

Long-term dynamics of tropical walking sticks in response to multiple large-scale and intense disturbances

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Abstract Understanding the effects of disturbance and secondary succession on spatio-temporal patterns in the abundance of species is stymied by a lack of long-term demographic data, especially in response to infrequent and high intensity disturbances, such as hurricanes. Moreover, resistance and resilience to hurricane-induced disturbance may be mediated by legacies of previous land use, although such interactive effects are poorly understood, especially in tropical environments. We address these central issues in disturbance ecology by analyzing an extensive dataset, spanning the impacts of Hurricanes Hugo and Georges, on the abundance of a Neotropical walking stick, *Lamponius portoricensis*, in tabonuco rainforest of Puerto Rico during the wet and dry seasons from 1991 to 2007. By synthesizing data from two proximate sites in tabonuco forest, we show that resistance to Hurricane Hugo (97% reduction in abundance) was much less than resistance to Hurricane Georges (21% reduction in abundance). Based on a powerful statistical approach (generalized linear mixed-effects models with Poisson error terms), we documented that the temporal trajectories of abundance during secondary succession (i.e., patterns of resilience) differed between

hurricanes and among historical land use categories, but that the effects of hurricanes and land use histories were independent of each other. These complex results likely arise because of differences in the intensities of the two hurricanes with respect to microclimatic effects (temperature and moisture) in the forest understory, as well as to time-lags in the response of *L. portoricensis* to changes in the abundance and distribution of preferred food plants (*Piper*) in post-hurricane environments.

Keywords Abundance · Hurricane · Phasmatidae · Resilience · Time-lag

Introduction

The role of disturbance in affecting the spatial and temporal dynamics of ecosystems is increasingly recognized as a dominant theme in ecology (Walker and Willig 1999; Willig and Walker 1999; Peters et al. 2010). Indeed, variation in the frequency, extent, and intensity of disturbance events has a profound effect on the nature of landscapes (see Pickett and White 1985), especially as human activities continue to expand and intensify throughout the globe. Moreover, the environmental context (i.e., the history or legacies of previous disturbances, including those of natural or anthropogenic origin) within which a particular disturbance event occurs can have a large effect on the severity of that event (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). Indeed, if multiple basins of attraction exist in a disturbance-mediated forest (sensu Vandermeer et al. 2004), then community composition and the abundances of species

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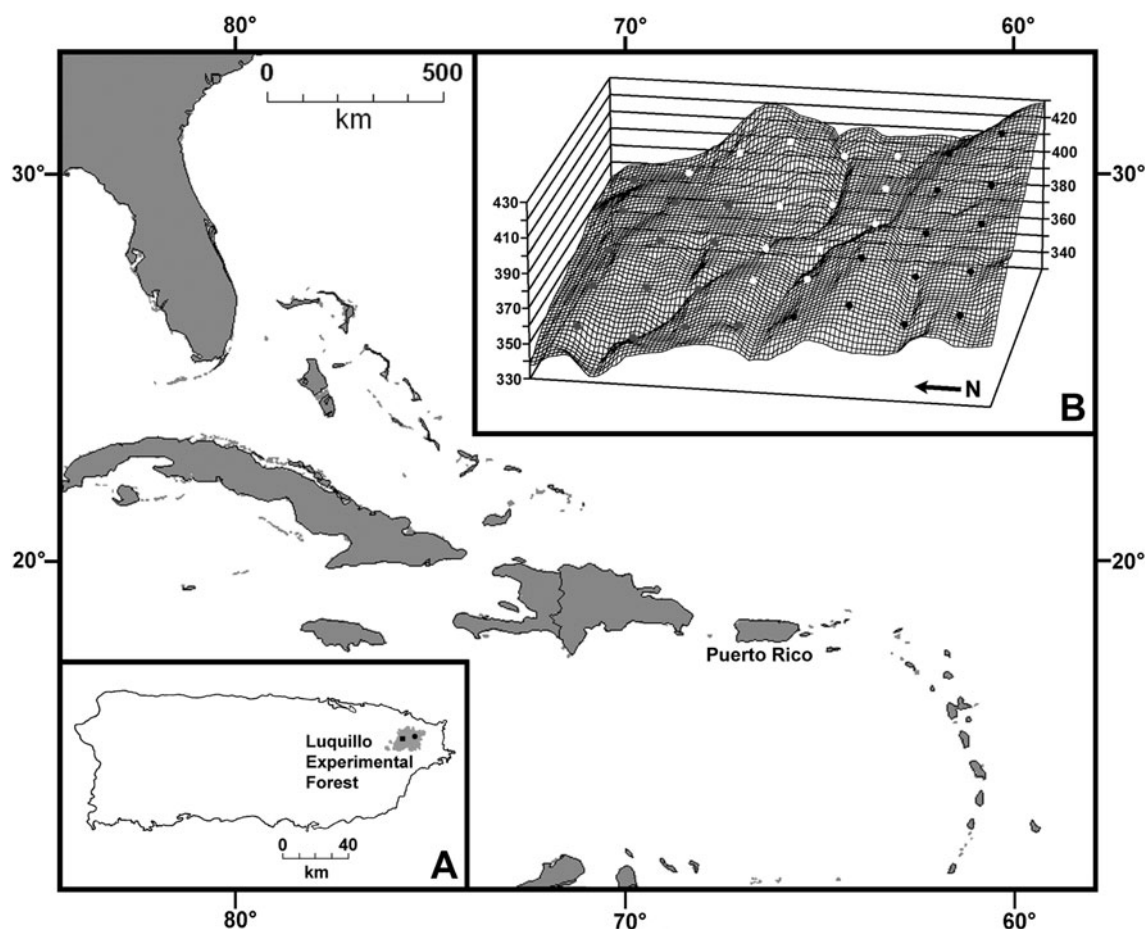


Fig. 1 Map of the Caribbean showing the location, size, and shape of Puerto Rico (labels on vertical borders are degrees north latitude and labels on horizontal axis are degrees west longitude). Within the Luquillo Experimental Forest (LEF) (gray shading of inset A), a square indicates the location of the Luquillo Forest Dynamics Plot (LFDP) at El Verde and a circle indicates the location of Bisley watersheds. Topographic map (inset B) of the 16-ha LFDP illustrates the topographic variability of the forest and the dispersion of sampling points (after Willig et al. 1998). Circles indicate the location

of sampling points (radius = 3 m) where surveys of *Lamponius portoricensis* were conducted over an 18-year period. Adjacent sample points were separated by 60 m. Shading of circles indicates historical land use (see text for details): white, land use class A (intensive logging and agriculture); gray, land use class B (shade coffee and small scale agriculture); and black, land use class C (light selective logging). Vertical axes (inset B) indicate elevation above sea level in meters

may not return to pre-disturbance conditions (multiple alternative states).

