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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Long-term spatiotemporal variation in density of a tropical folivore: responses to a complex disturbance regime

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Abstract

The Anthropocene is a time of unprecedented and accelerating rates of environmental change that includes press (e.g., climate change) and pulse disturbances (e.g., cyclonic storms, land use change) that interact to affect spatiotemporal dynamics in the density, distribution, and biodiversity of organisms. We leverage three decades of spatially explicit data on the density of a tropical folivore (*Lamponius portoricensis* [Insecta, Phasmida]) in a hurricane-mediated ecosystem (montane rainforest of Puerto Rico), along with associated environmental attributes, to disentangle the effects of interacting disturbances at multiple spatial scales. Spatiotemporal variation in density at a small spatial scale is affected by disturbance-related characteristics (hurricane severity, time after most recent major hurricane, ambient temperature, and understory temperature), legacies of previous land use, and understory habitat structure. Nonetheless, only a small proportion of spatiotemporal variation in density was related to those characteristics. In contrast, the majority of interannual variation in mean density at a larger scale was related to disturbance characteristics and understory habitat structure. These factors combine to affect a weak and declining trend in the density of *L. portoricensis* over time. The low resistance of *L. portoricensis* to Hurricane Hugo, as compared to Hurricanes Georges and Maria, likely arose because a drought followed Hurricane Hugo. The disturbance regime of the region is predicted to include increases in ambient temperatures, frequency of high-intensity storms, and frequency of droughts. Such trends may combine to threaten the conservation status of *L. portoricensis*, and other species with which it shares similar life history characteristics.

Keywords Climate change · Hurricane-induced disturbance · Luquillo experimental forest of Puerto Rico · Population dynamics · Succession

Introduction

The Anthropocene, an epoch of unprecedented and accelerating rates of environmental change (Monastersky 2015), has initiated a biodiversity crisis. Its magnitude constitutes the Earth's sixth mass extinction (Ceballos et al. 2015). Human-induced environmental changes include pulse (e.g., land use change, wildfires, cyclonic storms, and floods) and press (e.g., increasing temperature, ocean acidification, sea level rise) disturbances (Dukes and Mooney 1999; Sasaki et al. 2015). Pulse disturbances are relatively instantaneous and of short duration, after which the system responds to the episodic occurrence via succession, whereas press disturbances represent environmental changes that are maintained or exacerbated over extended time periods (Bender et al. 1984). Both types of disturbance can affect the same ecosystem, but their separate and combined effects rarely have been disentangled or comprehensively understood (Collins et al. 2016; Willig and Presley 2022).

The role of disturbance on spatial and temporal dynamics is a dominant theme in ecology (Walker and Willig 1999; Willig and Walker 1999; Peters et al. 2011; Pickett et al. 2011). Indeed, variation in the frequency, extent, and intensity of disturbance events has a profound effect on the nature of landscapes (Pickett and White 1985). Moreover, the environmental context (i.e., the history or legacies of previous disturbances, including those of natural or anthropogenic

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origin) within which a particular disturbance event occurs can have a substantial influence on the effect of that event on populations and communities (Grove et al. 2000; Lomascolo and Aide 2001), as well as on the subsequent trajectories of response that occur during secondary succession (Willig and Walker 1999; Bloch et al. 2007; Willig et al. 2007, 2011; Schowalter et al. 2017).

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 and Wyckhuys 2019; Salcido et al. 2020; Wagner 2020), as well as in the popular media (e.g., *Washington Post* 15 Oct 2018, *New York Times* 27 Nov 2018, *National Geographic* Feb 2019, *The Atlantic* Feb 2019), referring to the phenomenon as “Armageddon”. In particular, some (Lister and Garcia 2018) have claimed to document decreases in arthropod abundances that are attributed to global warming, leading to the collapse of food webs. In contrast, others have documented that such characterizations are misleading, premature, or not representative of other regions or other taxa (Schowalter et al. 2019; Willig et al. 2019; Crossley et al. 2020; van Klink et al. 2020; Willig and Presley 2022), in part because of interacting effects of multiple disturbances. For example, long-term, comprehensive, quantitative assessments found that the effects of hurricane-induced disturbances and subsequent secondary succession dwarfed those of global warming on arboreal arthropods (Schowalter et al. 2021) and understory gastropods (Willig and Presley 2022). Such long-term evaluations are difficult to effectively execute because they require synoptic (comprehensive) and syntopic (co-spatiotemporal) collection of demographic data on species and environmental drivers that transpire at regular intervals over decades. 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, droughts, ice storms, or floods. Consequently, insights are often derived from snapshots in time (Adams 2001; Willig and Camilo 1991), which are not able to clearly distinguish mechanistic bases for change or to characterize post-disturbance trajectories linked to secondary succession.

The Caribbean Basin (Fig. 1) is characterized by a history of high-intensity cyclonic storms (Landsea et al. 1999), with over 2000 hurricanes recorded in the Caribbean islands since 1851 (http://hurricane.csc.noaa.gov/hurricanes/). Consequently, the Caribbean Basin in general, and the island of Puerto Rico in particular, harbor disturbance-mediated ecosystems in which disturbance regimes produce a sequence

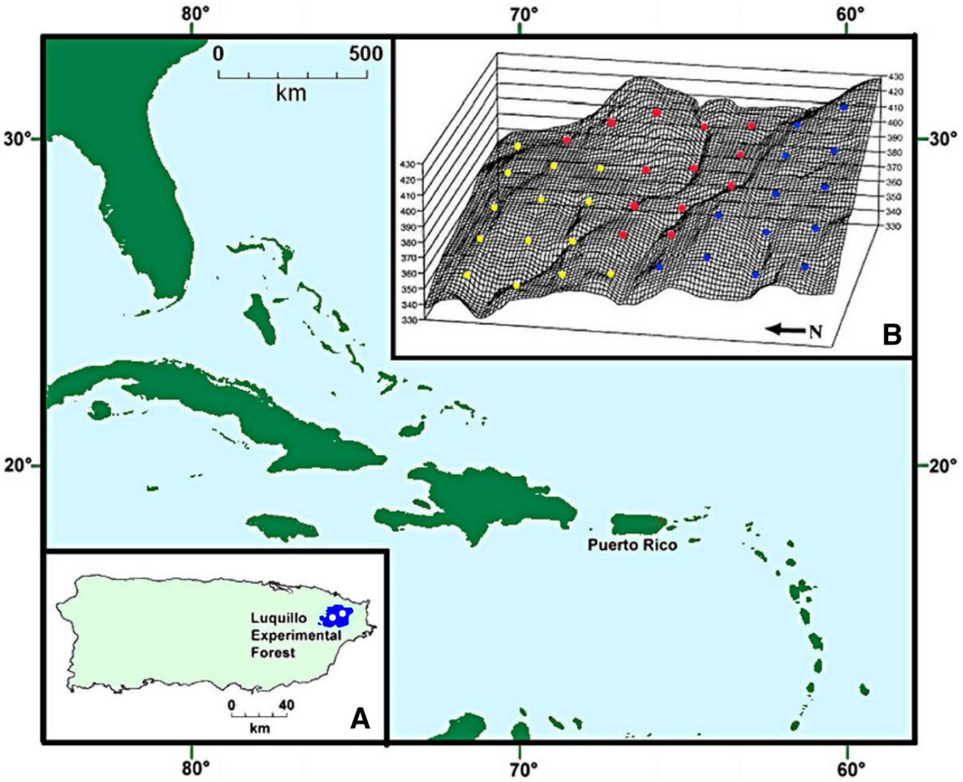

Fig. 1 Map of the Antilles. **a** Map of Puerto Rico indicating the location of the Luquillo Experimental Forest. Within the Luquillo Experimental Forest, a white dot represents the Bisley Watersheds (northeastern dot) as well as Luquillo Forest Dynamics Plot (LFDP; southwestern dot). **b** Elevational relief (contours represent meters above sea level) of the LFDP with red dots representing points in land use category A (intensive logging and agriculture), yellow dots representing points in land use category B (coffee-cultivation and smaller-scale agriculture), and blue dots representing points in land use category C (selective logging)

