



A canonical metacommunity structure over 3 decades: ecologically consistent but spatially dynamic patterns in a hurricane-prone montane forest

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Abstract

The Anthropocene is a time of rapid change induced by human activities, including pulse and press disturbances that affect the species composition of local communities and connectivity among them, giving rise to spatiotemporal dynamics at multiple scales. We evaluate effects of global warming and repeated intense hurricanes on gastropod metacommunities in montane tropical rainforests of Puerto Rico for each of 28 consecutive years. Specifically, we quantified metacommunity structure each year; assessed effects of global warming, hurricane-induced disturbance, and secondary succession on inter-annual variation in metacommunity structure; and evaluated legacies of previous land use on metacommunity structure. Gastropods were sampled annually during a 28-year period characterized by disturbance and succession associated with 3 major hurricanes (Hurricanes Hugo, Georges, and Maria). For each year, we evaluated coherence (the extent to which the environmental distributions of species are uninterrupted along a common latent environmental gradient), species range turnover, and species range boundary clumping; and conducted co-occurrence analyses for each pair of species. We used generalized linear mixed-effects model to evaluate long-term responses of the metacommunity to aspects of global warming and disturbance. Metacommunity structure was remarkably stable, with consistent patterns of species co-occurrence. Disturbance, warming, and successional stage had little effect on metacommunity structure. Despite great temporal variation in environmental conditions, groups of species tracked their niche through space and time to maintain the same general structure. Consequently, metacommunity structure was highly resistant and resilient to multiple disturbances, even those that greatly altered forest structure.

Keywords Disturbance · Ecological legacies · Long-term dynamics · Luquillo Experimental Forest of Puerto Rico · Resilience · Succession

Introduction

The Anthropocene is a time of rapid change, during which the influence of human activities has become a dominant feature that molds the biotic composition and structure of

landscapes throughout the world (Monastersky 2015). The consequences of anthropogenic modifications can arise from pulse disturbances, such as habitat conversion (Sasaki et al. 2015) or press disturbances, such as global warming (Dukes and Mooney 1999; Collins et al. 2016), that singly or in concert affect the species composition of local communities as well as the connectivity among them, giving rise to spatiotemporal dynamics that manifest at multiple scales. Secondary succession after naturally occurring pulse disturbances (e.g., hurricanes) contributes further to spatiotemporal variation.

A metacommunity perspective provides ecological insight into spatiotemporal dynamics, because it explicitly considers the structure and organization of communities along environmental gradients, and seeks to understand the ecological processes that generate these larger scale

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patterns. More specifically, a metacommunity is a network of communities that are potentially connected to each other via species-specific movement of individuals among communities (Leibold and Mikkelsen 2002). Local emigration and immigration, when coupled with other spatially explicit ecological processes such as species sorting, habitat filtering, priority effects, or interspecific competition, imbue the network with an emergent structure that corresponds to underlying environmental gradients (Leibold 2011; Leibold and Chase 2018).

Since its inception, the domain, theories, and hypotheses associated with metacommunity ecology have received increasing attention and amplification (Leibold et al. 2017; Leibold and Chase 2018). In general, there are complementary approaches for studying metacommunities. One approach uses four archetypical mechanistic models (i.e., neutral theory, patch dynamics, species sorting, and mass effects) that differ in assumptions about the role of particular processes (e.g., competition, dispersal) or sources of variation (e.g., habitat heterogeneity, species-specific capacity) to make predictions about community composition (Leibold and Chase 2018). The other approach focuses on emergent patterns of species distributions (e.g., nestedness, Clementsian, and Gleasonian) along environmental gradients (Leibold and Mikkelsen 2002; Presley et al. 2010). It is useful to first identify emergent patterns before hypothesizing the relative importance of mechanisms that give rise to those patterns.

A particular metacommunity structure reflects multiple ecological processes that arise from mechanisms that operate at multiple spatial scales (Leibold and Mikkelsen 2002). A fundamental principle in ecology is that species occurrences along an environmental gradient are Gaussian: modal in form with continuous distributions. More specifically, species should occupy a coherent range of sites along underlying environmental gradients (i.e., a species that occurs at temperatures of 10 °C and 20 °C should also occur at all temperatures between those values). For an entire metacommunity to exhibit coherence, the ranges of a majority of species must be associated with the same environmental gradient (Presley et al. 2010). However, the extent and location of species distributions along the gradient may differ, such that coherent metacommunities may evince many different discernable structures. If species do not respond to the same environmental gradient, distributions will not form a coherent structure and will represent a random metacommunity structure (Leibold and Mikkelsen 2002).

Metacommunity structure is evaluated with respect to a multidimensional continuum of possible structures, with idealized structures representing end points of variation in the amount of turnover among species ranges and in the form of distribution of range boundaries. Clements (1916) regarded communities to be discrete entities; a concept that

evolved into the community unit hypothesis (Whittaker 1975). In contrast, Gleason (1926) described a pattern of continual change in species composition along environmental gradients without the formation of discrete assemblages, which result from idiosyncratic, species-specific responses to the environment. In situations where strong interspecific competition exists, trade-offs in competitive ability may manifest as distributions that are more evenly spaced along environmental gradients than expected by chance (Tilman 1982). Finally, nested subsets form if the environmental ranges of species with more narrow distributions are contained within the ranges of species with more broad distributions (Patterson and Atmar 1986), with predictable patterns of environmental range breadth associated with variation in species-specific characteristics (dispersal ability, habitat specialization, and extinction risk). A set of objective criteria and a rigorous quantitative approach can simultaneously test the correspondence of an empirical structure to identified idealized structures (Leibold and Mikkelsen 2002; Presley et al. 2010). This approach combines evaluations of three elements of metacommunity structure (coherence, range turnover, and range boundary clumping, hereafter EMS) to identify which idealized metacommunity structure best approximates an empirical structure. Each non-random structure assumes that species distributions are molded by a combination of biotic and abiotic factors that differ among sites and constitute an environmental gradient. This allows for the testing of multiple hypotheses of structure, as well as for the generation of hypotheses related to structuring mechanisms.

The methodologies associated with EMS have enjoyed wide application in characterizing patterns and processes that organize a plethora of networks including those for vertebrates, invertebrates, plants, and microbes (see Appendix of Presley et al. 2019 for extensive list of studies). The EMS approach has been amplified (Presley et al. 2009, 2010) since its origin (Leibold and Mikkelsen 2002), and has been critiqued from multiple perspectives (Ulrich and Gotelli 2012; Schmera et al. 2018; Presley et al. 2019). Nonetheless, reassessments (Mihaljevic et al. 2015) and rejoinders (Presley 2020) have established that the EMS methodology provides considerable ecological insight (see also Supplementary Material, A critical history of the EMS framework) when considered from the perspective of species distributions along latent gradients, the original intent of the approach (Leibold and Mikkelsen 2002).

