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Context-dependence of long-term responses of terrestrial gastropod populations to large-scale disturbance

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Abstract: Large-scale natural disturbances, such as hurricanes, can have profound effects on animal populations. Nonetheless, generalizations about the effects of disturbance are elusive, and few studies consider long-term responses of a single population or community to multiple large-scale disturbance events. In the last 20 y, two major hurricanes (Hugo and Georges) have struck the island of Puerto Rico. Long-term population trends of 17 species of terrestrial gastropod were evaluated to determine whether gastropods respond to hurricane disturbances in a consistent fashion. Some species increased, some decreased, and some exhibited no simple trend in density or spatial variability following disturbance. In addition, some species responded differently to the two hurricanes with respect to population density, absolute spatial variability, or relative spatial variability. Population responses probably hinge on trade-offs between sensitivity to microclimatic changes and resource availability resulting from the relocation of biomass from the canopy to the forest floor. The historical context within which a hurricane occurs may be as important, or more so, than the intensity of the storm, per se.

Key Words: hurricane, land snails, population dynamics, Puerto Rico

INTRODUCTION

Large-scale natural disturbances, such as hurricanes, can have profound effects on animal populations, either directly, by causing mortality through the action of wind and rain, or indirectly, by altering the abiotic environment, habitat structure, resource availability, or density of predators or competitors. Disturbances caused by climatic events are generally unpredictable (Parmesan *et al.* 2000, Willig & Walker 1999), and the disturbance regime (i.e. the combination of severity, intensity, frequency, and extent of disturbances) is a dynamic characteristic unique to each ecosystem (White & Jentsch 2001). Thus, generalization about the effects of disturbance is difficult. Even within an ecosystem, disturbance events of a given type (e.g. hurricanes, fires, or landslides) differ in severity, intensity, and extent (Turner & Dale 1998, White 1979, White & Jentsch 2001). Moreover, components of disturbance regimes may change through time (e.g. climate change may increase the frequency of intense hurricanes in the Atlantic Ocean and the Caribbean Sea; Goldenberg *et al.* 2001).

Because of a variety of constraints, studies of large-scale, infrequent disturbances are few relative to studies of other types of disturbance (Turner *et al.* 1997) and generally focus on a single disturbance event (Turner & Dale 1998). A modest number of studies has examined the effects of multiple hurricanes (Hjerpe *et al.* 2001, Paerl *et al.* 2001, Pierson *et al.* 1996, Schoener *et al.* 2004), but these rarely consider long-term responses of the same geographic population or community following multiple disturbances. Such studies are necessary because short-term studies are snapshots that may provide misleading impressions of the general effects of disturbance (Adams 2001). The effects of successive disturbances can be highly variable (Bythell *et al.* 2000), and dynamics may be different in systems repeatedly affected by disturbance events than in those rarely subjected to disturbance (Lin *et al.* 2003, Paine *et al.* 1998). A comprehensive understanding of effects of disturbance requires more comparative work on disturbance events of different severity, intensity, and extent (Platt & Connell 2003, White & Jentsch 2001, Willig & Walker 1999).

Terrestrial gastropods are ideal organisms with which to study the effects of disturbance, in part because they are

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taxonomically well-known and numerically abundant, as well as ecologically important, particularly with respect to nutrient cycling (Jennings & Barkham 1979, Jones & Shachak 1990, Theenhaus & Scheu 1996). In addition, gastropods are ectotherms, are susceptible to desiccation, and are not very vagile; consequently, they may be affected strongly by disturbance and its often substantial modification of microclimate. Despite the clear ecological importance of terrestrial gastropods, little is known about the ecology of most species. Moreover, relatively few studies directly examine the responses of terrestrial snails to natural disturbance (but see Alvarez & Willig 1993, Karlin 1961, Secrest *et al.* 1996, Strayer *et al.* 1986, Willig & Camilo 1991, Willig *et al.* 1998). Most studies of the effects of disturbance on animal populations have focused instead on insects or vertebrates (Willig & McGinley 1999).

Although terrestrial gastropods respond to disturbance in a species-specific manner (Secrest *et al.* 1996, Willig & Camilo 1991, Willig *et al.* 1998), a few basic predictions are possible based on the biological characteristics of the group. The microclimate of canopy gaps is characterized by increased soil and air temperatures, enhanced rates of evaporation, and decreased relative humidity compared with undisturbed forest (Denslow 1980, Fernandez & Fetcher 1991). The degree of microclimatic difference between disturbed and intact forest increases with the size of the gap (Lee 1978). Hot, dry conditions, such as those found in gaps, often affect gastropods negatively (Cook 2001, Russell-Hunter 1983). Indeed, desiccation may be the primary cause of snail mortality (Solem 1984). Eggs and early growth stages are particularly vulnerable to elevated temperatures and reduced humidity (Baur & Baur 1993, Heatwole & Heatwole 1978, Riddle 1983). Thus, hurricanes, which generate large, widespread openings in the forest canopy, should decrease population densities of terrestrial gastropods, perhaps even extirpating less abundant species from some localities. Conversely, some species (especially those most tolerant to desiccation) may benefit from conditions generated by disturbance, either by exploiting a new or increased resource base or enjoying reduced rates of predation or competition. This may be particularly true of species that have evolved in disturbance-mediated environments, such as the Caribbean Basin.