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of disturbance events whose cumulative or interactive effects play a dominant role in determining the abundance and distribution of organisms (Waide and Lugo 1992). Indeed, northeastern Puerto Rico was impacted by three major hurricanes during a span of 28 years, resulting in an ideal situation for assessing context-dependent effects of intense disturbances on the spatial and temporal demographics of local populations (Walker et al. 1991, 1996). Because the frequencies of intense hurricanes (categories 3–5) may increase in the future as a consequence of global warming (Webster et al. 2005), understanding the long-term effects of successive disturbances on the resilience of ecological systems (i.e., the extent to which a system returns to pre-disturbance conditions or the amount of time required for a system to return to pre-disturbance conditions) is imperative (e.g., Holt 2006; Schoener and Spiller 2006). Our research in the tabonuco forest of Puerto Rico leverages 3 decades of annual data on the density of a tropical folivore (*Lamponius portoricensis*, hereafter *Lamponius*) to (1) quantify long-term variation; (2) evaluate resistance (i.e., the magnitude of short-term changes) of *Lamponius* to intense disturbances of different severity; (3) disentangle effects of various kinds of disturbance-related factors (hurricanes, variation in temperature, understory characteristics reflective of succession) with each other and with space; and (4) characterize such relationships at two spatial scales.

Materials and methods

Study site

Field work was conducted on a 16-ha grid, the Luquillo Forest Dynamics Plot (LFDP), located in tabonuco forest in the vicinity of El Verde Field Station in the northwestern sector (18° 19′ N, 65° 49′ W) of the Luquillo Experimental Forest of Puerto Rico (Fig. 1A). Tabonuco forest, a tropical montane rainforest, ranges in elevation between 250 and 600 m a.s.l. The dominant tree species in the forest, after which the forest is named, is *Dacryodes excelsa* (i.e., tabonuco). 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).

Study organism

The walking stick, *Lamponius*, is a useful model taxon to provide insights about the effects of disturbance on animal populations in the tabonuco forest of Puerto Rico (Garrison and Willig 1996; Willig et al. 2011). Although non-volant, it is ubiquitous there, and exhibits considerable spatiotemporal variation in density, reaching the greatest densities (i.e., mean estimate in wetter segment of the wet season, 55.9 [SD = 16.4] individuals per 100 m^2; mean estimate in a drier segment of the wet season, 56.5 [SD = 28.0] individuals per 100 m^2; estimates based on Manly–Parr mark-recapture method) in successional forest or small light gaps in otherwise closed-canopy forest (Willig et al. 1986, 1993). Moreover, local populations are dominated by nymphal instars (Willig et al. 1986), which may represent approximately 95% of the population, and likely much more, as newly hatched individuals and smaller instars may occupy habitats (e.g., litter) that are not easily perused during mark-recapture studies of long-term plots whose structure is not manipulated. Individuals, especially smaller nymphs, are generally philopatric, moving approximately 0.55 m per day. Some larger individuals may move 3 m per day, and the low recapture rates for adults suggest that they may be a dispersal stage during which individuals seek new canopy openings or mates. Food preferences of *Lamponius* are well documented and include a number of early successional and understory shrubs and trees, such as *Piper hispidum*, *P. glabrescens* (formerly *P. treleaseanum*), *Urera baccifera*, and *Dendropanax arboreus* (Sandlin and Willig 1993). Density of *Lamponius* in tabonuco forest was dramatically reduced as a consequence of disturbance associated with Hurricane Hugo (Willig and Camilo 1991), but that associated with Hurricane Georges caused little change in its density (Willig et al. 2011). Finally, herbivores like *Lamponius* play a key role in nutrient cycling and regulating decomposition rates that affect the composition of detritivorous microbes in the soil and litter, especially in disturbed areas of the forest where walking sticks can attain high densities (Willig et al. 1986; Garrison and Willig 1996; Fonte and Schowalter 2005; Prather et al. 2018). Moreover, *Lamponius* forages on early successional or understory plants; the frass produced by walking sticks therefore releases nutrients that are sequestered in their biomass, and makes it available for later successional species, potentially contributing to successional dynamics of plants and microbes (Willig et al. 1986). In an experimental study, Fonte and Schowalter (2005) documented that herbivory by *Lamponius* on an understory shrub (*P. glabrescens*) affected transfer of nitrate to the litter and decomposition rates. In another elegant manipulative experimental study involving *Lamponius*, Prather et al. (2018) quantified a 50% reduction in leaf litter decomposition associated with reductions in the abundance of high-quality litter that effected lower bacterial richness and abundance.

Hurricane history

Three major hurricanes (Hugo in 1989, Georges in 1998, and Maria in 2017) passed over northeastern Puerto Rico and caused extensive damage to forest on the LFDP. These major hurricanes differed in intensity, as well as in the extent and severity of damage that they caused to the forest

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(Zimmerman et al. 2020). Hurricane Hugo was a category 4 storm (maximum sustained winds of 227 km/h) that produced large canopy openings and deposited large quantities of coarse woody debris on the forest floor (Scatena and Larsen 1991). Hurricane Georges was a category 3 storm (sustained winds of 177 km/h) 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/h) that caused extensive tree mortality, killed twice as many trees as did Hurricane Hugo, removed nearly the entire forest canopy on the LFDP, and deposited large amounts of woody debris on the forest floor (Uriarte et al. 2019).

Land use history

Anthropogenic activities (e.g., logging and agriculture) represent important legacies of past disturbances on the LFDP (Thompson et al. 2002) that can manifest as contingencies (Pickett et al. 2011; Scheiner and Willig 2001; Waide and Willig 2012). The land was purchased by the U.S. Forest Service in 1934 and allowed to revert to closed-canopy forest. Nonetheless, differences in tree composition among areas of the LFDP continue to reflect the history of human activity and are relevant to 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). Points on the LFDP (Fig. 1B) can be classified into three categories (Thompson et al. 2002). Land use category A (0–50% canopy cover in 1936) experienced the most intensive logging and agriculture. Land use category B (50–80% canopy cover in 1936) was used for small-scale mixed agriculture (e.g., shade coffee plantation). Land use category C (80–100% canopy cover in 1936) was lightly and selectively logged until the 1950s.

Trends in temperature

To estimate the effects of global warming in the northeastern 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 weather 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 [T_{ambient}]), as these maxima likely have the greatest potential effects on invertebrate populations and communities (Schowalter 2016). Thus, we have only one estimate of average daily maximum temperature per year, without more point-specific resolution.

A critical effect of hurricane-induced disturbances on tropical forests is a change in the understory microclimate catalyzed by the loss of forest canopy (Willig et al. 2007; Richardson et al. 2010). Arthropods such as *Lamponius* experience understory temperatures that are influenced by global warming, hurricane-induced loss of canopy cover, and ensuing secondary succession during which the canopy regrows. An instrument failure occurred at the weather station at El Verde that resulted in an underestimate of maximum daily temperatures from 1988 to 1992 (see supplementary materials for Willig et al. 2019, https://luq.lter.network/pop-trends-yunque-luquillo). The instrument was replaced, providing a reliable estimate of maximum daily temperatures from mid-1992 until the present. Consequently, all analyses that included understory temperature considered only data from 1993 to 2019 to ensure use of accurate data. To estimate annual temperature in the understory ($T_{\text{understory}}$), we averaged daily maximum temperatures from the weather station located in the forest understory for each year. Thus, we have only one estimate of average understory temperature per year, without more point-specific resolution.