Although ecological understanding of the immediate and short-term responses of biota to disturbances has increased during the previous decade (e.g., Walker et al. 1991, 1996; Willig and McGinley 1999), fewer investigations have documented longer-term trajectories of response (e.g., Schowalter and Ganio 2003; Thibault and Brown 2008; Gannon and Willig 2009; Willig et al. 2011) by animals to high intensity disturbances. Because of logistic constraints, studies of multiple high-intensity disturbance events at the same site are rare (Turner et al. 1997), and these typically focus on short-term responses (e.g., Lopez et al. 2003; Schoener et al. 2004). With few exceptions (e.g., Bloch and Willig 2006; Bloch et al. 2007; Willig et al. 2007; Prates et al. 2010), long-term responses by

animals to multiple high-intensity disturbance events in the tropics are not well documented nor understood from a mechanistic perspective. Nevertheless, a long-term perspective is critical because short-term studies or before-and-after “snapshots” provide only an incomplete or even misleading impression of the effects of disturbance on populations, communities, or biogeochemical processes (Adams 2001).

The Caribbean Basin (Fig. 1) is characterized by high cyclonic activity (Landsea et al. 1999), with over 2,000 hurricanes recorded in the Caribbean islands from 1851 to 2008 (<http://hurricane.csc.noaa.gov/hurricanes/>). Consequently, the Caribbean Basin in general, and the island of Puerto Rico in particular, are disturbance-mediated environments in which disturbance regimes likely produce a sequence 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, Puerto Rico has experienced two major hurricanes in the past 20 years, resulting in a situation that is ideal for assessing context-dependent effects of intensive disturbances on the spatial and temporal demographics of local populations (Walker et al. 1991, 1996). Because the frequencies of intense hurricanes (Categories 4–5) may increase in the future as a consequence of global warming (Webster et al. 2005), it is all the more important to understand the long-term effects of successive disturbances on the resilience of biological systems (e.g., Holt 2006; Schoener and Spiller 2006).

Within this context, the overarching goal of this research was to employ an extensive dataset on the abundance of a tropical walking stick (*Lamponius portoricensis* Rehn 1903) to explore long-term spatio-temporal dynamics, including aspects of resistance and resilience, in response to intense disturbances during an 18-year period between 1991 and 2007. More specifically, our objectives were threefold: (1) to document and compare the resistance of walking stick populations to two high-intensity storms (Hurricane Hugo and Georges); (2) to quantify and compare resilience (i.e., trajectories of response to disturbance) during subsequent secondary succession; and (3) to synthesize autecological understanding of walking sticks with knowledge of environmental dynamics during disturbance and recovery to uncover possible mechanisms driving spatio-temporal dynamics. Because Hurricane Georges was less intense (Category 3 storm) than Hurricane Hugo (Category 4 storm) while passing over eastern Puerto Rico, we expected resistance and resilience to be greater with respect to Hurricane Georges than with respect to Hurricane Hugo.

Materials and methods

Study site

The Luquillo Experimental Forest (LEF) is a Man and the Biosphere Reserve (Franklin 1977) as well as a site in the National Science Foundation's Long-Term Ecological Research network (Hobbie et al. 2003). It occupies 11,300 ha of terrain in the northeastern corner of Puerto Rico (Fig. 1, inset A) and comprises four forest types (elfin, palo colorado, tabonuco, and palm) in association with elevational and edaphic features of the Luquillo Mountains. Research was conducted on the Luquillo Forest Dynamics Plot (LFDP), a 16-ha grid located in tabonuco forest near El Verde Field Station (Fig. 1, inset B), in the northwestern region of the LEF (18°10'N, 65°30'W). The LFDP was established to study long-term changes in forest

characteristics in response to hurricane-generated disturbances. Tabonuco forest occurs at elevations below 600 m, is the most extensive and best studied portion of the LEF, supports a well-documented flora and fauna (Reagan and Waide 1996), and is a subtropical wet forest according to the Holdridge classification system (Brown et al. 1983). The name “tabonuco” derives from the common epithet for the dominant hardwood species, *Dacryodes excelsa* (Burseraceae), which characterizes this forest. Other common trees of the canopy of tabonuco forest include *Manilkara bidentata*, *Sloanea berteriana*, *Guarea guidonia*, and *Prestoea acuminata* (Odum and Pigeon 1970).

Rainfall in tabonuco forest is substantial, averaging 346 cm per year (McDowell and Estrada-Pinto 1988), with a modestly drier period from January to April. Humidity is consistently high and relatively little seasonal or diurnal variation occurs in temperature (Odum and Pigeon 1970). As such, precipitation exceeds evapotranspiration in all months. The population- and community-level characteristics of the forest's biota have been long studied, as have been its associated ecosystem properties (e.g., Odum and Pigeon 1970; Brown et al. 1983; Reagan and Waide 1996).

In the last 20 years, two major hurricanes (Hugo in 1989 and Georges in 1998) have passed over eastern Puerto Rico. Although each produced considerable damage in the tabonuco forest, the two hurricanes differed in intensity, extent, and severity. Hurricane Hugo, a category 4 storm with maximum sustained winds of 227 km/h (Scatena and Larsen 1991), produced larger canopy openings and deposited more debris in the LEF than did Hurricane Georges, a category 3 storm with sustained winds of 177 km/h (Lomascolo and Aide 2001; Ostertag et al. 2003).

