

The Legacy of Disturbance on Habitat Associations of Terrestrial Snails in the Luquillo Experimental Forest, Puerto Rico¹

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ABSTRACT

Despite recent studies of the effect of disturbance on the abundance and distribution of organisms, little research has focused on the legacy of infrequent and large scale disturbances, especially from the perspective of habitat associations of animals. In 1989, Hurricane Hugo caused considerable damage to the Luquillo Experimental Forest of Puerto Rico, with the degree of disturbance strongly affected by topographic considerations. We examined the abundance, distribution, and habitat associations of four species of land snail (*Caracolus caracolla*, *Nenia tridens*, *Gaeotis nigrolineata*, *Polydotes acutangula*) in the tabonuco forest at two sites (El Verde and Bisley) which were differentially damaged by the hurricane. Five years after the impact of Hurricane Hugo, significant differences between sites in density persisted for all snails except *P. acutangula*. Moreover, significant differences in habitat characteristics (central tendency and dispersion) were detected between El Verde and Bisley based on univariate and multivariate analyses of a suite of 31 abiotic and biotic variables. Despite these differences, the basis of habitat association for each snail did not differ between sites. The factors that affected microspatial differences in snail density within sites accounted for differences in density between sites. Insight derived from research conducted at a single location (e.g., El Verde) adequately accounted for patterns of variation at another site (e.g., Bisley), even though differences between sites in the extent and severity of damage were well-documented. We hypothesize that the absence of scale-dependence with regard to habitat selection exists because the association among abiotic and biotic variables (character correlation matrix) within sites was not altered differentially by the hurricane or has recovered to a similar state as a consequence of secondary succession.

RESUMEN

A pesar que el rol del disturbio y su efecto sobre la abundancia y distribución de organismos se ha tornado más claro en los años recientes, escasa investigación se ha centrado en la consecuencia de disturbios grandes pero infrecuentes, especialmente desde la perspectiva de las asociaciones de hábitat animal. En 1989, el Huracán Hugo causó daño considerable al Bosque Experimental Luquillo de Puerto Rico, con el grado de disturbio fuertemente afectado por la topografía. Se examinaron la abundancia, distribución y asociaciones de hábitat de cuatro especies de caracoles terrestres (*Caracolus caracolla*, *Nenia tridens*, *Gaeotis nigrolineata*, *Polydotes acutangula*) en el bosque de tabonuco en dos sitios (El Verde y Bisley) que fueron dañados diferentemente por el huracán. Cinco años después del impacto del Huracán Hugo, persistían diferencias significativas en densidad entre los sitios para todos los caracoles excepto *P. acutangula*. Además, se detectaron diferencias significativas en características de hábitat (tendencia central y dispersión) entre El Verde y Bisley basadas en análisis univariado y multivariado de un conjunto de 31 variables abióticas y bióticas. A pesar de las diferencias, la base de la asociación de hábitat para cada especie de caracol no fue distinta entre sitios. Los factores que afectan las diferencias microespaciales en la densidad de caracoles dentro de cada sitio resulta en diferencias en densidad entre sitios. La percepción derivada de la investigación realizada en un sitio en particular (e.j., El Verde) explica adecuadamente los patrones de variación en el otro sitio (e.j., Bisley), a pesar que las diferencias en la extensión y severidad del daño están bien documentadas. Hipotetizamos que la ausencia de una dependencia de escala con respecto a la selección de hábitat persiste porque la asociación entre variables bióticas y abióticas (matriz de correlación de caracteres) dentro de los sitios no fue alterada diferencialmente por el huracán o se ha recuperado a un estado similar como consecuencia de sucesión secundaria.

Key words: Caracolus; disturbance; Gaeotis; habitat; habitat selection; hurricane; Nenia; Polydotes; habitat; snails.

