

Research article

Long-term responses to large-scale disturbances: spatiotemporal variation in gastropod populations and communities

Steven J. Presley[✉] and Michael R. Willig[✉]

Inst. of the Environment, Center for Environmental Sciences & Engineering, and Dept of Ecology & Evolutionary Biology, Univ. of Connecticut, Storrs, CT, USA

Correspondence: Steven J. Presley (steven.presley@uconn.edu)

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The Anthropocene is characterized by complex, primarily human-generated, disturbance regimes that include combinations of long-term press (e.g. climate change, pollution) and episodic pulse (e.g. cyclonic storms, floods, wildfires, land use change) disturbances. Within any regime, disturbances occur at multiple spatial and temporal scales, creating complex and varied interactions that influence spatiotemporal dynamics in the abundance, distribution and biodiversity of organisms. Moreover, responses to disturbance are context dependent, with the legacies of previous disturbances affecting responses to ensuing perturbations. We use three decades of annual data to evaluate the effects of repeated pulse disturbances and global warming on gastropod populations and communities in Puerto Rico at multiple spatial scales. More specifically, we quantify 1) the relative importance of large-scale and small-scale aspects of disturbance on variation in abundance, biodiversity and species composition; and 2) the spatial scales at which populations and communities integrate information in the spatially heterogeneous environments created by disturbances. Gastropods do not exhibit consistent decreases in abundance or biodiversity in association with global warming: abundance for many species has increased over time and species richness does not evince a temporal trend. Nonetheless, gastropods are sensitive to hurricane severity, spatial environmental variation and successional trajectories of the flora. In addition, they exhibit context dependent (i.e. legacy effects) responses that are scale dependent. The Puerto Rican biota has evolved in a disturbance-mediated system. This historical exposure to repeated, severe hurricane-induced disturbances has imbued the biota with high resistance and resilience to the current disturbance regime, resulting in an ability to persist or thrive under current environmental conditions. Nonetheless, these ecosystems may yet be threatened by worsening direct and indirect effects of climate change. In particular, more frequent and severe hurricanes may prevent the establishment of closed canopy forests, negatively impacting populations and communities that rely on these habitats.

Keywords: climate change, global warming, hurricane-induced disturbance, Luquillo Experimental Forest, population dynamics, Puerto Rico, pulse disturbance, press disturbance, succession, tropics



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Introduction

Human-induced environmental change is the defining feature of the current geological epoch with the proposed name of the 'Anthropocene' (Monastersky 2015). Current unprecedented and accelerating rates of environmental change associated with human activities have initiated a biodiversity crisis that may cause the Earth's sixth mass extinction (Cafaro 2015, Ceballos et al. 2015). Human-induced environmental changes occur at small and large spatial scales, persist over short- and long-time frames, and have direct and indirect effects on environmental conditions that affect the abundances of species and the composition and biodiversity of biotas. Ecological disturbances (hereafter 'disturbances') are events or forces of biological or non-biological origin that cause mortality and changes the distribution of resources in ecosystems (Paine 2019). Disturbances can play significant roles in shaping the structure of populations and the character of entire ecosystems. Anthropogenically-induced disturbances include pulse (e.g. land use change, wildfires, cyclonic storms and floods) and press (e.g. increasing temperature, ocean acidification, sea level rise, pollution) disturbances (Sasaki et al. 2015, Jentsch and White 2019). Pulse disturbances are relatively instantaneous and episodic events, after which the system responds via succession (Jentsch and White 2019), whereas press disturbances represent environmental changes that are maintained or exacerbated over extended time periods (Bender et al. 1984). In addition, some disturbances may initially represent pulse disturbance (e.g. clear-cut logging) but may come to represent press disturbances if their effects are maintained over time (e.g. clear-cut logging after which the cleared land is used for agriculture or human habitation). Currently, effects of press disturbances associated with climate change are ubiquitous. Consequently, any system that experiences pulse disturbances has a disturbance regime comprising both pulse and press components. Disentangling the relative effects of each component of a disturbance regime and identifying the spatiotemporal scales at which these effects manifest remain as a critical challenge for ecology and conservation biology (Collins et al. 2016, Willig and Presley 2022a, c).

Variation in the frequency, extent and intensity of each aspect of a disturbance regime can have wide-ranging effects on the regional biota (Pickett and White 1985). In systems with complex disturbance regimes, disturbances can initiate cross-scale interactions: processes at one spatial or temporal scale that interact with processes at other scales, resulting in nonlinear dynamics in populations and communities (Peters et al. 2007, Willig et al. 2007). Disturbances affect the demographics of species at fine spatial scales by altering the local abiotic, biotic or structural environment. In addition, disturbances create environmental variation among local habitats and alter landscape configuration, thereby modifying the effective connectedness among sites and the movement of individuals among communities (Thrush et al. 2013). As secondary succession advances, biotic, abiotic and structural characteristics of local sites change as a result of interactions

between fine-scale and broad-scale processes (Willig et al. 2007). Changes in local environmental characteristics alter the nature and configuration of habitat patches at broad scales, thereby creating a cascade of cross-scale interactions (Thrush et al. 2013, Buma 2015). Consequently, these interactions have the potential to significantly mold spatiotemporal patterns of abundance, composition and biodiversity, and will likely do so in complex ways in response to anthropogenically driven, dynamic disturbance regimes (Peters et al. 2007, Buma 2015). Moreover, the historical environmental context (i.e. the history or legacies of previous disturbances, including those of natural or anthropogenic origin) within which a particular disturbance event occurs can affect the severity of the disturbance (Grove et al. 2000, Lomascolo and Aide 2001), as well as immediate biotic responses (resistance) and long-term trajectories during secondary succession (Willig and Walker 1999, Bloch et al. 2007, Willig et al. 2011, Schowalter et al. 2017, Willig and Presley 2022a).

The Caribbean Basin (Fig. 1) is characterized by a history of high-intensity cyclonic storm activity (Johnson 2015), with over 2000 hurricanes recorded in the Caribbean Islands since 1851 (<http://hurricane.csc.noaa.gov/hurricanes/>). The cumulative or interactive effects of repeated high-intensity storms mold patterns of abundance and distribution of organisms on Caribbean Islands in general and Puerto Rico in particular (Waide and Lugo 1992). Eastern Puerto Rico has repeatedly experienced major hurricanes during the last few decades, resulting in an ideal opportunity to assess context-dependent effects of intense disturbances on the spatial and temporal demographics of local populations and communities (Walker et al. 1991, 1996). Because global warming may increase the frequency and intensity of hurricanes in the future (Webster et al. 2005), understanding the long-term effects of successive disturbances on the resilience of ecological systems is imperative (Holt 2006, Schoener and Spiller 2006). Despite links between global warming and increasing frequency and intensity of hurricanes, this relationship likely is not linear (Holland and Bruyère 2014), such that isolating the effects of global warming from those of hurricane-induced disturbances is especially challenging. Moreover, evaluations of responses at multiple spatial scales are necessary because of cross-scale interactions.

Terrestrial gastropods are diverse, abundant and easily sampled in many ecosystems, making them useful models for population (Willig and Camilo 1991, Willig et al. 1998b, 2014), community (Stanisic et al. 2007, Wronski and 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 conservationists (Lydeard et al. 2004). As ectotherms that are subject to desiccation stress, gastropods exhibit strong responses to changes in canopy openness, temperature or precipitation (Alvarez and Willig 1993, Nicolai and Ansart 2017). Consequently, direct (e.g. increasing temperature, more intense droughts) and indirect (e.g. changes in disturbance regimes) effects of