Disturbance events, especially those that are intense, alter abiotic and biotic characteristics of sites, as well as the nature of the intervening matrix, with considerable consequences at the level of populations or communities (Walker 1999; Brokaw et al. 2012). Consequently, disturbances redefine the environmental correlates of space and potentially alter the latent gradients associated with the distribution of

species. Moreover, secondary succession results in a temporal trajectory that may or may not lead to a return to the pre-disturbance structure of ecological systems (Willig and Walker 1999; Waide and Willig 2012). Indeed, if insufficient time has elapsed since a major pulse disturbance, local assembly processes associated with interspecific interactions and habitat filtering may be insufficient to countermand spatial processes such as dispersal in molding the composition of communities and the structure of metacommunities. This is akin to failing to attain a “quorum” (sensu Jenkins and Buikema 1998; Jenkins 2006). More specifically, a quorum is a situation in which multiple smaller scale or local processes (e.g., biotic factors such as competition and predation, or abiotic factors related to the tolerance limits of species) regulate community composition rather than a single larger scale or regional process (e.g., dispersal). More specifically, the combination of repeated disturbances and successional dynamics between disturbances may prevent a single process (e.g., interspecific competition, habitat filtering, or dispersal) from dominating the assembly of local communities. Because the frequency and intensity of disturbances is increasing due to global change drivers, it is important to understand the extent to which ecological systems are resistant, resilient, or vulnerable to such change, and the extent to which anthropogenic legacies persist in structuring ecological networks. Indeed, the Anthropocene may be increasingly characterized by novel combinations of species, with unknown consequences to the hierarchical structure of biodiversity (Young 2014; Kueffer 2015) or to the local and regional delivery of ecosystem services (Lugo 2013).

We take advantage of decades of work on long-term ecological monitoring in a tropical montane rainforest in Puerto Rico, as well as detailed understanding of local gastropod autecology (Secrest et al. 1996; Willig et al. 1998), disturbance ecology (Willig and Walker 1999; Bloch and Willig 2006; Bloch et al. 2007; Brokaw et al. 2012; Willig et al. 2014), and spatial ecology (Willig et al. 2007, 2011, 2014; Presley et al. 2011) to perform a novel evaluation of long-term variation in metacommunity structure. We explore annual variation in metacommunity structure of gastropods in Tabonuco rainforest of Puerto Rico, a disturbance-prone system in the Caribbean (Brokaw et al. 2012). Based on almost 3 decades of data, our goals were to (1) assess temporal variation in coherence, range turnover, and range boundary clumping (EMS); (2) assess the extent to which hurricane-induced disturbance, secondary succession, or global warming affect EMS; and (3) evaluate whether legacies of previous land use mold metacommunity structure decades later. Hurricanes can affect environmental gradients (e.g., variation in plant communities, productivity) that structure gastropod metacommunities in mature Tabonuco forest, creating environmental gradients that reflect tree loss and sources of environmental stress (e.g., increased understory

temperatures and decreased humidity). Consequently, we expected to observe random metacommunity structures (i.e., low gastropod incidence and non-coherence) during years immediately following hurricane impact and to observe increasingly compartmentalized structures (i.e., significant positive coherence, significant positive range turnover, and significant positive boundary clumping) along a dominant environmental gradient later in succession.

Materials and methods

Study site

Field work was conducted on the Luquillo Forest Dynamics Plot (LFDP), a 16-ha grid located in Tabonuco forest near El Verde Field Station in the northwestern sector (18°10' N, 65°30' W) of the Luquillo Experimental Forest (LEF) of Puerto Rico (Fig. 1). Tabonuco forest is a subtropical wet forest in the Holdridge classification system, and occurs at elevations between 250 and 600 m (Brown et al. 1983). Rainfall in Tabonuco forest averages 346 cm per year (McDowell and Estrada-Pinto 1988), with a modestly drier period from January to April.

History of disturbance

During the past few decades, three major hurricanes (Hugo in 1989, Georges in 1998, and Maria in 2017) have passed over eastern Puerto Rico. Each produced considerable damage to Tabonuco forest on the LFDP, but the three hurricanes differed in intensity, extent, and severity. Hurricane Hugo, a category 4 storm with maximum sustained winds of 227 km/h, produced large canopy openings and deposited much coarse woody debris on the forest floor (Scatena and Larsen 1991). Hurricane Georges, a category 3 storm with sustained winds of 177 km/h (Ostertag et al. 2003), caused extensive defoliation of trees, but did not produce large quantities of coarse woody debris. Hurricane Maria, a category 4 storm with sustained winds of 250 km/h, caused extensive tree mortality and canopy opening over much of the LEF, and deposited large amounts of coarse woody debris on the forest floor (Uriarte et al. 2019).

In addition to natural disturbances, anthropogenic activities (e.g., logging and agriculture) represent important legacies of past disturbance on the LFDP (Thompson et al. 2002). The land was purchased by the U.S. Forest Service in 1934 and allowed to revert to closed-canopy forest. Despite this dramatic reduction in anthropogenic land use, 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

