RESEARCH ARTICLE

Long-term trends in gastropod abundance and biodiversity: Disentangling effects of press versus pulse disturbances

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Abstract

Aim: Climate-induced pulse (e.g., hurricanes) and press (e.g., global warming) disturbances represent threats to populations, communities, and the ecosystem services that they provide. We leveraged three decades of annual data on tropical gastropods to quantify the effects of major hurricanes, associated secondary succession, and global warming on abundance, biodiversity, and species composition.

Location: Luquillo Mountains, Puerto Rico.

Methods: Gastropod abundance, biodiversity, and composition were estimated annually for each of 27 years in a tropical montane forest that experienced three major hurricanes (Hugo, Georges, and Maria). Generalized linear mixed-effects, linear mixed-effects, and linear models evaluated population- and community-level responses to year, ambient temperature, understorey temperature, hurricane, and time since hurricane. Variation partitioning determined the unique and shared variation in biotic responses associated with temperature, disturbance, and succession.

Results: Rather than declining, gastropod abundances generally increased through time, whereas the responses of biodiversity were weak and scale dependent. Hurricanes and associated secondary succession, rather than ambient atmospheric temperature, moulded long-term trends in abundances and biodiversity.

Main conclusions: Global warming over the past 30 years has not progressed sufficiently to elicit significant responses by gastropods in the Luquillo Mountains. Rather, effects from pulse disturbances (i.e., hurricanes) and secondary succession currently drive long-term variation in abundance and biodiversity. Gastropods evince high resilience in this tropical ecosystem. Historical exposure to recurrent hurricanes likely imbued the fauna with broad niches that make them resistant to current levels of global warming. We predict that biotic resiliency will be challenged once changes in temperature exceed interannual and inter-habitat differences that typify this hurricane-mediated system, or combine with an increased frequency of hurricanes and droughts to alter associations among environmental characteristics that define the fundamental niches of species. Only then might significant declines in abundance or the appearance of novel communities characterize the gastropod fauna in the Luquillo Mountains.

1 | INTRODUCTION

The Anthropocene heralds a time of unprecedented and accelerating rates of environmental change (Monastersky, 2015) that have created a biodiversity crisis whose magnitude represents the Earth's sixth mass extinction (Ceballos et al., 2015). Environmental changes associated with human activities include both pulse (e.g., land use change, habitat fragmentation, fires, hurricanes, floods, pesticides) and press (e.g., increasing temperature, ocean acidification, sea level rise) disturbances (Dukes & Mooney, 1999; Sasaki et al., 2015). Pulse disturbances are relatively instantaneous, after which the system responds to the episodic occurrence, whereas press disturbances represent environmental changes that are maintained for extended periods of time (E. A. Bender et al., 1984). Both types of disturbance often affect the same system, but the separate and combined effects of these types of anthropogenic disturbances have not been effectively disentangled or comprehensively understood (Collins et al., 2016). Disturbances may combine synergistically (combined effect greater than the sum of individual effects), antagonistically (combined effect less than the sum of individual effects), or additively (combined effect equal to the sum of individual effects) to affect ecosystems. The combined effects of such disturbances on populations and communities have profound consequences for the spatio-temporal dynamics of ecosystems, as well as on the delivery of critical services to humans (Prather et al., 2013; Schowalter, 2013; Wagner, 2020).

Recent concern and controversy about responses of insect populations to global warming have intensified, with some in the scientific literature (e.g., Harris et al., 2019; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020), as well as in the popular media (e.g., *Washington Post* 15 October 2018, *New York Times* 27 November 2018, *National Geographic* February 2019, *The Atlantic* February 2019), referring to the phenomenon as 'Insect Armageddon'. Similarly, some (Lister & Garcia, 2018) have claimed that decreases in arthropod abundances are a consequence of global warming and have led to the collapse of food webs. In contrast, others have documented that such characterizations are misleading, premature, or not representative of all regions or all taxa (Crossley et al., 2020; Schowalter et al., 2019; van Klink et al., 2020; Willig et al., 2019).

Recently, a long-term, comprehensive, quantitative assessment found that the effects of hurricane-induced disturbances and subsequent secondary succession dwarfed those of global warming on arboreal arthropods (Schowalter et al., 2021). Such long-term evaluations are difficult to effectively execute because they require synoptic (comprehensive) and syntopic (co-spatial) collection of demographic data on species and environmental drivers that transpire at regular intervals over many years. This is especially critical because the temporal onset of pulse disturbances may not be regular or predictable, making it challenging to characterize pre-disturbance conditions or variability, immediate post-disturbance effects, or subsequent secondary successional dynamics. Moreover, such pulse-associated dynamics can confound detection of effects from press disturbances, unless particularly long time series are available, spanning multiple cycles of pulse disturbances. Unfortunately, such data are not common, especially in disturbance-prone settings where the disturbance regime includes high intensity events such as cyclonic storms, wildfires, or floods. Consequently, insights are often derived from snapshots in time (Adams, 2001), which are not able to clearly distinguish mechanistic bases for change or to characterize post-disturbance trajectories linked to secondary succession.

Invertebrate species are particularly sensitive to disturbances, including those associated with climate change, and much research has leveraged the life history characteristics of insects to explore responses to changing temperature or precipitation (e.g., Forrest, 2016; Renner & Zohner, 2018; Strange & Ayers, 2010). Gastropods, the second-most species-rich group of animals represented by over 70,000 species (Brown & Lydeard, 2010), may provide critical insights about ecological effects of contemporary climate change and disturbances, just as they have provided deep insights about past climatic cycles and their associated effects on biotas (e.g., Cordellier & Pfenninger, 2009; Richiano et al., 2015).

Our research leverages almost three decades (1993 to 2019) of annual, census data of tropical gastropod species to attain two overarching goals: (a) quantification of long-term trends in population and community characteristics; and (b) assessment of the extent to which interannual variation in population and community characteristics is related to press (e.g., variation in temperature associated with climate change) versus pulse (e.g., cyclonic storms) disturbances. Because the biota of Puerto Rico has evolved in hurricane-mediated environments resulting in high variation in local environmental conditions, for gastropod populations and communities we predict that: (a) the effects of pulse disturbances and associated secondary succession will play a dominant role in affecting interannual variation; (b) warming trends at the regional level will play a minor role in affecting interannual variation; and (c) populations and communities will be resilient to both press and pulse disturbances.

2 | MATERIALS AND METHODS

2.1 | Study site

Fieldwork was conducted on the Luquillo Forest Dynamics Plot (LFDP), a 16-ha grid located in tabonuco forest near El Verde Field Station in the north-western sector (18°19′ N, 65°49′ W) of the Luquillo Experimental Forest of Puerto Rico (Figure 1). Tabonuco
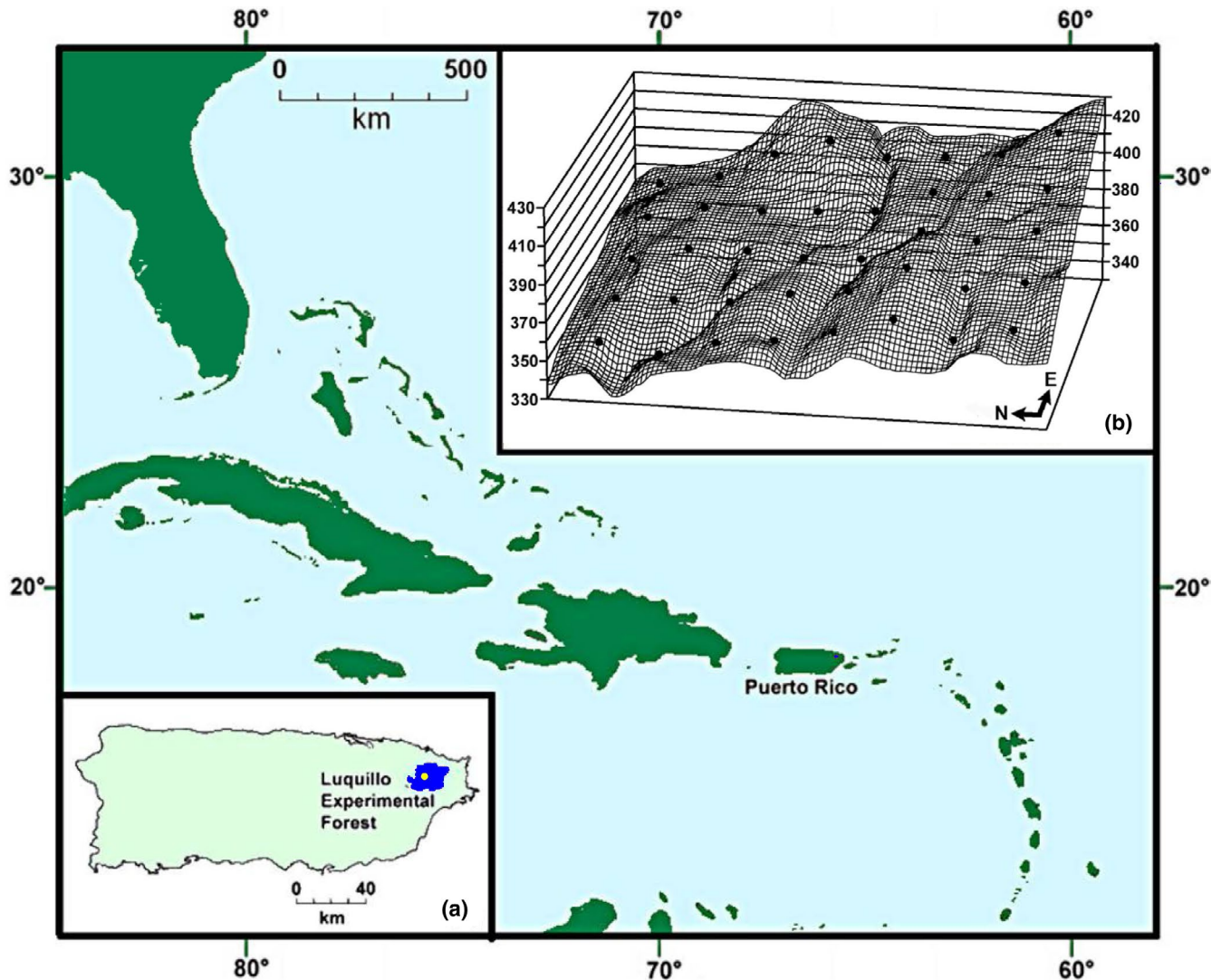
FIGURE 1 Map of the Antilles. (a) Map of Puerto Rico indicating the location of the Luquillo Experimental Forest (blue) and the Luquillo Forest Dynamics Plot (LFDP, yellow dot). (b) Elevational relief of the LFDP with dots representing 40 survey points

forest is a tropical montane rain forest occurring at elevations between 250 and 600 m a.s.l. in which *Dacryodes excelsa* (i.e., tabonuco) is a dominant tree species. Canopy height is >20 m with emergent trees over 35 m; average annual rainfall is 346 cm; and mean temperature is 23 °C with little seasonal or diurnal variation (Brokaw et al., 2012).