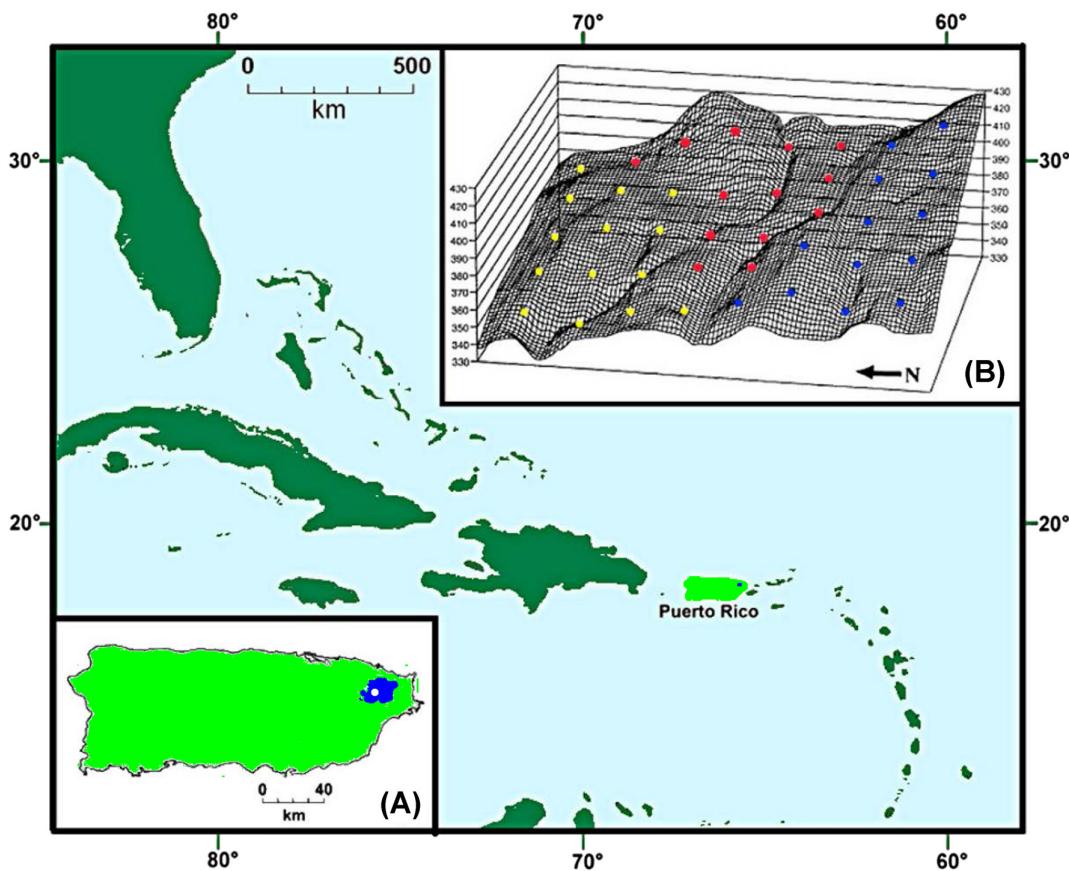


Figure 1. Map of the Antilles (modified from Willig et al. 2011) indicating the location of Puerto Rico (bright green) with respect to other islands. (A) Map of Puerto Rico indicating the location of the Luquillo Experimental Forest (blue) and the Luquillo Forest Dynamics Plot (LFDP, white dot), within the Luquillo Experimental Forest. (B) Elevational relief (contours represent meters above sea level) of the LFDP with red, yellow and blue dots representing points in land use category A (intensive logging and agriculture), B (coffee-cultivation and smaller-scale agriculture) and C (selective logging), respectively.

global warming, combined with increased intensity of other anthropogenic activities, may subject these faunas to greater risk of local or regional extirpation.

Terrestrial gastropods in lower montane rainforests of Puerto Rico have a ubiquitous spatial distribution, but responses to abiotic variation result in considerable spatial heterogeneity and interspecific variation in abundances (Bloch et al. 2007, Willig et al. 2014, 2021). These terrestrial gastropods represent multiple functional groups, including arboreal grazers, carnivores and detritivores (Bloch and Willig 2012), and are often highly abundant, making them important contributors to nutrient cycling in tropical rainforests (Willig and Presley 2022a). In general, competition does not structure these communities, species abundances are positively correlated in time and space, suggesting that variation in habitat quality or resource abundance influence shared population-level responses with no evidence of density compensation (Willig et al. 2021). 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 and Willig 2009, 2012).

Long-term, comprehensive assessments have found that the direct effects of hurricane-induced disturbances and subsequent secondary succession dwarfed the direct effects of global warming on arboreal arthropods (Schowalter et al. 2021) and understory gastropods (Willig and Presley 2022a). However, these approaches used only large-scale explanatory factors (e.g. hurricane identity, ambient temperature and time after most recent major hurricane) to account for ecological variation and lacked measures of spatial variation created by hurricane-induced disturbances, variation associated with local conditions (e.g. slope, aspect, soil type) or pre-disturbance conditions. Herein, we evaluate responses of gastropod populations and communities at small and large spatial scales to aspects of a complex disturbance regime and the spatial heterogeneity that it generates. More specifically, we 1) quantify the effects of large-scale disturbances and the spatial heterogeneity that they create at multiple spatial

scales on gastropod abundance, species composition and biodiversity; and 2) determine the spatial scales at which gastropods integrate information in the heterogenous environment created by hurricane-induced disturbances. Understanding biotic responses to disturbance events as well as to the spatial heterogeneity that they create contribute to the development of the theories of disturbance (Pickett and White 1985), succession (Pickett et al. 2011) and cross-scale interactions (Peters and Havstad 2006, Willig et al. 2007).

Material and methods

Study site

Field work was conducted in Puerto Rico (Fig. 1A) on the Luquillo Forest Dynamics Plot (LFDP), a 16-ha rectilinear grid established after Hurricane Hugo to evaluate long-term responses to hurricane-induced disturbances (Fig. 1B). The LFDP is in tabonuco forest in the western part ($18^{\circ}19'N$, $65^{\circ}49'W$) of the Luquillo Experimental Forest (LEF). Tabonuco forest is a tropical montane rainforest that grows between 250 and 600 m a.s.l. Canopy height is > 20 m, with emergent trees up to 35 m tall. Average annual rainfall is ~350 cm; humidity is high; and mean temperature is $23^{\circ}C$, with little seasonal or diurnal variation (Brokaw et al. 2012).

Study organisms

Terrestrial gastropods are taxonomically diverse and numerically abundant in many ecosystems, making them useful for studying the effects of press and pulse disturbances, as well as spatiotemporal dynamics associated with succession (Presley et al. 2011, Willig et al. 2011). High quality, spatially explicit, long-term, annual data on gastropod abundance exist for the LFDP (Willig et al. 1998b, Willig and Presley 2022b). Gastropod species have ubiquitous spatial distributions throughout tabonuco forest, but exhibit considerable spatial heterogeneity and interspecific variation in abundances associated with local environmental variation (Bloch et al. 2007, Willig et al. 2014, 2021). In addition, gastropods are subject to desiccation stress, making them vulnerable to changes in canopy openness, temperature and precipitation (Alvarez and Willig 1993, Nicolai and Ansart 2017).

Habitat use by gastropods in the LEF spans a gradient from species that occur almost exclusively on soil, leaf litter, rocks and fallen dead wood (e.g. *Alcadia alta*, *Megalomastoma croceum*, *Platysuccinea portoricensis*) to those that occur almost exclusively on live vegetation (e.g. *Gaeotis nigrolineata*, *Polydentes acutangula*); however, the majority of species commonly occur on litter, as well as on live vegetation. In general, particular species of gastropod do not maintain strong associations with particular species of plant; however, they may select or avoid particular plant species based on size and bark texture (Heatwole and Heatwole 1978). Gastropods in tabonuco forest include arboreal grazers, carnivores and detritivores (Bloch and Willig 2012).

Field methods

Gastropods were surveyed annually from 1991 through 2019 at each of 40 points on the LFDP. At each point, all surfaces (e.g. rocks, litter, debris, vegetation) within a 3 m radius and up to 3 m of height were inspected for gastropods. Surveys were conducted by two field technicians for 15 min or until all surfaces were exhaustively searched, whichever was longer. The same 40 points were surveyed two times in 1991, 1992 and 1993, three times in 1994, and four times all other years. All surveys were conducted during the wet season, typically June, July or August, and generally with 3–7 days between surveys. To minimize alteration of long-term study sites, litter was not manipulated and individuals were returned as closely as possible to the point of capture. Consequently, our inferences are restricted to gastropods that occur on or above ground litter that range in size from < 10 mm (*A. alta*, *Lamellaxis gracilis*) to > 60 mm (*Caracolus caracolla*, *P. acutangula*), but exclude species of micro snail (< 5 mm) that live in the soil or under the litter and cannot be reliably surveyed without modifying the habitats of these long-term study sites. Seventeen species of terrestrial gastropod typically occur in these surveyed habitats (Willig and Presley 2022a, b).