Field methods

A circular plot (3 m radius) was established at each of 40 points on the LFDP, and spaced evenly at 60 m intervals along rows and columns within a rectilinear grid (Fig. 1B). Of these points, 13 were located in land use category A (intensive logging), 14 in land use category B (shade coffee plantations), and 13 in land use category C (light and selective logging). Surveys of *Lamponius* were conducted during the wet season from 1991 to 2019 at each of the 40 points on the LFDP; however, the number of samples per annual survey varied over time. Each point was sampled twice per year in 1991, 1992, and 1993; three times per year in 1994; and four times per year thereafter. A minimum of 2 days was maintained between samples within each year. All surveys were conducted at night (19:30–03:00 h), coinciding with peak activity of walking sticks (Willig et al. 1986, 1993).

Each time a point was sampled, at least two people surveyed it for a minimum of 15 min, during which they searched for *Lamponius*—adults (body length $\geq$ 79 mm) and juveniles (body length $<$ 79 mm)—on all available surfaces (e.g., soil, litter, rocks, vegetation) from ground level to 3 m in the understory. Density estimates for a particular nightly survey were based on the total number of unique individuals detected during the corresponding survey period. To minimize alteration of long-term study sites, litter, debris, and vegetation were not manipulated. Individuals were only handled for measurement to determine age class, and were returned immediately to their original locations. For juveniles, adults, and their total, the abundance at a point during a particular year equaled the average number of individuals captured at that point, a metric that is not biased with regard to variation in effort (i.e., number of samples per year).

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We characterized each point based on spatial (latitude [northing], longitude [easting], elevation) and habitat characteristics. Only the latter varied over time. We estimated apparency (Cook and Stubbendiek 1986) of vegetation via a method that quantified the aerial density of plants at heights from ground level to 3 m above the forest floor in 0.5 m increments (Secrest et al. 1996). Using a plant apparency device (Secrest 1995), we determined the cumulative number of foliar intercepts, defined as a species-specific count of vegetation touching a wooden dowel at each of seven heights (0.0, 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m). The device comprised a set of four 0.5 m long dowels positioned at 90° angles at each height. Each year, the device was positioned 1.5 m from the center of each point in each of the four cardinal directions. We selected a number of apparency-based metrics to quantify habitat features known to influence variation in abundance of *Lamponius* (Willig and Camilo 1991; Willig et al. 1993). These include cumulative apparency at all heights with respect to (1) live plants, regardless of species ($\mathrm{PA}_{\mathrm{live}}$); (2) dead plants, regardless of species ($\mathrm{PA}_{\mathrm{dead}}$); (3) live plants in the genus *Piper*, regardless of species (PA_{Piper}); and (4) live ferns, regardless of species ($\mathrm{PA}_{\mathrm{fern}}$). We also characterized apparency of live plants regardless of species at each of seven heights: $\mathrm{PA}_{0.0\mathrm{m}}$, $\mathrm{PA}_{0.5\mathrm{m}}$, $\mathrm{PA}_{1.0\mathrm{m}}$, $\mathrm{PA}_{1.5\mathrm{m}}$, $\mathrm{PA}_{2.0\mathrm{m}}$, $\mathrm{PA}_{2.5\mathrm{m}}$, and $\mathrm{PA}_{3.0\mathrm{m}}$. Finally, canopy openness (CO) was measured each year using a spherical densiometer (~ 1.25 m above the ground) at the mid-point of the 4 cardinal radii of each sampling point.

Temporal trends

Simple linear regression was used to evaluate consistent temporal trends (i.e., annual rates of change [slopes]) in ambient or understory temperature. For each analysis, mean maximum daily temperature was the dependent variable and year was the independent variable. Temporal trends in temperature were evaluated based on a single estimate for ambient temperature (which does not vary among points) or understory temperature (for which point-specific data are not available) for the entire LFDP. In addition, there is no variation among points in hurricane identity or in time since last major hurricane for each year.

We conducted ordinary and orthogonal polynomial regressions (Dutka and Ewens 1971) to quantify linear and non-linear temporal trends in density of *Lamponius*. Ordinary polynomial regression facilitates the determination of the best-fit relationship between density (Y) and time (X) based on least-squares analyses ($Y = b_0 + b_1X + b_2X^2$), whereas orthogonal polynomial regression facilitates independent estimation of the significance of linear (b^*_1) and non-linear (b^*_2) components of change.

Factors affecting variation in density

We quantified variation in density of *Lamponius* at two spatial scales. At the smaller spatial scale, we explored causes of spatiotemporal variation at the point level. At the larger spatial scale, we explored causes of temporal variation at the level of the LFDP. At each of those scales, we used a generalized linear mixed-effects model (Bates et al. 2015) to determine the contributions of each of a number of characteristics related to disturbance and secondary succession on variation in density. Similarly, we used variation partitioning (Legendre 2007; Legendre et al. 2012) to determine the unique and total contributions of suites of characteristics on variation in density. Analyses for each combination of scale and statistical approach, were executed separately for densities of juvenile, adult, and all (total) *Lamponius*.

Point-scale focus

To understand factors affecting spatiotemporal variation in density at the point scale, we employed generalized linear mixed-effects models (GLMMs, Bates et al. 2015) based on Type II sums of squares. Negative binomial error terms were used in those analyses because the data are characterized by zero inflation (O'Hara and Kotze 2011). The model included four kinds of characteristics: (1) spatial attributes (northing, easting, and elevation); (2) habitat characteristics (CO, $\mathrm{PA}_{\mathrm{live}}$, $\mathrm{PA}_{\mathrm{dead}}$, PA_{Piper}, $\mathrm{PA}_{\mathrm{ferns}}$, $\mathrm{PA}_{0.0\mathrm{m}}$, $\mathrm{PA}_{0.5\mathrm{m}}$, $\mathrm{PA}_{1.0\mathrm{m}}$, $\mathrm{PA}_{1.5\mathrm{m}}$, $\mathrm{PA}_{2.0\mathrm{m}}$, $\mathrm{PA}_{2.5\mathrm{m}}$, and $\mathrm{PA}_{3.0\mathrm{m}}$); (3) climate-induced disturbance attributes (hurricane [H], identity of most recent hurricane [Hugo versus Georges versus Maria]; time after the most recent hurricane [TAH]; interaction between hurricane and time after the most recent hurricane [H × TAH]; ambient temperature [T_{ambient}], and understory temperature [$T_{\mathrm{understory}}$]; and (4) land use category. Spatial attributes, habitat characteristics, and land use were measured at the point scale, whereas disturbance attributes were measured at the LFDP scale (because they are effectively invariant among points within years). 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]).

We also evaluated if resistance to intense disturbances (i.e., the magnitude of short-term changes; Waide and Willig 2012) was consistent between hurricanes of different severity: a category 3 hurricane that caused moderate forest damage (Hurricane Georges) and a category 4 hurricane that caused extensive forest damage (Hurricane Maria). To do so, we used a GLMM with a negative binomial error distribution and Type II sums of squares to evaluate consistency of immediate responses of density to disturbance. Disturbance (before and after) and hurricane identity (Hurricanes Georges or Maria) were Model I treatment factors, and

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point was a random factor in each model. The disturbance by hurricane interaction term was included in the model to determine if responses to disturbance were contingent on hurricane identity (severity). These analyses of resistance could not incorporate responses to Hurricane Hugo, as no comparable data on density of *Lamponius* exist for the 40 points on LFDP until 1991. In addition, we used variation partitioning to evaluate the unique and total contribution of suites of characteristics on variation in density related to (1) spatial attributes (northing, easting, elevation), (2) disturbance attributes (H, TAH, T_{ambient}, $T_{\text{understory}}$, land use); or (3) habitat characteristics (CO, PA_{live}, PA_{dead}, PA_{Piper}, PA_{ferns}, $\text{PA}_{0.0\text{m}}$, $\text{PA}_{0.5\text{m}}$, $\text{PA}_{1.0\text{m}}$, $\text{PA}_{1.5\text{m}}$, $\text{PA}_{2.0\text{m}}$, $\text{PA}_{2.5\text{m}}$, and $\text{PA}_{3.0\text{m}}$).