2.2 | History of disturbance

Three major hurricanes (Hugo in 1989, Georges in 1998, and Maria in 2017) have passed over eastern Puerto Rico and caused extensive damage to the forest on the LFDP over the past three decades. The three hurricanes differed in intensity, extent, and severity of damage to the forest (Zimmerman, Wood, et al., 2020). Hurricane Hugo was a category 4 storm (maximum sustained winds of 227 km/hr) that produced large canopy openings and deposited large amounts of coarse

woody debris on the forest floor (Scatena & Larsen, 1991). Hurricane Georges was a category 3 storm (sustained winds of 177 km/hr) that caused extensive defoliation of trees, but did not produce appreciable coarse woody debris (Ostertag et al., 2003). Hurricane Maria was a category 4 storm (sustained winds of 250 km/hr) that caused extensive tree mortality, killing twice as many trees as did Hurricane Hugo, removing nearly the entire forest canopy on the LFDP, and depositing large amounts of woody debris on the forest floor (Uriarte et al., 2019).

2.3 | Trends in temperature

To estimate the effects of global warming in the north-eastern region of Puerto Rico, we used data from the National Centers for Environmental Information of the National Oceanic and Atmospheric Administration (Network ID: GHCND:RQW00011641) for the

station at the Luiz Muñoz Marin International Airport in San Juan, about 24 km from the LFDP. In doing so, we averaged the daily maximum temperatures for each year (hereafter 'ambient temperature'), as these maxima are thought to have the most profound effects on invertebrates (Schowalter, 2016).

A critical effect of hurricane-induced disturbances on tropical forests is a change in the understorey climate catalysed by the loss of forest canopy (Richardson et al., 2010; Willig et al., 2007). Terrestrial gastropods experience understorey temperatures that are influenced by global warming, hurricane-induced loss of canopy cover, and ensuing secondary succession. An instrument failure occurred at the weather station at El Verde that resulted in an underestimate of maximum daily temperatures from 1988–1992. The instrument was replaced, providing a reliable estimate of maximum daily temperatures from mid-1992 until the present. Consequently, all analyses that included understorey temperature considered only data from 1993–2019 to ensure use of accurate understorey temperature data. To estimate annual temperature in the understorey, we averaged daily maximum temperatures from the weather station located in the forest understorey for each year.

2.4 | Study organisms

Gastropods are useful for studying the effects of press (climate change) and pulse (hurricanes) disturbances on populations and communities in tabonuco forest of Puerto Rico. First, excellent long-term data on gastropod incidence and abundance exist for the LFDP (Garrison & Willig, 1996; Willig et al., 1998). Second, gastropods have a ubiquitous spatial distribution in tabonuco forest, but exhibit considerable spatial heterogeneity and interspecific variation in abundances (Bloch et al., 2007; Willig et al., 2014, 2021). Third, as ectotherms of relatively low vagility that are subject to desiccation stress, gastropods exhibit strong responses to changes in canopy openness, temperature or precipitation (Alvarez & Willig, 1993; Nicolai & Ansart, 2017). Gastropods in tabonuco forest can be classified into three functional groups: arboreal grazers, carnivores, or detritivores of the forest floor (Bloch & Willig, 2012). In general, competition does not structure these communities, as both spatial and temporal associations of species abundances are positive, suggesting that variation in habitat quality or resource abundance influences species similarly (positively or negative) without evidence of density compensation. Moreover, individuals are the largest in habitats with the most individuals, further indicating that high productivity has a positive influence on all gastropods, and that any density-dependent effects of intra- or interspecific competition are negligible (Bloch & Willig, 2009, 2012).

2.5 | Field methods

Gastropods were surveyed annually from 1993 through 2019 at each of 40 points on the LFDP. At each point, all surfaces (rocks, litter,

debris, vegetation) within a 3-m radius and up to 3 m of height were inspected for gastropods. Surveys were conducted at night, when terrestrial gastropods are most active (Heatwole & Heatwole, 1978). The same 40 points were surveyed twice in 1993, thrice in 1994, and four times all other years. To minimize alteration of long-term study sites, litter was not manipulated, and specimens were returned as closely as possible to the point of capture. Consequently, our considerations are restricted to gastropods that occur on or above ground litter. Seventeen species of terrestrial gastropod typically occur in these habitats, with some species being undetected in particular years (e.g., *Diplosolenodes occidentalis*, *Obeliscus terebraster*, *Subulina octona*) and other species occurring at over half of the survey points during most years (e.g., *Caracolus caracolla*, *Gaeotis nigrolineata*, *Nenia tridens*). All data are from the Luquillo Long-Term Ecological Research Site, whose collection is supported by the US National Science Foundation (NSF). Additional details on sampling (Willig et al., 1998) and gastropod autecology (Garrison & Willig, 1996) in the Luquillo Experimental Forest are available elsewhere.

2.6 | Estimation of abundance and biodiversity

Population- and community-level response variables were estimated at two focal scales (sensu Scheiner et al., 2000). The smaller focal scale pertained to characteristics of each point on the LFDP (i.e., each of 40 points was a replicate in analyses), whereas the larger focal scale pertained to combined data for the entire LFDP (i.e., a single value characterized the LFDP).

2.6.1 | Estimation at the smaller scale

For analyses at the point scale, we characterized the abundance of each species as the average of the number of captured individuals across all surveys within a year for each point. We estimated total gastropod abundance for each point as the sum of the average abundances of all species at that point. Similarly, metrics of biodiversity [i.e., species richness, Shannon diversity, Camargo's evenness, and Berger–Parker dominance (Magurran & McGill, 2011)] for each point were calculated based on the species abundance distribution at a particular point (i.e., the average abundance of each species at each point). The proportional abundance of a species equalled the ratio of the average of the number of captured individuals for a particular species at a point within a year to the average of the total number of captured individuals, regardless of species, at that point within that year.

2.6.2 | Estimation at the larger scale

For analyses at the scale of the LFDP, we characterized the abundance of each species, as well as total gastropod abundance, as the mean of the corresponding number of captured individuals per

survey across all 40 points on the LFDP within a year. Metrics of biodiversity at the grid scale (i.e., γ-biodiversity) were derived from species abundance distributions based on the sum of the average number of individuals for the 40 points within a year. The proportional abundance of a species equalled the ratio of the average number of individuals of a species for the 40 points within a year to the sum of such values for all species within a year.

Regardless of focal scale, metrics of biodiversity were expressed as Hill numbers or numbers equivalents (Jost, 2006). Greater values for any Hill number represent greater biodiversity, including those associated with dominance (i.e., larger values for Hill-transformed dominance indicate lower dominance and greater biodiversity). Metrics that represent taxon counts (e.g., richness) already represent numbers equivalents and require no transformation (Jost, 2006). Numbers equivalents for Shannon diversity, Camargo evenness, and Berger–Parker dominance were transformed from entropies into numbers equivalents following recommendations of Jost (2006), using functions written in MATLAB R2020a (ver. 9.8.0.1223502). For ease of exposition, hereafter we refer to these metrics simply as 'richness', 'diversity', 'evenness', and 'dominance', and use 'biodiversity' to refer to the general concept that comprises all four metrics.

2.7 | Quantitative analyses

Simple linear regression was used to evaluate consistent temporal trends [i.e., annual rates of change (slopes)] in ambient or understorey temperature at the larger spatial scale. For each analysis, mean maximum daily temperature was the dependent variable and year was the independent variable. Temporal trends at the smaller scale could not be executed because measures of understorey temperature or ambient temperature were not available for each point. In addition, there is no variation among points in hurricane identity or in time since last major hurricane during each year.

To evaluate temporal variation in each biotic response variable (i.e., abundances of each species, each metric of point or γ-biodiversity), we conducted a generalized linear mixed-effects model (point as a random factor, with random intercept and random slope terms to control for repeated measures over time) with a negative binomial error term (for abundances), a linear mixed-effects model (point as a random factor, with random intercept and random slope terms to control for repeated measures over time) with a Gaussian error term (for metrics of point biodiversity), or a linear model (for metrics of γ-biodiversity), with time (year) as the independent factor. To determine if disturbances associated with global warming or hurricanes influence interannual variation in each biotic response variable, we conducted a generalized linear mixed-effects model (point as a random factor, with random intercept and random slope terms to control for repeated measures over time) with a negative binomial error distribution for abundance, a linear mixed-effects model (point as a random factor, with random intercept and random slope terms to control for repeated measures over time) with a Gaussian error distribution for point biodiversity, or a linear

mixed-effects model (only a random intercept term) with a Gaussian error distribution for γ-biodiversity. For each of the analyses to evaluate effects of disturbance, ambient temperature, understorey temperature, hurricane identity (Hurricane Hugo, Georges, or Maria), time after most recent major hurricane (TAH, measured in years), and a hurricane by TAH interaction were explanatory factors, and all analyses used type II sums of squares. We used negative binomial error terms for gastropod abundances because they are appropriate for count data as well as for data that suffers from zero inflation (O'Hara & Kotze, 2011), such as abundances of rare gastropods. In contrast, biodiversity values represent continuous variables with error terms that that can be approximated by Gaussian distributions.

Although biotic response characteristics were quantified for each combination of point and year, none of the environmental characteristics were measured in a spatially explicit manner (e.g., understorey temperature or ambient temperature) or were point-specific (e.g., hurricane identity, time after most recent hurricane). Thus, variation among points in biotic response characteristics within years would not be explained by the independent variables in analyses at the small scale (points). Nonetheless, including point identity as a random factor for intercept and slope terms through time in mixed-effects models helps to control for other sources of spatial variation, and in combination with the repeated measures aspect of our study design, powerfully evaluates long-term responses to press and pulse disturbances.

We used mixed effects models to determine if resistance to intense disturbances (i.e., the magnitude of short-term changes) was consistent among hurricanes of different severity: a category 3 hurricane that caused moderate forest damage (Georges) and a category 4 hurricane that caused extensive forest damage (Maria). We used a generalized linear mixed-effects model with a negative binomial error distribution (for abundances) or a linear mixed-effects model with a Gaussian error distribution (for point biodiversity) to evaluate consistency of immediate responses of abundance (year before versus year after each hurricane) of each species separately, of total gastropod abundance, and of each point biodiversity metric separately. Disturbance (before and after) and hurricane (Georges or Maria) were Model I treatment factors, and point was a random factor (a random intercept term) in each model. The disturbance by hurricane interaction term was included in each model to determine if responses to disturbance were contingent on hurricane identity (i.e., severity). These analyses of resistance could not be executed with regard to Hurricane Hugo, as no gastropod data exist for the LFDP from before 1989.