A CURRENT PARADIGM IN ECOLOGY centers on disturbance and its effects on structural and functional aspects of populations and communities (Pickett &

White 1985). Historically, few ecologists focused on disturbance; most viewed communities as homogeneous and considered that communities and their constituent populations eventually reached equilibria following disturbance (Wiens 1977, Connell 1978). Disturbances were only rare occurrences that did not have much influence on abiotic

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or biotic features of an ecosystem (Karr & Freemark 1985). More recently, it has become apparent that few communities are equilibrational and most landscapes are mosaics resulting from various types of disturbance (Karr & Freemark 1985). Moreover, the impact of disturbances on some ecosystems is so great, that their communities are considered to be disturbance-mediated (Dayton 1971, Levin & Paine 1974, Platt 1975, Giesel 1976, West *et al.* 1981, McAuliffe 1984, Christensen 1985, Connell & Keough 1985, Sousa 1985). Unfortunately, consensus does not exist on a comprehensive definition of disturbance, and a complete understanding of its effects on communities and populations is elusive. Nonetheless, most ecologists agree that disturbances are important forces that modify the environment, depending on their frequency, intensity, and scale (Waide & Lugo 1992).

HURRICANE AND HABITAT ASSOCIATIONS.—Habitat associations may be defined operationally by the suite of abiotic or biotic characteristics that affect the abundances of species in a spatially explicit fashion (Sites & Willig 1991, Willig *et al.* 1993). Infrequent, large-scale disturbances of high intensity, such as hurricanes, can alter the magnitude, variation, or correlation among biotic and abiotic components of an ecosystem. Consequently, they have tremendous potential to alter the spatial distribution and habitat associations of animals. Changes in the variability of, or correlation among, abiotic characteristics may result in organisms occupying a wider range of conditions or, conversely, being limited to a narrower range of conditions than observed prior to a disturbance. Habitat modifications imposed by such changes in abiotic conditions directly appear as differences in habitat associations. Moreover, groups of plant species are often found together as a result of similar adaptations to topography or abiotic conditions (Basnet 1992). Hurricanes differentially affect the appearance and distribution of plants, potentially killing more of one plant species than another (Zimmerman *et al.* 1994). When this occurs, animals may be unable to locate specific combinations of plants which represent high value habitat and, as a consequence, must inhabit areas which contain only one of the preferred plants or occupy sites with distinctly different combinations of plants than before the hurricane. By altering the frequency and intensity of inter-specific interactions in a site-specific fashion, disturbances indirectly alter habitat associations as well. In particular, competitors or predators modify the value of a habitat by deter-

mining the cost of obtaining necessary elements for survival and reproduction (Krebs 1985, Ricklefs 1990). Consequently, hurricane-induced alterations in competitor or predator densities likely affect the ecological and microgeographic distribution of species with whom they interact. Finally, density-dependent selection can result in changes in habitat associations as a consequence of the ideal-free distribution (Fretwell & Lucas 1970) and intra-specific interactions. The presence of conspecifics may reduce the utility of an area to a point where an alternate site may be the more profitable choice for additional individuals. Clearly, disturbances such as hurricanes can modify habitat associations via a number of mechanisms. As a result, species that exist in a landscape subject to different levels of disturbance should exhibit heterogeneity across that landscape in terms of habitat association.

In September 1989, the center of Hurricane Hugo passed within 10 km of the Luquillo Experimental Forest (LEF) of Puerto Rico. Subsequently, short-term studies of the effects of the hurricane were conducted on a variety of animal taxa; most, but not all taxa, suffered reductions in the aftermath of the disturbance (Covich *et al.* 1991, Dolloff *et al.* 1994, Gannon & Willig 1994, Haney *et al.* 1991, Reagan 1991, Waide 1991a, Willig & Camilo 1991, Woolbright 1991). Five years have elapsed since Hurricane Hugo modified the landscape of the LEF; consequently, we can begin to evaluate long-term response and the legacy of infrequent events on population attributes (Willig *et al.*, in press). Tree snails are ideal organisms with which to study these phenomena because they are not as mobile as many macro-invertebrates, and they are unable to easily escape a disturbance or the changed environment that follows. As a consequence, they may more readily reflect the disturbance history of a site (Strayer *et al.* 1986) than do more mobile invertebrates or vertebrates.