Hurricanes produce a mosaic of environmental conditions that become less disparate over time as canopy gaps close. If the effect of hurricanes on terrestrial gastropods is primarily indirect through changes in microclimate, then population densities of snails should mirror the mosaic pattern of disturbance intensity; densities will remain relatively unaffected in undisturbed refugia and be reduced severely in the most disturbed locations. Unless disturbance is so intense as to devastate a population throughout its geographic range, variance in density should be highest after recent disturbance and decline thereafter as the canopy regenerates, microclimatic conditions become more uniform, and snail densities and distributions become less restricted by desiccation. Rare or hypodispersed species may be an exception. Reduction of their densities by disturbance may result in increased homogeneity simply because they will not be locally abundant anywhere, or because they decline at one or more of the sites where abundance is high.

In the last 20 y, two major hurricanes (Hugo in 1989 and Georges in 1998) have struck the island of Puerto Rico. The two hurricanes differed in intensity and severity, with Hurricane Hugo producing larger canopy openings and depositing more debris than did Hurricane Georges (Lugo & Frangi 2003, Ostertag *et al.* 2003). Additionally, the historical context of the two storms differed. Hurricane Hugo was the first major hurricane to make landfall in north-eastern Puerto Rico in over 30 y (Scatena & Larsen 1991, Turner *et al.* 1997), whereas Hurricane Georges arrived only 9 y after Hurricane Hugo. This study evaluated long-term population-level trends of terrestrial gastropods, to determine whether species respond to hurricane disturbances in a consistent fashion, or whether differences in hurricane intensity or disturbance history result in disparate population-level responses.

METHODS

Study site and field methodology

The Luquillo Experimental Forest (LEF) is an 11 330-ha tract of land located in the Luquillo Mountains of north-eastern Puerto Rico. It ranges in elevation from 100 to 1075 m and encompasses four distinct forest types: tabonuco, palo colorado, dwarf, and palm forests (Brown *et al.* 1983). Of these, the tabonuco forest, which is the most extensively studied (Odum & Pigeon 1970, Reagan & Waide 1996), is the setting for this research. This forest type occurs below 600 m and takes its name from the dominant tree, tabonuco (*Dacryodes excelsa*). The climate is typical of tropical forests. Rainfall is substantial (245–400 cm y^{-1}, depending on elevation; Brown *et al.* 1983), with the driest months being January through April. Relatively little seasonal or diurnal variation occurs in temperature (Odum *et al.* 1970).

Long-term censuses of terrestrial gastropods were undertaken on the Luquillo Forest Dynamics Plot (LFDP), a 16-ha grid near El Verde Field Station, in the north-west of the LEF (18°10′N, 65°30′W). Circular plots (3 m radius) were established at 40 points on the LFDP in 1991 (Willig *et al.* 1998). Plots were spaced evenly such that 60 m separated adjacent points along a row or column within a rectilinear grid. From 1991 to 2004, gastropod surveys were conducted twice annually to account for seasonal variation in rainfall. The first survey each year was conducted in March (dry season) and the second during June, July or August (wet season). The lone exception was the dry season of 1999, when dry-season sampling was conducted in January rather than March to assess the effects of Hurricane Georges as soon as possible after the storm. Sampling intensity differed 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 d was maintained between sampling periods to allow gastropods to recover from displacement during previous surveys. All surveys were conducted at night (19h30–03h00) to coincide with peak snail activity (Heatwole & Heatwole 1978, Willig *et al.* 1998).

Each time a plot was sampled, at least two people surveyed it for a minimum of 15 min, during which time they searched for snails and slugs on all available surfaces (e.g. soil, litter, rock cover, vegetation). Searches extended upward to about 5 m from the ground. To minimize damage to long-term study sites, substrate was not manipulated in searching for specimens. All individuals were identified to species in the field and returned as closely as possible to the point of capture and always within the plot of capture.

Population density of each species within each plot in each season was estimated as the mean number of individuals captured per night and converted to number of individuals per ha. As it is unlikely that all individuals on a plot will be located during each survey, averaging number of captures certainly underestimates true density; however, it has advantages over other metrics (e.g. minimum number known alive, Lincoln–Peterson index) in that it does not require tagging of individuals, imposes few assumptions, and is not biased as a consequence of interannual differences in sampling intensity. On the other hand, visual searches inevitably are biased against detection of small species or juveniles. Mean number of captures therefore provides only a relative measure of density for each species and is unsuitable for comparison of density among species. Nevertheless, this relative measure of density correlates strongly with mark–recapture estimates for *Caracolus caracolla*, one of the largest and most conspicuous snail species on the LFDP, and *Nenia tridens*, a smaller, more cryptic species (Bloch 2004).

Characterization of temporal trends in density

Analysis of covariance (ANCOVA) was used to evaluate trends in density and spatial variation in density over time. To guard against the possibility that observed trends in variance are confounded by the correlation between means and variances, both absolute (sample variance) and relative variation (variance of $\log_{10}$-transformed densities, which removes the correlation between mean and variance; Lande 1977, Wright 1952) were considered as measures of spatial variability. Separate ANCOVAs were conducted for each species and for the total snail assemblage using SPSS version 9.0. In each analysis, the factor of interest (hurricane) indicated whether an observation came from the time period following Hurricane Hugo (1991–1998) or that following Hurricane Georges (1999–2004). The covariate was time since disturbance, measured in seasons. Thus, because the dry season of 1999 was the first sampling season following Hurricane Georges, the value of the covariate for data from this season was 1. Similarly, data collected prior to Hurricane Georges were assigned a value for time elapsed since the impact of Hurricane Hugo in 1989. Sampling began in the dry season of 1991, so a value of 3 was assigned to the covariate for data from the first sample, to indicate that two seasons had elapsed since Hurricane Hugo. Therefore, time period 3 post-Hurricane Hugo indicated the passage of the same amount of time following disturbance as did time period 3 post-Hurricane Georges.