LFDP-scale focus

Using the same statistical approach (GLMMs) as was done at the point scale, we evaluated temporal variation in mean density at the scale of the LFDP (average density of the 40 points) with a model that included two kinds of characteristics: (1) mean habitat characteristics (CO, PA_{live}, PA_{dead}, PA_{Piper}, PA_{ferns}, $\text{PA}_{0\text{m}}$, $\text{PA}_{0.5\text{m}}$, $\text{PA}_{1.0\text{m}}$, $\text{PA}_{1.5\text{m}}$, $\text{PA}_{2.0\text{m}}$, $\text{PA}_{2.5\text{m}}$, and $\text{PA}_{3.0\text{m}}$) for each year; and (2) disturbance attributes (H, TAH, H × TAH, T_{ambient}, and $T_{\text{understory}}$). Because all variables were quantified at the scale of the LFDP, no spatial or land use attributes were included in the model, and year was incorporated as a random factor. In addition, we used variation partitioning to evaluate the unique and total contribution of suites of factors related to (1) disturbance attributes (H, TAH, T_{ambient}, $T_{\text{understory}}$, land use); and (2) mean habitat characteristics (CO, PA_{live}, PA_{dead}, PA_{Piper}, PA_{ferns}, $\text{PA}_{0.0\text{m}}$, $\text{PA}_{0.5\text{m}}$, $\text{PA}_{1.0\text{m}}$, $\text{PA}_{1.5\text{m}}$, $\text{PA}_{2.0\text{m}}$, $\text{PA}_{2.5\text{m}}$, and $\text{PA}_{3.0\text{m}}$) on variation in mean density (average density of the 40 points).

Linear models were conducted using the lm function from the stats package (R Core Team 2021). Generalized linear mixed-effects models were conducted using the glmer.nb function from the lme4 package (Bates et al. 2015). 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). Variation partitioning was conducted using the varpart function from the vegan package (Oksanen et al. 2019). Significance can only be determined for unique and total effects of each factor, as well as for the entire model. Shared effects (e.g., spatially structured effects of habitat or habitat-dependent effects of disturbance) can be quantified but cannot be evaluated statistically. Small negative shared partitions exist 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. Orthogonal and ordinary polynomial regressions were conducted using the lm function from the stats package (R Core Team, 2021). Type II sums of squares were implemented via the Anova function in the car package (Fox and Weisberg 2019). All analyses were executed in R version 4.1.1 (R Core Team 2021), with an α of 0.05, although we noted effects that approached significance ($0.10 \geq p > 0.05$) as well.

Results

Temporal trends

From 1991 through 2019, ambient temperature did not evince a significant temporal trend (Fig. 2A). In contrast, from 1993 through 2019 understory temperature significantly decreased over time (Fig. 2B), primarily because the canopy closed during secondary succession following Hurricane Hugo (Willig et al. 2019; Willig and Presley 2022). Hurricane Georges did not appreciably re-open the forest canopy on the LFDP, and the large increase in canopy openness and understory temperature after Hurricane Maria represented only a small proportion (~7%) of the data (2 of 27 years).

No significant linear or non-linear trend characterized temporal variation in density of *Lamponius* in general, or of juveniles or of adults (Table 1; Fig. 3). Nonetheless, long-term trends for juvenile and for total density of *Lamponius* approached significance, mostly as a consequence of a strong negative linear component (b^*_1).

Factors affecting variation in density

In part because adult *Lamponius* were rare with a low frequency of occurrence, adults evinced little variation in density (Fig. 3) and responses by adults to predictor characteristics were generally non-significant. In contrast, juveniles were more abundant and variable, as well as having higher frequencies of occurrence compared to adults, resulting in greater power to identify important environmental predictors that may affect spatiotemporal variation. Consequently, we focus on results for total density (i.e., juveniles and adults combined), and only comment on the results for particular age groups when they provide additional insight into spatiotemporal dynamics.

Point-scale focus

The magnitude of resistance did not differ between Hurricanes Georges and Maria (non-significant interaction terms), with no evidence of a consistent immediate

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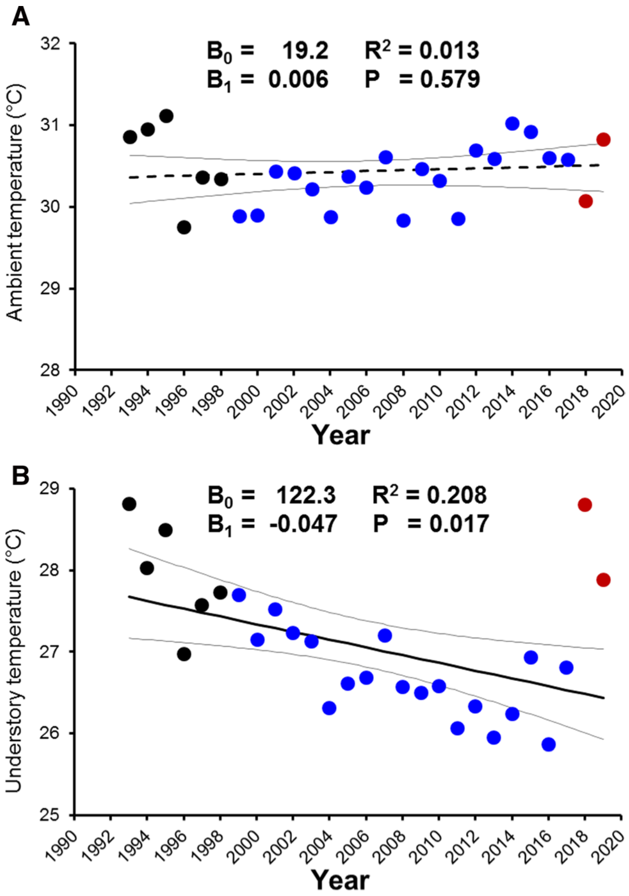

Fig. 2 Ambient temperature did not exhibit long-term trends, whereas understory temperature significantly decreased from 1993 to 2019. **a** Annual mean daily maximum temperature from Luiz Muñoz Marín International Airport, San Juan, Puerto Rico (approximately 24 km from the Luquillo Experimental Forest) represents variation in ambient temperatures that could be driven by global climate change. **b** Annual mean daily maximum temperature from the understory of tabonuco forest in the Luquillo Experimental Forest represents variation in temperatures in the habitats occupied by *Lamponius portoricensis* that are affected by 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. Gray lines represent upper and lower 95% confidence limits of predicted values

effect of hurricane-induced disturbance on total density (Table 2). The lack of significance arises in part because variation among points in the change in density was high compared to the mean change in density. Moreover, many points did not change in total density in response to either hurricane (i.e., 27 of 40 points did not evince a change after Hurricane Georges, and 26 of 40 points did not evince a change after Hurricane Maria) because pre-disturbance densities were zero, thereby precluding the ability of populations to decline immediately after a disturbance and enhancing the likelihood of non-significant responses.

Based on the GLMM (Table 3), many characteristics (5 significant and 2 approaching significance) affected spatiotemporal variation in density at the point scale, but the cumulative explained variation was quite small (R^2_{Marginal}, 0.118; $R^2_{\text{Conditional}}$, 0.171). Factors related to hurricane disturbance and subsequent secondary succession (i.e., H, TAH, and $T_{\text{understory}}$) significantly affected spatiotemporal variation in total density. Moreover, H and TAH played a consistent role in doing so (i.e., no significant H × TAH interaction). Although ambient temperature did not show a strong or significant temporal trend (Fig. 2A), its interannual variation had a significant effect on total density. In addition, land use approached significance in affecting interannual variation (total density of category C > total density of category B > total density of category A), with density decreasing with intensity or severity of historical land use. In contrast, spatial relationships of points (easting, northing, and elevation) had little effect. Finally, two understory characteristics, PA_{dead} and $PA_{3.0\text{m}}$, were significant or approached significance.