SNAIL SPECIES.—In terrestrial ecosystems, land mollusks rank second in species richness after arthropods (Russell-Hunter 1983). Because of their numbers and trophic position as litter-feeders and herbivores, terrestrial snails likely are of considerable ecological importance (Mason 1970). Still, the ecology of land snails is more poorly understood than that of other invertebrates (*e.g.*, insects) or vertebrates.

Thirty-four species of land snails inhabit the tabonuco forest of Puerto Rico (Alvarez 1991). *Caracolus caracolla* (Camaenidae), *Nenia tridens* (Clausiliidae), *Polydotes acutangula* (Camaenidae),

and *Gaeotis nigrolineata* (Bulimulidae) are among the more common taxa (Willig *et al.*, in press). The activity of these species is primarily nocturnal or associated with high relative humidity during diurnal rain showers. Although many snail species are soil inhabitants, these four usually are found on the surfaces of living plants or recently fallen branches or leaves, and rarely are found above a height of 5 m. The densities of *C. caracolla* and *N. tridens* are far greater than those of the other two species; *P. acutangula* is the least common (Willig *et al.*, in press). With regard to microhabitat affinities, *C. caracolla* appears most catholic, whereas *G. nigrolineata* is most restricted, being associated mainly with the undersides of leaflets of *Prestoea montana* (Sierra palm). *Nenia tridens* frequently is found on trunks or recently fallen leaves of *Prestoea*, although it commonly occurs on the stems of woody vines as well.

The life history of *C. caracolla* is better known than that of most other invertebrates. Various aspects of its autecology have been studied, including habitat associations and distribution (Van der Schalie 1948, Alvarez & Willig 1993), behavior (Drewry 1968), life history (Heatwole & Heatwole 1978), reproductive cycle (Marcos 1992), home-range size and site fidelity (Heatwole & Heatwole 1978, Cary 1992), and immediate response to Hurricane Hugo (Willig & Camilo 1991). Life history characteristics of *N. tridens* remain unstudied; however, ecological studies have included evaluations of habitat associations (Alvarez 1991, Alvarez & Willig 1993), distribution (Van der Schalie 1948), and immediate response to Hurricane Hugo (Willig & Camilo 1991). Knowledge concerning the ecology of *P. acutangula* is cursory; studies include considerations of snail activity patterns, habitat associations, reproductive cycle, longevity, and immediate response to Hurricane Hugo (Heatwole & Heatwole 1978, Willig & Camilo 1991). Similarly, information regarding the ecology and behavior of *G. nigrolineata* is limited, although Willig and Camilo (1991) did evaluate its immediate response to Hurricane Hugo.

METHODS

STUDY AREA.—The LEF includes 11,330 ha within the Luquillo Mountains, ranging in elevation from 100 m to 1,075 m (Brown *et al.* 1983). The LEF comprises four life zones: subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rain forest (Brown *et al.* 1983). The zones are a result of rapid increases in elevation

accompanied by changes in precipitation, temperature, soil structure, and vegetation (Brown *et al.* 1983). The most intensely studied life zone is the subtropical wet forest (100–600 m), commonly called the tabonuco forest because of the abundance of *Dacryodes excelsa* (tabonuco).

Long-term ecological monitoring of land snails within the tabonuco forest was conducted at two sites, El Verde and Bisley. El Verde (18°20'N, 65°49'W; 69 ha) is located in the northwestern corner of the LEF; the Bisley Watersheds (18°18'N, 65°50'W; 28 ha) are located in the northeastern corner of the LEF. Many of the current differences between El Verde and Bisley can be attributed to Hurricane Hugo (Scatena & Larsen 1991). Boose *et al.* (1994) found an east-to-west damage gradient across the LEF associated with Hurricane Hugo. The extent of damage also depended on exposure, elevation, and vegetation type. Most of the damage was concentrated on north-facing slopes, with little impact on south-facing slopes (Scatena & Larsen 1991). El Verde suffered moderate damage (Walker 1991), experiencing 50 percent canopy defoliation and 7 percent tree mortality, whereas Bisley (Walker *et al.* 1992) experienced 100 percent canopy defoliation and 54 percent tree mortality.