Using such an analysis, it was possible to assess whether each response variable (mean density, absolute variability in density, relative variability in density) changed linearly over time, whether such a response was consistent following both hurricanes, and whether means differed between time sequences (following Hurricane Hugo versus Hurricane Georges) after accounting for the effect of time since disturbance. Significant F-tests for individual terms of an ANCOVA model were interpreted only if the overall model achieved significance ($P \leq 0.05$). A significant interaction between hurricane and time since disturbance would indicate that the effects of hurricane identity and time since disturbance are contingent on each other; that is, the trajectory of population response (i.e. slope) differs between hurricanes. If the interaction was non-significant, that term was removed from the model, the overall slope for the relationship between the response variable and time since disturbance was estimated using pooled data (Sokal & Rohlf 1995), and significant main effects were interpreted. A significant effect of time since disturbance would indicate a consistent linear response to elapsed time following a hurricane, regardless of identity. A significant effect of hurricane would imply that means differed between hurricanes, after accounting for the effect of time since disturbance. These ANCOVAs assume linearity of responses to the covariate, time since disturbance. No *a priori* biological reason exists, however, to presume such linearity. Therefore, an additional set of ANCOVAs was conducted, incorporating a quadratic term to model the association between density of each species and time since disturbance.

Because we were interested primarily in the particular response of each species to disturbance, rather than overall multivariate evidence of a hurricane effect, results were interpreted without application of Bonferroni sequential adjustments (Rice 1989) to maintain experiment-wise error rate at 0.05. Recently, the use of this adjustment has engendered considerable controversy, largely because it is highly conservative, resulting in a high rate of Type II error (Hurlbert 2003, Moran 2003). The exploratory nature of this study thus argues against the use of such an adjustment (Roback & Askins 2005). Nevertheless, a Bonferroni sequential adjustment was applied to each suite of analyses and is presented for comparative purposes.

RESULTS

A total of 18 species of terrestrial gastropod was recorded at the study site from 1991 to 2004: *Alcadia alta* (Sowerby), *A. striata* (Lamarck), *Austroselenites alticola* H.B. Baker, *C. caracolla* (Linnaeus), *C. marginella* (Gmelin), *Cepolis squamosa* (Férussac), *Gaeotis nigrolineata* Shuttleworth, *Lamellaxis gracilis* (Hutton), *Megalomastoma croceum* (Gmelin), *N. tridens* (Schweigger), *Obeliscus terebraster* (Lamarck), *Oleacina glabra* (Pfeiffer), *O. interrupta* (Shuttleworth), *O. playa* (H.B. Baker), *Platysuccinea portoricensis* (Shuttleworth), *Polydontes acutangula* (Burrow), *Subulina octona* (Bruguière), and *Vaginulus occidentalis* (Guilding). Two species (*Oleacina interrupta* and *O. playa*) are relatively uncommon, morphologically similar, and sometimes difficult to differentiate in the field. Because it is impossible subsequently to verify identities of released and unmarked individuals, the two species are treated hereafter as a single entity and referred to as *O. playa*, for a total of 17 species.

Patterns of population dynamics of the 17 species were heterogeneous. Indeed, each of the five possible patterns of response to disturbance that ANCOVA could reveal was represented by at least one species (Figure 1). Disturbance affected the magnitude of density or population trajectories for six of 17 species (*Alcadia striata*, *N. tridens*, *O. glabra*, *Platysuccinea portoricensis*, *Polydontes acutangula* and *Subulina octona*; Table 1). For three species, density differed between time frames: *P. acutangula* was more abundant from 1991 to 1998 (following Hurricane Hugo and prior to Hurricane Georges) than from 1999 to 2004 (following Hurricane Georges), whereas *P. portoricensis* and *S. octona* were more abundant following Hurricane Georges. Significant linear relationships between density and time since disturbance existed for *A. striata*, *N. tridens* and *P. portoricensis*. Densities of *N. tridens* and *P. portoricensis* increased through time following disturbance, whereas those of *A. striata* declined. These three responses were consistent regardless of hurricane identity (Hugo versus Georges). Densities

Table 1. Results of analyses of covariance assessing temporal trends in density of terrestrial gastropod species. F-ratios and P-values indicate significance levels for terms of the model. Bold type indicates components of ANCOVA models that were significant at the 0.05 level. Individual terms of the model were interpreted only if the overall model was significant. If the interaction between time since disturbance and hurricane was non-significant, then values for all other terms and for the overall model were calculated for a model excluding the interaction. If the interaction was significant, slopes differ between hurricanes and are not reported. Degrees of freedom for models including the interaction term were 1 (interaction), 1 (time since disturbance), 1 (hurricane) and 24 (error). Degrees of freedom for models excluding the interaction term were 1 (time since disturbance), 1 (hurricane) and 25 (error). Bold italics indicate overall ANCOVA models that remain significant after the application of Bonferroni's sequential adjustment.