In addition to natural disturbances, anthropogenic activities (e.g., logging and agriculture) have also disturbed the land that now comprises the LFDP (Thompson et al. 2002). The land was purchased by the US Forest Service in 1934 and allowed to revert to closed-canopy forest, although limited selective logging persisted until the 1950s. Despite this dramatic reduction in land use, differences in tree composition among areas of the LFDP continue to reflect the history of human activity (Willig et al. 1996; Thompson et al. 2002). As such, the history of anthropogenic disturbance is relevant to extant patterns of species composition and abundance of plants (Thompson et al. 2002; Rice et al. 2004), animals (Bloch and Weiss 2002; Bloch et al. 2007), and microbes (Willig et al. 1996). Using aerial photographs and US Forest Service records, locations on the LFDP (Fig. 1, inset B) can be allocated into three categories (hereafter, land use classes; Thompson et al. 2002). Land use class A (0–50% canopy cover in 1936; classes 1 and 2 of Thompson et al. 2002) experienced the most intensive logging and agriculture prior to 1934.

Land use class B (50–80% canopy cover in 1936; class 3 of Thompson et al. 2002) was used for small-scale mixed agriculture (especially cultivation of shade coffee) before 1934. Land use class C (80–100% canopy cover in 1936; land use class 4 of Thompson et al. 2002) was lightly and selectively logged until the 1950s.

Study organism

For a variety of reasons, the walking stick, *L. portoricensis* (hereafter, *Lamponius*), is a useful species for studying the effects of disturbance on animal populations in the tabonuco forest of Puerto Rico (Garrison and Willig 1996). First, it has a ubiquitous spatial distribution in tabonuco forest, but exhibits considerable spatial variation in abundance, reaching the greatest densities in successional forest or small light gaps in otherwise closed-canopy forest (Willig et al. 1986, 1993). Second, its food preferences are well documented and include a number of early successional shrubs and trees, such as *Piper hispidum*, *P. glabrescens* (formerly *P. treleaseanum*), *Urera baccifera*, and *Dendropanax arboreus* (Sandlin and Willig 1993). Third, its abundances in tabonuco forest of Puerto Rico were dramatically reduced as a consequence of hurricane-induced disturbance (Willig and Camilo 1991). Fourth, *Lamponius* may be a keystone species because of its role in herbivory and nutrient cycling, as well as in stimulating decomposition rates and affecting the composition of detritivorous fungi in litter, especially in disturbed areas of the forest where they can attain high densities (Willig et al. 1986; Garrison and Willig 1996; Fonte and Schowalter 2005).

Field methods

Circular plots (3 m radius) were established at 40 points on the LFDP and spaced evenly such that 60 m intervene between adjacent points along a row or column within a rectilinear grid (Fig. 1, inset B). Of these plots, 13 were located in land use class A (intensive logging), 14 in land use class B (shade coffee plantations), and 13 in land use class C (light and selective logging). Surveys of *Lamponius* were conducted twice per year (wet and dry seasons) from 1991 to 2007 at all 40 plots on the LFDP. Nonetheless, the number of samples per seasonal survey varied over time. Each plot was sampled once in the dry season of 1991, twice in each season from the wet season of 1991 to the wet season of 1993, three times per season from the dry season of 1994 to the dry season of 1995, and four times per season thereafter, except for the dry season of 2003 (two surveys). A minimum of 2 days was maintained between samples within seasons. All surveys were conducted at night (1930 to 0300 hours), coinciding

with peak activity of walking sticks (Willig et al. 1986, 1993).

Each time a plot was sampled, at least two people surveyed it for a minimum of 15 min, during which they searched for *Lamponius*—adults (body length ≥ 79 mm) and juveniles (body length < 79 mm)—on all available surfaces (e.g., soil, litter, rocks, vegetation). To minimize alteration of long-term study sites, leaf litter was not manipulated and specimens were returned as closely as possible to the point of capture, usually on the same plant and within 0.5 m, and always within the same plot. For adults and juveniles separately, the abundance at a plot during a particular season equaled the average number of individuals captured at that plot. In subsequent analyses, time represents a sequence of alternating dry and wet seasons after each hurricane.

We estimated the apparency (Cook and Stubbendiek 1986) of *Piper* via a method that quantified the aerial density of *P. glabrescens* and *P. hispidum* at heights up to 3 m above the forest floor (see 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, 0.5, 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. The device was positioned 1.5 m from the center of each plot in each of the four cardinal directions. Apparency was measured during each wet season.

Quantitative analyses

To evaluate the extent to which the temporal trajectory of response by *Lamponius* to Hurricane Hugo differed from that to Hurricane Georges and depended on previous land use on the LFDP, we conducted a generalized linear mixed-effects model using the R programming environment (R Development Core Team 2009) and the MASS and nlme libraries. We did so separately for adults and juveniles because these stages differ greatly in size and mobility, as well as in associated physiological and behavioral characteristics (Sandlin and Willig 1993; Willig et al. 1986, 1993). Land use category was a between subjects factor, whereas time and hurricane were within subjects (i.e., repeated measures) factors because the same plots were sampled during all time periods after each hurricane (i.e., were not independent). These statistical analyses excluded the first two time periods after each hurricane (i.e., periods 1 and 2 in Figs. 2, 3 and 4) because we did not have data from the LFDP until 1½ years after Hurricane Hugo and the analytical design required all time periods to be represented equally after each hurricane.