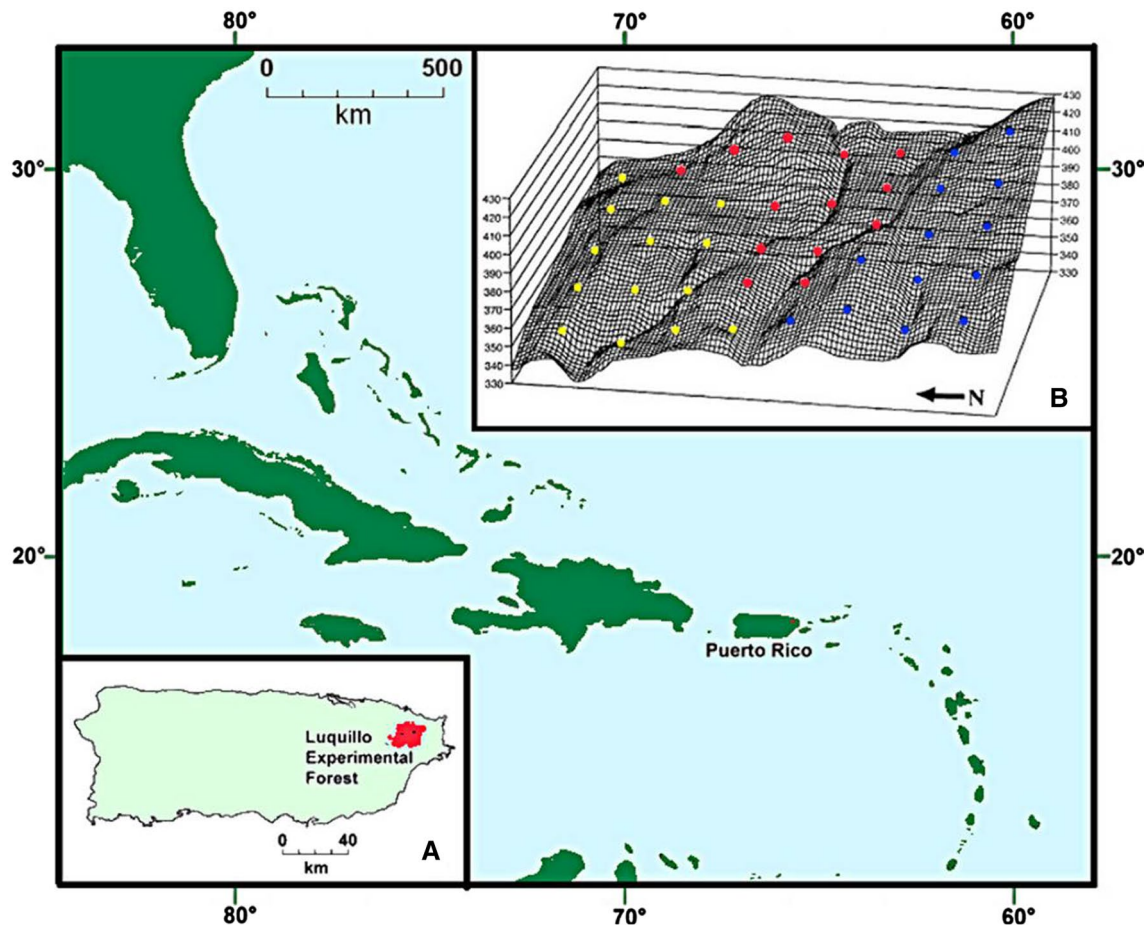


Fig. 1 Map of the Antilles. **A** Map of Puerto Rico indicating the location of the Luquillo Experimental Forest and the Luquillo Forest Dynamics Plot (LFDP). **B** Elevational relief of the LFDP with red dots representing plots in land-use category A (intensive logging and

agriculture), yellow dots representing plots in land-use category B (coffee cultivation and smaller scale agriculture), and blue dots representing plots in land-use category C (selective logging)

(Bloch and Weiss 2002; Bloch et al. 2007). The LFDP (Fig. 1B) can be allocated into three categories (hereafter, land-use classes; 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. Land-use category C (80–100% canopy cover in 1936) was lightly and selectively logged until the 1950s.

Trends in temperature

To estimate effects of global warming, we used data provided by the National Centers for Environmental Information of the National Oceanic and Atmospheric Administration from the station at the Luiz Muñoz Marín International Airport in San Juan, Puerto Rico (Network ID: GHCND:RQW00011641). To estimate annual ambient temperature in the northeastern region of Puerto Rico,

we averaged the daily maximum temperatures for each year (hereafter “ambient temperature”).

One of the effects of hurricane-induced disturbances on tropical forests is a change in the understory climate precipitated by removal of the forest canopy (Willig et al. 2007; Barbara et al. 2010). Terrestrial gastropods experience understory temperatures, which can be influenced by both global warming and by the state of the forest due to loss of canopy cover and ensuing succession. An instrument failure occurred at the weather station at El Verde that resulted in an underestimate of maximum daily temperatures from 1988 to 1992. 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 2018 to ensure accurate data. To estimate annual temperature in the understory, we averaged daily maximum temperatures from the weather station located in the forest understory for each year.

Study organisms

Gastropods are useful for studying the effects of press (climate change) and pulse (hurricanes) disturbances on populations and communities in Tabonuco forest of Puerto Rico. First, excellent long-term data on gastropod incidence and abundance exist for the LFDP. Second, gastropods have a ubiquitous spatial distribution in Tabonuco forest, but exhibit considerable spatial heterogeneity and interspecific variation in abundances (Bloch et al. 2007; Willig et al. 2014). Third, as ectotherms of relatively low vagility, responses of gastropods to variation in temperature and precipitation can be appreciable (Nicolai and Ansart 2017). To minimize alteration of long-term study sites used to study ecosystem processes, microbes, fungi, plants, and animals, litter was not manipulated, and specimens were returned as closely as possible to the point of capture. Consequently, the surveyed gastropod fauna represents terrestrial species that use habitats on or above the leaf litter, including open soil, rocks, woody debris, and live vegetation, omitting small gastropods that live under leaf litter or in the soil.

Field methods

Circular plots (3 m radius) were established at 40 points spaced 60 m apart within a rectilinear grid on the LFDP (Fig. 1B). Of these plots, 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). Nocturnal surveys of gastropods were conducted annually during the wet season from 1991 to 2018 at all 40 plots. During each survey of each plot, two field technicians searched all surfaces (vegetation, rocks, woody debris, soil, and leaf litter) within 3 m of the plot center and up to a height of 3 m from the forest floor for 15 min or until all surfaces were exhaustively searched, whichever was longer. Data were recorded by a third technician, and surveys typically took longer than 30 min. Only living animals were counted. The number of samples per survey varied over time. Each plot was sampled twice from 1991 to 1993, three times from 1994 to 1995, and four times per year thereafter. Data from all surveys within a year were combined to determine incidence at each site for each year (Table S1). All data are from the National Science Foundation (NSF) supported Luquillo Long-Term Ecological Research Site. Gastropod data are archived publicly in accordance with NSF guidelines (<https://luq.lter.network/data/luqmetadata171>).

Metacommunity structure

Using presence–absence data for plots (i.e., incidence based on all surveys for each plot each year), metacommunity structure of gastropods along a latent environmental

gradient was determined separately for each year using the EMS framework (Leibold and Mikkelsen 2002; Presley et al. 2010). The best-fit pattern of metacommunity structure for each year (Fig. S1) was determined based on three characteristics of species environmental distributions (i.e., coherence, species range turnover, and range boundary clumping) that were derived from an ordinated presence–absence matrix. Each matrix was ordinated via reciprocal averaging (RA), which simultaneously optimizes the proximity of communities with similar species composition and the proximity of species with similar distributions in the ordinated space.

To evaluate coherence, a null model that constrained community richness to equal observed totals and that maintained equal probabilities of species occurrence was chosen a priori, because it has a desirable combination of type I and type II error properties when applied to small matrices (i.e., those with fewer than 30 species or 30 communities), and creates a biologically realistic null space in which the number of species in each community is fixed, but the number of communities in which a species occurs is random (Presley and Willig 2010; Presley et al. 2010, 2011). For each year, 1000 randomly generated matrices were created and subjected to RA. Embedded absences in each randomly generated matrix were counted and used to create a null distribution. A z test based on the mean and variance of the null distribution was used to determine significance. A metacommunity was considered significantly and positively coherent if the likelihood due to chance of having fewer embedded absences than observed was $\leq \alpha$. Analyses of coherence were conducted as one-tailed tests as no biological mechanism is known that could give rise to more-embedded absences than expected by chance (Presley et al. 2019). Embedded absences are filled prior to analysis of range turnover or range boundary clumping. This is a simple form of multi-species occupancy modeling, as embedded absences represent communities in which a species should occur but was not detected (Leibold and Mikkelsen 2002).