	Interaction term		Time since disturbance			Hurricane		Overall model	
Species	F	P	Slope	F	P	F	P	F	P
Alcadia alta	0.01	0.927	−1.01	1.83	0.188	3.41	0.077	1.90	0.171
Alcadia striata	0.50	0.485	**−5.98**	**9.00**	**0.006**	1.21	0.281	**4.52**	**0.021**
Austroselenites alticola	0.04	0.849	−0.07	0.02	0.881	3.79	0.063	2.49	0.103
Caracolus caracolla	0.62	0.439	**39.4**	**5.62**	**0.026**	0.48	0.493	2.88	0.075
Caracolus marginella	0.98	0.332	−1.06	3.67	0.067	3.13	0.089	2.38	0.113
Cepolis squamosa	0.66	0.423	**−3.21**	**4.83**	**0.038**	1.52	0.229	2.46	0.106
Gaeotis nigrolineata	0.00	0.974	−30.6	1.90	0.180	0.44	0.511	0.95	0.399
Lamellaxis gracilis	0.91	0.350	−0.21	0.52	0.478	1.30	0.265	0.68	0.515
Megalomastoma croceum	1.16	0.291	0.58	1.33	0.260	1.69	0.361	1.06	0.361
Nenia tridens	2.81	0.107	**109**	**39.9**	< **0.001**	3.56	0.071	***32.9***	< ***0.001***
Obeliscus terebraster	2.24	0.147	0.26	2.91	0.101	1.85	0.186	1.69	0.204
Oleacina glabra	**4.37**	**0.047**	–	2.73	0.111	0.40	0.535	**3.53**	**0.030**
*Oleacina playa**	0.07	0.802	0.08	0.05	0.83	0.38	0.543	0.19	0.827
Platysuccinea portoricensis	0.00	0.986	**4.93**	**12.7**	**0.001**	**25.1**	< **0.001**	***13.8***	< ***0.001***
Polydontes acutangula	0.27	0.609	−2.52	3.84	0.061	**19.1**	< **0.001**	***9.55***	< ***0.001***
Subulina octona	2.96	0.098	0.12	0.01	0.939	**9.70**	**0.005**	**5.83**	**0.008**
Vaginulus occidentalis	0.13	0.723	−0.91	3.86	0.061	0.11	0.739	2.09	0.145
Total gastropods	0.25	0.622	**109**	**11.1**	**0.003**	1.05	0.316	**9.22**	***0.001***

* Includes *O. interrupta*.