STUDY PLOTS.—Two study plots were established in the tabonuco forest, the Hurricane Recovery Plot (HRP) at El Verde and the Bisley grid. The HRP is a 16 ha rectangular (500 m × 320 m) area, with 442 grid points spaced at 20 m intervals. The Bisley Grid (13 ha) is contained within Bisley Watersheds One and Two, with 88 points spaced at 40 m intervals. Previous surveys of the HRP (Cary 1992) and Bisley grid (Willig & Camilo 1991) each included 40 points; this study examined the same points to facilitate temporal comparisons within a site. Land snails were surveyed three times in 1994, from June 13 to August 6, at each of 40 points (60 m spacing) on the HRP and 36 points (40 m spacing) on the Bisley Grid. At Bisley, four of the original 40 points were inaccessible to survey teams in 1994.

A circle, 10 m in diameter, was surveyed around each of the 76 points. Two investigators surveyed each circle for a minimum of 20 min, during which all snails were located by visually inspecting soil, rocks, leaf litter, and vegetation up to a height of approximately 5 m. Snails within reach were measured, identified to species, and replaced within the circle as near as possible to the exact location of capture. Surveys alternated between El

Verde and Bisley to allow snails ample time to recover from handling and displacement from preferred microhabitat as a result of prior surveys. As a consequence, each of the 76 points was surveyed once every 2 wk over a 6 wk period. Surveys were conducted at night because snails are characteristically nocturnal (Heatwole & Heatwole 1978, Cary 1992). Snail density was estimated as the minimum number known alive (MNKA) from the three different surveys. Although MNKA is an underestimate of true density, relative differences in density among sites are reflected by differences in MNKA (Willig *et al.*, in press).

HABITAT CHARACTERIZATION.—Habitats at El Verde and Bisley were characterized during a two wk period following the completion of snail surveys. Habitat characterizations were conducted during the day, with a minimum of three people surveying a circular area (10 m diameter) centered on a point. Thirty-one descriptors, reflecting structural and taxonomic attributes of the canopy, subcanopy, and forest floor (Table 1) were used to characterize habitat. Descriptors were quantified as ranked, discrete, or continuous variables. Ranked variables (Cary 1992, Secrest 1995) assumed one of five states depending on the relative amount of cover (1, 0%–20%; 2, 21%–40%; 3, 41%–60%; 4, 61%–80%; 5, 81%–100%). Measures of canopy openness, dead vegetation, roots, litter, and plant apparency (Cook & Stubbendieck 1986) were considered discrete variables, although the underlying distribution of each was continuous. Plant apparency is an estimate of foliar volume at different heights. The number of foliar intercepts, defined as a species-specific count of vegetation (e.g., leaf, stem) touching a wooden dowel, was counted at each of 7 heights (0, 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m) using a plant apparency device (Cary 1992, Secrest 1995). Four 0.5 m dowels were positioned at 90° angles at each height. The device was positioned 1.5 m from the central point in each cardinal direction, and the number of intercepts recorded. Height-specific apparency and species-specific apparency (Cary 1992, Willig *et al.* 1993) were calculated as the total number of foliar intercepts at each height regardless of species, and the total number of foliar intercepts by each common species or category (*i.e.*, dead vegetation) regardless of height, respectively. Canopy openness was evaluated using a densiometer positioned 0.5 m away from the point in each of the cardinal directions. The mean of those four readings described openness at each point. The amount of dead vegetation

TABLE 1. *The suite of 31 habitat variables used to characterize El Verde and Bisley. Apparency measures the number of foliar intercepts at a particular height or by a particular taxon at any height.*