Variation partitioning was used to determine the unique and shared variation associated with ambient temperature, understorey temperature, or hurricanes and subsequent secondary succession (hurricane identity and TAH), with respect to (a) abundance of each species of gastropod, (b) total gastropod abundance, (c) each of four metrics of γ-biodiversity, (d) a multivariate representation of biodiversity (i.e., all four metrics as a group), and (e) a multivariate representation of species composition (relative abundances of each of 17 species). Because variation partitioning does not allow

for the inclusion of random effects to control for repeated measures of the same point, all such analyses were conducted only at the larger scale. Redundancy analyses determined the significance of each unique partition, each total partition, and the overall model. Significance of shared partitions cannot be determined statistically (Legendre, 2007; Legendre et al., 2012). Small negative shared partitions existed in many variation partitioning analyses because adjusted R^2 values are not strictly additive (Legendre et al., 2012). For interpretive purposes, the variation explained by these partitions should be considered to be zero.

Generalized linear mixed-effects models were conducted using the glmer.nb function from the lme4 package (Bates et al., 2015) or the lme function from the nlme package (Pinheiro et al., 2021). Linear models were conducted using the glm functions from the stats package (R Core Team, 2020). Variation partitioning was conducted using the varpart function from the vegan package (Oksanen et al., 2019). Type II sums of squares were implemented via the ANOVA function in the car package (Fox & Weisberg, 2019). Except for the conversion of entropies into numbers equivalents, all analyses were conducted in R version 3.6.1 (R Core Team, 2020). All statistical analyses were conducted with an α of .05, although we noted effects that approached significance ($.10 \geq p > .05$) as well. Following Sokal and Rohlf (2012), when interaction terms were significant in a particular model, we did not interpret the significance of constituent main effects (i.e., a significant interaction between hurricane and TAH denotes that the effect of TAH depends on hurricane identity, obviating the need to evaluate consistent main effects). Finally, all minor manipulations of the data (i.e., calculations of sums or ratios) were executed via Microsoft EXCEL for Office 365.

3 | RESULTS

3.1 | Temporal trends

3.1.1 | Temperature

Although the empirical slope of the relationship between ambient temperature and time is positive ($B_1 = 0.006$), it is not significant ($p = .579$) and little of the variation ($R^2 = .013$) in ambient temperature was related to time (Figure 2a). Ambient temperature displayed potential autoregressive structure that could confound the ability to detect temporal patterns; however, an autoregressive moving average (ARMA) model also found no evidence of a consistent temporal change in ambient temperature ($p = .784$). In contrast, understorey temperature significantly cooled over time ($B_1 = -0.047$; $p = .017$; $R^2 = .208$). The post-Hurricane Hugo cooling in the understorey is associated with post-hurricane canopy closure (black circles, Figure 2b) during secondary succession, a process that was essentially unaffected by Hurricane Georges (blue circles, Figure 2b). However, Hurricane Maria initiated a spike in understorey temperature, but this was followed by a decline, at least in the short term (red circles, Figure 2b). Although ambient temperature surely affects
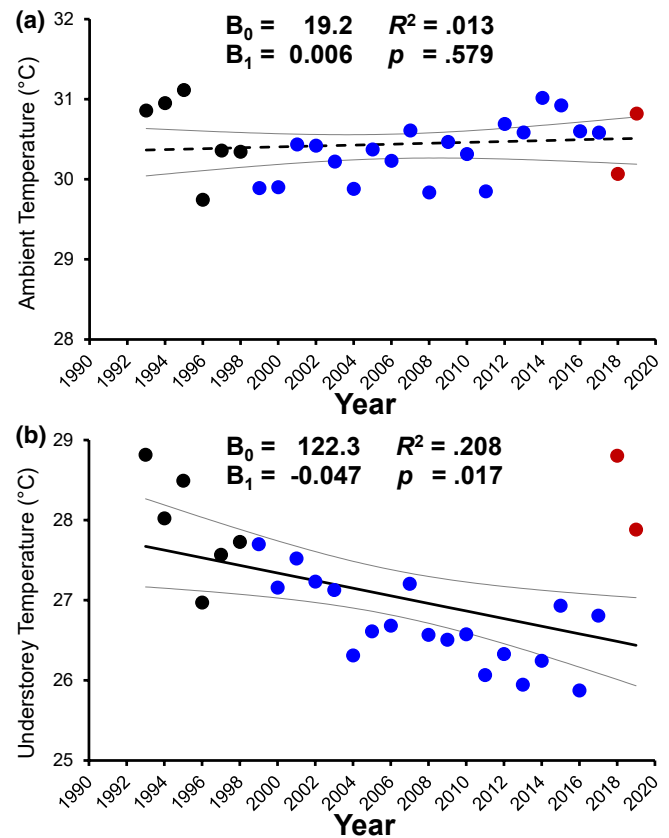
FIGURE 2 Ambient temperature did not exhibit consistent long-term trends, whereas understorey temperature significantly decreased from 1993 to 2019. (a) Annual mean daily maximum temperature from Luiz Muñoz Marín International Airport, San Juan, Puerto Rico (approximately 24 km from the Luquillo Experimental Forest). This is a measure of the ambient temperatures that could be driven by global climate change. (b) Annual mean daily maximum temperature from the understorey of tabonuco forest in the Luquillo Experimental Forest. This is a measure of temperatures in the habitats occupied by terrestrial gastropods that are affected by both global climate change and changes to canopy openness related to hurricane-induced disturbances and succession. Black, blue, and red dots represent temperatures after Hurricanes Hugo (1989), Georges (1998), and Maria (2017), respectively. B_0, B_1, R^2, and p are results from simple linear regressions for each measure of temperature through time. Dashed and solid lines represent non-significant and significant relationships, respectively. Grey lines represent upper and lower 95% confidence limits of the predicted values

understorey temperature, the two measures were not significantly correlated (Person correlation, $r = .211$, $p = .291$); the status of forest canopy likely decouples the relationship.

3.1.2 | Population-level characteristics

Almost half of the gastropod species (8 of 17) did not evince consistent linear trends through time: six species (*Alcadia striata*, *Austroselenites alticola*, *D. occidentalis*, *Lamellaxis gracilis*, *Megalomastoma croceum*,

and *N. tridens*) significantly increased in abundance over time; and three species significantly (*O. terebraster* and *Polydontes acutangula*) or marginally (*Platysuccinea portoricensis*) decreased in abundance over time (Table 1; Figure 3). As a consequence of the cumulative responses of species, total gastropod abundance significantly increased over time (Table 1). Each of the three most abundant species of gastropod (*N. tridens*, mean = 5.57; *C. caracolla*, mean = 4.23; *G. nigrolineata*, mean = 1.24) increased over time, two significantly so (Table 1).

The magnitude of resistance differed significantly between Hurricanes Georges and Maria for each of the four most abundant species (*C. caracolla*, *G. nigrolineata*, *N. tridens*, and *P. portoricensis*) and for total gastropod abundance, and approached significance for *S. octona* (Table 2). Resistance was lower in response to Hurricane Maria in all cases, with abundance decreasing in response to hurricanes in all cases except for *S. octona* after Georges. Only one species (*Oleacina glabra*) exhibited a consistent significant decrease in abundance regardless of Hurricane.

3.1.3 | Community-level characteristics

Species richness did not evince a consistent linear trend through time at the point or γ scale (Table 1). In contrast, Hill-transformed metrics sensitive to interspecific variation in abundance (i.e., Shannon diversity, Camargo evenness, and Berger–Parker dominance) decreased significantly over time at the point scale, but did so only marginally ($.10 \geq p > .05$) at the γ scale (Table 1; Figure 4). This decline in biodiversity was driven by the combination of increasing relative abundance of numerically dominant species during succession, especially *N. tridens*, as well as by the decreasing relative abundance of species that are early successional and gap specialists (e.g., *A. striata*, *Caracolus marginella*, *Cepolis squamosa*, *D. occidentalis*, *P. acutangula*). Importantly, even species with positive temporal trajectories in abundance may evince declining relative abundances because *N. tridens* is by far the most numerically dominant taxon on the LFDP (accounting for almost half of all gastropod individuals) and has a significant rate of increase ($B_1 = 0.210$) that is more than twice that of the species (*L. gracilis*) with the second-most rapid rate of increase.

The magnitude of resistance did not differ significantly between Hurricanes Georges and Maria for any measure of point biodiversity (Table 2). Species richness exhibited consistent significant decreases regardless of Hurricane. All metrics of point biodiversity were consistently greater near (before and after) the time of Hurricane Georges than near (before and after) the time of Hurricane Maria, consistent with the temporal trends of decreasing biodiversity through time (Table 1).

3.2 | Environmental variation

3.2.1 | Population-level characteristics

Environmental variation accounted for significant interannual variation in abundance for all but four species (i.e., *C. marginella*, *O. terebraster*, *Oleacina playa*, and *S. octona*) of gastropod (Table 3), each of

TABLE 1 Generalized linear mixed-effects models quantify the effects of year separately on the abundance of each species of gastropod and on total abundance, linear mixed-effects models quantify the effects of year separately on each metric of point biodiversity, and linear models quantify the effects of year separately on each metric of γ-biodiversity

			Year	
	Mean	SD	B_1 ($\pm$ SE)	p
Population				
Alcadia alta	0.05	0.38	0.000 ($\pm$ 0.001)	.774
Alcadia striata	0.20	0.44	0.020 ($\pm$ 0.009)	**.043**
Austroselenites alticola	0.07	0.20	0.078 ($\pm$ 0.001)	**<.001**
Caracolus caracolla	4.23	4.74	0.014 ($\pm$ 0.003)	.258
Caracolus marginella	0.03	0.12	−0.016 ($\pm$ 0.002)	.500
Cepolis squamosa	0.09	0.32	0.021 ($\pm$ 0.001)	.156
Diplosolenodes occidentalis	0.01	0.06	0.012 ($\pm$ 0.042)	**<.001**
Gaeotis nigrolineata	1.24	2.02	0.003 ($\pm$ 0.008)	.674
Lamellaxis gracilis	0.04	0.20	0.049 ($\pm$ 0.002)	**<.001**
Megalomastoma croceum	0.03	0.20	0.108 ($\pm$ 0.009)	**<.001**
Nenia tridens	5.57	6.28	0.201 ($\pm$ 0.021)	**<.001**
Obeliscus terebraster	0.00	0.04	−0.037 ($\pm$ 0.062)	**<.001**
Oleacina glabra	0.04	0.13	0.010 ($\pm$ 0.019)	.592
Oleacina playa	0.03	0.09	0.005 ($\pm$ 0.001)	.843
Platysuccinea portoricensis	0.21	0.64	−0.004 ($\pm$ 0.007)	.091
Polydontes acutangula	0.09	0.26	−0.066 ($\pm$ 0.001)	**<.001**
Subulina octona	0.10	0.57	−0.001 ($\pm$ 0.002)	.452
Total abundance	12.03	9.41	0.229 ($\pm$ 0.029)	**<.001**
Point biodiversity				
Species richness	4.24	1.60	−0.001 ($\pm$ 0.006)	.932
Shannon diversity	2.71	0.90	−0.015 ($\pm$ 0.003)	**<.001**
Camargo evenness	2.25	0.72	−0.012 ($\pm$ 0.003)	**<.001**
Berger–Parker dominance	1.79	0.53	−0.008 ($\pm$ 0.001)	**<.001**
γ-biodiversity				
Species richness	11.42	1.25	0.003 ($\pm$ 0.031)	.920
Shannon diversity	3.64	0.72	−0.033 ($\pm$ 0.017)	.059
Camargo evenness	2.93	0.54	−0.025 ($\pm$ 0.013)	.059
Berger–Parker dominance	2.12	0.42	−0.020 ($\pm$ 0.010)	.054