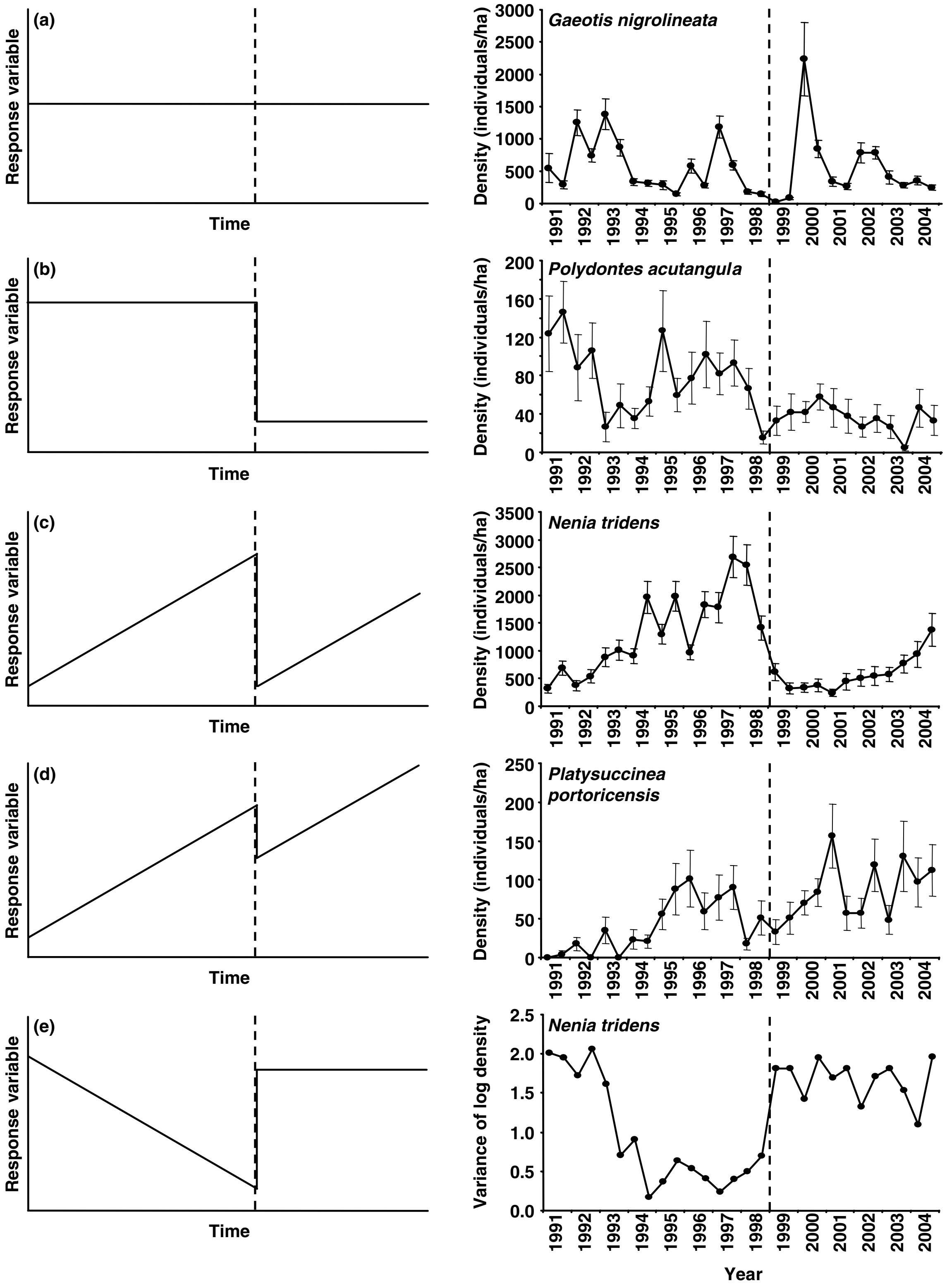

Figure 1. Idealized representations of possible statistical outcomes of population responses to disturbance by two hurricanes (left column), with an example of each for terrestrial gastropods on the LFDP (right column). Potential patterns are: (a) no response to disturbance (i.e. non-significant ANCOVA model), (b) mean of response variable differs between disturbances after accounting for time since disturbance (significant effect of hurricane identity), (c) consistent linear response to both disturbances (significant effect of time since disturbance), (d) both b and c simultaneously, and (e) trajectory of response depends on hurricane identity (significant interaction term). Slopes and differences in magnitude of response variables between hurricanes may be positive or negative. Error bars represent 1 SE about the mean.

of *O. glabra*, in contrast, did not respond to the two hurricanes in the same fashion (interaction term, $F_{1,24} = 4.37$, $P = 0.047$). Rather, densities increased more rapidly following Hurricane Georges than following Hurricane Hugo (slopes: $b_1 = 1.79 \pm 1.05$ versus -0.21 ± 0.37, mean ± SE). Although significant effects of disturbance were not consistent for all species, total density of gastropods increased linearly through time following disturbance ($b_1 = 109$, $F_{1,25} = 11.1$, $P = 0.003$), and the response was consistent for the two hurricanes. The effects on *N. tridens*, *P. portoricensis* and *P. acutangula* remained significant after application of the Bonferroni sequential adjustment.

Quadratic relationships between density and time since disturbance were not prevalent. Indeed, ANCOVA models incorporating a quadratic term were significant for only three species: *A. striata*, *C. squamosa* and *M. croceum*. The significant quadratic term for *M. croceum* was driven strongly by a single datum (an unusually high density in the wet season of 1998) and probably is not indicative of a biologically meaningful trend. For *A. striata* and *C. squamosa*, on the other hand, a genuinely nonlinear response was apparent. Densities of each were greatest approximately 2 y after each hurricane and declined in a quadratic fashion thereafter (Figure 2).

Similarly to mean density, absolute spatial variability in density exhibited a significant effect of disturbance (i.e. a significant ANCOVA model) for only a subset of the snail assemblage (*A. striata*, *Caracolus marginella*, *N. tridens*, *P. portoricensis* and *P. acutangula*; Table 2). *Alcadia striata*, *C. marginella* and *P. portoricensis* exhibited both a difference in variability between the two time sequences (recovery from Hurricane Hugo versus Hurricane Georges) and a consistent linear relationship between variability and time since disturbance. *Polydontes acutangula* displayed only the former, whereas *N. tridens* displayed only the latter. The interaction between hurricane identity and time since disturbance was never significant. Densities of *A. striata*, *C. marginella* and *P. acutangula* were more variable following Hurricane Hugo than Hurricane Georges. *Platysuccinea portoricensis* was the only species to exhibit greater variability in density following the second hurricane. Variabilities of densities of *N. tridens* and *P. portoricensis* increased through time following disturbance, whereas those of *A. striata* and *C. marginella* declined. For total snail abundance, disturbance had no apparent effect on absolute variability. The effects of disturbance on three species (*A. striata*, *N. tridens* and *P. portoricensis*) remained significant after the application of the Bonferroni sequential adjustment.

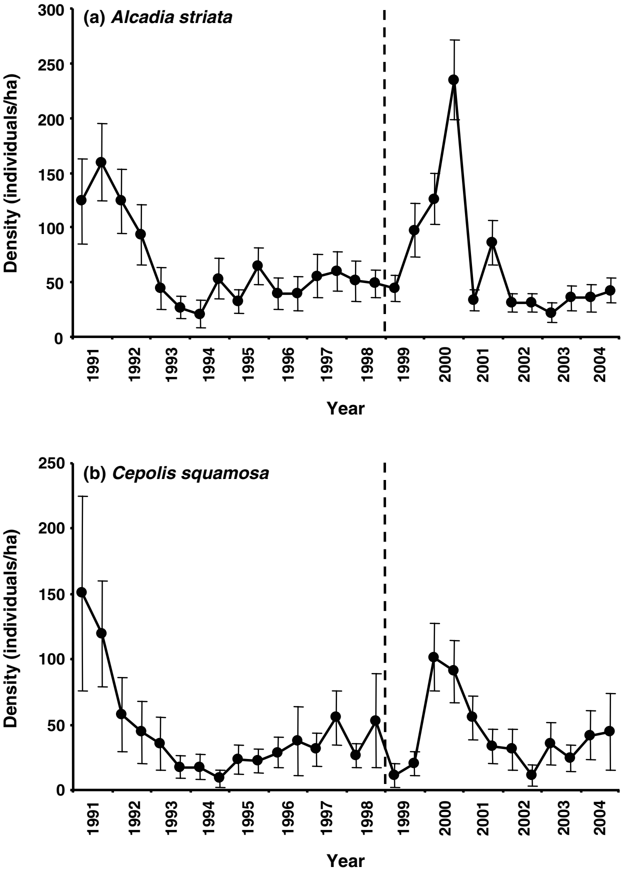

Figure 2. Population density of (a) *Alcadia striata* and (b) *Cepolis squamosa* on the Luquillo Forest Dynamics Plot from 1991 to 2004. Error bars encompass 1 SE about the mean. Dashed lines indicate the impact of Hurricane Georges.