At the smaller spatial scale, variation partitioning generally corroborated the results from the corresponding GLMM (Table 4; Fig. 4). The unique effects of each suite of characteristics was significant, but explained only a small proportion of the variation in total density (spatial, $R^2 = 0.005$; disturbance, $R^2 = 0.075$; understory, $R^2 = 0.012$). Similarly, total effects were significant for disturbance and for understory suites of characteristics, but not for the spatial suite of characteristics, with only small proportions of the variation in total density associated with any particular suite (spatial, $R^2 = 0.002$; disturbance, $R^2 = 0.086$; understory, $R^2 = 0.024$).

LFDP-scale focus

Based on the GLMM (Table 3), an appreciable number of characteristics (4 significant and 2 approaching significance) affected temporal variation in mean total density at the LFDP scale, and the cumulative explained variation was quite high (R^2_{Marginal}, 0.826; $R^2_{\text{Conditional}}$, 0.979). Moreover, the effect of time after most recent hurricane (secondary succession) on mean total density was contingent on hurricane identity (i.e., a significant H × TAH interaction). Neither T_{ambient} nor $T_{\text{understory}}$ had a significant effect on mean total density. Finally, five understory characteristics (PA_{live}, PA_{dead}, PA_{piper}, $PA_{0.0\text{m}}$, and $PA_{1.0\text{m}}$) were significant or approached significance in affecting variation in mean total density.

At the spatial scale of the LFDP, variation partitioning generally corroborated results from the corresponding

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Table 1 Results of ordinary and orthogonal polynomial regressions characterizing the relationship between juvenile, adult, or total density of *Lamponius* and time

	Ordinary polynomial regression					Orthogonal polynomial regression					Model fit	
	b_0	b_1	P_{b1}	b_2	P_{b2}	b^*_0	b^*_1	P_{b^*1}	b^*_2	P_{b^*2}	R^2	p
Total	23,901.0	− 18.83	0.988	0.003	0.991	111.24	− 220.81	**0.040**	1.17	0.991	0.115	0.088
Adults	734,359.4	− 732.06	0.064	0.182	0.064	19.41	− 21.01	0.513	61.40	0.064	0.072	0.144
Juveniles	− 710,458.4	713.23	0.468	− 0.179	0.465	91.82	− 199.79	**0.021**	− 60.23	0.465	0.141	0.053

Orthogonal polynomial regression decomposes the relationship from ordinary polynomial regression into a suite of additive components whose coefficients represent the independent contributions of magnitude, linear, and non-linear components (b^*_0, b^*_1, b^*_2, respectively). Accordingly, the fit of the full model is the same for both regression approaches. Significant ($p \leq 0.05$) orthogonal coefficients are bold

GLMM (Table 4; Fig. 4). The unique effects of each suite of characteristics was significant, and explained an appreciable proportion of the variation in mean total density (disturbance, $R^2 = 0.258$, understory characteristics, $R^2 = 0.298$). Similarly, total effects were significant for disturbance and understory characteristics, with large proportions of the variation in mean total density associated with the suite of disturbance characteristics ($R^2 = 0.412$) or the suite of understory characteristics ($R^2 = 0.453$).

Discussion

Complexities of disturbance and response

The effects of particular disturbance events (e.g., hurricanes) and the nature of subsequent secondary succession, must be integrated in the context of other aspects of a disturbance regime (e.g., warming), including legacies of previous disturbances (e.g., land use history) to understand likely causes of population-level variation. This multifaceted aspect of the disturbance regime, and the extent to which various components interact, result in complex ecological dynamics. Consequently, the relative contributions of different aspects of the disturbance regime to variation in density of *Lamponius* are especially challenging to quantify (e.g., Marquis et al. 2019; Schowalter et al. 2021), particularly when some disturbances are episodic at unpredictable intervals (i.e., pulses), and others are gradual and enduring over time (presses).

Temperature effects

Ambient temperature did not evince a 30-year directional trend in northeastern Puerto Rico (Fig. 2A), but its interannual variation was significantly associated with variation in density of *Lamponius* at the point scale, including variation in the mean density of adults and juveniles, separately (Table 3). At the same time, the significant cooling of the understory, likely associated with canopy closure after Hurricane Hugo (and the only minor effects of Hurricane Georges on this successional development), contributed significantly to variation in density (Table 3). Thus, the effects of variation in ambient temperature on density of *Lamponius* are both direct, and indirect, as mediated by the status of the canopy during succession as well as by the effect of ambient temperature on the frequency and intensity of hurricanes in the Caribbean (Bender et al. 2010). Changes in ambient temperature associated with global warming can affect many aspects of behavior, development, demography, and distribution of insects, including earlier flight times, enhanced winter survival, acceleration of development, disruption of phenological synchrony between insects and hosts or food supply, and removal or relocation of the barriers that define the geographical limits of species ranges (Bale et al. 2003; Robinet and Roquest 2010). The degree to which the trend in warming at the global scale manifests at the regional scale in northeastern Puerto Rico remains uncertain, but it will likely interact with canopy closure in complex ways during succession to affect trends in understory temperature and variation in the density of *Lamponius* and other understory invertebrates (Willig and Presley 2022).

Resistance to Hurricanes

Hurricane-induced disturbances are well known to have short-term effects on the dynamics of biotic populations (Walker et al. 1991, 1996; Willig and McGinley 1999; Lopez et al. 2003; Schoener et al. 2004), including those in the tabonuco forest of Puerto Rico (e.g., Reagan 1991; Waide 1991; Woolbright 1991; Gannon and Willig 1994; Zimmerman et al. 1996). Indeed, the resistance of *Lamponius* populations was quite low in response to Hurricane Hugo (1989) in the Bisley Watersheds (Willig and Camilo 1991), a site < 10 km northeast of the LFDP. At Bisley Watersheds, total density of *Lamponius* dramatically decreased by more than 95%, from 369.2 individuals per ha before Hurricane Hugo in 1989 to 12.7 individuals per ha after Hurricane Hugo in 1990 (Fig. 3). Data from or in the vicinity of the LFDP similarly documented low resistance in response to

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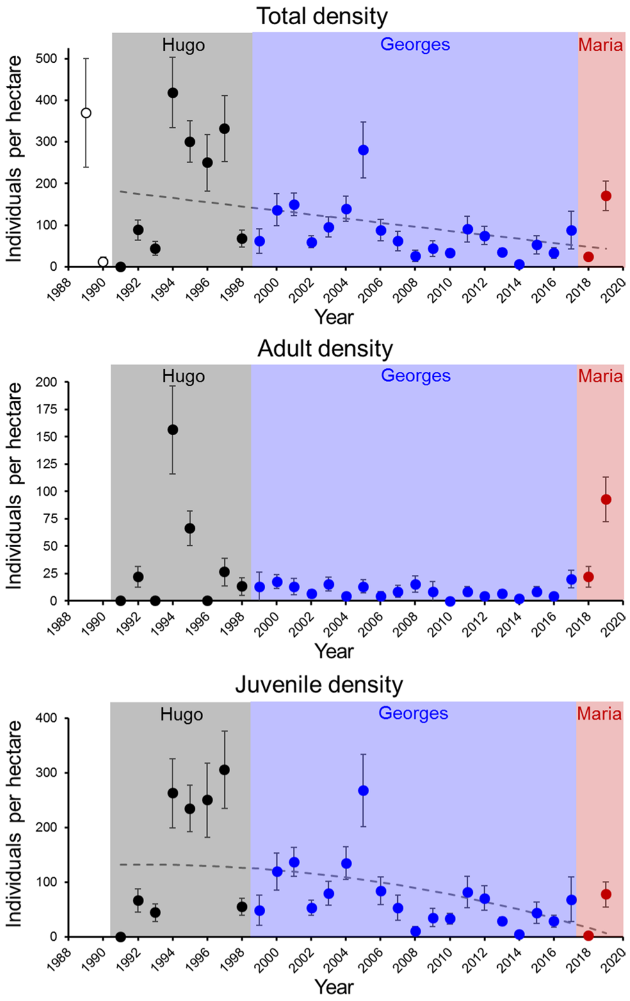