Note: Error terms for analyses of abundance were based on a negative binomial distribution, error terms for analyses of biodiversity were based on a Gaussian distribution. Analyses of abundance and point biodiversity used point as a random factor with both a random intercept term and a random slope term to control for repeated measures through time. Analyses of γ-biodiversity were conducted at the scale of the Luquillo Dynamics Forest Plot (LFDP). Significant results ($p \leq .05$) are bold. Regression coefficients (B_1) indicates the direction and magnitude of relationships and the standard error (SE) associated with the estimate of B_1. Inference space for means and standard deviations (SD) of abundance or point biodiversity is a point, whereas it is the entire LFDP for γ-biodiversity.

which is generally rare (mean abundance ≤ 0.10; Table 1). Ambient temperature significantly affected variation in abundance of seven species (i.e., *Alcadia alta*, *A. alticola*, *C. caracolla*, *G. nigrolineata*, *L. gracilis*, *O. glabra*, and *P. portoricensis*), whereas understorey temperature affected variation in abundance of nine species (i.e., *A. alta*, *A. alticola*, *C. caracolla*, *C. squamosa*, *G. nigrolineata*, *L. gracilis*, *N. tridens*, *O. glabra*, and *P. portoricensis*). Hurricane identity or subsequent successional status (i.e., time after hurricane, and the interaction between hurricane identity and time after hurricane) affected all but five species, the same four that did not respond to any environmental characteristic plus *A. alticola* (Table 3). Moreover, when either factor had an effect, it generally reflected an interaction in which successional dynamics were hurricane-specific (10 of 12 species). Finally, total gastropod abundance responded significantly to all factors, although responses to factors related to pulse disturbances (understorey temperature and the interaction between hurricane and time after hurricane) were stronger than those to ambient temperature (Table 3).

The amount of variation in abundance related to hurricane (identity or TAH), ambient temperature, or understorey temperature differed considerably among species (Table 4). Nonetheless, the amount of variation in abundance associated with unique partitions, when significant, was greater for hurricane (six species, R^2 ranging from .252 to .445) than for ambient temperature (four species, R^2 ranging from .122 to .240), and lowest for understorey temperature (five species, R^2 ranging from .114 to .282). The amount of variation in abundance associated with total partitions, when significant, was greatest for hurricane (seven species, R^2 ranging from .206 to .712), intermediate for understorey temperature (six species, R^2 ranging from .149 to .416), and least for ambient temperature (one species, $R^2 = .133$). The full model, including all environmental characteristics, significantly accounted for variation in abundance of nine species (R^2 ranging from .360 to .697). Finally, the full model of environmental characteristics significantly accounted for 73.4% of the variation in total gastropod abundance (Figure 5), with the unique partition associated with hurricane ($R^2 = .099$) being greater than that for each of the others ($R^2 = .054$, understorey temperature; $R^2 = .041$, ambient temperature) and with the total partition associated with hurricane ($R^2 = .681$) being greater than that for each of the others ($R^2 = .393$, understorey temperature; $R^2 = .087$, ambient temperature).

3.2.2 | Community-level characteristics

At the point scale, each metric of biodiversity responded to ambient temperature, understorey temperature, hurricane, and time after hurricane (Table 3). Evenness, diversity, and dominance responded to time after hurricane in a consistent manner (i.e., no significant hurricane by time after hurricane interaction), whereas the effect of time after hurricane depended on hurricane identity for richness (a significant hurricane by time after hurricane interaction). At the γ scale, each metric of biodiversity responded to time after hurricane in a consistent manner, and was unaffected by any other environmental factor, except for richness, which was significantly related to understorey temperature.

The amount of variation in metrics of biodiversity related to ambient temperature, understorey temperature, or hurricane (identity and time after hurricane), differed among metrics (Table 4). The full models for richness, evenness, and diversity were significant, accounting for at least a third of the total variation (i.e., $R^2 = .355$, $R^2 = .472$, and $R^2 = .429$, respectively). In contrast, the full model for dominance was not significant and accounted for less than 10% of the total variation. In general, the unique partition related to hurricane (range of R^2, .164–.336) was greater than those associated with ambient temperature ($R^2 \sim 0$) or understorey temperature ($R^2 \sim 0$) for metrics that are weighted by abundance. In the case of species richness, unique effects of understorey temperature ($R^2 = .376$) were greater than those of hurricane ($R^2 = .235$) or ambient temperature ($R^2 = .034$). For metrics of biodiversity weighted by abundance, the total effects of hurricane (range of R^2, .151–.484) were generally greater than those for ambient temperature (range of R^2, ~ 0–.140) or understorey temperature ($R^2 \sim 0$). In contrast, the total amount of variation associated with understorey temperature ($R^2 = .138$) was greater than that for either ambient temperature ($R^2 = .007$) or hurricane ($R^2 = .016$) when considering species richness. From a multivariate perspective based on all four metrics of biodiversity (Figure 5), the unique effect of hurricane ($R^2 = .261$) was greater than that of understorey temperature ($R^2 = .227$) or ambient temperature ($R^2 = .011$). Similarly, the total effect of hurricane ($R^2 = .172$) was greater than that of understorey temperature ($R^2 = .072$) or ambient temperature ($R^2 = .043$).

Variation in environmental factors accounted for significant variation (42.4%) in species composition (Table 4; Figure 5). The unique effect of hurricane ($R^2 = .312$) was greater than that of ambient temperature ($R^2 \sim 0$) or of understorey temperature ($R^2 \sim 0$), and the total effect of hurricane ($R^2 = .444$) was greater than that of ambient temperature ($R^2 = .074$) or of understorey temperature ($R^2 \sim 0$).

FIGURE 3 Six species (*Alcadia striata*, *Austroselenites alticola*, *Diplosolenodes occidentalis*, *Lamellaxis gracilis*, *Megalomastoma croceum*, and *Nenia tridens*) as well as total gastropod abundance increased in abundance, whereas three species (*Obeliscus terebraster*, *Platysuccinea portoricensis*, and *Polydontes acutangula*) decreased in abundance between 1993 and 2019. Temporal variation in means of point abundance for each of nine species of gastropod as well as for total gastropod abundance, each of which exhibited significant trends through time (Table 1). Black, blue, and red dots represent mean data for each year following Hurricane Hugo (1989), Hurricane Georges (1998), and Hurricane Maria (2017), respectively. Solid black lines represent predicted values based on a generalized linear mixed-effects models with negative binomial error terms. Grey lines represent upper and lower 95% confidence limits of the predicted values (i.e., abundance at the point scale)
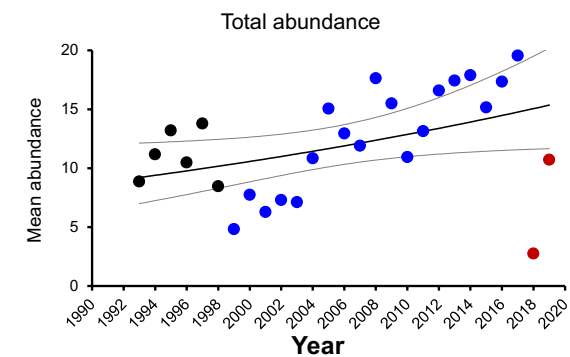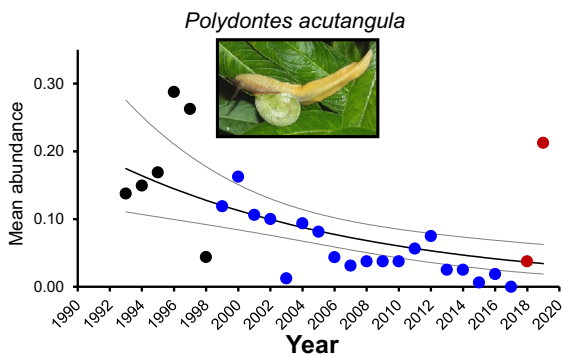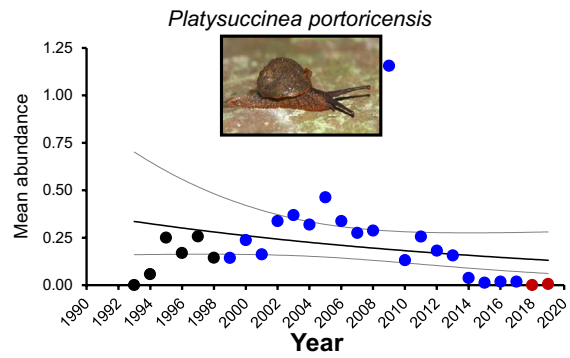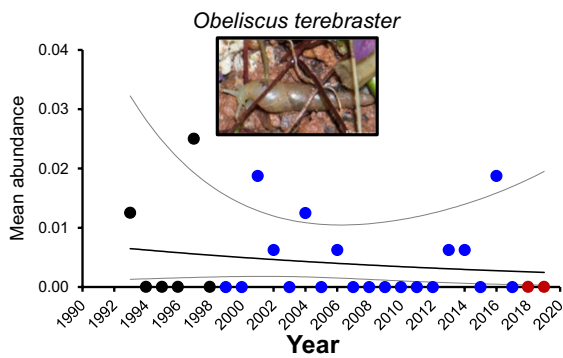
Alcadia striata