Disturbance effects were slightly more prevalent for relative variability (variance of log density) than for absolute variability; seven of 17 species displayed significant ANCOVA models, including three (*N. tridens*, *P. portoricensis* and *P. acutangula*) of the five with significant ANCOVA models for absolute variance (Table 3). Relative variability in abundance of *P. acutangula* was greater following Hurricane Hugo than Hurricane Georges. The converse was true of *Austroselenites alticola*, *O. glabra*, *P. portoricensis* and *S. octona*. Relative variability increased over time following disturbance for *P. portoricensis*. This effect was consistent for both hurricanes. *Gaeotis nigrolineata* and *N. tridens* differed from other species in that relative variability in abundance responded differently to each hurricane (interaction terms $F_{1,24} = 5.05$, $P = 0.033$ for *G. nigrolineata* and $F_{1,24} = 7.55$, $P = 0.011$ for *N. tridens*). For both species, variance of density (log-transformed) decreased over time following Hurricane Hugo but not following Hurricane Georges ($b_1 = -0.066 \pm 0.025$ versus 0.038 ± 0.038 for *G. nigrolineata* and $b_1 = -0.117 \pm 0.022$ versus -0.018 ± 0.023 for *N. tridens*). Relative variability of the total snail assemblage was unaffected by either hurricane identity or time since disturbance. Effects of disturbance remained significant after application of the Bonferroni

Table 2. Results of analyses of covariance assessing temporal trends in absolute variance in density of terrestrial gastropod species. F-ratios and P-values indicate significance levels for terms of the model. Bold type indicates components of ANCOVA models that were significant at the 0.05 level. Individual terms of the model were interpreted only if the overall model was significant. In all cases, the interaction between time since disturbance and hurricane was non-significant; therefore, values for all other terms and for the overall model were calculated for a model excluding the interaction. Degrees of freedom were 1 (time since disturbance), 1 (hurricane) and 25 (error). Bold italics indicate overall ANCOVA models that remain significant after the application of Bonferroni's sequential adjustment.

	Time since disturbance			Hurricane		Overall model	
Species	Slope	F	P	F	P	F	P
Alcadia alta	−136	0.12	0.727	1.72	0.201	0.89	0.423
Alcadia striata	**−2295**	**15.4**	**0.001**	**7.56**	**0.011**	***8.40***	***0.002***
Austroselenites alticola	−101	0.98	0.331	0.45	0.510	1.23	0.310
Caracolus caracolla	41969	1.10	0.305	0.31	0.586	1.16	0.329
Caracolus marginella	**−423**	**5.83**	**0.023**	**5.56**	**0.027**	**3.98**	**0.031**
Cepolis squamosa	−3509	3.69	0.066	3.66	0.067	2.57	0.096
Gaeotis nigrolineata	−149552	1.82	0.190	0.03	0.868	1.25	0.303
Lamellaxis gracilis	−265	2.63	0.117	2.22	0.148	1.70	0.203
Megalomastoma croceum	688	2.21	0.150	0.37	0.551	1.11	0.347
Nenia tridens	**235652**	**26.9**	< **0.001**	0.01	0.947	***16.3***	< ***0.001***
Obeliscus terebraster	15	0.55	0.464	0.65	0.429	0.42	0.661
Oleacina glabra	−35	0.22	0.645	0.38	0.545	0.52	0.603
*Oleacina playa**	−17	0.05	0.822	0.14	0.716	0.16	0.854
Platysuccinea portoricensis	**2519**	**9.51**	**0.005**	**11.5**	**0.002**	***7.37***	***0.003***
Polydontes acutangula	−1299	3.46	0.075	**14.0**	**0.001**	**7.02**	**0.004**
Subulina octona	−2936	0.59	0.451	2.01	0.169	2.16	0.136
Vaginulus occidentalis	−319	3.34	0.080	1.39	0.249	1.77	0.192
Total gastropods	244843	3.60	0.070	0.01	0.942	2.14	0.139

* Includes *O. interrupta.*

Table 3. Results of analyses of covariance assessing temporal trends in relative variance in density (i.e. variance of log density) of terrestrial gastropod species. F-ratios and P-values indicate significance levels for terms of the model. Bold type indicates components of ANCOVA models that were significant at the 0.05 level. Individual terms of the model were interpreted only if the overall model was significant. If the interaction between time since disturbance and hurricane was non-significant, then values for all other terms and for the overall model were calculated for a model excluding the interaction. If the interaction was significant, slopes differ between hurricanes and are not reported. Degrees of freedom for models including the interaction term were 1 (interaction), 1 (time since disturbance), 1 (hurricane) and 24 (error). Degrees of freedom for models excluding the interaction term were 1 (time since disturbance), 1 (hurricane) and 25 (error). Bold italics indicate overall ANCOVA models that remain significant after the application of Bonferroni's sequential adjustment.