Species range turnover along the latent environmental gradient was evaluated for each metacommunity. To quantify range turnover, the number of times one species environmental range replaced another species environmental range between each possible pair of communities was counted in the ordinated empirical matrix. A replacement only occurs when the environmental range of one species (Species A) extends beyond that of another (Species B) in one direction along the gradient and the range of Species B extends beyond that of Species A in the other direction. Importantly, replacements cannot occur within the ranges of species. To determine significance, the empirical number of replacements was compared to a null distribution of such replacements that was derived from 1000 matrices that contained randomly shifted species ranges along the latent environmental gradient whose extents were the same

as in the empirical metacommunity (Leibold and Mikkelsen 2002). A metacommunity exhibited positive species range turnover when the likelihood of randomly generating more replacements than observed was $\leq \alpha/2$; a metacommunity exhibited negative species range turnover when the likelihood of randomly generating fewer replacements than observed was $\leq \alpha/2$.

Morisita's index (I) measures the clumping of species range boundaries with respect to an environmental gradient by counting the number of distributional termini at each plot (Hurlbert 1990). Because analyses of EMS are explicitly related to environmental gradients, environmental range boundaries exist even for species whose geographical distribution spans the entire study area. When the niche characteristics of a species allow it to ubiquitously occur on the LFDP, the termini of its environmental distribution will occur at the ends of the latent environmental gradient, and not therefore contribute to boundary clumping (Leibold and Mikkelsen 2002). Significance was determined via a Chi-square goodness-of-fit test that compared the observed distribution of range boundaries along the environmental gradient to an expected uniform distribution. Environmental range boundaries that occurred at random have a Morisita's index of ~ 1.0 and a non-significant Chi-square test. Index values > 1.0 with a significant Chi-square test indicate clumped boundaries, whereas index values < 1.0 with a significant Chi-square test indicate hyperdispersed boundaries.

We followed Presley et al. (2010) in recognizing quasi-structures. If range turnover was non-significant and less than the average number from randomly generated matrices, we considered the metacommunity to be quasi-nested. In contrast, if range turnover was non-significant and more than the average number from randomly generated matrices, we considered the metacommunity to be quasi-evenly spaced, quasi-Gleasonian, or quasi-Clementsian, depending on results of analysis of boundary clumping (Fig. S1).

To evaluate the overall significance of each element of metacommunity structure, we conducted a meta-analysis based on Stouffer's (inverse normal) method (Zaykin 2011), which combines probabilities from all 28 years into a single P value. Based on these combined probabilities for each element, we characterized the overarching metacommunity structure. Because the 28 tests for each EMS are not independent (i.e., they are repeated on the same metacommunity), we modified α to account for the lack of independence (Benjamini and Hochberg 1995) in which $\alpha_{\text{adjusted}} = \alpha(k+1)/(2 \times k)$, where k is the number of tests. For this analysis, with $\alpha = 0.10$, $\alpha_{\text{adjusted}} = 0.10(28+1)/(2 \times 28) = 0.052$. Approaches for combining probabilities may be biased if temporal autocorrelation characterizes the data. To assess this, we determined effect sizes for each EMS each year. We then compared the distribution of differences between effect sizes of adjacent years (i.e., $T_i - T_{i+1}$) to the distribution of

all such possible interannual pairwise differences to evaluate the importance of temporal autocorrelation. To disentangle possible effects of each hurricane from estimations of temporal autocorrelation, we estimated the mean difference between adjacent years before and after Hurricane Hugo, and before and after Hurricane Maria, and compared those differences to all possible interannual differences.

Effects of hurricane disturbance, secondary succession, and temperature

To determine whether disturbances associated with hurricanes or temperature influence interannual variation in coherence, species range turnover, or species boundary clumping, we conducted separate generalized linear models (GLM) with Gaussian error terms, type II sums of squares, effect size of each element as the response variable, and hurricane identity (Hurricane Hugo, Georges, or Maria), time after most recent major hurricane (TAH), a hurricane by TAH interaction, understory temperature, and ambient temperature as explanatory variables. In addition, we performed a multivariable GLM to simultaneously evaluate the effects of hurricane and temperature on coherence, species range turnover, and range boundary clumping using the same design as for the univariate GLMs.

Land-use legacies

We determined if the position of communities along a latent environmental gradient (i.e., community scores on primary axis from RA) differed among historical land-use categories for each year separately via analysis of variance. Subsequently, post hoc tests identified the contribution of particular land-use categories to such differences. Post hoc comparisons were conducted using a Tukey test with a Holm–Šidák adjustment of P values. Analyses were conducted in R 3.2.2 using the `glht` function from the `multcomp` library (Hothorn et al. 2008). In addition, we combined probabilities from the analysis of variance for each year via Stouffer's Method to determine if the effect of historical land use was pervasive over time. As data are repeated on the same metacommunity each year, we adjusted α to account for a lack of independence (Benjamini and Hochberg 1995). Moreover, we explored if the latent environmental gradients mapped onto space in a similar fashion during consecutive years by quantifying the correspondence of community scores from RA between consecutive years of the study. This was achieved via Spearman rank correlations, as we had no reason to expect associations to be linear.

We conducted co-occurrence analyses for all pairs of gastropod species separately for each year (Griffith et al. 2016) using the combinatorics approach of Veech (2013). We used mantel matrix correlations (Legendre and Legendre 1998) to

determine if pairwise species co-occurrence structure was similar between consecutive years. Finally, we conducted meta-analyses for each pair of species via Stouffer's method to evaluate the overall significance of negative or positive co-occurrence over the 28-year time frame. For this meta-analysis, we extracted the P values that estimated the likelihood of positive or negative co-occurrence for each pair of species for each of the 28 years. For each pair of species, two separate meta-analyses were conducted: one for positive co-occurrence and one for negative co-occurrence. As the P values generated by co-occurrence analyses conducted via the "cooccur" function of the cooccur library (Griffith et al. 2016) are for one-tailed tests, we converted these P values to represent P values of two-tailed tests to reduce the likelihood of type I errors in meta-analyses.

Analyses of coherence, species range turnover, and range boundary clumping were performed in Matlab 9.2.0.556344, release 2017a (script files for Matlab are available for download at <https://faculty.tarleton.edu/higgins/metacommunity-structure.html>). Scores for communities along primary axes as defined by RA were obtained using the simple correspondence analysis option in Mini-Tab 17.3.1. GLMs were conducted using the glm function from the stats package (R Core Team 2020). Multivariate GLMs were conducted using the manova function from the stats package (R Core Team 2020). Type II sums of squares were implemented via the Anova function in the car package (Fox and Weisberg 2019). Tukey tests were conducted using the glht function from the multcomp package (Hothorn et al. 2008). Stouffer's method was conducted using the sumz function from the metapack package (Dewey 2020). Analysis of variance, including post hoc tests, Spearman rank correlation, Stouffer's method, co-occurrence analysis, and Mantel tests were executed in R 3.2.2.