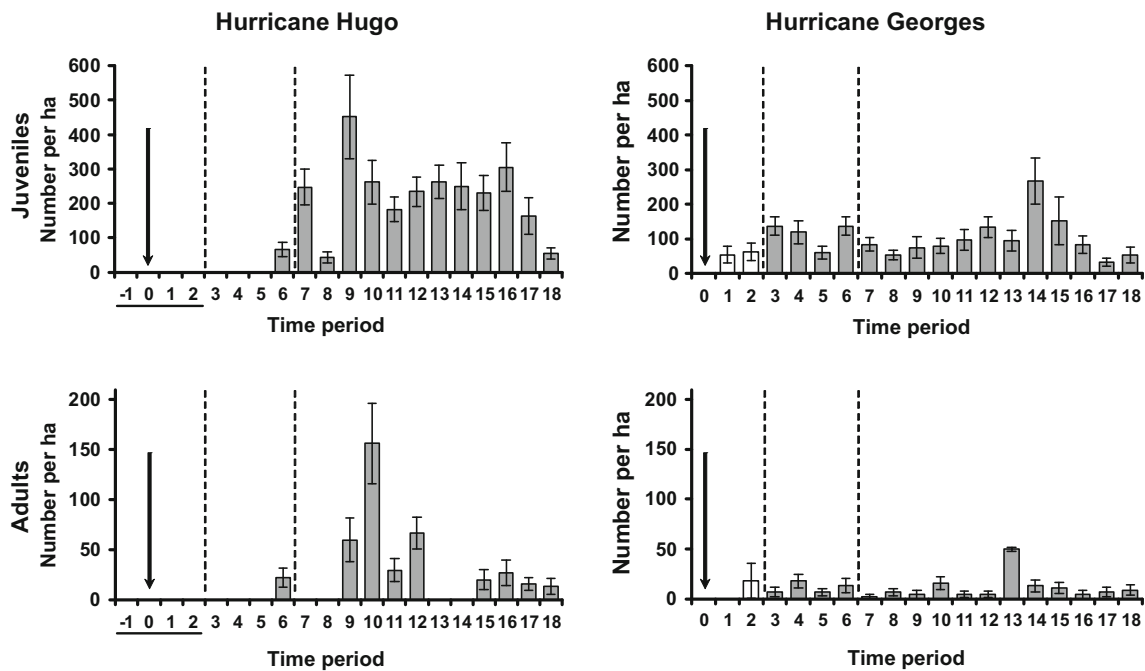


Fig. 2 Bar graphs displaying mean density of juvenile (top row) or adult (bottom row) *Lamponius portoricensis* for each of 16 time periods after each hurricane, consistent with statistical analyses (i.e., a significant hurricane by time interaction, but a non-significant hurricane by time by land use interaction; Table 1). *Odd-numbered* time periods correspond to samples collected during dry seasons, and *even-numbered* time periods correspond to samples collected during wet seasons. A *negative number* represents a time period prior to Hurricane Hugo. Hurricane events are indicated by *vertical arrows* at

time 0. *Vertical dashed lines* delimit immediate (<12 months), short-term (between 12 and 36 months), and long-term (>36 months) responses to hurricanes. *Error bars* represent 1 SE. Time periods for which data are not available from the Luquillo Forest Dynamics Plot are *underlined* (note that abundances for time periods 3, 4, and 5, post Hurricane Hugo, were zero and were included in analyses). Data included in analyses are in *gray*. Data from the first year after Hurricane Georges are in *white* and were not included in analyses because corresponding data for Hurricane Hugo are not available

We used Pearson product moment correlations to evaluate associations between abundances of adult or juvenile *Lamponius* and apparency of *Piper* plants on which they forage. Because *Lamponius* and *Piper* may not respond to hurricane-induced disturbance in the same time frame, we performed a series of correlation analyses to evaluate possible time lags between plant responses and those of adult or juvenile walking sticks. Each series consisted of a contemporary comparison (i.e., correlation between abundance of *Lamponius* and apparency of *Piper* from the same time period) as well as correlations between apparency of *Piper* and abundance of *Lamponius* with time lags of 1, 2, 3, 4, 5 or 6 years.

To assess the assumption of spatial independence of walking stick abundances among plots, we conducted tests of spatial autocorrelation based on Moran's I (1950) using the Biotas software package (<http://www.ecostats.com/>) for adults and juveniles separately. We did so for all combinations of time and land use (32 times for each of three land use categories), as well as for the entire LFDP at each time period. To ensure that results were biologically meaningful as well as to avoid enhanced Type II error rates, we conducted test of autocorrelation only if at least

five plots contained walking sticks at the level of land use category, or if at least ten plots contained walking sticks for the entire LFDP. Analyses of combinations of time and land use that are characterized by a high proportion of zeros (absences) have low power to detect spatial autocorrelation; thus, if spatial autocorrelation is rare in our analyses, we are confident in the accuracy of that assessment and the appropriateness of subsequent statistical analyses.

Results

Spatial (~3 orders of magnitude) and temporal (~2.5 orders of magnitude) variation in abundance of walking sticks was considerable for adults and for juveniles (Fig. 2). This was true for all three land use classes, as well as for time periods after each hurricane.

Spatial autocorrelation

Abundances of walking sticks, regardless of developmental stage, displayed little evidence of significant spatial