	Interaction term		Time since disturbance			Hurricane		Overall model	
Species	F	P	Slope	F	P	F	P	F	P
Alcadia alta	0.05	0.825	−0.02	3.32	0.081	2.54	0.123	2.06	0.148
Alcadia striata	0.42	0.523	**−0.03**	**6.00**	**0.022**	1.85	0.186	3.06	0.065
Austroselenites alticola	0.08	0.775	0.00	0.14	0.712	**8.98**	**0.006**	**5.00**	**0.015**
Caracolus caracolla	0.68	0.418	**−0.03**	**4.68**	**0.040**	**4.65**	**0.041**	3.26	0.055
Caracolus marginella	0.56	0.462	−0.01	1.31	0.264	0.74	0.398	0.74	0.489
Cepolis squamosa	0.05	0.829	−0.01	1.05	0.315	0.02	0.886	0.58	0.568
Gaeotis nigrolineata	**5.15**	**0.033**	–	0.37	0.547	**7.72**	**0.010**	**3.00**	**0.050**
Lamellaxis gracilis	3.80	0.063	0.00	0.01	0.907	0.30	0.587	0.23	0.797
Megalomastoma croceum	0.75	0.395	0.01	0.57	0.458	**4.42**	**0.046**	2.22	0.129
Nenia tridens	**7.55**	**0.011**	–	**14.2**	**0.001**	1.45	0.241	***21.4***	< ***0.001***
Obeliscus terebraster	2.68	0.115	0.01	4.02	0.056	2.39	0.134	2.30	0.121
Oleacina glabra	3.43	0.076	0.02	1.98	0.172	**7.66**	**0.010**	**3.86**	**0.035**
*Oleacina playa**	0.06	0.803	0.01	0.57	0.456	1.12	0.300	0.62	0.548
Platysuccinea portoricensis	2.01	0.169	**0.06**	**22.0**	< **0.001**	**35.1**	< **0.001**	***20.4***	< ***0.001***
Polydontes acutangula	0.29	0.597	−0.02	2.78	0.108	**15.7**	**0.001**	***7.84***	***0.002***
Subulina octona	3.20	0.086	0.01	0.90	0.352	**21.8**	< **0.001**	***11.6***	< ***0.001***
Vaginulus occidentalis	1.68	0.208	−0.02	3.34	0.079	0.32	0.579	2.79	0.081
Total gastropods	2.74	0.111	**−0.03**	**4.82**	**0.038**	2.65	0.116	2.69	0.087

* Includes *O. interrupta.*

sequential adjustment for four species (*N. tridens*, *P. portoricensis*, *P. acutangula* and *S. octona*).

DISCUSSION

Although previous studies have documented effects of disturbance on terrestrial gastropod populations, this study represents the longest regularly sampled assemblage examined in this context. Time since disturbance for a variety of disturbance types (i.e. agriculture, fire or logging) had no effect on density of any species of gastropod in New England forests, but the small size of disturbed patches and their proximity to undisturbed forest probably accounted for a rapid return to pre-disturbance densities (Strayer *et al.* 1986). Elsewhere, abundance of snails typically decreases following fire (Karlin 1961) and logging (Hylander *et al.* 2004). Recovery of populations occurs over a period of years to decades. Young stands of conifers harbour low numbers of gastropods relative to old growth forests (Shikov 1984), but as regenerating forests enter later successional stages, densities of gastropods can exceed those in old growth (Ström 2004). Similarly, some gastropod species in the LEF exceeded pre-disturbance densities within 5 y after Hurricane Hugo (Secrest *et al.* 1996, Willig *et al.* 1998) despite large initial declines (Willig & Camilo 1991).

The most directly comparable results to the present study are those of Willig and colleagues (Alvarez & Willig 1993, Secrest *et al.* 1996, Willig & Camilo 1991, Willig *et al.* 1998), who used similar sampling techniques to examine the effects of natural disturbance on terrestrial gastropods in the LEF prior to Hurricane Georges. These studies clearly demonstrated that early responses of gastropod populations can differ among disturbance types (i.e. hurricanes vs. individual treefalls). Current results extend this finding, suggesting that long-term responses also may differ among disturbance events of the same type (i.e. Hurricanes Hugo vs. Georges).

Nenia tridens represents an example of context-dependent responses to disturbance. This species was low in density following both hurricanes, and increased in density over time following disturbance, suggesting that initial environmental conditions produced by hurricanes are inhospitable. In contrast, prior to Hurricane Hugo, density of *N. tridens* was greater in treefall gaps than in undisturbed forest, suggesting that *N. tridens* could exploit resources available in gaps (i.e. dead plant material and the algae and fungi that grow on it; Alvarez & Willig 1993, J. de Jesus, *pers. comm.*) without experiencing severe desiccation (Alvarez & Willig 1993). At that time, however, over 30 y had passed since the last major hurricane (Scatena & Larsen 1991, Turner *et al.* 1997). In tabonuco forest that had not recently experienced a major hurricane, treefall gaps may have been too small or topographically heterogeneous to develop extreme environmental differences from undisturbed forest (Alvarez & Willig 1993). The effect of a hurricane covers a greater area and produces many gaps comprising multiple treefalls, and may therefore produce more noticeable or different effects. Patterns of succession of trees, for example, differ between open patches created by hurricanes and gaps resulting from individual treefalls; pioneer species may be more important in treefall gaps than in patches generated by hurricanes (Vandermeer *et al.* 2000).

Although Hurricane Hugo initially caused precipitous declines in population densities of terrestrial gastropods (Willig & Camilo 1991), a variety of species-specific population trajectories developed in subsequent years (Willig *et al.* 1998). No evidence in the present study contradicts these findings. Some species increased in density over time following disturbance, whereas others declined. Many species, in contrast, displayed no clear linear or quadratic response to disturbance. More interesting, perhaps, are differences in the effects of the two hurricanes. Post-hurricane density or spatial variability of several species differed after Hurricane Hugo (from 1991 to 1998) compared with after Hurricane Georges (1999 to 2004). Moreover, patterns of change in population size or relative spatial variability of three species differed between the two hurricanes.