Fig. 3 Temporal variation in density of *Lamponius portoricensis* for total, adult, and juvenile individuals from tabonuco forest in the Luquillo Experimental Forest of Puerto Rico. Black, blue, and red circles represent mean densities ($N=40$) on the Luquillo Forest Dynamic Plot for each year following Hurricane Hugo (1989) but before Hurricane Georges (gray shaded area), following Hurricane Georges (1998) but before Hurricane Maria (blue shaded area), and following Hurricane Maria (2017; red shaded area), respectively. White circles represent mean densities ($N=40$) of *L. portoricensis* from Bisley Watersheds, a nearby site in tabonuco forest, estimated immediately before (1989) and after (1990) Hurricane Hugo (Willig and Camilo 1991); these serve as context for assessment of resistance and early resilience after Hurricane Hugo but were not incorporated into any statistical analyses. Dashed lines represent predicted values based on a best-fit polynomial models that approached significance ($0.05 \leq p \leq 0.10$) for density from 1991 to 2019 on the LFDP (Table 1). Error bars are 1 ± standard error

Hurricane Hugo. At a site in tabonuco forest < 0.5 km from the LFDP, total density of *Lamponius* was quite high (2,111 individuals per hectare) before Hurricane Hugo (Willig et al. 1993) but quite low at those same locations immediately thereafter (M.R. Willig personal observation), as well as on the nearby LFDP within a few years of the hurricane (Willig et al. 2011).

Compared to Hurricane Hugo, Hurricane Georges was a much less severe disturbance, and the total density of *Lamponius* was quite resistant, changing from 68.5 individuals per ha in 1998 to 61.9 individuals per ha in 1999 (Table 2), an approximate 10% reduction. Hurricane Maria was the most severe of the three major hurricanes, and total density changed from 88.4 individuals per ha in 2017 to 24.3 individuals per ha in 2018 (Table 2), representing a 72.5% reduction. Nonetheless, the non-significant effect of these two recent hurricanes on the change in total density of *Lamponius* was consistent (i.e., no hurricane by time interaction). Such non-significance may arise because of the rarity of these insects and their spatial heterogeneity in abundance. More specifically, the mean magnitude of change in total density was low, in part because many points did not harbor any *Lamponius* before or after a particular hurricane (27 points for Hurricane Georges; 26 points for Hurricane Maria) and those points harboring *Lamponius* before the impact of a hurricane varied greatly in their response to disturbance (i.e., the change in total density was variable across space). Consequently, the mean magnitude of the response was low compared to its spatial variation for both hurricanes, suggesting high resistance to those pulse disturbances. This contrasts with the low resistance exhibited in response to Hurricane Hugo in the Bisley Watersheds: pre-disturbance densities were high and consistently non-zero in 1988, but post-disturbance densities were consistently zero at those same points in 1989 (Fig. 3; Willig and Camilo 1991), and on the LFDP stayed close to zero through 1991 (Fig. 3). Critically, Hurricane Hugo was followed by an extended period of drought (Walker et al. 1991; Heartsill-Scalley et al. 2007), whereas Hurricanes Georges or Maria were not. This extended drought could have affected survivorship of *Lamponius*, especially eggs and early instars, as well as early successional plant communities, including understory plants on which *Lamponius* forage, potentially exacerbating any negative effects of the immediate damage caused by Hurricane Hugo. Consequently, *Lamponius* may be resistant to pulse disturbances associated with hurricanes, but are not resistant to a combination of disturbances derived from sequential hurricanes and droughts. As both hurricane frequency (Bender et al. 2010) and drought frequency (Herrera and Ault 2017) are predicted to increase in the coming centuries in the Caribbean, conservation of species with life history characteristics similar to those of *Lamponius* may become of increasing concern and will require additional vigilance from a management perspective.

Resilience to Hurricanes

At the point scale, interannual variation in density was strongly associated with large-scale disturbance factors, including hurricane identity, time after the most recent

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Table 2 Results (p and Wald χ^2 values) of generalized linear mixed-effects models (GLMM) evaluating the effect of hurricane identity (Georges vs. Maria) and disturbance (year before vs. after a hurricane) on the density of *Lamponius* at the point scale in the Luquillo Experimental Forest of Puerto Rico

	Mean density (individuals per hectare)				GLMM					
	Georges		Maria		Hurricane		Disturbance		Disturbance × hurricane	
	Before	After	Before	After	p	χ^2	p	χ^2	p	χ^2
Total	68.53	61.89	88.42	24.32	0.698	0.151	0.205	1.605	0.194	1.691
Adults	13.26	13.26	19.89	22.10	0.525	0.404	0.929	0.008	0.941	0.005
Juveniles	55.26	48.63	68.53	2.21	0.890	0.019	0.479	0.501	0.129	2.304

Analyses were conducted separately for juvenile, adult, and total density of Lamponius. Point was a random factor to take into account repeated measures of each point during all four time periods

Table 3 Results (p and Wald χ^2 values) from generalized linear mixed-effects models that evaluate factors affecting variation in density of *Lamponius*, with density per point as the dependent variable and year given point (year|point) as a random factor for analyses at the point scale, and with mean density (40 points) and year as a random factor for analyses at the Luquillo Forest Dynamics Plot (LFDP) scale. At the point scale, predictors include characteristics related to disturbance, space, and understory habitat that change during secondary succession. At the LFDP scale, predictors include characteristics related to disturbance and mean understory habitat that change during secondary succession

	Point scale						LFDP scale					
	Total		Adults		Juveniles		Total		Adults		Juveniles	
	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2
Disturbance												
Hurricane	**<0.001**	65.908	**0.029**	7.047	**<0.001**	56.637	0.106	4.495	0.654	0.851	**0.019**	7.930
Time after hurricane	**<0.001**$^{-}$	30.807	0.067^{-}	3.357	**<0.001**$^{-}$	25.174	0.701	0.148	0.934	0.007	0.615	0.253
Understory temperature	**<0.001**$^{+}$	17.117	0.686	0.164	**<0.001**$^{+}$	19.191	0.258	1.278	**0.025**$^{+}$	4.992	0.478	0.503
Ambient temperature	**<0.001**$^{+}$	12.190	**0.012**$^{+}$	6.367	**<0.001**$^{+}$	11.152	0.890	0.019	0.543	0.371	0.718	0.131
Land use	0.076	5.160	0.969	0.063	**0.048**	6.070	–		–		–	
Space												
Elevation	0.106	2.606	0.202	1.626	0.140	2.178	–		–		–	
Northing	0.269	1.220	0.868	0.028	0.187	1.743	–		–		–	
Easting	0.939	0.006	0.464	0.537	0.759	0.094	–		–		–	
Understory habitat												
Canopy openness	0.736	0.114	0.690	0.159	0.472	0.518	0.385	0.756	0.856	0.033	0.307	1.046
PA_{live}	0.430	0.622	0.491	0.473	0.259	1.276	0.074^{+}	3.185	**0.016**$^{+}$	5.765	**0.003**$^{+}$	8.767
PA_{dead}	**0.027**$^{+}$	4.906	0.120	2.420	0.094^{+}	2.798	**0.018**$^{+}$	5.642	0.895	0.018	**0.004**$^{+}$	8.451
PA_{piper}	0.653	0.202	0.712	0.136	0.926	0.009	**<0.001**$^{+}$	13.482	0.296	1.090	**<0.001**$^{+}$	17.918
PA_{fern}	0.343	0.898	0.495	0.466	0.109	2.575	0.991	0.000	0.153	2.039	0.648	0.209
$PA_{0.0}$	0.138	2.202	0.866	0.028	0.087^{+}	2.930	0.068^{+}	3.337	**0.026**$^{+}$	4.943	**0.003**$^{+}$	8.749
$PA_{0.5}$	0.881	0.022	0.367	0.814	0.440	0.595	0.253	1.309	**0.050**$^{+}$	3.832	0.417	0.659
$PA_{1.0}$	0.106	2.619	0.340	0.911	**0.032**$^{+}$	4.619	**<0.001**$^{+}$	13.467	0.519	0.416	**<0.001**$^{+}$	22.611
$PA_{1.5}$	0.332	0.941	0.788	0.073	0.210	1.574	0.484	0.491	0.358	0.845	0.559	0.341
$PA_{2.0}$	0.177	1.827	0.063^{+}	3.444	0.459	0.548	0.343	0.901	0.582	0.303	0.314	1.014
$PA_{2.5}$	0.352	0.865	0.154	2.028	0.686	0.164	0.158	1.993	0.453	0.564	**0.047**$^{+}$	3.942
$PA_{3.0}$	0.094^{+}	2.797	0.368	0.809	**0.041**$^{+}$	4.180	0.517	0.419	0.123	2.377	0.200	1.645
Hurricane × TAH	0.134	4.020	0.657	0.841	0.084	4.950	**0.025**	7.391	0.326	2.242	**0.006**	10.080
R^2 Marginal	0.118		0.043		0.160		0.826		0.884		0.832	
R^2 Conditional	0.171		0.043		0.207		0.979		0.986		0.979	