Austroselenites alticola

Diplosolenodes occidentalis

Lamellaxis gracilis

Megalomastoma croceum

Nenia tridens

Obeliscus terebraster

Platysuccinea portoricensis

Polydontes acutangula

Total abundance
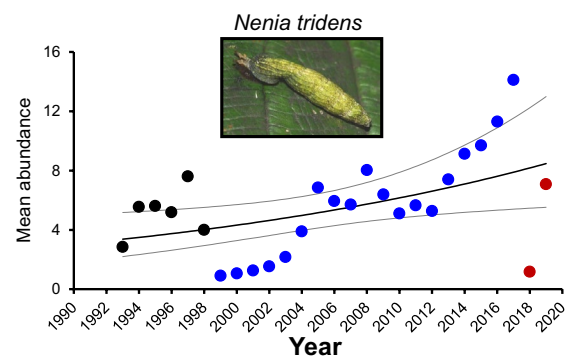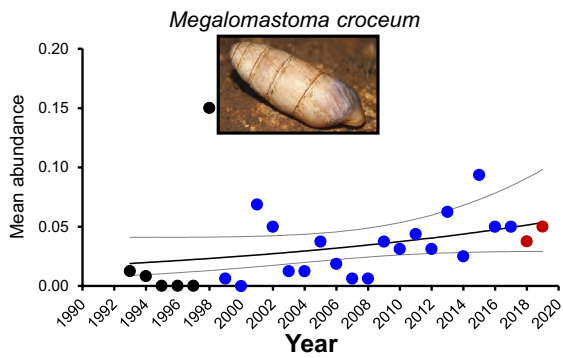
TABLE 2 Generalized linear mixed-effects models (GLMM) quantifying the effect of hurricane identity (Georges and Maria), hurricane disturbance (year before versus year after), and their interaction on the abundance and point biodiversity of gastropods in the Luquillo Experimental Forest for the years immediately before or after each hurricane

	Abundance or biodiversity				GLMM		
	Georges		Maria				Disturbance ×
	Before	After	Before	After	Identity	Disturbance	identity
Abundance							
Alcadia alta	0.00	0.01	0.01	0.01	0.777	0.777	0.999
Alcadia striata	0.14	0.28	0.13	0.14	0.279	0.223	0.474
Austroselenites alticola	0.03	0.03	0.03	0.01	0.821	0.672	0.517
Caracolus caracolla	3.11	2.54	4.14	1.13	0.985	**<0.001**	**<0.001**
Caracolus marginella	0.03	0.05	0.01	0.10	0.548	0.182	0.442
Cepolis squamosa	0.15	0.06	0.01	0.04	0.367	0.476	0.215
Diplosolenodes occidentalis	0.00	0.01	0.00	0.00	1.000	1.000	1.000
Gaeotis nigrolineata	0.43	0.23	1.01	0.03	**0.021**	**0.006**	**0.003**
Lamellaxisgracilis	0.01	0.02	0.00	0.01	0.824	0.634	1.000
Megalomastoma croceum	0.15	0.01	0.05	0.04	0.359	0.297	0.172
Nenia tridens	4.00	0.91	14.11	1.17	**<0.001**	**<0.001**	**0.001**
Obeliscus terebraster	0.00	0.00	0.00	0.00	1.000	1.000	1.000
Oleacina glabra	0.03	0.00	0.02	0.00	0.576	**<0.001**	0.234
Oleacina playa	0.02	0.01	0.03	0.02	0.509	0.513	0.775
Platysuccinea portoricensis	0.14	0.14	0.02	0.00	**<0.001**	0.492	**<0.001**
Polydontes acutangula	0.04	0.12	0.00	0.04	0.218	0.259	1.000
Subulina octona	0.19	0.44	0.01	0.00	**0.043**	0.060	0.080
Total abundance	8.46	4.84	19.57	2.74	**<0.001**	**<0.001**	**<0.001**
Point biodiversity							
Species richness	3.85	3.30	3.73	2.58	0.055	**<0.001**	0.175
Shannon diversity	2.71	2.49	2.12	1.99	**<0.001**	0.209	0.723
Camargo evenness	2.29	2.14	1.75	1.77	**<0.001**	0.601	0.476
Berger–Parker dominance	1.87	1.73	1.46	1.50	**<0.001**	0.567	0.291

Note: Error terms for analyses of abundance were based on a negative binomial distribution, whereas error terms for analyses of biodiversity were based on a Gaussian distribution. Analyses of abundance and point biodiversity incorporated sampling point as a random factor to control for repeated measures. Significant results ($p \leq .05$) are bold. Before and After are the mean point abundance or point biodiversity for the year before or year after Hurricane Georges or Hurricane Maria.

4 | DISCUSSION

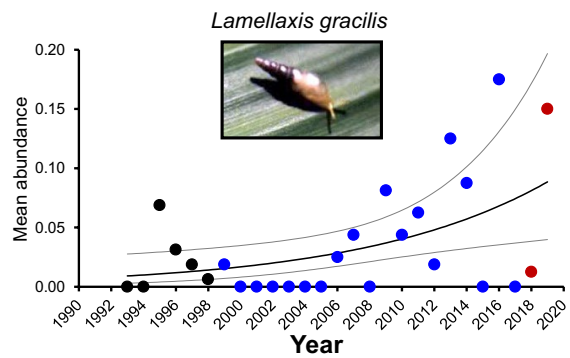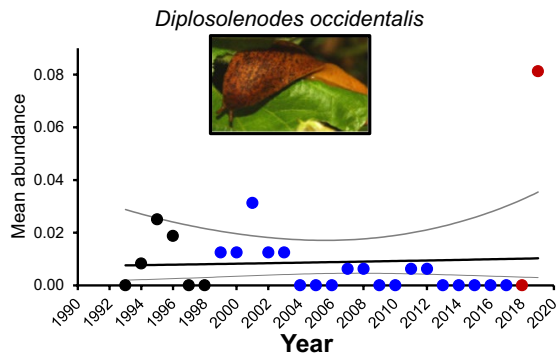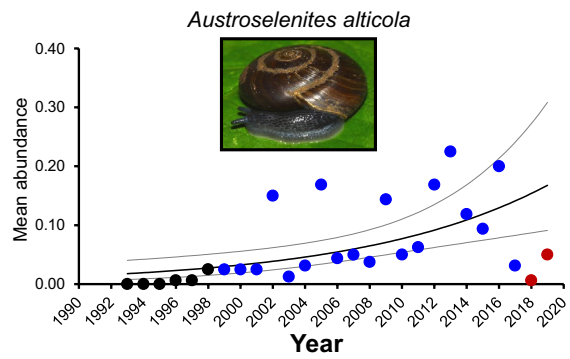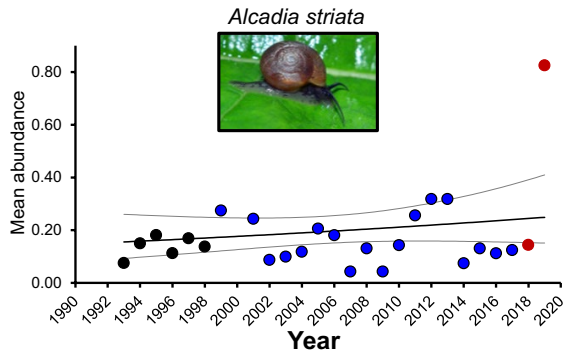Many taxa in other environments are declining in abundance, likely in response to a combination of biocides, habitat loss and fragmentation, and an increasingly warm world (Dirzo et al., 2014; Hallman et al., 2017; Rosenberg et al., 2019; Sánchez-Bayo & Wyckhuys, 2019; Thomas, 2004; Wagner, 2020), thereby generating alarm about a pending mass extinction and collapse of ecological systems across the planet. In contrast to this phenomenon, declines have not been detected for arthropods in the sub-canopy (Schowalter et al., 2021; Willig et al., 2019) or for dominant vertebrate groups in tabonuco forest of Puerto Rico (Willig et al., 2019). Even when significant long-term declines have been quantified, as for walkingsticks (*Lamponius portoricensis*), the temporal decline was related to hurricane-induced disturbance and secondary succession

rather than to ambient temperature (Schowalter et al., 2021; Willig et al., 2011, 2019).

Herein, we show that long-term trends in a dominant group of ectotherms (gastropods), known to be sensitive to climatic variation in general and to warming in particular, provide no support for pervasive declines in abundance or biodiversity associated with climate change. In fact, we observe just the opposite: total abundance of gastropods is increasing significantly over time (Table 1). This general trend is a consequence of three phenomena: (a) the significant temporal increase in the most abundant species of gastropod (*N. tridens*); (b) the empirical increases (positive slopes) in almost 70% of the other species (11 of 16), five of which are significant (*A. alticola, D. occidentalis, L. gracilis, M. croceum,* and *O. playa*); and (c) the relatively low abundance of the three species that evinced a significant decline over time (*O. terebraster, P. portoricensis,* and *P. acutangula*). Regardless
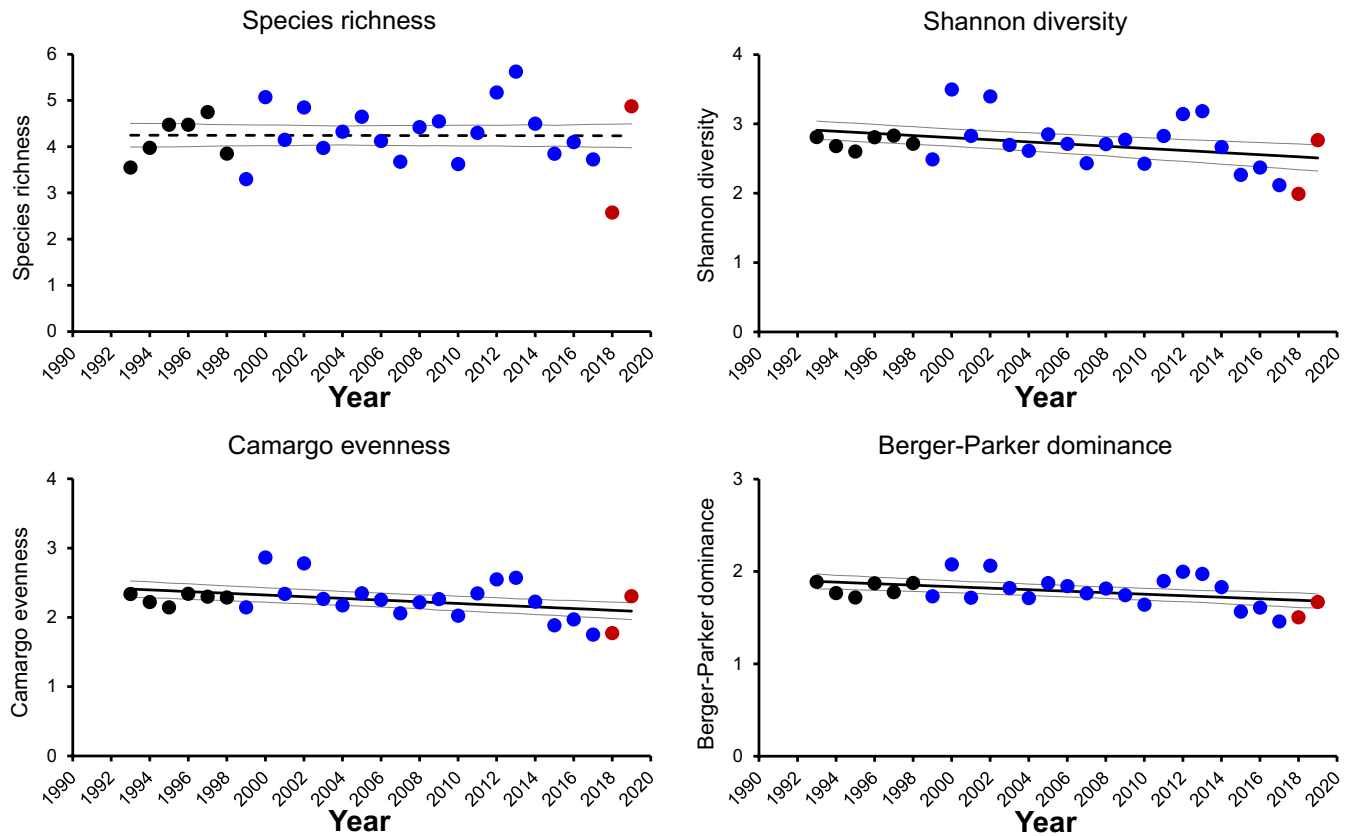
FIGURE 4 Species richness did not exhibit a consistent temporal trend between 1993 and 2019, whereas Shannon diversity, Camargo evenness, and Berger–Parker dominance each decreased significantly during this period. Dashed and solid lines represent non-significant and significant relationships, respectively, based on data at the point scale (Table 1). Black, blue, and red dots represent mean data for each year following Hurricane Hugo (1989), Hurricane Georges (1998), and Hurricane Maria (2017), respectively. Regression lines represents predicted values for metrics at the point scale based on a linear mixed-effects model with sampling point as a random factor, with random intercept and random slope terms to control for repeated measures over time. Grey lines represent upper and lower 95% confidence limits of the predicted values