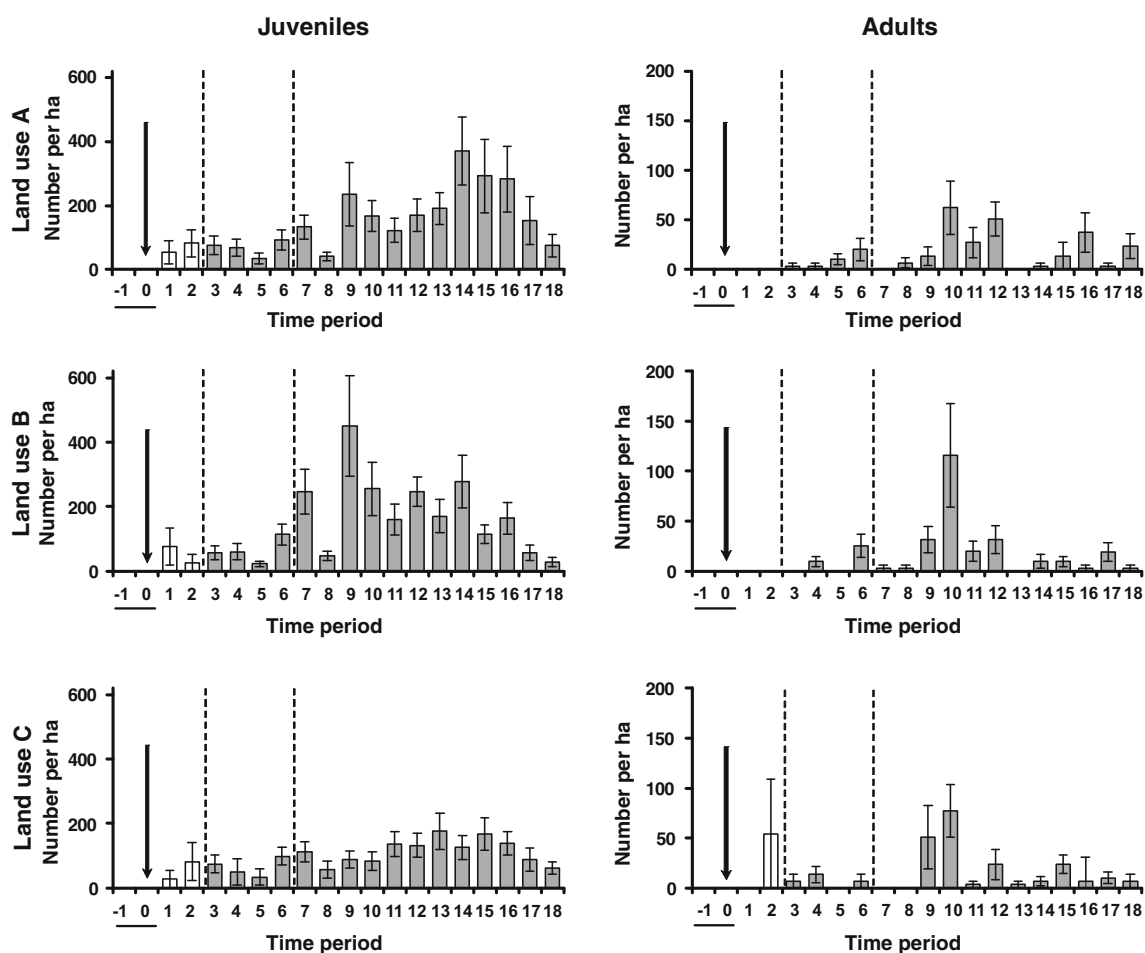


Fig. 3 Bar graphs displaying mean juvenile or adult walking stick density for each combination of land use and time, consistent with results of statistical analyses (i.e., a significant land use by time interaction, but a non-significant hurricane by time by land use interaction, Table 1). *Odd-numbered* time periods correspond to samples collected during dry seasons, and *even-numbered* time periods correspond to samples collected during wet seasons. A *negative number* represents a time period prior to Hurricane Hugo. Hurricane events are indicated by *vertical arrows* at time 0. *Vertical*

dashed lines delimit immediate (<12 months), short-term (between 12 and 36 months), and long-term (>36 months) responses to hurricanes. *Error bars* represent 1SE. Time periods for which data are not available from the Luquillo Forest Dynamics Plot are *underlined*. Data included in analyses are in *gray*. Data from the first year after Hurricane Georges are in *white* and were not included in analyses because corresponding data for Hurricane Hugo are not available

autocorrelation on the LFDP. Indeed, the numbers of significant tests of autocorrelation were similar to the number expected by chance (i.e., 5%). For juveniles, 4.8% (4 of 83) of analyses suggested spatial autocorrelation for any land use category or for the entire LFDP. Similarly for adults, 20% (2 of 10) of analyses suggested spatial autocorrelation for any land use category or for the entire LFDP. Spatial autocorrelation of adults was not analyzed in the majority of cases (118 of 128) because their frequencies were inadequate for analyses to have reasonable power to detect autocorrelation. Indeed, the likelihood of significant spatial autocorrelation for data with such structure is low. As a result, the frequency of autocorrelation for adults likely was much lower than 20%, and estimates of autocorrelation based on juveniles were more accurate. As such, analyses

based on spatial independence of abundances among plots are reasonable and unlikely to have had a major impact on conclusions.

Effects of hurricane, land use, and time on abundance

Based on a rigorous statistical analysis of adult and juvenile stages, the temporal trajectories of abundances in response to disturbance differed between hurricanes (Fig. 2) and differed among land use categories (Fig. 3), but effects of hurricanes and land use on temporal trajectories were independent of each other (i.e., a non-significant three-way interaction among hurricane, land use, and time, Table 1). For adults, differences in average abundance among land use categories depended on hurricane