To enhance power at detecting ecological patterns, especially given the high variability of the system and the heuristic nature of this research, we recognized significance when $P \leq 0.10$ (overall conclusions were not markedly different using $\alpha = 0.05$). Of course, blind adherence to any α -level can be counterproductive (Amrhein et al. 2019), and the decision to rely on the magnitude of P values is complex and controversial (Ellison et al. 2014). Consequently, we report all P values, so that interpretations can be assessed independently using other standards of significance.

Results

Elements of metacommunity structure

Coherence was statistically greater than expected due to chance alone in each of 28 years (Table 1), indicating that the preponderance of gastropod species responded to

a common latent environmental gradient within each year. Similarly, species range turnover was statistically greater than expected due to chance in 23 of 28 years and significantly less than expected due to chance during none of the years, indicating the absence of nested structures (see Fig. S2 for examples). Finally, boundary clumping was significantly greater than expected due to chance during 21 of 28 years. In over 2/3 of years (19 of 28), a compartmentalized structure with positive range turnover (i.e., Clementsian or quasi-Clementsian structure) characterized the metacommunity. The separate meta-analyses for coherence, range turnover, and range boundary clumping confirmed that through time, the metacommunity was coherent ($P < 0.001$), with greater than expected range turnover ($P < 0.001$) and range boundary clumping ($P < 0.001$), thereby corroborating the generality of a Clementsian structure.

Coherence exhibited significant responses to hurricane, ambient temperature, and TAH (Table 2). Coherence increased with increasing TAH, but decreased with increasing ambient temperature. In addition, coherence differed in response to hurricanes, with coherence being greater during years after Hurricane Hugo than during years after Hurricane Maria ($P = 0.066$), and greater during years after Hurricane Georges ($P = 0.077$) than during years after Hurricane Maria. Coherence during years after Hurricane Hugo (1991–1998) and during years after Hurricane Georges (1999–2017) were not significantly different ($P = 0.805$; Fig. 2B). Although the level of coherence changed in response to hurricane and temperature, metacommunities always remained significantly coherent (Table 1).

Neither species range turnover nor range boundary clumping exhibited a significant response to hurricane or temperature. Similarly, a multivariate GLM found no consistent effects of hurricane or temperature on metacommunity structure as simultaneously measured by coherence, range turnover, and range boundary clumping (Table 1).

We evaluated the potential for temporal autocorrelation in EMS by comparing the differences between adjacent years (based on standardized effect sizes) to all pairwise differences between years. Mean adjacent year changes in coherence, range turnover, and range boundary clumping were not significantly different than pairwise differences between all possible years (Fig. 2A). Comparisons of EMS immediately before and immediately after hurricane disturbances revealed a large decrease in coherence as a result of Hurricane Maria and a large decrease in range turnover as a result of Hurricane Georges (Table 1, Fig. 2A).

Although considerable temporal variation characterized the extent to which land use accounted for differences among communities in their positions along the latent environmental gradient (i.e., community scores on axis 1 from RA), a meta-analysis of those results for the entire time domain suggests that land use had a pervasive effect in producing

Table 1 For each year from 1991 to 2018, results of the analyses for coherence, species turnover, and boundary clumping and the corresponding metacommunity structure of terrestrial gastropods on the Luquillo Forest Dynamics Plot (LFDP). In addition, total species richness for the LFDP and abundance (mean abundance per survey) are displayed for each year

	Year	Coherence		Species turnover		Boundary clumping		Species richness	Abundance	Metacommunity Structure
		Abs	P	Rep	P	I	P			
Hurricane Hugo	1989									
	1990									
	1991	179	< 0.001	1145	0.457	3.130	< 0.001	16	295	Quasi-nested subsets
	1992	93	< 0.001	1000	0.002	2.242	0.064	12	266	Clementsian
	1993	72	< 0.001	1027	0.031	3.455	0.004	12	354	Clementsian
	1994	162	< 0.001	1359	0.026	2.088	0.061	14	447	Clementsian
	1995	184	< 0.001	1321	0.773	0.000	0.066	14	528	Quasi-evenly spaced
	1996	158	< 0.001	2227	0.004	2.073	0.111	14	419	Gleasonian
	1997	132	< 0.001	1892	0.022	2.171	0.040	14	551	Clementsian
Hurricane Georges	1998	160	< 0.001	4183	< 0.001	1.904	0.055	14	337	Clementsian
	1999	181	< 0.001	2290	0.309	1.515	0.092	15	194	Quasi-Clementsian
	2000	144	< 0.001	1913	< 0.001	2.895	0.004	13	310	Clementsian
	2001	157	< 0.001	1067	0.157	3.083	< 0.001	16	252	Quasi-nested subsets
	2002	179	< 0.001	4141	< 0.001	1.490	0.163	15	292	Gleasonian
	2003	162	< 0.001	3425	0.003	1.558	0.111	15	285	Gleasonian
	2004	202	< 0.001	2982	0.026	1.810	0.035	15	339	Clementsian
	2005	174	< 0.001	3089	0.069	2.484	0.006	13	603	Clementsian
	2006	152	< 0.001	3230	0.014	2.689	< 0.001	16	519	Clementsian
	2007	183	< 0.001	3242	0.010	1.152	0.331	17	477	Gleasonian
	2008	143	< 0.001	3689	0.002	2.850	0.003	15	706	Clementsian
	2009	172	< 0.001	3819	0.001	1.739	0.081	15	620	Clementsian
	2010	91	< 0.001	2135	< 0.001	1.152	0.394	13	438	Gleasonian
	2011	137	< 0.001	2573	< 0.001	2.222	0.012	17	527	Clementsian
	2012	211	< 0.001	4239	0.003	2.203	0.003	16	664	Clementsian
	2013	159	< 0.001	3189	< 0.001	1.778	0.063	15	698	Clementsian
	2014	163	< 0.001	2430	0.030	1.900	0.069	14	716	Clementsian
	2015	131	< 0.001	1392	0.801	1.448	0.221	13	607	Quasi-nested subsets
	2016	198	< 0.001	4175	< 0.001	2.400	0.004	16	694	Clementsian
Hurricane Maria	2017	109	< 0.001	1121	< 0.001	3.333	< 0.001	12	783	Clementsian
	2018	123	0.034	677	0.005	3.182	0.006	12	110	Clementsian
Meta-analysis			< 0.001		< 0.001		< 0.001			Clementsian

Times of occurrence of major hurricanes, Hugo (1989), Georges (1998), and Maria (2017), are shown to the left

Abs number of embedded absences, Rep number of replacements, I Morisita's index

Results that were significant ($P \leq 0.10$) are bold. Meta-analyses are results from Stouffers method for combining probabilities for all years

compartments (Table 3). Moreover, post hoc analyses (Tukey tests) of all possible pairwise contrasts between land-use categories, after adjustment based on Stouffer's method, identified significant differences in the position of communities along latent environmental gradients between land-use category B representing coffee cultivation and smaller scale agriculture, and land-use category C, representing selective logging (Table 3).