Land use history

Anthropogenic activities represent important legacies of past disturbances on the LFDP (Thompson et al. 2002). The U.S. Forest Service purchased the land of the LEF in 1934 and allowed it to revert to closed-canopy forest. The legacy of land use continues to influence extant patterns of species composition and abundance of plants (Thompson et al. 2002, Rice et al. 2004) and animals (Bloch and Weiss 2002, Bloch et al. 2007, Willig et al. 2011, Willig and Presley 2022c). Three historical land use categories occur in roughly equal extent across the LFDP (Fig. 1B, Thompson et al. 2002). Land use category A experienced the most intense land use, with intensive logging and agriculture resulting in less than 50% canopy cover in 1936. Land use category B was used for small-scale mixed agriculture, mostly shade coffee, with 50–80% canopy cover in 1936. Land use category C was lightly and selectively logged forest with over 80% canopy cover in 1936.

Hurricane history

During the past four decades, three major hurricanes (Hugo in 1989, Georges in 1998, Maria in 2017) have impacted northeastern Puerto Rico and caused extensive damage to tabonuco forest in the LEF. These hurricanes differed in intensity and severity of damage caused to the forest (Zimmerman et al. 2020). In 1989, Hurricane Hugo was a category 4 storm (227 km h^{-1} winds) that produced large canopy openings and deposited large quantities of woody debris on the forest floor (Scatena and Larsen 1991). In 1998, Hurricane Georges was a category 3 storm (177 km h^{-1}

winds) that caused defoliation of trees, but did not produce appreciable canopy openings or woody debris (Ostertag et al. 2003). In 2017, Hurricane Maria was a category 4 storm (250 km h⁻¹ winds) that caused extensive tree mortality, removing the majority of forest canopy on the LFDP and killing twice as many trees as did Hurricane Hugo (Uriarte et al. 2019).

Ambient and understory temperatures

To estimate the effects of global warming in northeastern 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 weather station at the Luis Muñoz Marin International Airport in San Juan, which is ~24 km from the LFDP. We averaged the daily maximum temperatures for each year to estimate annual ambient temperature (hereafter ambient temperature (T_{ambient})).

We define the understory as the vertical space between the forest floor and the forest subcanopy, and understory habitat as the biotic, abiotic and structural components of this vertical space. The loss of canopy in a tropical forest changes the understory climate (Richardson et al. 2010, Schowalter et al. 2021). Consequently, animals that live in the understory experience temperatures that are influenced by ambient temperature as well as by canopy cover. Hurricane-induced loss of the forest canopy has resulted in a larger and more immediate increase in understory temperatures than has global warming over multiple decades (Schowalter et al. 2021), with closure of the canopy during succession resulting in net cooling of understory temperatures despite ongoing climate change (Willig et al. 2019). Continuous and reliable estimates of maximum daily understory temperatures for the LFDP exist only from mid-1992 until the present. Consequently, all analyses that included understory temperature considered only data from 1993 to 2019. To estimate annual temperature in the understory ($T_{\text{understory}}$), we averaged daily maximum temperatures for each year from a weather station located in the forest understory near the LFDP.

Characterization of space, habitat and disturbance

We characterized each point using spatial (northing, easting, elevation) and habitat characteristics. We quantified the aerial density of plants (i.e. plant apperancy) at heights from ground level to 3.0 m in 0.5 m increments (Secrest et al. 1996). We selected apperancy-based metrics to quantify habitat features known to influence variation in abundance or biodiversity of gastropods in tabonuco forest (Secrest et al. 1996, Willig et al. 1998a). These include cumulative apperancy at all heights with respect to 1) all live plants, regardless of species (PA_{live}); 2) all dead plants (PA_{dead}); 3) live plants in the genus *Piper* (PA_{piper}); and 4) live *Prestoea acuminata* (PA_{prestoea}). We also characterized apperancy of all live plants at each of seven heights: $PA_{0\text{m}}$, $PA_{0.5\text{m}}$, $PA_{1.0\text{m}}$, $PA_{1.5\text{m}}$, $PA_{2.0\text{m}}$, $PA_{2.5\text{m}}$ and $PA_{3.0\text{m}}$. Finally, canopy openness was measured

each year using a spherical densiometer, with higher numbers representing greater canopy openness. Apperancy of *Piper* spp. and *P. acuminata* were chosen because they can positively affect abundances of particular species of gastropod (e.g. *G. nigrolineata*, *Nenia tridens*, *P. acutangula*) in tabonuco forest (Secrest et al. 1996, Willig et al. 1998a). We used generalized variance inflation factor (GVIF) analysis to assess multicollinearity among independent variables (Fox and Monette 1990). This resulted in the removal of all height-specific plant apperancy characteristics (i.e. $PA_{0\text{m}}$, $PA_{0.5\text{m}}$, $PA_{1.0\text{m}}$, $PA_{1.5\text{m}}$, $PA_{2.0\text{m}}$, $PA_{2.5\text{m}}$ and $PA_{3.0\text{m}}$) from all analyses.

Disturbance was characterized based on historical land use, occurrence of major hurricanes, successional time after each hurricane and global warming. Because only historical land use was evaluated at the point scale, it was the only characteristic with the potential to exhibit spatial variation on the LFDP. More specifically, each point was assigned to one of the three land use categories based on historical land use (Thompson et al. 2002): 13 were located in land use class A (intensive logging), 14 in land use class B (shade coffee plantations) and 13 in land use class C (light and selective logging). Temporal variation in disturbance and succession on the LFDP was estimated via identity of most recent major hurricane (Hurricane; a proxy for variation in hurricane severity), time after the most recent major hurricane (TAH; a measure of successional time after disturbance), $T_{\text{understory}}$ (understory temperature) and T_{ambient} (ambient temperature).

Estimations of abundance and biodiversity

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, a metric that is not biased with regard to variation in the number of samples per year. We estimated total gastropod abundance for each point as the sum of the average abundances of all species at that point. Metrics of point biodiversity, including species richness, Shannon diversity, Camargo's evenness and Berger–Parker dominance (Magurran and McGill 2011) were calculated based on the species abundance distribution at a particular point (i.e. the average abundance of each species at each point). For ease of exposition, we refer to these metrics simply as 'richness', 'diversity', 'evenness' and 'dominance', and reserve 'biodiversity' to refer to the general concept that comprises all four metrics. Separately for each combination of year and metric, α biodiversity was calculated as the average point biodiversity for the 40 points.

For analyses at the LFDP scale, we characterized the abundance of each species, as well as total gastropod abundance, as the sum of the average number of captured individuals per survey across all 40 points on the LFDP within a year. Metrics of biodiversity at the LFDP 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. Regardless of scale, each metric of biodiversity was expressed as a Hill number (Jost 2006).

Spatial scales

Explanatory characteristics, abundance and biodiversity were estimated at two focal scales: point scale and LFDP scale. At the point scale, characteristics were measured separately at each of the 40 points on the LFDP with each point as a replicate within years. At the LFDP scale, characteristics were measured for the entire LFDP with a single value characterizing the LFDP each year. All measures of abundance, biodiversity and plant apparentness were estimated at both the point and LFDP scales. In contrast, some explanatory variables were either spatially invariant (e.g. hurricane identity, TAH, T_{ambient}) or were only measured in one location ($T_{\text{understory}}$) resulting in a single estimate for each year.

Analytical methods

Point scale

To understand the relative contributions of space, disturbance and habitat factors to spatiotemporal variation in gastropod abundance and point biodiversity at the point scale, we employed GLMMs and used type II sums of squares. Negative binomial error terms were used for analyses of gastropod abundance, which are count data characterized by zero inflation (O'Hara and Kotze 2011), whereas Gaussian distributions were used for analyses of metrics of biodiversity. The model included four kinds of characteristics: 1) spatial attributes (northing, easting and elevation); 2) habitat characteristics (canopy openness, PA_{live} , PA_{dead} , PA_{piper} and PA_{prestoea}); 3) disturbance attributes (Hurricane, TAH, Hurricane \times TAH; T_{ambient} and $T_{\text{understory}}$); and 4) land use category. Spatial attributes, habitat characteristics and land use were measured at the point scale, whereas disturbance attributes are spatially invariant and measured at the LFDP scale. To control for spatiotemporal autocorrelation and pseudoreplication, we employed a random factor that adjusts for point-specific trends (i.e. year given point (Year|Point)).