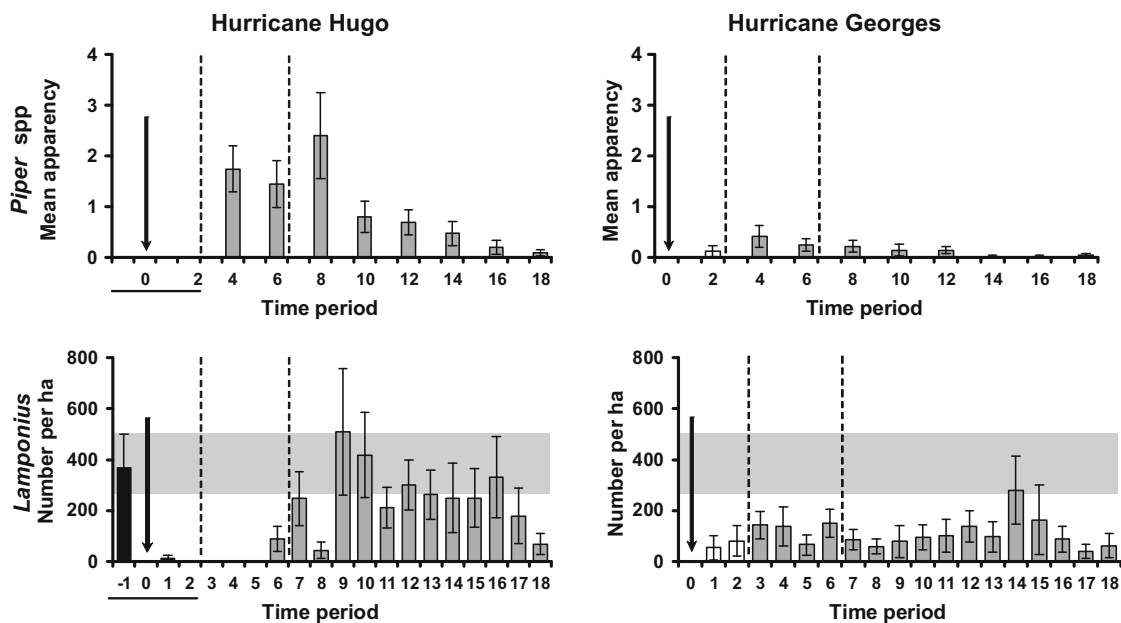


Fig. 4 Bar graphs displaying mean appearance (average number of foliar intercepts per plot) for *Piper* spp. (top row) and mean *Lamponius portoricensis* density with juveniles and adults combined (bottom row) after each hurricane. Hurricane events are indicated by vertical arrows at time 0. Vertical dashed lines delimit immediate (<12 months), short-term (between 12 and 36 months), and long-term (>36 months) responses to hurricanes. Appearance data were available only for even-numbered time periods (i.e., wet seasons). Error bars represent 1 (top row) or 2 (bottom row) SE. Time periods for which data are not available from the Luquillo Forest Dynamics Plot are

underlined. Data included in analyses are in gray. Data from the first year after Hurricane Georges are in white and were not included in analyses because corresponding data for Hurricane Hugo are not available. Densities of *L. portoricensis* from Bisley watersheds, a nearby site in tabonuco forest, estimated immediately before and after Hurricane Hugo (Willig and Camilo 1991) are in black and serve as context assessment of resilience. Gray horizontal bands in the bottom row indicate mean abundance $\pm 2SE$ of *L. portoricensis* from Bisley watersheds just prior to Hurricane Hugo

(Table 1). For each land use category, mean abundances were greater after Hugo than after Georges; however, the magnitude of the difference was greater for land use B (18.2 individuals per ha) than it was for land use A (10.8 individuals per ha) or for land use C (11.3 individuals per ha).

Time lag of recovery

Responses of *Lamponius* were not contemporary with those of their food plants (Table 2). Rather, changes in abundance of adult *Lamponius* exhibited a 1- to 2-year time lag with respect to changes in *Piper* appearance, whereas changes in abundance of juvenile *Lamponius* exhibited a 3- to 4-year time lag with respect to changes in *Piper* appearance (Figs. 2 and 4).

Discussion

The conceptual foundations of disturbance and succession are intimately interlinked in both basic and applied dimensions of ecological research (Walker and Willig 1999; Willig and Walker 1999; Peters et al. 2010).

Table 1 Significance levels (exact *P* values) from generalized linear mixed effects models that quantify the effects of historical land use, hurricane, and time since disturbance (i.e., 16 seasons after each hurricane) on abundances of juvenile or adult *Lamponius portoricensis* from tabonuco forest in the Luquillo Mountains of Puerto Rico

Treatment factors	Juveniles	Adults
Between subjects		
Land use	0.256	0.818
Within subjects		
Time	<0.001	<0.001
Land use \times time	0.006	0.042
Hurricane	<0.001	<0.001
Land use \times hurricane	0.438	0.040
Time \times hurricane	<0.001	0.005
Land use \times time \times hurricane	0.313	1.000

Land use is a between subjects factor, whereas time since disturbance and hurricane are within subjects factors (i.e., each of the 40 points are repeated for all combinations of time and hurricane. Bold font indicates significant results (i.e., $P \leq 0.05$)

Resistance to disturbance and resilience during subsequent secondary succession may be inversely related to each other or to alternative life history strategies of disturbance-

Table 2 Pearson product moment correlations and associated significance of the association between apparency of *Piper* spp. and abundance of juvenile or adult *Lamponius portoricensis* (Fig. 4)

Time lag (years)	Juveniles		Adults	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
0	-0.241	0.368	0.063	0.818
1	0.294	0.287	0.776	<0.001
2	0.354	0.215	0.527	0.053
3	0.577	0.039	0.315	0.295
4	0.703	0.011	0.411	0.185
5	0.139	0.684	0.268	0.425
6	0.002	0.996	0.547	0.102

Analyses were conducted for contemporary values, as well as for time lags in 1 year intervals from 1 to 6 years. Significant results (i.e., $P \leq 0.05$) or results approaching significance (i.e., $0.05 < P \leq 0.10$) are in bold

adapted species (Holling 1973; Boucher et al. 1994; Miller and Chesson 2009), but long-term data that are required to fully explore this are often lacking. This is particularly true for successions after large, infrequent, unpredictable natural disturbances, such as hurricanes (Turner et al. 1998). Fortunately, 17 years of data from a synoptic network of sites from the tabonuco forest of Puerto Rico, augmented by intensive data from nearby locations, facilitated an understanding of the tempo and mode of response by walking sticks to disturbances for which these insects rank among the least resistant species in the biota (Willig and Camilo 1991; Zimmerman et al. 1996). Based on ecological and behavioral characteristics of walking sticks, and understanding of post-hurricane succession in tabonuco forest, we discuss the potential mechanistic bases for trajectories of response by *Lamponius* to Hurricanes Hugo and Georges, and do so for three general time periods reflecting immediate effects (months 1–12 post hurricane), short-term effects (months 13–36 post hurricane), and long-term effects (≥ 37 months post hurricane). Of course, the Luquillo Experimental Forest is subject to other disturbances such as drought (1993–1994) or hurricanes of less intensity (e.g., Hurricanes Luis and Marilyn in 1995, Hurricane Jeanne in 2004), but for the purposes of this exposition, these are considered sources of error (as a visual inspection of long-term data failed to detect clear signals related to these events). Finally, our association of mechanism to pattern does not arise from manipulative experiments or concurrent assessment of environmental characteristics (e.g., temperature, humidity, light) and walking stick abundances, and thus should be considered a mechanistic hypothesis rather than a firm conclusion based on causal analyses.