of these temporal trends in abundance (Table 3), we demonstrate that interannual variation in only three species is related to ambient temperature, whereas most species (>75%), including those three, respond to climate-induced hurricane disturbances or associated secondary succession. Moreover, gastropods in tabonuco forest exhibit positive associations with respect to abundance from both temporal and spatial perspectives, suggesting that they exhibit shared responses to variation in habitat quality or resource abundance (Bloch & Willig, 2009; Willig et al., 2021). These shared responses likely arise from a combination of considerations: (a) all snails are sensitive to desiccation stress, and (b) high productivity has positive effects on all foraging guilds (grazers, detritivores, and carnivores).

Community-level metrics that characterize species abundance distributions evince complicated temporal responses (Table 1). Richness does not exhibit a significant linear temporal trend at either large or small focal sales. In contrast, all abundance-weighted metrics evince temporal declines that are significant (point biodiversity) or that approach significance (γ-biodiversity). These patterns arise because *N. tridens* disproportionally increased in abundance over time, resulting in increases in dominance (decreases in the Hill

transformation of dominance) and decreases in evenness and diversity. Regardless, interannual variation in biodiversity is only related to ambient temperature at small focal scales (point biodiversity), and is generally related to hurricane-induced secondary succession at all focal scales (point and γ-biodiversity), and to hurricanes and understorey temperature at small scales (Table 3).

At the metacommunity level, there is no evidence of temporal trends in range coherence, range turnover, or range boundary clumping (i.e., elements of metacommunity structure, sensu Leibold & Mikkelson, 2002) for gastropods occupying the LFDP. Rather, a canonical, compartmentalized structure has persisted over the past three decades that is spatially variable but environmentally consistent (Willig et al., 2021). Importantly, elements of metacommunity structure are based on incidence rather than relative abundance, making them less sensitive to the current level of climate change than are abundance-based approaches. In tabonuco forest of Puerto Rico, 'Biodiversity Armageddon' has not yet occurred for gastropods, arthropods (Schowalter et al., 2021), frogs, or birds (Willig et al., 2019), as this disturbance-mediated system exhibits remarkable resilience.

TABLE 3 Generalized linear mixed-effects models quantify the effects of a suite of environmental factors separately on the abundance of each species of gastropod and on total gastropod abundance; and linear mixed-effects models quantify the effects of a suite of environmental factors separately on each metric of point and γ-biodiversity. Environmental factors include: ambient temperature, understorey temperature, hurricane (Hugo, Georges, Maria), time after most recent major hurricane (TAH), and a hurricane × TAH interaction

	Ambient temperature	Understorey temperature	Hurricane	TAH	Hurricane × TAH
Population					
Alcadia alta	**0.042**	**0.046**	**0.036**	0.746	**0.040**
Alcadia striata	0.526	0.512	**<0.001**	**<0.001**	**0.006**
Austroselenites alticola	**<0.001**	**<0.001**	0.686	0.215	0.270
Caracolus caracolla	**0.003**	**<0.001**	**<0.001**	0.507	**0.020**
Caracolus marginella	0.398	0.426	0.552	0.621	0.097
Cepolis squamosa	0.851	**0.035**	**<0.001**	**0.009**	**0.033**
Diplosolenodes occidentalis	0.575	0.866	0.764	0.225	**<0.001**
Gaeotis nigrolineata	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Lamellaxis gracilis	**0.037**	**0.002**	**<0.001**	0.681	0.940
Megalomastoma croceum	0.196	0.644	0.304	**0.027**	**0.023**
Nenia tridens	0.662	**0.021**	**<0.001**	**<0.001**	**<0.001**
Obeliscus terebraster	0.498	0.496	0.785	0.573	0.952
Oleacina glabra	**<0.001**	**0.006**	**<0.001**	**0.004**	**<0.001**
Oleacina playa	0.421	0.711	0.468	0.724	0.798
Platysuccinea portoricensis	**0.015**	**<0.001**	0.115	**<0.001**	**0.022**
Polydontes acutangula	0.721	0.056	**<0.001**	**<0.001**	0.441
Subulina octona	0.601	0.788	0.177	0.763	0.121
Total abundance	**0.047**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Point biodiversity					
Species richness	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.032**
Shannon diversity	**0.001**	**<0.001**	**<0.001**	**<0.001**	0.518
Camargo evenness	**0.004**	**<0.001**	**<0.001**	**<0.001**	0.586
Berger–Parker dominance	0.069	**<0.001**	**<0.001**	**<0.001**	0.858
γ-biodiversity					
Species richness	0.292	**0.009**	0.618	**<0.001**	0.377
Shannon diversity	0.687	0.311	0.225	**<0.001**	0.669
Camargo evenness	0.605	0.308	0.304	**<0.001**	0.761
Berger–Parker dominance	0.517	0.233	0.125	0.059	0.356

Note: Error terms for analyses of abundance were based on a negative binomial distribution, whereas error terms for analyses of biodiversity were based on a Gaussian distribution. Analyses of abundance and point biodiversity incorporated point as a random factor with both a random intercept term and a random slope term to control for repeated measures through time and temporal autocorrelation. Analyses of γ-biodiversity were conducted at the scale of the Luquillo Dynamics Forest Plot and incorporated year as a random factor to control for temporal autocorrelation. Significant results ($p ≤ .05$) are bold.

4.1 | Resistance, resilience, and secondary succession

Hurricanes cause two drastic changes to tropical forests (Brokaw et al., 2012; Shiels & González, 2014; Shiels et al., 2014, 2015). They create gaps in the canopy of various sizes that persist to the level of the forest floor. These gaps alter the microclimatic conditions (e.g., light penetration, temperature, and humidity) of the understorey. Simultaneously, hurricanes deposit large quantities of debris

(fine and coarse wood as well as green leaves) on the forest floor that alter the microclimatic conditions of the litter, the physical structure of understorey, and nutrient availability. These immediate effects of hurricanes are confounded in any non-manipulative experiment, such as this one, that explores biotic responses over time because the additive and interactive effects of canopy opening and debris deposition cannot be disentangled. Nonetheless, initial effects of hurricane-initiated disturbances promote a temporal sequence of biotically driven site-specific changes that manifest with regard to
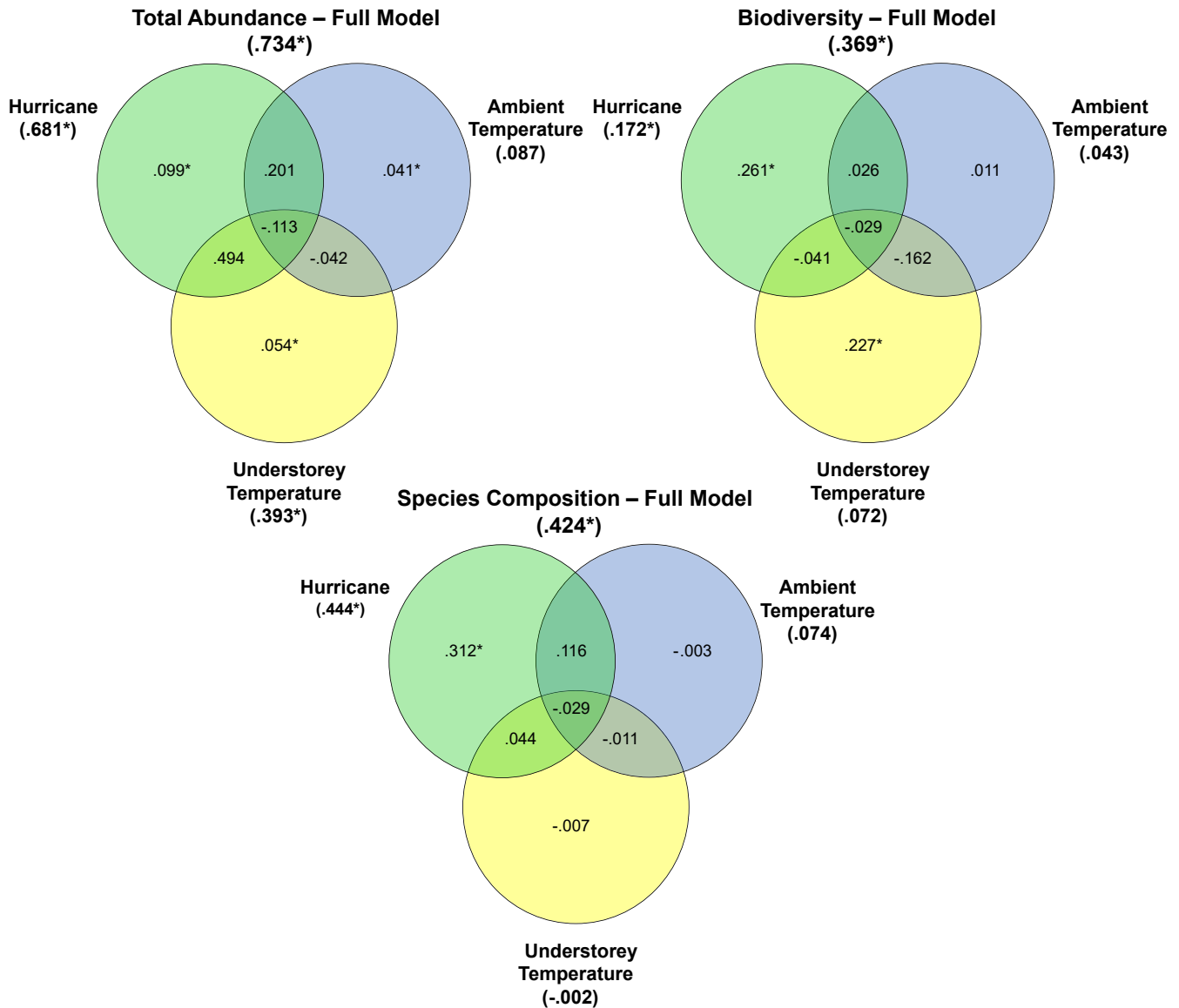
TABLE 4 Results of variation partitioning to evaluate the relative contributions of ambient temperature (AT), understorey temperature (UT), and hurricane (H, including hurricane identity and time after most recent major hurricane) on variation in abundance of each of 17 species of gastropod, total abundance, each of four metrics of biodiversity, the four biodiversity metrics as a multivariate group (Biodiversity matrix), and the relative abundances of each of 17 species as a multivariate group (Composition matrix)