To determine the unique, total and shared contributions of factors associated with space, disturbance and habitat characteristics on gastropod abundance and biodiversity, we conducted variation partitioning (Borcard et al. 1992, Legendre 2007, Legendre et al. 2012). Analyses were conducted separately for the abundance of each species of gastropod, for total gastropod abundance, for each metric of point biodiversity, for species composition (relative abundances of all 17 species) and for multivariate point biodiversity (simultaneous consideration of all four metrics of point biodiversity). Spatial attributes included northing, easting and elevation; disturbance attributes included Hurricane, TAH, T_{ambient} , $T_{\text{understory}}$ and land use; and habitat characteristics included canopy openness, PA_{live} , PA_{dead} , PA_{piper} and PA_{prestoea} . In variation partitioning, shared effects can be quantified, but their significance cannot be evaluated statistically (e.g. spatially structured effects of habitat or habitat-dependent effects of disturbance). All R^2 values reported for variation partitioning are adjusted R^2 values (Peres-Neto et al. 2006). Small negative shared partitions are common in variation partitioning because adjusted R^2 values are not strictly additive (Legendre et al.

2012). For interpretive purposes, the variation explained by these partitions is considered to be zero; however, we present these negative values to demonstrate how sets of factors sum to equal the variation explained by the full model.

LFDP scale

To understand the relative contributions of disturbance and habitat factors on temporal variation in abundance, α biodiversity and γ biodiversity at the LFDP scale, we used a similar statistical approach to that at the point scale, except that models were linear mixed-effects models (LMEs) with type II sums of squares and Gaussian error terms, and included year as a random factor to account for temporal autocorrelation and repeated measures. Because these analyses were based on mean abundances at the LFDP scale, data were neither counts nor zero inflated, and Gaussian error terms were appropriate. Models included two kinds of explanatory characteristics: 1) mean habitat characteristics (canopy openness, PA_{live} , PA_{dead} , PA_{piper} and PA_{prestoea}); and 2) disturbance attributes (Hurricane, TAH, $H \times TAH$, T_{ambient} and $T_{\text{understory}}$).

We conducted variation partitioning to determine the unique, total and shared contributions of factors associated with temporal variation in disturbance and habitat characteristics on gastropod abundance and biodiversity. Analyses were conducted separately for the abundance of each species of gastropod, for total gastropod abundance, for each metric of α biodiversity, for each metric of γ biodiversity, for species composition (relative abundances of all 17 species) and multivariate point biodiversity (simultaneous consideration of all four metrics of point biodiversity). Disturbance attributes included Hurricane, TAH, T_{ambient} and $T_{\text{understory}}$; and mean habitat characteristics included canopy openness, PA_{live} , PA_{dead} , PA_{piper} and PA_{prestoea} .

For all mixed-effects models, we report marginal R^2 values to quantify the variation explained only by the fixed effects (e.g. spatial, habitat, disturbance and land use characteristics) included in the model, as well as conditional R^2 values to quantify the variation explained by the complete model (both fixed and random effects). All analyses were executed in R ver. 4.1.1 (www.r-project.org). GLMMs 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. 2022). GLMM marginal and conditional R^2 were estimated via the *r.squaredGLMM* function in *MuMin* package (Barton 2018). Variation partitioning was conducted using the *varpart* function from the *vegan* package (Oksanen et al. 2019). Type II sums of squares and variance inflation factors were implemented via the *Anova* and *VIF* functions, respectively, in the *car* package (Fox and Weisberg 2019). All analyses were conducted with an α of 0.05, although we also note and discuss effects that approached significance ($0.10 \geq p > 0.05$).

Results

A total of 50 808 gastropods representing 17 species was recorded from the LFDP between 1993 and 2019. All 17 of

the typically occurring species of terrestrial gastropod from on or above the leaf litter in tabonuco forest were recorded (Willig et al. 2021). Although introduced species of gastropod occur on Puerto Rico, none are common in high elevation montane rainforests and none were recorded during the study. *Nenia tridens* (23 619 individuals), *C. caracolla* (17 852) and *G. nigrolineata* (5127) were the most abundant species, and represented 91.7% of all captures during the study. Among the remaining species, only *Platysuccinea portoricensis* (923) and *Alcadia striata* (847) represented > 1% of all captures. Five species (*A. striata*, *C. caracolla*, *Cepolis squamosa*, *G. nigrolineata* and *N. tridens*) were captured during each of the 27 years of the study, whereas only three species were captured during fewer than 20 years, *L. gracilis* (16 years), *Diplosolenodes occidentalis* (13) and *Obeliscus terebraster* (9). Between 12 and 16 species were recorded each year, with an average of 14.4 species.

Long-term responses

At the point scale, GLMMs that included characteristics of disturbance, space and understory habitat explained over 30% (marginal $R^2 > 0.30$) of the variation in the abundance of each of six species and in total gastropod abundance (Table 1). Aspects of press and pulse disturbances, succession and historical land use were primarily responsible for the variation explained by these models. At the LFDP scale, these characteristics explained over 50% (marginal $R^2 > 0.50$) of variation in the abundance of each of 11 species and in total gastropod abundance (Table 2). Aspects of succession (TAH and $T_{\text{understory}}$) most often contributed significantly to variation in abundance or in biodiversity.

Space

Spatial characteristics explained a significant amount of unique variation for each of 11 species, for total gastropod abundance, for each of three measures of point biodiversity, for species composition and for multivariate point biodiversity (Fig. 2, Supporting information); however, variation partitioning cannot account for temporal autocorrelation or repeated measures. In the GLMMs that can account for these aspects of experimental design, space had little effect on variation in gastropod abundances or biodiversity, with abundances of only three species showing effects related to each of elevation, northing or easting (Table 1).

Legacies

Total gastropod abundance as well as the abundance of each of four species, including the two most abundant species of gastropod (*C. caracolla*, *N. tridens*), were affected by historical land use. The abundances of *C. caracolla* and of *N. tridens*, and consequently total gastropod abundance, were greatest in forest that had the most intensive historical land use (category A), whereas the abundances of *M. croceum* and of *P. portoricensis* were greatest in forest with the least intensive historical land use (category C). Importantly, historical land use was spatially structured on the LFDP

(Fig. 1B), and three of these four species, as well as total gastropod abundance, also responded to at least one spatial characteristic (Table 1). Effectively, responses to space may represent fine-scale variation in abundance associated with historical land use.

Hurricanes and succession

At the point scale, the abundances of each of 13 species, as well as total gastropod abundance, responded to hurricane identity, succession after hurricane-induced disturbances (TAH) or their interaction (Table 1). In addition, all four metrics of point biodiversity exhibited responses to hurricane identity, succession or their interaction. In general, abundances were greatest after Hurricane Georges, the least severe of the major hurricanes (Willig and Presley 2022a); however, these greater abundances were driven largely by the most abundant species (*N. tridens*), which resulted in decreases in abundance-based measures of biodiversity during succession after Hurricane Georges (Willig and Presley 2022a).

At the LFDP scale, effects of succession (TAH) on the abundances of each of four species (*Austroselenites alticola*, *C. squamosa*, *D. occidentalis*, *M. croceum*) were contingent on hurricane identity, whereas the abundances of each of two species (*N. tridens*, *Oleacina glabra*) increased consistently during succession after each hurricane and abundances of one species (*P. acutangula*) decreased consistently during succession after each hurricane (Table 2). Some of the cases of apparent interaction between hurricane identity and succession may be artefacts of having only early successional data after Hurricane Maria. For example, the abundances of *A. alticola* increased during succession after Hurricanes Hugo and Georges, whereas the abundances of *D. occidentalis* decreased during succession after Hurricanes Hugo and Georges, whereas late successional data are not yet available after Hurricane Maria.

Temperature

Responses to temperature were similar at point and LFDP spatial scales, but were in opposing directions with respect to temperatures associated with global warming (T_{ambient}) versus canopy closure ($T_{\text{understory}}$): abundances and biodiversity generally increased with increasing T_{ambient} and decreased with increasing $T_{\text{understory}}$. At the point scale, the abundances of each of four species and point richness increased with increasing T_{ambient} , whereas the abundance of one species and each abundance-based measure of point biodiversity decreased with increasing T_{ambient} (Table 1). In contrast, the abundances of each of seven species, total gastropod abundance and all four metrics of point biodiversity decreased with increasing $T_{\text{understory}}$.

At the LFDP scale, the abundances of each of three species and α richness increased with increasing T_{ambient} , whereas no measures of abundance or biodiversity decreased with increasing T_{ambient} (Table 2). In contrast, the abundances of each of three species, all metrics of α biodiversity, γ richness and γ dominance decreased with increasing $T_{\text{understory}}$, whereas the abundances of one species increased with increasing $T_{\text{understory}}$.