Descriptors	Code	Descriptor type
Geographic		
Slope	SLOPE	Continuous
Elevation	ELEV	Continuous
Height-specific apparency		
0.0 m	HT1	Discrete
0.5 m	HT2	Discrete
1.0 m	HT3	Discrete
1.5 m	HT4	Discrete
2.0 m	HT5	Discrete
2.5 m	HT6	Discrete
3.0 m	HT7	Discrete
Species-specific apparency		
<i>Casearia arborea</i>	CASARB	Discrete
<i>Cecropia schreberiana</i>	CECSCH	Discrete
<i>Didymopanax morototoni</i>	DIDMOR	Discrete
<i>Heliconia caribaea</i>	HEL CAR	Discrete
<i>Ichmanthus pallens</i>	ICHPAL	Discrete
<i>Palicourea riparia</i>	PALRIP	Discrete
<i>Philodendron</i> spp.	PHILO	Discrete
<i>Piper glabrescens</i>	PIPGLA	Discrete
<i>Piper hispidum</i>	PIPHIS	Discrete
<i>Prestoea montana</i>	PREMON	Discrete
<i>Psychotria berteriana</i>	PSYBER	Discrete
<i>Rourea surinamensis</i>	ROU	Discrete
<i>Sloanea berteriana</i>	SLOB	Discrete
<i>Miconia</i> spp.	MIC	Discrete
Rubiaceae spp.	RUB	Discrete
Other		
Canopy openness	ADEN	Continuous
Litter cover	ANAIL	Continuous
Dead wood cover	DW	Ranked
Litter cover	LC	Ranked
Rock cover	RC	Ranked
Vine cover	VC	Ranked
Dead vegetation	DEAD	Discrete

and roots was determined as the number of intercepts of each by the plant apparency device. A nail was driven into the forest floor 1 m from the point in each of the cardinal directions, the average number of leaves from the four replicates was used to produce an estimate of litter cover. Finally, slope, and elevation were obtained for each point from topographic maps.

STATISTICAL ANALYSES

All statistical analyses were performed on SPSS (SPSS Inc. 1990) and are described in Sokal and Rohlf (1981) or Tabachnick and Fidell (1989). Un-

less otherwise stated, significance was detected if $P \leq 0.05$.

ANALYSES OF HABITAT.—Differences between the HRP and Bisley with respect to the 31 habitat variables were assessed from multivariate and univariate perspectives (Willig 1993, Lacher & Willig 1993). Overall significance, with respect to central tendency (centroids), was determined by Multivariate Analysis of Variance (MANOVA), with likely contributions of particular characteristics to overall differences identified by Bonferroni's Sequential Adjustment (Rice 1989). Differences in variance between the HRP and Bisley for each habitat characteristic were assessed by Bartlett's Test.

In addition to affecting the magnitude or variance of habitat characteristics, Hurricane Hugo could have differentially altered associations among habitat characters within sites. Such differences in the correlation of habitat characteristics were assessed by Mantel Analyses (Manly 1986). Non-significance in the Mantel Test suggests that the spatial association of habitat characteristics is different between El Verde and Bisley.

ANALYSIS OF DENSITY.—Intra-specific comparisons of density between the HRP (moderate disturbance) and Bisley Grid (severe disturbance) were conducted for each of the four common snail species. Because heteroscedasticity was detected in these comparisons of sites (Bartlett's Test), mean differences were identified via t-tests based on unequal variances.

ANALYSIS OF HABITAT ASSOCIATIONS.—For each species, three step-wise multiple regressions were conducted with snail density as the dependent variable and the 31 habitat descriptors (Table 1) as independent variables. The first two analyses were site-specific, one for the HRP and one for Bisley. They assessed if the suite of habitat characteristics accounted for a significant quantity of variation in density among points within sites (overall F-tests) and identified the specific characteristics that likely contribute to those differences. Because some important characteristics may not appear in regression equations as a consequence of high communality with those already in the regression, we also examined simple correlations between snail density and each habitat descriptor. These inferential statistics assess linear relationships between snail abundances and habitat descriptors. As a consequence, we may fail to recognize the importance of some variables to the extent that actual relationships

are non-linear. We have minimized this likelihood by restricting our focus to tabonuco forest; moreover, visual inspection of scattergrams failed to suggest obvious non-linearities (Gaussian or asymptotic relationships).