	Unique partitions						Total partitions						Shared partitions				Residual	Full model	
	AT		UT		H		AT		UT		H		AT∩UT	AT∩H	UT∩H	3-way shared	variation		
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	R^2	R^2	R^2		R^2	p
Population																			
Alcadia alta	.027	.236	.002	.307	-.040	.520	.055	.104	.077	.080	-.078	.770	.043	-.005	.110	-.077	.940	.060	.278
Alcadia striata	.016	.252	.082	.085	.298	**.049**	-.038	.851	-.033	.716	.177	.053	-.050	-.055	-.116	.050	.774	.226	.098
Austroselenites alticola	.155	**.006**	.173	**.007**	.002	.422	.016	.234	.416	**.001**	.354	**.004**	-.133	-.024	.359	.017	.451	.549	**.002**
Caracolus caracolla	.005	.289	.043	.127	.029	.268	-.024	.544	.304	**.003**	.356	**.005**	-.031	.035	.325	-.033	.627	.373	**.005**
Caracolus marginella	-.028	.833	.026	.178	.050	.215	-.024	.561	.338	**.001**	.333	**.013**	.030	.000	.309	-.026	.640	.360	**.023**
Cepolis squamosa	-.017	.516	.282	**.002**	.385	**.017**	.022	.220	-.040	.935	.090	.153	.016	.042	-.318	-.020	.629	.371	**.017**
Diplosolenodes occidentalis	.122	**.014**	.078	.058	.363	**.036**	-.019	.490	.063	.112	.282	.054	-.028	-.155	-.089	.102	.606	.394	**.042**
Gaeotis nigrolineata	.029	.243	.003	.320	-.077	.755	-.007	.367	.061	.115	.020	.302	-.039	.000	.094	.003	.986	.014	.375
Lamellaxis gracilis	.141	**.033**	.234	**.009**	.252	**.013**	.057	.129	.064	.116	.206	**.041**	-.147	-.022	-.110	.086	.566	.434	**.010**
Megalomastoma croceum	-.047	.970	-.032	.581	-.005	.395	-.003	.375	-.032	.648	.041	.251	.007	.053	.009	-.016	1.030	-.030	.507
Nenia tridens	-.003	.404	-.009	.575	.279	**.002**	.114	.058	.187	**.023**	.712	**.001**	-.004	.233	.313	-.113	.303	.697	**.001**
Obeliscus terebraster	-.032	.545	-.023	.481	-.072	.659	-.034	.731	-.038	.852	-.078	.791	-.013	-.004	-.017	.014	1.146	-.146	.894
Oleacina glabra	.240	**.010**	.204	**.008**	.131	.079	-.006	.356	.178	**.021**	.097	.148	-.181	-.188	.033	.122	.639	.361	**.010**
Oleacina playa	.019	.254	.008	.304	-.023	.499	.010	.265	-.033	.684	-.039	.586	-.040	-.016	-.048	.047	1.052	-.052	.609
Platysuccinea portoricensis	-.040	.812	.023	.227	.026	.298	.010	.283	.035	.183	.063	.206	.005	.030	-.008	.015	.949	.051	.294
Polydontes acutangula	-.011	.552	.114	**.012**	.445	**.002**	-.030	.620	.149	**.028**	.494	**.001**	.001	.015	.070	-.035	.402	.598	**.001**
Subulina octona	.022	.193	-.022	.559	.117	.140	.043	.144	-.013	.410	.233	**.035**	-.013	.094	-.008	.030	.779	.221	.087
Total abundance	.041	**.048**	.054	.471	.099	**.027**	.074	.055	.393	**.002**	.681	**.001**	-.042	.201	.494	-.113	.266	.734	**.001**
Community																			
Species richness	.034	.161	.376	**.002**	.235	**.030**	.007	.285	.138	**.036**	.016	.340	-.071	-.052	-.264	.097	.645	.355	**.006**
Shannon diversity	-.024	.895	-.002	.351	.336	**.005**	.140	**.031**	-.033	.693	.484	**.002**	.013	.193	-.002	-.042	.528	.472	**.002**
Camargo evenness	-.026	.924	-.005	.389	.323	**.010**	.100	.061	-.025	.557	.455	**.002**	.005	.157	.012	-.037	.571	.429	**.010**
Berger–Parker dominance	-.026	.571	-.021	.477	.164	.088	-.026	.584	-.040	.922	.151	.077	-.009	-.004	-.021	.012	.905	.095	.231
Biodiversity matrix	.011	.253	.227	**.004**	.261	**.005**	.043	.144	.072	.075	.172	**.038**	-.162	.026	-.041	.047	.631	.369	**.002**
Composition matrix	-.003	.456	-.007	.471	.312	**.003**	.074	.055	-.002	.401	.444	**.001**	-.011	.116	.044	-.029	.576	.424	**.002**

Note: Shared partitions cannot be tested for statistical significance. Because adjusted R^2 values are not strictly additive, adjustments to R^2 often result in small negative values for partitions as well as for variation explained by the full model, sometimes leading to 'residual variation' >1.0. Importantly, such small negative values should be considered to be zero (Legendre et al., 2012). Significant results ($p \le .05$) for full models or individual partitions are bold.

Total Abundance – Full Model
(.734*)

Hurricane
(.681*)

.099* .201 .041*

-.113

.494 -.042

Ambient
Temperature
(.087)

.054*

**Understorey
Temperature
(.393*)**

Biodiversity – Full Model
(.369*)

Hurricane
(.172*)

.261* .026 .011

-.029

-.041 -.162

Ambient
Temperature
(.043)

.227*

**Understorey
Temperature
(.072)**

Species Composition – Full Model
(.424*)

Hurricane
(.444*)

.312* .116 -.003

-.029

.044 -.011

Ambient
Temperature
(.074)

-.007

**Understorey
Temperature
(-.002)**

FIGURE 5 Hurricane identity and succession after each hurricane explained more variation in gastropod abundance, biodiversity, or species composition than did understorey or ambient temperature. Variation partitioning for total gastropod abundance, biodiversity (based on Hill numbers for species richness, Shannon diversity, Camargo evenness, and Berger–Parker dominance), and species composition (based on annual relative abundances of each of 17 species) from the Luquillo Forest Dynamics Plot (LFDP) during 1993–2019. Partitions included hurricane, represented by hurricane identity (Hurricanes Hugo, Georges, Maria) and time after most recent major hurricane; ambient temperature (mean daily maximum temperature for each year); and understorey temperature (mean daily maximum temperature for each year). Total partitions are displayed outside each corresponding circle, unique partitions are in the corresponding non-overlapping portion of each circle, and shared partitions are in the corresponding overlapping portions of the diagram. Numerical values are explained amounts of variation related to partitions or models; significant effects are indicated by an asterisk; shared partitions cannot be tested for significance

microclimatic, abiotic, biotic and structural characteristics of the forest (secondary succession). In our analyses, we do not include any of these site-specific characteristics (or their variability) that are directly linked to such successional changes. Instead, we use TAH as a univariate surrogate that is common to all 40 sites within years, as an admittedly imperfect representation of those changing multivariate characteristics. Similarly, we use understorey temperature (UT) as a

surrogate that is common to all 40 sites within years whose temporal trend reflects the process of canopy closure, a well-documented successional trend that on the LFDP plays a dominant role driving ecosystem dynamics (Shiels et al., 2015).

Responses of gastropods to immediate effects of intense hurricanes (i.e., before and after comparisons) can be quite substantial (e.g., Willig & Camilo, 1991) and indicate low resistance.
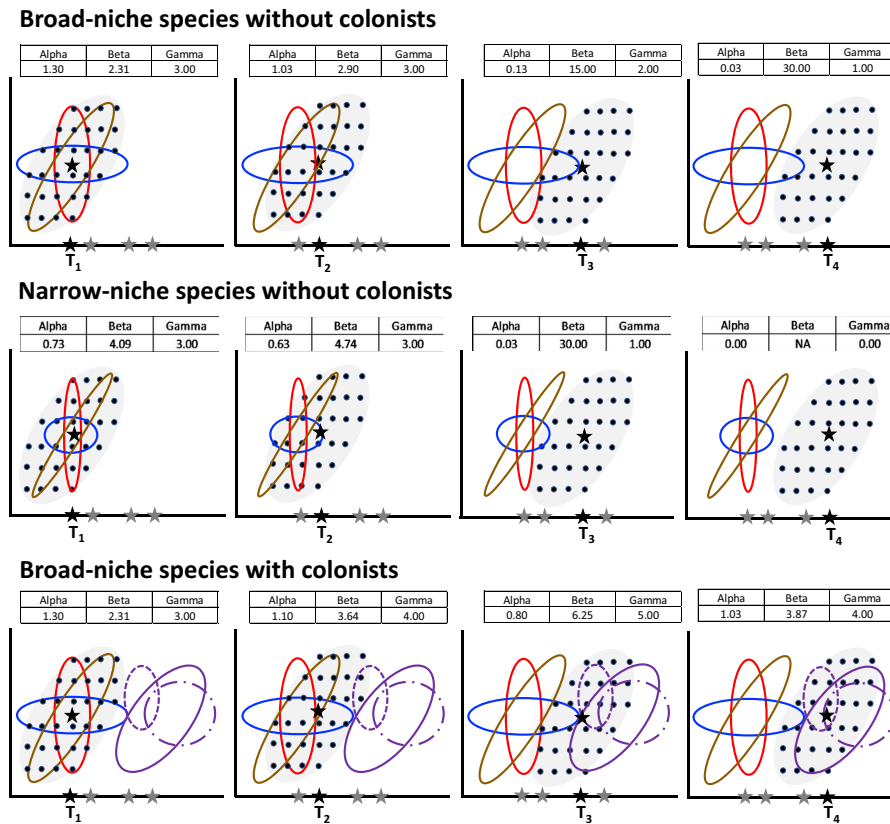
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Broad-niche species without colonists