Table 1. Evaluation of small-scale (point) responses (p-values) from generalized linear mixed effects models, with year given point (year|point) as a random factor, to assess the importance of characteristics related to press (global warming) or pulse disturbances (hurricane-induced disturbances and secondary succession), as well as to habitat characteristics and space, on variation in the abundance of each of 17 species, in total abundance, and in each of four metrics of biodiversity. Marginal R^2 (R_{M}^2) reflects the proportion of variation in abundance or biodiversity related to the suite of characteristics, whereas conditional R^2 (R_{C}^2) reflects the proportion of variation in abundance or biodiversity related to the combined effects of the suite of characteristics and random effects. Positive and negative significant associations between continuous predictors and abundance or biodiversity are indicated by + and - superscripts, respectively. Significant effects ($p \leq 0.05$) are bold.

	Hurricane (H)	TAH	H \times TAH	T _{understory}	T _{ambient}	Land use	Elevation	Northing	Easting	Canopy openness	PA _{tree}	PA _{dead}	PA _{upper}	PA _{prestera}	R _M ²	R _C ²
Abundance																
<i>Alcadia alta</i>	0.033	0.946	0.041	0.009 ⁻	0.268	0.246	0.025 ⁻	0.061	0.201	0.270	0.527	0.097	0.716	< 0.001 ⁺	0.085	0.101
<i>Alcadia striata</i>	< 0.001	< 0.001 ⁻	0.003	0.665	0.485	0.778	0.247	0.323	0.764	0.835	0.121	0.535	0.539	0.353	0.042	0.051
<i>Austroselenites alticola</i>	0.397	0.176	0.008	< 0.001 ⁻	< 0.001 ⁺	0.302	0.292	0.160	0.796	0.076	0.981	0.979	0.936	0.212	0.229	0.237
<i>Caracolus caracolla</i>	< 0.001	0.930	0.002	< 0.001 ⁻	0.085	0.015	0.253	0.437	< 0.001 ⁻	0.225	< 0.001 ⁻	0.036 ⁺	0.149	0.678	0.299	0.725
<i>Caracolus marginella</i>	0.900	0.981	0.293	0.474	0.551	0.297	0.880	0.560	0.007 ⁻	0.857	0.322	0.744	0.524	0.364	0.022	0.022
<i>Cepolis squamosa</i>	< 0.001	0.017 ⁻	0.005	0.055	0.960	0.633	0.944	0.641	0.258	0.853	0.995	0.011 ⁺	0.014 ⁺	0.815	0.052	0.071
<i>Diplosolenodes occidentalis</i>	0.903	0.256	0.877	0.555	0.516	0.803	0.463	0.845	0.856	0.249	0.085	0.656	0.484	0.379	0.101	0.101
<i>Gaeditis nigrolineata</i>	< 0.001	< 0.001 ⁺	< 0.001	< 0.001 ⁻	< 0.001 ⁺	0.174	0.698	0.003 ⁺	0.191	< 0.001 ⁻	0.696	0.003 ⁺	0.450	0.046 ⁺	0.425	0.478
<i>Lamellaxis gracilis</i>	0.022	0.834	0.897	0.006 ⁻	0.042 ⁺	0.461	0.546	0.159	0.193	0.152	0.864	0.636	0.481	0.783	0.089	0.105
<i>Megalomastoma croceum</i>	0.596	0.210	0.037	0.547	0.274	< 0.001	0.418	< 0.001 ⁻	0.021 ⁻	0.652	0.768	0.530	0.731	0.571	0.069	0.069
<i>Nenia tridens</i>	< 0.001	< 0.001 ⁺	< 0.001	0.095	0.943	0.001	0.040 ⁻	0.261	0.226	0.023 ⁻	< 0.001 ⁻	0.003 ⁺	0.354	0.229	0.432	0.603
<i>Obeliscus terbraster</i>	0.190	0.324	0.980	0.308	0.400	0.550	0.915	0.404	0.966	0.152	0.969	0.546	0.656	0.802	0.092	0.092
<i>Oleacina glabra</i>	0.548	0.013 ⁺	0.963	0.012 ⁻	0.006 ⁺	0.431	0.355	0.252	0.780	0.888	0.658	0.637	0.544	0.667	0.327	0.327
<i>Platyscincus portoricensis</i>	0.638	0.650	0.806	0.665	0.422	0.707	0.513	0.573	0.265	0.566	0.907	0.802	0.875	0.970	0.005	0.005
<i>Polydolones acutangula</i>	< 0.001	< 0.001 ⁻	0.611	0.063	0.632	0.644	0.188	0.934	0.449	0.883	0.643	0.772	0.525	0.835	0.066	0.082
Total abundance	< 0.001	< 0.001 ⁺	< 0.001	< 0.001 ⁻	0.076	0.011	0.302	0.235	0.011 ⁻	0.015 ⁻	0.011 ⁻	0.088	0.311	0.617	0.354	0.625
Point biodiversity	< 0.001	< 0.001 ⁺	0.046	< 0.001 ⁻	< 0.001 ⁺	0.965	0.094	0.796	0.318	0.032 ⁻	0.784	0.303	0.066	0.121	0.271	
Species richness	< 0.001	< 0.001 ⁻	0.583	< 0.001 ⁻	< 0.001 ⁻	0.162	0.073	0.999	0.839	0.342	0.042 ⁻	0.083	0.487	0.002 ⁺	0.107	0.231
Shannon diversity	< 0.001	< 0.001 ⁻	0.140	< 0.001 ⁻	0.018 ⁻	0.012 ⁺	< 0.001 ⁻	0.690	0.047 ⁻	0.131	0.146	0.736	0.018 ⁺	0.613	0.664	
Camargo evenness	0.004	< 0.001 ⁻	0.864	< 0.001 ⁻	0.032 ⁻	0.497	0.360	0.947	0.730	0.667	0.059	0.561	0.003 ⁺	0.063	0.145	
Berger–Parker dominance																

Understory habitat

Understory habitat at the point scale was generally a poor predictor of gastropod abundance or biodiversity at the point scale (Table 1). Indeed, only total gastropod abundance, Shannon diversity and the abundances of each of five species (*C. caracolla*, *C. squamosa*, *G. nigrolineata*, *N. tridens*, *P. portoricensis*) responded to more than one of the five understory habitat characteristics. Only canopy openness, PA_{dead} and $PA_{prestoea}$ were significantly associated with the abundance of more than two species (Table 1).

Understory characteristics at the LFDP scale were generally poor predictors of gastropod abundance or biodiversity (Table 2). The abundances of only three species (*C. caracolla*, *L. gracilis* and *O. glabra*) and no metric of α or γ biodiversity responded to more than one of the five understory characteristics. Only PA_{live} and $PA_{prestoea}$ were significantly associated with the abundances of more than two species (Table 2).

Scale

Point scale

Full models based on disturbance, spatial and understory habitat characteristics explained a significant amount of variation for 15 of 17 species, for total gastropod abundance, for each measure of point biodiversity, for species composition and for a multidimensional point biodiversity (Fig. 2, Supporting information). At least 18% of the variation in response variables was explained by models for the two most abundant species (*C. caracolla* and *N. tridens*), total abundance and species composition. In general, disturbance explained more variation in abundance, biodiversity and species composition at the point scale than did space or understory characteristics, but all partitions typically explained significant variation (Fig. 2, Supporting information).

LFDP scale

Although variation partitioning models were pervasively significant at the point scale, disturbance and understory habitat characteristics at the LFDP scale only explained significant variation for seven of 17 species, total gastropod abundance, α richness, species composition, multidimensional α biodiversity and multidimensional γ biodiversity (Fig. 3, Supporting information). Significant models explained at least 33% and as much as 74% of variation in abundance or biodiversity. In general, disturbance explained four to eight times more variation in abundance, biodiversity or species composition at the LFDP scale than did understory habitat (Fig. 3, Supporting information).

Discussion

Issues of scale are critical in ecology in general (Levin 1992, Chave 2013) and in disturbance ecology in particular (Pickett et al. 1989, 2011). Indeed, responses of the biota to disturbance events are related to multiple aspects of scale,

including the spatial extents at which a disturbance occurs and the scales at which such disturbances and responses to them are quantified. For example, previous studies of long-term responses of invertebrates to the disturbance regime in the LEF (Schowalter et al. 2021, Willig and Presley 2022a) have focused on the relative contributions of press versus pulse disturbances (i.e. global warming effects versus hurricane effects) on variation in abundance or biodiversity. Those studies only considered large-scale, spatially invariant characteristics of disturbance (e.g. ambient temperature, hurricane identity, TAH), with random effects accounting for some aspects of local spatial variation. Critically, those analyses did not evaluate the consequences of variation in local environmental characteristics on variation in abundance or biodiversity. Although hurricanes affect large areas, they produce spatial heterogeneity in environmental characteristics that influences local responses of the biota, as well as the ability of species that have experienced local extirpation to re-colonize those sites (Willig et al. 2007). Herein, we assume a more nuanced approach to evaluate the relative importance of large-scale events that are effectively considered to be spatially invariant (e.g. climate change, hurricane occurrence) versus small-scale spatial environmental variability (e.g. canopy openness, forest structure) in molding patterns of gastropod abundance and biodiversity. Moreover, we determine if the effects of large- and small-scale factors differ between considerations of populations and communities at small and large spatial resolution (i.e. point versus LFDP scales).