Lamponius is a specialist folivore in the understory of early successional areas and light gaps in tabonuco forest

(Willig et al. 1986, 1993; Garrison and Willig 1996). Many aspects of its natural history are poorly known, especially those related to demography. Generally, *Lamponius* is quite philopatric (mean daily movement ~ 0.5 m; mean maximum movement between 2.5 and 3.0 m), although adults may disperse much more broadly across the landscape (see Willig et al. 1986). The extensive damage to the forest canopy caused by Hurricane Hugo (Brokaw and Greer 1991; Scatena and Larsen 1991; Walker et al. 1991), and to a somewhat lesser extent by Hurricane Georges (Ostertag et al. 2003), as well as associated vegetation dynamics during post-hurricane secondary succession (Zimmerman et al. 1994; Brokaw et al. 2004), led to great fluctuations in the abundance and distribution of walking sticks during the ensuing 17 years (Figs. 2 and 3).

Immediate effects of Hurricane Hugo

Lamponius exhibited little resistance to disturbance associated with Hurricane Hugo. Field work in the Bisley watersheds of the LEF, another site in tabonuco forest located 4.1 km from the LFDP (Fig. 1, inset A), documented severe reductions in the abundance of *Lamponius* in response to Hurricane Hugo (Willig and Camilo 1991): average abundance decreased by more than 97% from 369.2 individuals per ha (SE = 65.4) before the hurricane to 12.7 individuals per ha (SE = 5.4) after the hurricane. Similarly, *Lamponius* was quite abundant (mean = 2,111 individuals per ha; SE = 212.3 individuals per ha) in tabonuco forest <0.5 km from the LFDP prior to Hurricane Hugo (Willig et al. 1993), but was absent or rare immediately after the hurricane at those same sites (M.R. Willig, personal observation), as well as on the LFDP within 2–3 years of the hurricane (Fig. 2). In contrast, after Hurricane Georges, average abundance decreased only by 21% on the LFDP, from 68.5 (SE = 20.4) to 54.4 (SE = 24.1) individuals per ha, which was a non-significant change [i.e., compare total abundance at time period 18 after Hurricane Hugo (=pre-Hurricane Georges data) to time period 1 after Hurricane Georges (=post-Hurricane Georges data) in Fig. 4].

Large reductions in the extent of forest canopy associated with Hurricane Hugo created hot, dry microclimates at the forest floor that were not conducive to survival of walking sticks. Moreover, a 3-month drought following Hurricane Hugo (Waide 1991) exacerbated the initial effects of the storm. From the perspective of walking sticks, early developmental stages, including highly resistant eggs, would be susceptible to the effects of flooding associated with torrential rains and subsequent desiccation that arose from an open canopy and extended drought. Indeed, the eggs of tropical walking sticks have a relatively short diapause (Berger 2004), and observations on

Lamponius (Willig and Camilo 1991) indicate that the egg stadium can persist for 60–80 days. Thus, recruitment of nymphal individuals from litter following Hurricane Hugo probably was slight, because even the most resistant stage in the life cycle was unable to survive the long period of inclement conditions.

Short-term effects of Hurricane Hugo

During the second and third years after the disturbance, abundances of *Lamponius* remained quite low; in fact, *Lamponius* were undetectable on the LFDP for much of this time (Fig. 2). Two factors likely contributed to this phenomenon. First, the high immediate mortality of walking sticks, including their eggs, that was associated with Hurricane Hugo would severely reduce the capacity for subsequent recruitment of individuals via in situ demographic processes. Second, the large spatial extent of the initial disturbance and associated drought would diminish the likelihood that local populations of *Lamponius* could be rescued by immigration from nearby areas of the forest via mass or rescue effects (Hanski 2002). This highlights the critical role of the landscape-level distribution of biotic residuals (Turner et al. 1998) or, more accurately, their absence during post-hurricane secondary succession.

Long-term effects of Hurricane Hugo

The loss of canopy foliage during Hurricane Hugo increased subsequent penetration of light to the forest floor. Coupled with increased nutrient input from the decomposition of hurricane-produced debris, this facilitated an increase in the growth of understory and successional plants, such as *P. glabrescens* and *P. hispidum*, for ~3 years following the hurricane (Fig. 4). Once established, these plants typically persist in the understory for many years (Greig 1993). Indeed, the longevity of individual leaves of some species of *Piper* may be as great as 5 years, though 1–2 years is more common (Williams et al. 1989). Species of *Piper* that occur in tabonuco forest are food sources for *Lamponius* (Sandlin and Willig 1993). Moreover, abundance of *Lamponius* was significantly correlated with the understory development (i.e., apparency) of *Piper* before the hurricane (Willig et al. 1993). Thus, beginning in the third year post-hurricane, abundances of *Lamponius* began to increase with this flush in understory productivity.