Marginal R^2 reflects the proportion of variation in density related to the suite of predictor characteristics, whereas conditional R^2 reflects the proportion of variation in density related to the combined effects of predictor characteristics and random effects. Positive and negative significant associations (Pearson Product coefficients) based on Pearson Product between continuous predictors and *Lamponius* density are indicated by + and − superscripts, respectively. Significant ($p \leq 0.05$) results are bold

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Table 4 Results of variation partitioning at the focal scale of points and at the focal scale of the Luquillo Forest Dynamics Plot (LFDP), which quantify the contributions of suites of characteristics on variation in density of *Lamponius* in the tabonuco forest of Puerto Rico. Analyses were conducted separately for juvenile, adult, and total densities. At the point scale, the dependent variable is density at a point, and the three partitions represent characteristics related to disturbance, space, or understory habitat. At the LFDP scale, the dependent variable is mean density across all 40 points on the LFPD, and the partitions represent characteristics related to disturbance or mean understory characteristics across all 40 points on the LFDP

	Unique partitions						Total partitions						Shared partition R^2				Residual	Full model	
	Disturbance		Space		Understory		Disturbance		Space		Understory								
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	D∩S	D∩P	S∩P	D∩S∩U	R^2	R^2	p
Point scale																			
Total	0.075	**0.001**	0.005	**0.035**	0.012	**0.032**	0.086	**0.001**	0.002	0.203	0.024	**0.006**	−0.002	0.014	−0.001	0.000	0.898	0.102	**0.001**
Adults	0.064	**0.001**	0.001	0.254	0.035	**0.005**	0.088	**0.001**	0.003	0.110	0.060	**0.001**	0.000	0.023	0.001	0.001	0.876	0.124	**0.001**
Juveniles	0.069	**0.001**	0.004	**0.047**	0.010	**0.040**	0.074	**0.001**	0.001	0.254	0.018	**0.014**	−0.003	0.008	−0.001	0.000	0.912	0.088	**0.001**
LFDP scale																			
Total	0.258	**0.035**	–	–	0.298	**0.050**	0.412	**0.010**	–	–	0.453	**0.045**	–	0.154	–	–	0.290	0.710	**0.023**
Adults	0.279	**0.027**	–	–	0.409	**0.027**	0.330	**0.049**	–	–	0.460	0.088	–	0.051	–	–	0.261	0.739	**0.019**
Juveniles	0.221	0.073	–	–	0.244	0.111	0.393	**0.010**	–	–	0.415	**0.046**	–	0.171	–	–	0.363	0.637	**0.028**

Significance (indicated by bold *p* values) can only be determined for the full model, unique partitions, or total partitions

hurricane, and both ambient and understory temperatures (Table 3). Despite large differences in the intensity of hurricanes and in the severity of damage to the forest caused by them, trends in *Lamponius* density were not dependent on the identity of the hurricanes (i.e., no hurricane × TAH interaction), suggesting that trends during succession were similar after each hurricane, even if the magnitude of response differed among hurricanes. Generally, density of *Lamponius* increases during early succession, a time when understory plants and early successional plants on which *Lamponius* feeds also reach high density, followed by gradual decreases as the forest matures during later in succession (Fig. 3; Willig et al. 2011). In contrast, at the LFDP scale, *Lamponius* density was contingent on hurricane identity. Although the same general trends are evident after each hurricane, it is also true that the magnitude of response was contingent on hurricane severity. Hurricane Hugo caused large gaps in the forest canopy, which resulted in a large increase in the density of food plants (e.g., *Piper* spp.) for *Lamponius* a few years later, a phenomenon that did not manifest after the relatively modest forest damage caused by Hurricane Georges (Willig et al. 2011).

Succession: habitat characteristics and scale

Theory and empirical data (Peters and Havstad 2006; Peters et al. 2007; Willig et al. 2007; Prates et al. 2022) suggest that local conditions and fine scale processes, interact with broad scale patterns as well as neighborhood effects that relate to the surrounding landscape, to affect spatiotemporal dynamics. Of the habitat characteristics at the point scale, only PA_{dead} was a significant predictor of total density, whereas $PA_{1.0m}$ and $PA_{3.0m}$ were significant predictors of juvenile density. In contrast, habitat characteristics dominated the analyses at the LFDP scale, with PA_{live}, PA_{dead}, PA_{piper}, $PA_{0.0m}$, $PA_{0.5m}$, $PA_{1.0m}$, and $PA_{2.5m}$ explaining significant variation in density of adult, juvenile, or total *Lamponius* (Table 3). In addition, the model at the LFDP scale explained considerable variation in density (marginal and condition R^2 in Table 3). This stark difference in results of analyses at point and LFDP scales likely arises from multiple factors, including, but not limited to the scale at which *Lamponius* responds to the environment, neighborhood effects, ontogenetic changes in habitat use, and time lags between environmental changes and responses by populations of *Lamponius*.

The grain (Turner et al. 1989) at which *Lamponius* perceives the environment may diminish the strength of associations between point-specific density and point-specific habitat characteristics. This is particularly true if the focal scale of analyses is considerably different than the grain at which the environment is perceived by *Lamponius*. In addition, neighborhood effects (Bonan 1988) can be important in