Global warming

The threat of global warming to the biota in disturbance mediated systems is of general concern, as there is considerable evidence that climate change could exacerbate the already alarming negative effects of human activities on biotas from local to global scales (Monastersky 2015, Sasaki et al. 2015). At present, global warming in the LEF does not appear to be threatening species of gastropods with extinction. Only one negative effect to increasing ambient temperature was documented, whereas abundances consistently increased with increasing temperature in seven cases (Table 1, 2). The biota in this disturbance-mediated system may be highly resilient to changing temperatures because the effect of forest canopy loss due to hurricanes has a much larger effect on understory temperature than does the current level of global warming (Schowalter et al. 2021). This does not mean that ecosystems in the LEF will not eventually be threatened by a combination of phenomena related to climate change and anthropogenic activities. Increasing temperatures in the future may have direct and indirect negative effects on the fauna, directly if thermal conditions lie outside species tolerance levels and indirectly by effecting more frequent and severe hurricanes (Webster et al. 2005, Bender et al. 2010) that prevent the establishment of closed canopy forest and consequently reduce the size of populations below their critical minima. This combination of effects may ultimately result in novel communities (Willig and Presley 2022a).

Table 2. Evaluation of large-scale (Luquillo Forest Dynamics Plot) responses (p-values) from generalized linear mixed effects models with year as a random factor, to assess the importance of characteristics related to press (global warming) or pulse disturbances (hurricane-induced disturbances and secondary succession), as well as to habitat characteristics on variation in the abundance of each of 17 species, in total abundance, in each of four metrics of α biodiversity (mean point biodiversity) and each of four metrics of γ biodiversity (Luquillo Forest Dynamics Plot scale biodiversity). Marginal R^2 (R_M^2) reflects the proportion of variation in abundance or biodiversity related to the suite of characteristics, whereas conditional R^2 (R_C^2) reflects the proportion of variation in abundance or biodiversity related to the combined effects of the suite of characteristics and random effects. Positive and negative significant associations between continuous predictors and abundance or biodiversity are indicated by + and – superscripts, respectively. Significant effects ($p \leq 0.05$) are bold.

	Hurricane (H)	TAH	H x TAH	T _{understory}	T _{ambient}	Canopy openness	PA _{live}	PA _{dead}	PA _{paper}	PA _{nestosa}	R _M ²	R _C ²
Abundance												
<i>Alcadia alta</i>	0.758	0.666	0.635	0.329	0.206	0.630	0.986	0.440	0.771	0.780	0.257	0.908
<i>Alcadia striata</i>	0.938	0.093	0.109	0.793	0.731	0.728	0.217	0.375	0.503	0.563	0.277	0.946
<i>Astroselemites alticola</i>	0.675	0.369	0.010	< 0.001 [–]	0.219	0.043 [–]	0.277	0.805	0.809	0.690	0.962	
<i>Caracolus caracolla</i>	0.676	0.969	0.124	0.258	0.799	0.107	0.033 [–]	0.904	0.337	0.123	0.558	0.945
<i>Caracolus marginella</i>	< 0.001	0.318	0.052	0.032 ⁺	0.829	0.577	0.696	0.540	0.005 [–]	< 0.001 ⁺	0.472	0.799
<i>Cepolis squamosa</i>	0.052	0.001 [–]	< 0.001 [–]	< 0.001	0.308	0.032 ⁺	0.986	0.716	0.775	0.823	0.106	0.364
<i>Diplosolenodes occidentalis</i>	0.488	< 0.001 [–]	< 0.001		0.308	0.843	0.206	0.937	0.095	0.028 ⁺	0.106	0.847
<i>Gaeotis nigrolineata</i>	0.825	0.456	0.410	0.062	0.118	0.378	0.727	0.733	0.059	0.861	0.309	0.915
<i>Lamellaxis gracilis</i>	0.023	0.253	0.480	< 0.001 [–]	0.757	0.022 ⁺	0.005 ⁺	0.038 ⁺	0.013 [–]	0.067	0.116	0.765
<i>Megalomastoma croceum</i>	0.802	0.151	0.002		0.246	0.841	0.691	0.288	0.288	0.067	0.328	0.463
<i>Nenia tridens</i>	0.546	< 0.001 ⁺	0.139	0.270	0.418	0.609	0.551	0.787	0.092	0.465	0.750	0.969
<i>Obeliscus teretbraster</i>	0.331	0.554	0.110	0.110	0.148	0.925	0.066	0.773	0.385	0.382	0.271	0.910
<i>Oleacina glabra</i>	0.057	< 0.001 ⁺	0.906	< 0.001 [–]	0.585	< 0.001 ⁺	0.257	0.002 [–]	0.908	0.453	< 0.001 ⁺	0.699
<i>Oleacina playa</i>	0.308	0.139	0.893	0.740	0.428	0.740	0.754	0.400	0.877	0.319	0.319	0.916
<i>Platysuccinea portoricensis</i>	0.776	0.081	0.640	0.269	0.381	0.430	0.396	0.106	0.310	0.237	0.327	0.917
<i>Polydentes acutangula</i>	< 0.001	< 0.001 [–]	0.453	0.183	0.522	0.209	0.109	0.396	0.379	0.001 ⁺	0.761	0.971
<i>Subulina octona</i>	0.013	0.747	0.290	0.195	0.187	0.239	0.199	0.452	0.543	0.472	0.523	0.941
Total abundance	0.431	0.024 ⁺	0.215	0.375	0.717	0.960	0.535	0.903	0.412	0.935	0.727	0.966
α biodiversity												
Species richness	0.073	< 0.001 ⁺	0.785	0.001 [–]	0.022 ⁺	0.451	0.823	0.550	0.602	0.421	0.535	0.943
Shannon diversity	0.478	< 0.001 [–]	0.455	0.003 [–]	0.066	0.583	0.720	0.913	0.080	0.648	0.484	0.936
Camargo evenness	0.492	< 0.001 [–]	0.358	0.002 [–]	0.071	0.723	0.680	0.997	0.055	0.668	0.499	0.938
Berger-Parker dominance	0.449	0.001 [–]	0.401	0.004 [–]	0.165	0.758	0.273	0.781	0.038 ⁺	0.693	0.459	0.933
γ biodiversity												
Species richness	0.674	0.003 [–]	0.493	0.006 [–]	0.219	0.300	0.945	0.357	0.971	0.514	0.470	0.935
Shannon diversity	0.419	0.001 [–]	0.180	0.081	0.333	0.873	0.753	0.821	0.109	0.797	0.552	0.945
Camargo evenness	0.537	0.001 [–]	0.232	0.076	0.285	0.955	0.962	0.838	0.095	0.916	0.520	0.941
Berger-Parker dominance	0.769	0.033 [–]	0.609	0.050 [–]	0.228	0.748	0.246	0.851	0.042	0.463	0.408	0.927