Subsequent closure of the forest canopy was associated with decreases in the amount of light that reached the forest floor and decreases in understory and soil temperature, resulting in increased humidity in the lower understory. These microclimatic conditions are favorable for

Lamponius, especially for survivorship of eggs and hatchlings. Moreover, these microclimatic ameliorations were accompanied by a temporary, widespread increase in food resources throughout much of the forest, which led to a rapid increase in walking stick abundance between 3 and 5 years after the hurricane (time periods 5–10 in Fig. 2). The recovering forest and closing canopy shaded many of the successional and understory plants on which *Lamponius* feeds. Although understory plants on which *Lamponius* forages may persist under a closed canopy, the reduced light levels slow the rate at which plants are able to produce new leaves to replace those consumed via herbivory. As a consequence, the food supply of walking sticks decreased over time (compare time periods 4–8 with time periods 10–18 for *Piper* in Fig. 4), leading to a decline in abundance of *Lamponius*, especially that of adults. Well before the time Hurricane Georges landed on the island, 9 years after Hurricane Hugo, *Lamponius* populations likely were within levels of density that were characteristic of tabonuco forest prior to Hurricane Hugo [i.e., the mean \pm 1 SE of abundances on the LFDP overlapped the 95% CI of mean abundance (238.4–500.1 individuals per ha) at Bisley before Hurricane Hugo; Fig. 4].

Comparisons with Hurricane Georges

In contrast to Hurricane Hugo, Hurricane Georges was less damaging to the trees and physiognomy of tabonuco forest (Ostertag et al. 2003) and was not accompanied by a subsequent drought. Consequently, Hurricane Georges did not have as severe an effect on the density of *Lamponius* or on its primary food sources (e.g., *Piper* spp.; Figs. 3 and 4). Walking stick densities generally were below pre-Hurricane Hugo levels before Hurricane Georges and remained low thereafter (Fig. 2). Two explanations are tenable: (1) abundances of *Lamponius* were lower in tabonuco forest at El Verde than at Bisley prior to Hurricane Hugo (i.e., the estimates of pre-Hurricane abundance on the LFDP based on data from Bisley were overestimates), or (2) patch dynamics in a landscape are modified for many years after a hurricane. Natural landslides and tree falls occur regularly in tabonuco forest and create canopy openings that represent the preferred habitat for *Lamponius* (Willig et al. 1993). Intense, large-scale disturbances, such as hurricanes, may uproot trees and trigger landslides that otherwise would not have occurred for some time. As a result, trees that were approaching senescence or injured from natural causes (candidates for initiating future light gaps) would be at low frequency in a post-hurricane forest (i.e., the trees that would have produced light gaps were “selectively removed” by hurricane winds). In such a scenario, intense hurricanes may disrupt patch dynamics at small spatial scales for many years, resulting in fewer new light gaps and

associated patches of early successional forest. In this case, abundance of early successional plants on which *Lamponius* feeds may decline below baseline levels several years after a hurricane (Fig. 4), thereby negatively affecting walking stick abundance. Indeed, *Lamponius* may be food-limited during secondary succession, as changes in its abundance more-or-less followed those of *Piper*, but with significant time-lags between 2 and 4 years, depending on age cohort of *Lamponius* (Table 2; Figs. 2 and 4). The time lag between *Piper* proliferation and *Lamponius* recovery likely represents the time required for individuals to emigrate into newly recovered habitats. Adults are more vagile than are juveniles. The shorter time lag for adults than for juveniles likely represents emigration of adults from nearby less disturbed areas, whereas the time lag for juveniles is longer as they are the offspring of the emigrant adults. Thus, the temporal trajectories of abundance of *Lamponius* differed between Hurricanes, and did so in a consistent fashion in all three areas of the LFDP that were defined by land use history (i.e., for both adults and juveniles, a significant Hurricane \times Time interaction without a significant Hurricane \times Time \times Land use interaction; Table 1).

Landscape considerations

Previous land use practices on the LFDP have had lasting effects on the structure and functioning of tabonuco ecosystems (e.g., Secrest et al. 1996; Thompson et al. 2002; Bloch et al. 2007). This is also true with regard to trajectories of recovery from hurricane-induced disturbances. Indeed, temporal responses to hurricanes with regard to abundances of *Lamponius* differed among areas of the LFDP based on land use history, and these differences were consistent for both hurricanes (i.e., for adults and for juveniles, a significant Land use \times Time interaction without a significant Hurricane \times Time \times Land use interaction; Table 1). Unfortunately, the effect of previous land use history cannot be decoupled from the severity of damage caused by Hurricanes Hugo or Georges. More specifically, northern portions of the LFDP, land use classes A and B, were more disturbed than were southern portions of the LFDP, land use class C, from the perspectives of previous human land use and hurricane-induced disturbance (Rice et al. 2004). For example, stem damage as reflected in percent basal area for tree stems that were snapped off or tipped up was $\sim 20\%$ in the northern area and $\sim 13\%$ in the southern area during Hurricane Hugo and $\sim 18\%$ in the northern area and $\sim 12\%$ during Hurricane Georges (J. Thompson, unpublished data, as reported in Rice et al. 2004). Trajectories in abundances of walking sticks, especially that of juveniles (the largest portion of the total population at any time), paralleled these differences in initial severity of effects associated with

human- and hurricane-induced disturbances (Fig. 3). Abundances of juvenile walking sticks in the least disturbed area (Land use C) showed the least variation, neither increasing nor decreasing greatly in response to hurricanes. In contrast, abundances of juvenile walking sticks in the most disturbed areas (Land use A and B) varied greatly in time, following similar patterns: increasing to relatively high values during time periods 9–14, and then decreasing to lower values by time period 18. Differences in temporal trajectories of abundance of adult walking sticks among areas of different land use were more idiosyncratic. Adult *Lamponius* generally are not common; therefore, analysis of their abundances may be less informative than comparable data for juveniles.

Concluding remarks

The theory of disturbance (Pickett et al. 1989; Walker and Willig 1999; Willig and McGinley 1999; Willig and Walker 1999) has matured considerably since the seminal publication of Pickett and White (1985). It has provided a rich lexicon with which to characterize disturbance and response, and to facilitate development of a conceptual framework for assessing the extent to which population, community, or biogeochemical attributes are molded by such events. Demographic responses of *Lamponius* to hurricane-induced disturbance document the rich complexity of interactions that occur during secondary succession as well as the extent to which they can be modified by legacies of previous human land use.

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