Narrow-niche species without colonists

Broad-niche species with colonists

FIGURE 6 Three scenarios, defined by rows (broad-niche species without colonists, narrow-niche species without colonists, and broad-niche species with colonists), demonstrating how the interactions between the fundamental niches of species (coloured ellipses) and changing environmental conditions (grey shaded ellipses) due to disturbances can result in changes in species composition and the emergence of novel communities over time. The large grey shaded ellipse in each panel represents the available environmental characteristics in two-dimensional (x and y axes) space for a landscape that comprises multiple sampling sites (black dots). The four panels within each row represent sequential periods within a time series. The mapping of environmental characteristics onto the sampling sites with time (T_i) changes in a directional manner (i.e., the location of the grid in environmental space differs among T_1, T_2, T_3, and T_4) because of shifts with respect to characteristics associated with the x axis (compare panels within rows). For convenience, the centroid of the available environmental space at each time period is indicated by a black star and is projected onto the x axis to illustrate environmental change (e.g., warming); the grey stars on the x axis denote centroids of environmental space at earlier or later periods in the time series. The blue, red, and brown ellipses represent the fundamental niches of each of three species with respect to environmental characteristics (species do not evolve, niches remain constant). The overlap of species distributions at a site defines its composition and species richness. The three purple ellipses (see bottom row of panels) represent the fundamental niches of species in the regional species pool that did not occur in the landscape at T_1 because the environmental characteristics of the landscape did not correspond to the fundamental niches of those species. The temporal sequence of changes in the environmental characteristics of the sampling points is the same in the top, middle, and bottom rows, but the fundamental niches of species are broader in the top row compared to the middle row. In the bottom row, the fundamental niches of species are the same as in the top row, but the consequences of environmental change are expanded to include the possible addition of species from a regional pool that were not present at the sampling points at T_1. α represents the average species richness of communities at the sampling points, γ represents the total species richness of the entire landscape (as if the data for the sampling points were combined into a single sample). β represents the 'turnover' among communities in the landscape and derives from a multiplicative model (α × β = γ; Jost, 2007). Richness decreases more quickly at the γ and α level if species have narrow niches with respect to the biota originally on the grid at T_1 (compare top and middle rows). Moreover, if environmental characteristics shift over time and species can colonize the landscape from outside areas (bottom row), novel communities may appear, replacing the original community. For example, species composition for the grid or suite of points at T_1 includes the red, blue, and brown species (bottom row, left-most panel), whereas species composition at T_3 may represent a novel community that includes the blue species plus three invading species designated by different purple ellipses (bottom row, third panel from the left)

For example, *C. caracolla*, *N. tridens*, and *G. nigrolineata*, three of the more common gastropod species in tabonuco forest, declined greatly in abundance after Hurricane Hugo in the Bisley Watersheds, less than 10 km from the LFDP (Willig & Camilo, 1991). Similarly, each of those three species as well as

O. glabra, *P. portoricensis*, and *S. octona* declined in response to Hurricanes Maria and Georges, with species typically exhibiting low resilience (i.e., declining in abundance) after each hurricane and much lower resilience after more severe hurricanes. Hurricane Georges was a much less intense disturbance than were

Hurricanes Hugo or Maria. Consequently, fewer species significantly declined in response to Georges, and the proportional declines in total abundance were much smaller compared to those in response to Hurricane Maria (Table 2) or to Hurricane Hugo (Willig & Camilo, 1991). As expected, resistance to hurricane-induced disturbance was greatest for the least intense storm (Hurricane Georges) and least for the more intense storms (Hurricanes Hugo and Maria), reflecting the effects of desiccation stress arising from greater temperatures and lower humidity that are effected by canopy loss. The effects of hurricane intensity on biotic responses are consistent with results from a long-term experiment involving repeated, simulated hurricane-like disturbances in tabonuco forest (Shiels & González, 2014). Simulated hurricanes created 30 × 30 m gaps in the canopy, which were surrounded by mature forest that could provide source populations to disturbed areas. Gastropod populations and communities were resistant and resilient to these simulated disturbances, exhibiting quick recovery from any short-term changes in abundance or biodiversity, similar to responses to Hurricane Georges (Presley & Willig, 2021).

Although our analyses do not provide support for consistent declines in abundance or in richness over time associated with warming, they do suggest that interannual variation is driven by climate-induced environmental changes. More specifically, we can significantly account for 73.4% of the interannual variation in total gastropod abundance using hurricane-related attributes, ambient temperature, and understorey temperature (Table 4). The vast majority of that variation is related to total effects of hurricane (68.1% of the total variation) because variation in understorey temperature is related to severity and recency of hurricane damage to the forest (large hurricane–understorey temperature shared partition in Figure 5). These same environmental factors explain appreciable proportions of variation in biodiversity and in species composition, reinforcing the contention that climate-induced variation associated with hurricanes and ensuing succession override any direct effects of global warming (Table 4; Figure 5). Of course, disturbance and succession induced by increasingly frequent and intense cyclonic storms are an indirect effect of global warming, indicating that anthropogenic activities affect this disturbance-mediated system despite considerable resilience to warming, per se.

4.2 | Prognosis for the future

The inferences drawn from this study formally pertain only to the three decades considered in these analyses, including the domain of independent variables. Moreover, extrapolations of these results outside of such domains may be uninformative, especially if the rate of change in ambient temperature or the frequency of high energy storms increases, potentially creating new combinations of environmental characteristics that are outside of the 'evolutionary history' of the system or diminishing the likelihood of rescue effects or compensatory source–sink dynamics. Consistent with palaeontological, biogeographic, and ecological theory (Waide &

Willig, 2012), we predict that species extinctions or changes in the combination of species that are syntopic (i.e., community patterns) in the form of direct responses to anthropogenically induced climate change have not yet occurred in tabonuco forest of Puerto Rico because (a) the fundamental niches of species are sufficiently large or (b) the extent of change in critical, limiting environmental characteristics to which a biota responds is too small (Figure 6). In general, resistance and resilience should be enhanced when the ratio of species niche breadth to environmental change is large and should be diminished when that ratio is small (Figure 6). At the metacommunity level, a shift in environmental characteristics would result in changes in the hierarchical organization of biodiversity at α (i.e., mean species richness of points) and γ (i.e., total species richness of the LFDP) levels, as well as changes in the heterogeneity in or turnover among sites (i.e., β = γ/α; Jost, 2007) in species composition.

Species in the tabonuco forest in particular, and in Puerto Rico in general, have experienced a history of hurricane-induced disturbances for millennia (Zimmerman, Willig, et al., 2020), likely resulting in broad fundamental niches, especially those related to temperature, to ensure species persistence. Indeed, differences in temperature between open and closed canopy forest at any point in time are greater than the extent of change in ambient temperature that has characterized the last three decades, and year-to-year variation in temperature are as large or larger than any directional changes experienced during the past 30 years (Figure 2). Thus, both spatial and temporal considerations of variability that are related to existence in a hurricane-mediated environment may predispose the biota to high resistance and resilience to global warming at the decadal scale (Zellweger et al., 2020).

If the rate of change in warming over the coming decades results in a thermal environment that is outside the fundamental niches of some of the species in the current gastropod fauna, we will likely begin to see the local extirpation of species (Figure 6; T_3 and T_4 of the top and middle rows). Moreover, the forest may become colonized by gastropods from the regional species pool, perhaps those from lower elevations, that can tolerate or thrive in warmer and drier conditions, depending on species-specific dispersal limitations (Figure 6; T_1 and T_2 of the bottom row). Eventually, novel communities will likely arise (Figure 6; T_3 and T_4 of the bottom row). For example, 29 of the 30 points in the hypothetical landscape of Figure 6 support novel communities (T4, right panel), those with only newly immigrating taxa and without any of the species originally in the landscape at T_1 (left panel of Figure 6). Such taxa immigrating to tabonuco forest will likely be resistant to desiccation stress. Moreover, the likelihood of novel communities occupying the landscape will be enhanced if the interval between intense cyclonic storms decreases as is predicted by some climatological forecasts (M. A. Bender et al., 2010). Because the degree of canopy openness will increase and persist, it will further increase understorey temperature and potentially alter the structural environment (Zellweger et al., 2020), as well as the abundance and composition of taxa on which gastropods feed.

4.3 | Perspectives on synoptic and syntopic networks

The severity of predictions about a sixth extinction crisis combines with the scientific and public controversies about the veracity of declines in abundance to suggest a number of recommendations. First, long-term monitoring of populations and communities needs to become a scientific priority. Second, such biotic monitoring should be coupled with parallel monitoring of a comprehensive suite of environmental indicators. Third, the temporal plan for monitoring (at least annual) should be designed to quantify historical reference conditions, short-term effects of episodic disturbances, subsequent secondary successional dynamics, and longer-term trends beyond cycles of disturbance and recovery. Fourth, synoptic monitoring needs to be undertaken for a variety of taxa in multiple habitats across the planet to fully evaluate generality of patterns, and to encourage integration and synthesis that leads to predictive understanding that can inform conservation, adaptive management, and environmental policy. The challenges to do so are far from trivial, although the guidelines for establishing effective monitoring programmes are reasonably well known (e.g., Didham et al., 2020; Lindenmayer & Likens, 2010). The costs of failure are enormous, as the ecosystem services provided by biota underwrite the long-term health and vitality of human society in general.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

Both authors contributed substantially to all aspects of this research, resulting in similar overall contribution to this work.

DATA AVAILABILITY STATEMENT

Gastropod and temperature data are archived publicly and openly available in the Luquillo Long-Term Ecological Research data catalogue, https://luq.lter.network/data/luqmetadata107 or https://portal.edire pository.org/nis/mapbrowse?packageid=knb-lter-luq.107.9996737. In addition, the code and data used to conduct these analyses are provided in the Supporting Information and are archived on DRYAD: https://doi.org/10.5061/dryad.1zcrjdft4, https://datadryad.org/stash/share/Lf99Zllrmrtyf1C_LkmKcC-nt-putS723Sv91UxOHs8.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Willig, M. R., & Presley S. J. (2022). Long-term trends in gastropod abundance and biodiversity: Disentangling effects of press versus pulse disturbances. *Global Ecology and Biogeography*, 31, 247–265. https://doi.org/10.1111/geb.13425