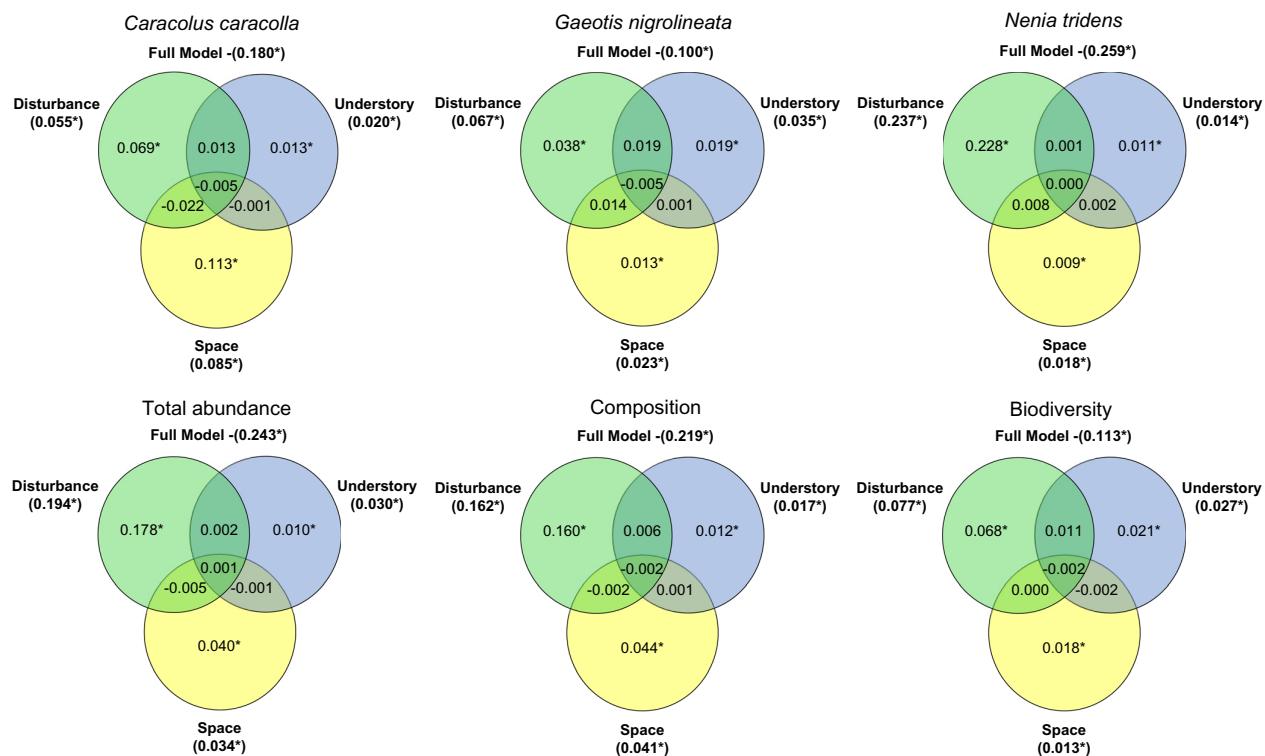


Figure 2. Venn diagrams representing the results of variation partitioning at the point scale, which quantify the proportion of variation in abundance of each of the three most abundant species of gastropod, total gastropod abundance, species composition (a multivariate assessment reflecting abundances of all 17 species) and multivariate biodiversity (a multivariate assessment of all four biodiversity metrics) that can be ascribed to three suites of characteristics (green, disturbance (land use history, hurricane identity, time after most recent hurricane, ambient temperature and understory temperature); yellow, space (northing, easting and elevation); and blue, habitat (canopy openness, apparence of live plants, apparence of dead plants, apparence of *Prestoea acuminata* and apparence of *Piper*)). Significant ($p \leq 0.05$) full models, total partitions or unique partitions are indicated by an asterisk; significance cannot be assessed for shared partitions. All R^2 values are adjusted R^2 values (Peres-Neto et al. 2006).

Large-scale disturbance versus spatial heterogeneity

Disturbances occur at different spatiotemporal scales. Climate change is a large-scale press disturbance, occurring over large spatial scales (globally) and persisting over long temporal scales (decades). In contrast, hurricanes are intense pulse disturbances that occur over large spatial scales (regionally) but are short in duration (days). The effects of global warming or hurricanes on populations and communities over small spatial extents, such as the LFDP, generally result in the explanatory factors that exhibit spatial invariance (e.g. hurricane identity, TAH or mean annual ambient temperature are effectively the same for all points on the LFDP). For example, effects of global warming on temperature experienced across the LFDP will not differ among points. Similarly, points on the LFDP experienced the same hurricanes at the same time. Nonetheless, the effects of these disturbances are spatially variable. General trends in warming may not be experienced by all points on the LFDP in the same way, depending on their slope, aspect and other features of the surrounding landscape that affect local temperature (Estrada et al. 2021). Similarly, hurricanes are dynamic storms whose effects on local habitats

depend on their directionality as well as on slope, aspect and the age and composition of trees (Uriarte et al. 2004, 2019, Muscarella et al. 2019). Consequently, a single large-scale disturbance can create spatially explicit environmental variation that affects local responses of the fauna to the same disturbance event. This spatial heterogeneity can facilitate source–sink dynamics and likely affects the rates at which species re-colonize habitats (Presley and Willig 2022). Forest patches that maintain a closed canopy after a hurricane serve as refugia for animal populations in the region and become source populations during secondary succession. This spatial heterogeneity created by hurricanes can mirror that created in human dominated landscapes in which forestry practices create patches of habitat in various stages of succession. The same kind of source–sink dynamics have been observed for gastropods in New England after clear-cut logging of forests, with gastropods from nearby forest patches serving as source populations that facilitate re-colonization during early succession (Strayer et al. 1986). The spatially heterogeneous nature of these refugia may help to speed recovery of local communities, especially those that contain species that are not particularly vagile, such as gastropods. Consequently,

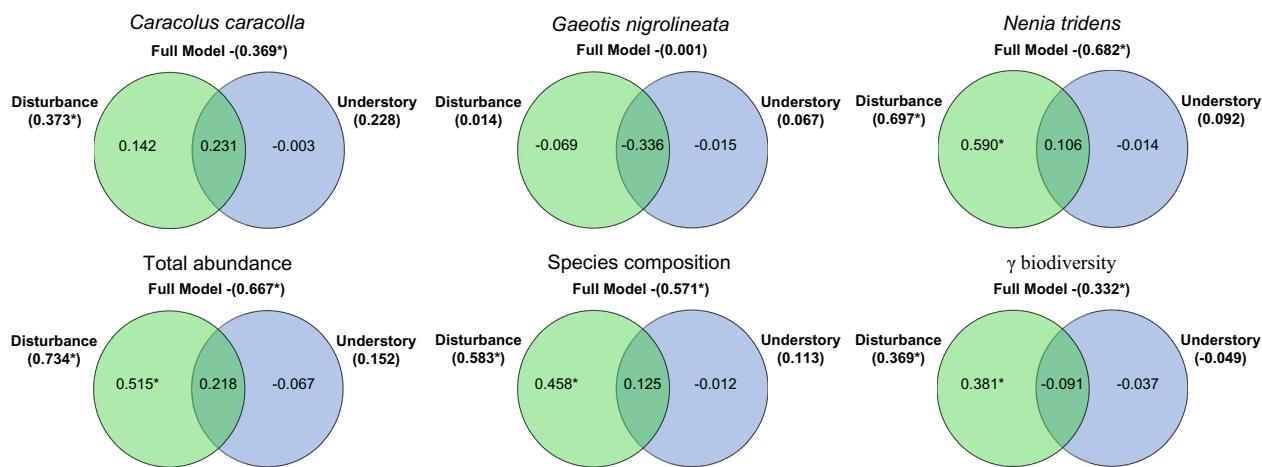


Figure 3. Venn diagrams representing the results of variation partitioning at the scale of the Luquillo Forest Dynamics Plot (LFDP) that quantify the proportion of variation in abundance of each of the three most abundant species of gastropod, total gastropod abundance, species composition (a multivariate assessment reflecting abundances of all 17 species) and multivariate γ -biodiversity (a simultaneous assessment of all four metrics of γ -biodiversity) that can be ascribed to two suites of characteristics (green, disturbance (hurricane identity, time after most recent hurricane, ambient temperature and understory temperature); and blue, understory characteristics (mean canopy openness, mean apparenacy of live plants, mean apparenacy of dead plants, mean apparenacy of *Prestoea acuminata* and mean apparenacy of *Piper*)). Significant ($p \leq 0.05$) full models, total partitions or unique partitions are indicated by an asterisk; significance cannot be assessed for shared partitions. All R^2 values are adjusted R^2 values (Peres-Neto et al. 2006).

large- (e.g. global warming, hurricanes) and small-scale factors (e.g. slope, aspect, composition and structure of forest) combine to determine local and regional responses to a complex disturbance regime via cross-scale interactions (Peters et al. 2007, Willig et al. 2007). However, isolating the relative effects of large-scale events from the spatial heterogeneity created by them remains challenging and rarely studied.