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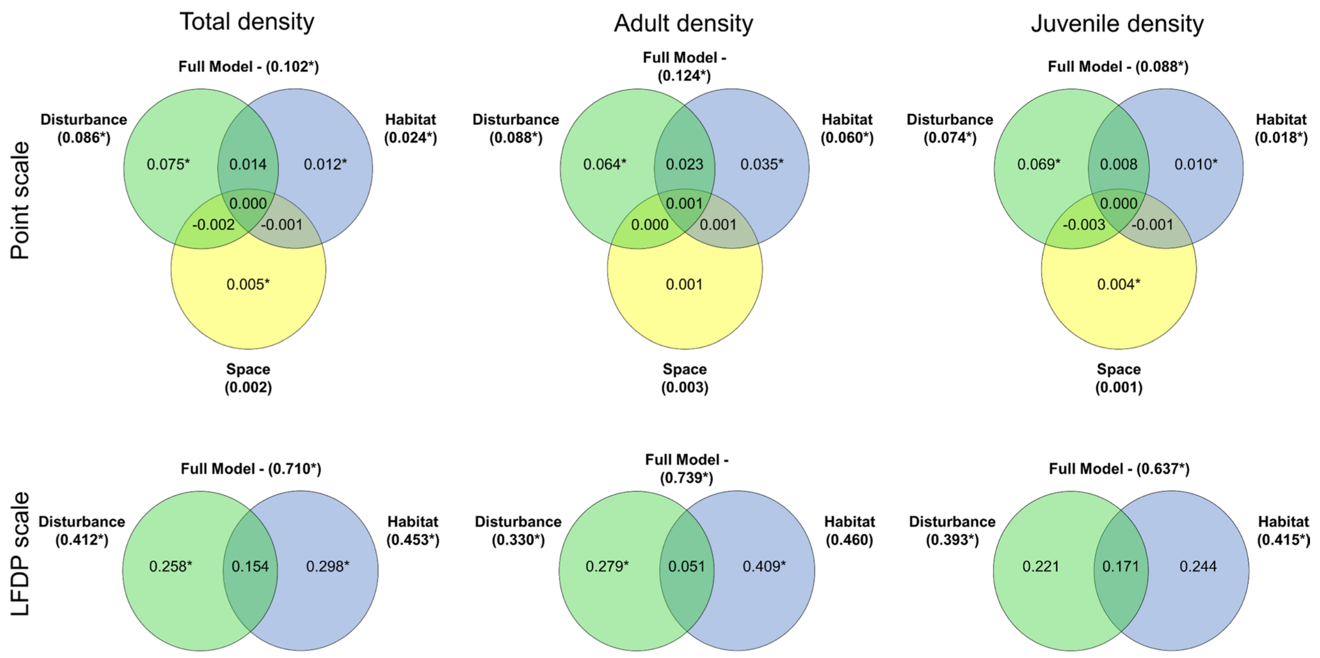

Fig. 4 Venn diagrams representing the results of variation partitioning, which quantify the proportion of variation in density of *Lamponius portoricensis* on the Luquillo Forest Dynamics Plot (LFDP) that can be ascribed to three suites of characteristics (green, disturbance [land use history, hurricane identity, time after most recent hurricane, ambient temperature, and understory temperature]; yellow, space [northing, easting, and elevation]; and blue, habitat [canopy openness, apparency of live plants, apparency of dead plants, apparency of ferns, apparency of *Piper*, apparency of live plants at each of seven heights, at 0.5 m intervals, from the forest floor to 3.0 m] at the focal scale of points (upper row) or to two suites of characteristics (green, disturbance [land use history, hurricane identity, time after most recent hurricane, ambient temperature, and understory temperature] and blue, habitat characteristics [mean canopy openness, mean apparency of live plants, mean apparency of dead plants, mean apparency of ferns, mean apparency of *Piper*, and mean apparency of live plants at each of seven heights, at 0.5 m intervals from the forest floor to 3.0 m]) at the focal scale of the LFDP (lower row)

predicting spatiotemporal variation of invertebrates (Prates et al., 2015, 2022), and should be considered in future research, as should considerations of age- or stage-specific grain size (i.e., early, less mobile instars may perceive the environment in different ways than do larger, more mobile instars or adults of the same species). This may arise because ontogenetic niche shifts may be associated with foraging, adult needs to locate mates or suitable oviposition sites, or the locations of first instar juveniles are determined by adult oviposition preferences in the past (e.g., Horgan et al. 2020; Rudolph 2020). Moreover, demographic responses of *Lamponius* to disturbances may be mediated by time lags associated with the abundance and distribution of preferred food plants in post-hurricane environments (Willig et al. 2011), further reducing the variation in density that can be explained by predictors concurrently measured at the point scale.

Our study design made the trade-off of sampling more, smaller points throughout the LFDP rather than sampling fewer, larger points. One consequence of this design is that the area (28.27 m^2) of each point could be smaller than the area over which individuals integrate habitat information, especially larger individuals, which may result in some variables (e.g., plant apparency data) being poor predictors of the occurrence, abundance, or biodiversity of some taxa (e.g., density of *Lamponius*). In such cases, highly significant predictors may result in low explained variation (point scale in Table 3). However, averaging each predictor variable and averaging the response variable across the entire LFDP each year can diminish the mismatch between focus and grain, as well as account for neighborhood effects, resulting in a better representation of the predictive value of particular habitat characteristics and changes in *Lamponius* density over time. This improvement in matching the scale of response to the scale of predictors likely is why analyses at the LFDP scale account for more variation in *Lamponius* density than do those at smaller scales (Table 3; Fig. 4). Moreover, the identity and strength of environmental attributes that account for spatial variation in density within years may be different from those that account for variation among years. The importance of particular variables in accounting for spatial variation within years may be predicated on time, reflecting the nature of habitat heterogeneity in the landscape that is molded by particular disturbance events and subsequent succession. In short, it is difficult to accurately

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predict the density of *Lamponius* at each point based on environmental information from that point, but it is easier to predict the density of *Lamponius* at a larger scale based on data from throughout the entire LFDP.

Legacy of previous disturbance

Comparable to results for other arthropods in different environments (Jeffries et al. 2006; Goßner et al. 2008; Boege et al. 2019), previous land use history created significant legacies that are reflected in variation in density of *Lamponius* (Table 3). Indeed, density of *Lamponius* remains inversely associated with intensity or severity of historical land use. The least disturbed areas on the LFDP, land use categories C (light selective logging) and B (shade coffee), had greater densities (123 and 122 individuals per ha, respectively) than did areas in land use category A (intensive logging followed by agriculture), with 91 individuals per ha. Despite a complex disturbance regime that includes major hurricanes, drought, and landslides, the legacy of land use from over 80 years ago affects the species composition of plants (Thompson et al. 2002) as well as the density of folivorous insects, such as *Lamponius*, that depend on particular plant species for food. Importantly, this does not appear to be an issue of dispersal or a spatial effect as location on the grid (northing, easting) is not associated with variation in density of *Lamponius*.

Prospectus

Ambient temperature in northeastern Puerto Rico did not evince a temporal tread during the past three decades. Nonetheless, its interannual variation and that of understory temperature affect variation in density of *Lamponius* at the point scale, along with understory habitat characteristics and previous land use. These factors, which represent legacy, disturbance, and succession effects, combine to result in a weak and declining trend in density of walking sticks over time. The apparent high and indistinguishable resistance of *Lamponius* to Hurricanes Georges and Maria are likely consequences of the low density and low frequency of occurrence of walking sticks after Hurricane Hugo. In contrast, the low resistance of *Lamponius* to Hurricane Hugo was likely a consequence of the higher density and frequency of occurrence of walking sticks prior to disturbance, and the immediate post-disturbance drought that followed the hurricane. Indeed, research on forest trees in the LEF (Smith-Martin et al. 2022) suggests that droughts and hurricanes favor different adaptive traits, and that vulnerability to droughts is exacerbated by hurricanes. A similar trade-off may exist for tropical herbivores, both in terms of adaptive traits directly favored by hurricane-induced disturbances versus droughts, and indirectly favored by the changing composition of forage plants on which animals feed. Because the next few centuries will be characterized by warming ambient temperatures, an increased frequency of high-intensity hurricanes, and an increased frequency of droughts, populations of *Lamponius* may become imperiled. The ability to distinguish factors affecting such dynamics for *Lamponius*, as well as for other species in ecosystems that experience complex disturbance regimes, is predicated on continuous long-term monitoring in the context of a synoptic and syntopic network of sites that captures demographic data for species of concern as well as a diversity of environmental factors that may affect those dynamics.

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Author contribution statement MRW conceived and managed all aspects of the project. SJP executed quantitative analyses. MRW and SJP designed the analytical phases of the work and wrote the manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Data availability statement *Lamponius portoricensis* (walking stick) and temperature data are archived publicly and openly available in the Luquillo Long-Term Ecological Research data catalog: *Lamponius portoricensis* data https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.107.9996737), temperature data (https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-luq&identifier=16&revision=538557).

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