The creation of canopy openings by hurricanes has two major effects: deposition of organic matter on the forest floor and modification of microclimate. An obvious trade-off exists between these two effects; a hurricane that deposits more material on the forest floor will necessarily have a greater effect on microclimate, as a function of the larger size or wider distribution of canopy openings. Both hurricanes, therefore, increased the resource base for terrestrial gastropods (e.g. litter and debris, either directly or as a substrate for algae, fungi, and other microbes; Heatwole & Heatwole 1978), while simultaneously producing unfavourable microclimatic conditions. Although Hurricane Georges deposited less debris than did Hurricane Hugo (Lugo & Frangi 2003, Ostertag *et al.* 2003), it also produced less extensive openings in the canopy (M.R. Willig *et al.*, unpubl. data), which required less recovery time before canopy closure and the restoration of initial microclimatic conditions. Different responses of different species (or of a single species among disturbance types or particular hurricanes) probably hinge on the relative sensitivities of species to microclimate, habitat structure, and resource availability. *Alcadia striata* and *C. squamosa* may be prime examples. Both species appear to respond in lagged fashion. Immediately following a hurricane, when environmental conditions are most extreme, they exhibit low densities. Within 2 y, densities peak, perhaps because conditions have ameliorated sufficiently to allow these species to exploit increased resource availability. Changing conditions (e.g. degradation of resources, alteration of microclimate, interspecific interactions) may conspire to limit the ability of *A. striata* and *C. squamosa* to maintain high densities thereafter.

Within a group as diverse as the Gastropoda, different species probably would be adapted differentially to conditions created by hurricanes. This variety of responses is not limited to snails. Tree species exhibit considerable differences in the degree of damage they suffer from hurricanes and their ability to recover thereafter (Zimmerman *et al.* 1994). Responses of spiders to Hurricane Hugo depended strongly on locations of webs: species that build webs close to the ground, anchoring to dead leaves or debris, increased in density, whereas those that attach webs to living leaves declined (Pfeiffer 1996). For birds and bats, effects of hurricanes were more pronounced for frugivores and nectarivores than for other groups (Jones *et al.* 2001, Waide 1991). Insect species may be driven locally extinct (Schowalter 1994, Willig & Camilo 1991), or they may undergo outbreaks in response to resource pulses (Torres 1992).

Disturbance types differ in extent, frequency or intensity (Walker & Willig 1999, White & Pickett 1985), or in degree of resultant landscape heterogeneity (Turner *et al.* 1997). Less frequently acknowledged, though, is the distribution of extents and intensities within a disturbance type. Nevertheless, even disturbances with wide-ranging effects, such as hurricanes, differ in severity. Differences in wind speed and amount of rainfall obviously influence the severity of damage caused by a storm (Tanner *et al.* 1991). The trajectory of the storm also can be important. For example, Hurricane Hugo passed over only the eastern third of Puerto Rico (Scatena & Larsen 1991), whereas Hurricane Georges devastated the entire island. The Jamaican fruit bat, *Artibeus jamaicensis*, suffered declines in density following both hurricanes (Gannon & Willig 1994, Jones *et al.* 2001, Rodríguez-Durán & Vázquez 2001) but recovered more rapidly following Hurricane Hugo, at least in part because of immigration from undisturbed parts of the island, which were less common following Hurricane Georges (Rodríguez-Durán & Vázquez 2001).

Historical factors can modify the effects of a disturbance. Catastrophic disturbance by windstorms removes large numbers of mature canopy trees, thus reducing rates of canopy gap formation by treefalls as the dead trees are replaced by smaller individuals, which are unlikely to senesce in the short term (Whigham *et al.* 1999). Thus, older forests generally suffer greater damage than do younger ones (Grove *et al.* 2000, Lomascolo & Aide 2001), because older, taller trees are more likely to be damaged by wind (Brokaw 1985, Runkle 1985). Before Hurricane Hugo struck Puerto Rico in 1989, over 30 y had passed since the previous major hurricane (Scatena & Larsen 1991, Turner *et al.* 1997), whereas only 9 y elapsed between Hurricane Hugo and Hurricane Georges. Thus, the smaller, younger forest probably sustained less damage than would have transpired had the landfall of Hurricane Georges occurred in 1989. Alternatively, repeated disturbance can exacerbate effects on native species. Cyclones striking in consecutive years reduced resources so much that the flying fox, *Pteropus tonganus*, declined to less than 0.1% of pre-cyclone densities (Pierson *et al.* 1996).

In addition, the variety of responses observed for gastropods may in part reflect the influence of other disturbance types during the 15-y study. For example, a period of high rainfall that caused extreme flooding in March of 1998 may be partly responsible for a decline in some species (e.g. *Nenia tridens*; see Figure 1c) even before the arrival of Hurricane Georges. Although treefall gaps, landslides, and, to a lesser extent, flash floods are localized in their effects, droughts often influence ecosystem and community dynamics throughout the LEF (Burrowes *et al.* 2004, Covich *et al.* 2003, Schowalter & Ganio 2003). In an extreme drought, activity of terrestrial gastropods undoubtedly is reduced and mortality increased. Such signals may be evident for some gastropod species (e.g. a pronounced decrease in density of *G. nigrolineata* in 1994, a drought year; see Figure 1a), but the extent to which their effects persist and interact with those of hurricanes remains unclear.

Clearly, historical contingencies and differences between disturbance events can result in heterogeneous responses of species. In this context, there is little wonder that some snail species responded differently to Hurricane Hugo than to Hurricane Georges. In future studies of large-scale disturbance, researchers should avoid the implicit assumption that all hurricanes are equal in severity or equivalent with respect to the trajectory of recovery that follows them. The historical context within which a storm occurs may be as important, if not more so, than the intensity of the storm, per se.

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