A simultaneous evaluation of large-scale disturbances and aspects of the spatial heterogeneity that they generate shows that gastropods responded primarily to large-scale factors associated with hurricane severity, succession and temperature (Table 1, 2, Supporting information). Regardless of the severity of damage caused to the forest, each hurricane (Hugo, Georges and Maria) created habitat heterogeneity that set the stage for ensuing successional trajectories (Walker et al. 1996). Less severe disturbances (e.g. Hurricane Georges) leave most of the forest canopy intact, with isolated canopy openings that result in fast re-colonization of more impacted areas (Presley and Willig 2022). Whereas more severe disturbances (e.g. Hurricane Maria) remove most of the forest canopy, leaving only a few isolated patches of canopy cover. This results in a less hospitable environment for gastropods in general, and fewer opportunities for re-colonization from refugia to areas that lost forest canopy. Some species (e.g. *G. nigrolineata*, *N. tridens*, *O. glabra*) consistently respond positively during succession (forest recovery after a hurricane) as they prefer closed canopy habitats, whereas other species (e.g. *A. striata*, *C. squamosa*, *P. portoricensis*, *P. acutangula*) prefer more open habitats and have greatest abundances soon after the initial impact of hurricanes but decline in abundance as the canopy closes. Nonetheless, the most abundant species generally increased in abundance during succession, and all

species are capable of persisting in closed canopy forest. This combination of factors results in increasing point richness during succession, but decreasing biodiversity in terms of abundance-based metrics, as dominant species become disproportionately abundant as the forest canopy closes during succession. Additional evidence of the importance of forest-wide canopy openness to gastropod populations is the universally negative response to increasing understory temperature (Table 1). Understory temperature is primarily driven by changes to canopy openness, with more severe and recent hurricanes resulting in more open canopies and higher temperatures (Willig et al. 2019, Schowalter et al. 2021). Because of source–sink dynamics, increasing canopy cover (and resultant decreasing temperature) increases abundances of gastropods throughout the forest, even in locations where the canopy remains open or partially closed.

In contrast to the relatively consistent responses to large-scale aspects of disturbance, responses to understory plant characteristics (i.e. species-specific or height-specific representations) were relatively few and idiosyncratic (Table 1, 2), reflecting the fine-scale habitat preferences of each species in an environmentally heterogeneous forest. A similar number of positive and negative responses to measures of plant apparenacy occurred, reflecting species-specific microhabitat and substrate preferences. Such species-specific responses to spatial variation in microhabitat and microclimate by members of gastropod communities have also been observed in fragmented landscapes in Germany (Kappes et al. 2009), suggesting that niche partitioning associated with these environmental characteristics is typical of terrestrial gastropods. The apparenacy of *P. acuminata* ($PA_{prestoea}$) and of live plants (PA_{live}), as well as canopy openness, were the most influential

in affecting variation in point abundance and biodiversity, with each having only positive effects. Although gastropods are commonly found foraging on the surfaces of some plant species (e.g. *Dacryodes excelsa*, *Heliconia* spp., *Philodendron* spp., *Piper* spp., *P. acuminata*), many plants (e.g. grasses, ferns, *Urena baccifera*) are common and abundant in understory habitats but are avoided by gastropods. Consequently, the negative effects of vegetation density (a composite measure) on the abundance or biodiversity of gastropods reflect the avoidance of many early successional and understory plants by gastropods.

Local versus forest-level responses

In general, responses were consistent between point and LFDP scales, but with two notable exceptions: responses to hurricane identity and responses to the hurricane identity \times TAH interaction (Table 1, 2). At the point scale, hurricane identity (a proxy for hurricane severity) and its interaction with succession (TAH) were among the most prominent predictors of abundance and biodiversity, whereas these common effects did not manifest at the LFDP scale. This difference likely occurred because hurricane-induced environmental heterogeneity among points results in spatial heterogeneity in successional stage among points (i.e. successional asynchrony). The spatial variation in initial post-disturbance environmental conditions and the landscape context in which such dynamics transpire creates variation among points in the stage at which successional trajectories are initiated. Consequently, point-level analyses that control for repeated measures effectively track variation in successional trajectories of populations or communities, and assess consistent point-specific responses during post-disturbance succession after hurricanes that differ in severity. In contrast, LFDP-level analyses that average responses for all points do not effectively evaluate differences in responses after hurricanes because they cannot account for spatial variation in successional starting points (i.e. point-specific successional trajectories cannot be evaluated). In short, averaged data across the LFDP did not effectively account for successional asynchrony that arises from spatial variation generated by hurricane-induced disturbances.

Contrasting results of GLMMs and variation partitioning at the point scale provides additional evidence regarding the importance of controlling for point-level trajectories to identify local responses to disturbance. When controlling for point-specific responses through time, few responses to space occurred (Table 1). However, the spatial partitions from variation partitioning, an approach that cannot evaluate point-specific responses through time, typically accounted for significant variation in abundance, biodiversity and species composition. In combination, these results suggest that the spatial component of variation partitioning is identifying spatial structure that reflects disturbance characteristics. Specifically, some parts of the LFDP suffered greater damage than did other parts, resulting in spatial structure in the starting points for successional trajectories. This spatial

variation in disturbance likely contributes to relatively few significant responses to any measures of plant apprenacy. Context for understory vegetational structure matters. For example, the apprenacy of *Piper* species in a patch with no canopy cover does not have the same effect on gastropod abundance or biodiversity as does the apprenacy of *Piper* species in a patch with a closed canopy. Similarly, *P. acuminata* is a common subcanopy and understory palm, the effects of its apprenacy on gastropods depends on the presence or absence of a canopy, likely because of overriding effects of light intensity and temperature.

Synthesis

The complexity and scale-sensitive nature of results for gastropods on the LFDP are consistent with the theory of cross-scale interactions. More specifically, the effects of local environmental conditions on abundance or biodiversity depend on aspects of the surrounding landscape and their effects on source–sink dynamics (Pulliam and Danielson 1991). The consequences of smaller scale variation in local characteristics likely transpire because of habitat filtering (Leibold and Chase 2018), whereas the consequences of larger scale variation within a landscape (composition and configuration) likely manifest because of source–sink dynamics that determine the movement of individuals among patches, specifically between local refugia that survive disturbances mostly intact and sites dramatically modified by disturbance. If the frequency of high intensity storms or droughts increases, the biota of the LEF may be increasingly characterized by transient dynamics (Hastings 2004, Townley et al. 2007) and emergence of novel or no-analog communities (Williams and Jackson 2007, Willig and Presley 2022a).

In general, effects of interactions between climate change and other disturbances on forested ecosystems and the services they provide are increasingly concerning (Weed et al. 2013). For example, climate change has exacerbated the severity of biotic disturbances (i.e. disease and insect outbreaks) in temperate forests, devastating forested ecosystems (Weed et al. 2013). In addition, drought associated with climate change affects productivity in forests, makes trees more susceptible to pathogens and reduces decomposition rates, which can cause a buildup of organic material and contributes to forest fires (Hanson and Weltzin 2000). In contrast, small scale disturbances are expected to ameliorate some of the negative effects of climate change in temperate forests, with the biodiversity of Hemiptera, Hymenoptera, Mollusca, Symphyta, Syrphidae and understory vegetation each benefitting from this combination of disturbances (Thom et al. 2017). In contrast, the biodiversity of Araneae, Carabidae, saproxylic beetles and canopy trees each experience negative effects from climate change that are not counteracted by other forms of disturbance (Thom et al. 2017). These dynamic interactions will challenge the ability of ecologists and conservation managers to link changes in habitat characteristics to population or community level

variation (Gamelon et al. 2014, Maldonado-Chaparro et al. 2018), as well as to understand or predict responses to longer term variation, such as global warming.

Understanding the causes and consequences of spatio-temporal variation in the abundance and biodiversity of plants and animals caused by dynamic and complex disturbance regimes during the Anthropocene remains a significant challenge in ecology and biogeography. Future research should explicitly include considerations of scale, including cross-scale interactions, within the context of multiple aspects of disturbance regimes (e.g. climate change, drought, fire, flood, cyclonic storms, land use change, fragmentation). Moreover, manipulative experiments designed to disentangle the effects of particular aspects of disturbance regimes will be necessary to distinguish correlation from causation (Richardson et al. 2010, Willig et al. 2014, Presley and Willig 2022). Finally, these research efforts should be complemented by an increased focus on documenting and understanding the autecological and synecological aspects of plants and animals. Although not the vogue in contemporary ecology, a true mechanistic understanding of the ecology of populations and communities is predicated on concerted efforts to amplify the depth and breadth of natural history information that forms the foundations of scientific understanding.

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Author contributions

Steven J. Presley: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Michael R. Willig:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.44j0zpcj8> (Presley and Willig 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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