At the scale of the LFDP, the co-occurrence structure of gastropod species was quite similar between each pair of consecutive years (Table 4). In contrast, the spatial structure

of the latent environmental gradient, as represented by primary axis scores from RA, was correlated between consecutive years only in a minority of cases. Nonetheless, a meta-analysis of correlations between consecutive years suggests significant overall correlations in spatial structure exist (Table 4).

Species co-occurrences

Of the 136 possible pair of species, meta-analysis of co-occurrence over 28 years suggested that only 1 pair

significantly co-occurred less than expected due to chance (*Megalomastoma croceum* and *Caracolus caracolla*), whereas 28 pairs of species co-occurred more than expected due to chance (Table S2). Although each species significantly co-occurred with at least one other species, frequent and abundant taxa (e.g., *C. caracolla*, *Nenia tridens*, and *Gaeotis nigrolineata*) as well as infrequent and rare taxa (e.g., *Obeliscus terebraster*, *Platysuccinea portoricensis*) did not evince many significant co-occurrences with other species. In contrast, each of seven moderately abundant species significantly co-occurred with at least 4 other species (i.e., *Austroselenites alticola* with 4 species; *Caracolus marginella* with 5 species; *Lamelaxis gracilis* with 5 species, *M. croceum* with 6 species; *Oleacina playa* with 7 species; *Subulina octona* with 5 species, and *Diplosolenodes occidentalis* with 6 species).

Discussion

A strong motivation for conducting long-term ecological research is the concern that short-term “snapshots” fail to capture temporal dynamics. Moreover, short-term studies that represent before-and-after snapshots can provide incomplete or misleading impressions of the effects of disturbance on the biota (Adams 2001). Consequently, considerable attention has been devoted to quantifying temporal variation in abundance of populations (Proença et al. 2017) or species of conservation concern (Pedler et al. 2016). Nonetheless, a few studies have documented temporal variation in species composition or biodiversity of communities at regular intervals for extensive periods of time for invertebrates (Bloch et al. 2007; Willig et al. 2007, 2011; Schowalter et al. 2021), or have explored such temporal variation in the structure of metacommunities.

Temporal trends in metacommunity structure have been evaluated for many groups of organisms (e.g., vascular plants in forests, grasslands, and wetlands; gastropods; parasitoids; marine benthic invertebrates; freshwater fish; amphibians; birds; bats; non-volant small mammals) and at different temporal resolutions, including seasonally (Erős et al. 2014; Fernandes et al. 2014; Cisneros et al. 2015), annually over a span of 2–4 years (Presley et al. 2011; Willig et al. 2011; Erős et al. 2014; Fernandes et al. 2014; Ochoa-Ochoa and Whittaker 2014), or episodically between time periods that span 1–12 decades (Keith et al. 2011; Newton et al. 2012; Bonthoux and Balent 2015; Delciellos et al. 2018; Josefson et al. 2018). Such studies have been undertaken over the short term to explore effects of seasonal pulses in resource availability (Cisneros et al. 2015) or seasonal flooding (Fernandes et al. 2014), or over the long term to evaluate effects of broad-scale anthropogenic activities (e.g., agriculture, marine trawling) on local communities

(Keith et al. 2011; Newton et al. 2012; Josefson et al. 2018). To date, no study has evaluated interannual variability of metacommunity structure over regular intervals that characterize extensive spans of time (> 10 years) or continually over several generations, especially in dynamic environments associated with disturbance-mediated systems. Due to desiccation stress, gastropod mortality resulting from hurricanes occurs quickly (Willig et al. 2019), and short generation times combined with high reproductive capacity allow populations to increase quickly as early successional forest becomes established (Bloch and Willig 2006). Nonetheless, studies that evaluate metacommunity structure have shown it to be stable, even when exposed to press disturbances such as eutrophication associated with agriculture or changes in land-use regimes (Keith et al. 2011; Newton et al. 2012; Bonthoux and Balent 2015; Delciellos et al. 2018).

Temporal variation in metacommunity structure of gastropods

During the 28-year time frame for which we evaluated metacommunity structure, the LEF experienced three major hurricanes (Hugo, Georges, and Maria), noteworthy droughts (1993, 1994, 2015), and temperature changes associated with climate change (Willig et al. 2019). Nonetheless, the metacommunity structure of gastropods was remarkably stable throughout these events (i.e., Clementsian or quasi-Clementsian). These phenomena lead to the conclusion that the gastropod metacommunity exhibits a canonical structure characterized by compartments, and that quorum constraints (sensu Jenkins and Buikema 1998; Jenkins 2006) are not relevant, even though the system is disturbance-mediated and was often in early seral stages of succession.

Gradients and hurricanes

Metacommunity structure did not map onto space in the same way every year (i.e., compartments were not represented by the same sets of sites every year and intersite relationships based on species composition differed over time). In fact, the spatial representation of the latent environmental gradients that induced metacommunity structure were not correlated between consecutive years in most cases (17 of 27 pairs). Instead, the spatial distributions of gastropod species responded to spatiotemporal dynamics in environmental characteristics.

The only EMS that exhibited a response to effects of hurricanes or ambient temperature was coherence (Table 2). The metacommunity was less coherent (but still significantly coherent) after Hurricane Maria than after other hurricanes; however, this result may reflect the lack of a longer post-Maria time frame for analysis. Coherence consistently increased with time after each major hurricane, suggesting

Table 2 Results of general linear models (GLM) for each element of metacommunity structure, as well as a multivariate GLM for all three elements of metacommunity structure, that evaluate the effects of hurricane (Hugo, Georges, Maria), ambient temperature, understory

	Hurricane	Ambient temperature	Understory temperature	TAH	Hurricane × TAH
Coherence	0.061	0.078	0.254	0.039	0.161
Range turnover	0.550	0.104	0.430	0.401	0.543
Range boundary clumping	0.524	0.236	0.800	0.633	0.507
Multivariate GLM	0.115	0.191	0.186	0.244	0.568

Significant ($P \leq 0.10$) are bold

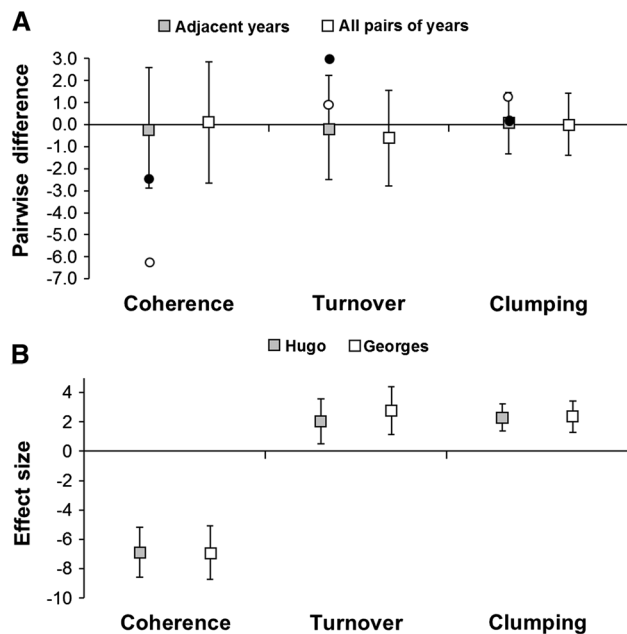


Fig. 2 **A** Mean pairwise differences between adjacent years (year_i – year_{i+1}) and between all possible pairs of years (year_i – year_{i+x}) for coherence, range turnover, or range boundary clumping and **B** mean standardized effect size for coherence, range turnover, and range boundary clumping during years following Hurricanes Hugo and Georges (effect sizes were not plotted for Hurricane Maria because there was only 1 year of data). Error bars are ± 1 SD. Dots indicate difference before and after Hurricane Georges (black; 1998–1999) or Maria (white; 2017–2018). Negative values of coherence indicate a loss of coherence over time, whereas negative values of range turnover or range boundary clumping indicate increases in those elements over time

that the strength of response to a common gradient increased as secondary succession proceeded. In contrast, climate change, represented by increasing ambient temperature, had a slight negative effect on coherence when effects of hurricanes (hurricane identity, TAH, and understory temperature) were taken into account. This suggests that an increasing magnitude of climate change in the future may change the

temperature, time after most recent major hurricane (TAH), and the interaction between hurricane and TAH on the standardized effect size for coherence, range turnover, and range boundary clumping)

structure of this metacommunity or result in a different gradient along which it is structured.

Importantly, the combined effects of hurricanes and climate change have not altered the species that compose the gastropod metacommunity in the LFDP. The same group of species has generally been present throughout the time frame of the study. Although the relative abundances and incidence of some species change during secondary succession, the same three species (*C. caracolla*, *N. tridens*, *G. nigrolineata*) are the most abundant, and the same pool of rare species persist in the forest. To date, we have not documented local extirpation of a species of terrestrial gastropod nor the addition of species previously not found in Tabonuco forest. The temporal stability of the gastropod species pool in the LFDP may contribute to consistent Clementsian structure despite the occurrence of repeated cycles of secondary succession caused by hurricanes during a time of rapid climate change.

Compartmentalization

Analyses of co-occurrence facilitate identification of suites of species with similar environmental distributions that contribute to the compartmentalized structure of the metacommunity. Statistical constraints associated with taxa that have high frequencies of occurrence or low frequencies of occurrence result in those species not evincing significant associations. Fortunately, this corresponds to the fact the neither ubiquitous species nor infrequent species contribute greatly to the detection of metacommunity structure. Because of their positive associations with multiple species, *A. alticola*, *C. marginella*, *L. gracilis*, *M. croceum*, *O. playa*, *S. octona*, and *D. occidentalis* are the primary contributors to the compartmentalized structures that characterize the gastropod metacommunity on the LFDP during secondary succession. These species are largely associated with early successional habitats and canopy openings that have higher light levels, which harbor different plant species than do mature areas of Tabonuco forest (Secrest et al.

Table 3 For each year from 1991 to 2018, analysis of variance (ANOVA) evaluated the extent to which historical land use affected the position of plots along the latent environmental gradient (Axis 1 from reciprocal averaging). Post hoc comparisons (Tukey's test with a Holm–Šidák adjustment) evaluated differences between particular land-use categories in each year

Year	ANOVA	Contrast		
		A–B	A–C	B–C
1991	0.919	1.000	1.000	1.000
1992	0.078	0.412	0.294	0.078
1993	0.884	1.000	1.000	1.000
1994	0.258	0.306	0.806	0.806
1995	0.224	0.370	0.312	0.731
1996	0.973	1.000	1.000	1.000
1997	0.145	0.580	0.580	0.153
1998	0.109	0.267	0.610	0.131
1999	0.011	0.123	0.236	0.010
2000	0.004	0.005	0.445	0.025
2001	0.426	0.947	0.740	0.740
2002	0.004	0.542	0.021	0.005
2003	0.021	0.480	0.083	0.022
2004	0.503	0.830	0.830	0.771
2005	0.543	0.850	0.907	0.907
2006	0.799	1.000	1.000	1.000
2007	0.041	0.881	0.074	0.074
2008	0.054	0.433	0.216	0.055
2009	0.314	0.502	0.868	0.502
2010	0.229	0.386	0.757	0.326
2011	0.238	0.388	0.779	0.348
2012	0.204	0.602	0.602	0.232
2013	0.032	0.616	0.041	0.080
2014	0.038	0.736	0.084	0.053
2015	0.919	1.000	1.000	1.000
2016	0.042	0.066	0.788	0.082
2017	0.747	1.000	1.000	1.000
2018	0.734	1.000	1.000	1.000
Meta-analysis	< 0.001	0.377	0.274	< 0.001

Abbreviations for land-use categories are: *A* for intensive logging and agriculture, *B* for coffee cultivation and smaller scale agriculture, and *C* for selective logging (see text for details)

Comparisons that were significant ($P \leq 0.10$) are bold, indicating the contrasts that most contributed to overall differences between land-use categories. Thereafter, a meta-analysis (Stouffer's method) evaluated overall evidence for significant differences among land-use categories, as well as for each pairwise contrast separately

1996; Bloch and Willig 2006). The lack of ubiquitous negative co-occurrences over time (only one species pair), which might have been expected for Clementsian structures, likely arises, because such species would generally only occur on a small proportion of sites, making it a challenge to distinguish between negative and random associations.

Table 4 Results (P values) of Mantel matrix correlations determining the correspondence in interspecific gastropod co-occurrence for each pair of consecutive years, results of Spearman rank correlations of sites scores for the primary axis of reciprocal averaging for each pair of consecutive years, and results from a meta-analysis based on Stouffer's method

Initial year	Ensuing year	Correlation of inter-specific co-occurrence matrices	Spearman rank correlation
1991	1992	< 0.001	0.273
1992	1993	< 0.001	0.183
1993	1994	< 0.001	0.086
1994	1995	< 0.001	0.859
1995	1996	< 0.001	0.077
1996	1997	< 0.001	0.190
1997	1998	< 0.001	0.665
1998	1999	< 0.001	0.737
1999	2000	< 0.001	0.811
2000	2001	< 0.001	0.367
2001	2002	< 0.001	0.141
2002	2003	< 0.001	< 0.001
2003	2004	< 0.001	0.502
2004	2005	< 0.001	0.050
2005	2006	< 0.001	0.216
2006	2007	< 0.001	0.947
2007	2008	< 0.001	0.033
2008	2009	< 0.001	0.016
2009	2010	< 0.001	0.002
2010	2011	< 0.001	0.112
2011	2012	< 0.001	0.070
2012	2013	< 0.001	0.001
2013	2014	< 0.001	0.028
2014	2015	< 0.001	0.317
2015	2016	< 0.001	0.367
2016	2017	< 0.001	0.473
2017	2018	< 0.001	0.463
Meta-analysis		< 0.001	< 0.001

Significant ($P \leq 0.10$) results are bold

Complex nature of legacies

The strength of associations between historical land use and latent environmental gradients were variable over time, but sufficiently strong to suggest a lasting effect (Table 3). Land-use category likely serves as a crude proxy for space as selective logging occurred on the southern part of the LFDP, coffee plantations and agriculture were located on the northern part of the LFDP, and a mix of logging and agriculture occurred in the central part of the LFDP. Only communities from locations with the least similar land-use histories (selective logging versus coffee plantations or agriculture) exhibited consistently significant differences in their

positions along the latent environmental gradient representing variation in the composition of gastropod communities (Table 3).

Interannual correspondences of the ordering of communities along the latent environmental gradient that structured the metacommunity were typically weak with the exception of 2007 through 2014, a period of relatively mature rainforest (Table 4). Two opposing factors may contribute to these phenomena. Each of the three land-use categories represents sites that are a contiguous, geographical subset of the LFDP (Fig. 1B). To some extent, sites within land-use categories may have been historically identified for particular anthropogenic land uses because of similar topographic or environmental characteristics. Moreover, the intensity and severity of tropical storms and hurricanes are unlikely to be spatially random, even at the scale of the LFDP, because the winds and attendant structural damage to the forest are spatially molded by the direction of the storms as they intercept the topographic relief and vertical profile of the landscape (Everham and Brokaw 1996). In essence, land-use legacies may not be independent of pre-existing differences in environmental attributes among regions of the LFDP or the intensity and severity of storms (i.e., effects of previous land use may be confounded with earlier environmental heterogeneity or subsequent disturbance effects). Moreover, storm damage was not homogeneous within land-use categories, and secondary succession will transpire at site-specific rates and trajectories, enhancing variation within land-use categories and diminishing differences among land-use categories. The balance between these processes leads to complex spatial patterning of the latent environmental gradient and a weak-to-modest effect of previous land use on metacommunity structure over time.

Mechanisms of resistance and resilience

The canonical nature of compartmentalized metacommunity structure on the LFDP likely arises, because groups of species share fundamental niche characteristics that distinguish them from other such groups. Consequently, species within each group will evince similar environmental distributions, even when the spatial mapping of critical environmental characteristics varies over time as a result of disturbance and secondary succession. Thus, the spatial component of metacommunity structure (the groups of sites that represent compartments) will vary over time, and may be weekly correlated during some stages of secondary succession, depending on the rate of environmental change experienced by each community. In contrast, the correspondence of species distributions should be correlated over time because of the preeminence of niche-based assembly processes that are linked to environmental attributes of sites within the landscape. Indeed, species co-occurrences were highly correlated

between all possible pairs of successive years ($P < 0.001$ in all 27 pairs of years; Table 4), corroborating the niche-based mechanism for maintenance of a canonical, compartmentalized, metacommunity structure.

Maintenance of a compartmentalized structure in a disturbance-mediated system requires two conditions. First, individuals of most species must be capable of dispersing among communities sufficiently quickly to exceed the rate of change in environmental characteristics of those communities so as to assure that environmental filtering occurs. Second, the correlations among environmental characteristics, particularly those that are associated with the fundamental niches of species in the metacommunity, need to be maintained over time, even if the central tendency and dispersion in environmental attributes changes greatly in response to disturbance and succession. If these two conditions persist in a metacommunity characterized by groups of species with similar fundamental niches, Clementsian structure should be pervasive over time.

We do not have data to support or refute the claim about the correspondence of rates of environmental change and rates of gastropod movement associated with the first condition. Nonetheless, based on first principals, such rates of movement would be dependent on cross-scale interactions (Peters et al. 2007), involving consideration of the environmental characteristics of particular sites and the environmental characteristics of the landscape through which individuals must move to emigrate to other sites (Willig et al. 2007, 2012). If such movement occurs at a rate that approaches or exceeds the pace of environmental change during secondary succession, quorum constraints should characterize the system (Jenkins 2006). Although preferred habitat characteristic may be taxon-specific, each species may have adapted considerable tolerance to a broad range of hydric, thermal, and habitat characteristics, as a consequence of evolving in a disturbance-prone system. Indeed, tolerances may be sufficiently broad to allow movement by most species through less favorable sites until they encounter more favorable sites, thereby enhancing the effective rate of emigration. In addition, species likely have evolved different strategies for dealing with periodic hurricane-induced loss of canopy. The largest species (*C. caracolla*) seems to weather post-hurricane conditions well compared to other gastropods, with their small surface-to-volume ratio and thick shell buffering them against warm, dry conditions. In contrast, the small *N. tridens* suffers massive mortality after hurricanes, persisting only in areas with some amount of canopy cover, with a rapid increase in abundance as early successional plant species provide cover (Bloch and Willig 2006).

The system features associated with the second condition are corroborated for Tabonuco forest, to the extent that spatial variation can provide insights about temporal variation. Although only 20 km apart, the Bisley watersheds suffered

much more damage from Hurricane Hugo than did those at El Verde (Walker 1991; Boose et al. 1994; Willig et al. 1998). Even 5 years after the storm (1994), the mean and variance of habitat characteristics differed greatly between watersheds, while the correlation structure of habitat characteristics was indistinguishable between watersheds (Secrest et al. 1996). Moreover, the association of gastropod abundances with habitat characteristics was indistinguishable between Bisley and El Verde for four common species (i.e., *C. caracolla*, *G. nigrolineata*, *N. tridens*, and *P. acutangula*), even though the mean and variance in abundances of all but *P. acutangula* differed between watersheds (Secrest et al. 1996).

To the extent that the spatial correlation of environmental attributes, especially those that are linked to the fundamental niches of most species in a Clementsian metacommunity, is unaffected by a changing disturbance regime, we predict that compartmentalized structures will persist unless new combinations of environmental characteristics emerge, especially at the extremes of gradients. These novel combinations essentially represent environments outside of the evolutionary history of the constituent species, and will likely select for novel communities and result in altered metacommunity structure (Lugo et al. 2012; Lugo 2013).

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Data availability statement Gastropod and temperature data are archived publicly and openly available in the Luquillo Long-Term Ecological Research data catalog: gastropod data (<https://luq.lter.network/data/luqmetadata107> or <https://portal.edirepository.org/nis/mapbrowse?packageid=knbn-lter-luq.107.9996737>), temperature data (<https://luq.lter.network/data/luqmetadata16> or <https://portal.edirepository.org/nis/mapbrowse?packageid=knbn-lter-luq.16.538551>).

Declarations

Conflicts of interest The authors have no relevant financial or non-financial interests to disclose.

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