The third analysis combined data for both sites and included a dummy variable that coded for the HRP (0) and Bisley (1). If the dummy variable was included in the regression, then differences between locations beyond those represented by variation in the suite of habitat characteristics accounted for differences in density among sites, and disturbance may have altered critical aspects of habitat associations.

RESULTS

HABITAT CHARACTERISTICS.—El Verde and Bisley represented significantly different combinations of habitat characteristics (MANOVA; $F = 36.4$; $P < 0.001$) based on the suite of 31 variables (Table 1). This difference persisted when characteristics unaffected by the hurricane (*i.e.*, slope, elevation) are removed from consideration (MANOVA; $F = 5.75$; $P < 0.001$). Bonferroni's sequential adjustment procedure confirmed the overall significance in both circumstances, suggesting that multivariate results were robust with respect to potential deviations from model assumptions. Examination of character-specific significance from the Bonferroni procedure for the analysis based on the combined data revealed that slope, elevation, and height-specific apparency at 0.5 m and 1 m significantly contributed to the overall difference (Table 2). In the same manner, variances were unequal for over 65 percent of the habitat variables; in most cases of significance, Bisley was more variable than El Verde (Table 2). Despite differences in central tendency and dispersion, the correlation among habitat variables at El Verde was quite similar to that at Bisley (Mantel Analysis; $P = 0.004$).

DENSITY.—The mean and variance of density (per unit area of 78.25 m²) significantly differed between the HRP and Bisley for three of the four snail species (*C. caracolla*, *N. tridens*, and *G. nigrolineata*), but not for *P. acutangula* (Table 3). The densities of *C. caracolla* (HRP, 14.33; Bisley, 8.92) and *G. nigrolineata* (HRP, 3.50; Bisley, 1.64) were approximately twice as great on the site experiencing moderate damage from Hurricane Hugo (HRP at El Verde). In contrast, the density of *N. tridens* on the severely disturbed site (Bisley) was twice as great as that at the moderately disturbed site (HRP,

TABLE 2. Mean and standard error (SE) for each of 31 descriptors (Table 1) that characterized habitat at El Verde (N = 40) and Bisley (N = 37). Assessments of equality of variance (Bartlett's Test) and equality of means (t-test, unpaired variances) are provided; for mean comparisons, Bonferonni's sequential adjustment indicates significance (*, P ≤ 0.05; NS, not significant) after controlling overall error rate for the number of variables under examinations. Variable codes appear in Table 1.

Variable code	El Verde		Bisley		Bartlett's test (significance)	t-test (significance)	Bonferonni's sequential adjustment
	Mean	SE	Mean	SE			
SLOPE	23.38	0.28	43.39	0.65	<0.001	<0.001	*
ELEV	378.94	0.43	333.61	1.14	<0.001	<0.001	*
HT1	85.98	1.04	111.47	1.46	0.160	0.023	NS
HT2	6.38	0.10	11.97	0.23	<0.001	<0.001	*
HT3	4.65	0.08	8.22	0.16	0.001	0.001	*
HT4	5.48	0.12	7.67	0.22	0.001	0.154	NS
HT5	5.48	0.11	8.08	0.19	0.007	0.054	NS
HT6	6.75	0.17	7.42	0.21	0.570	0.686	NS
HT7	7.43	0.16	11.78	0.34	<0.001	0.063	NS
CASARB	1.13	0.07	0.08	0.01	<0.001	0.025	NS
CECSCH	0.73	0.05	2.69	0.14	<0.001	0.037	NS
DIDMOR	0.03	0.00	0.06	0.01	<0.001	0.618	NS
HELCAR	0.55	0.04	0.33	0.03	0.020	0.483	NS
ICHPAL	2.03	0.12	0.78	0.04	<0.001	0.131	NS
PALRIP	4.18	0.21	1.72	0.15	0.013	0.125	NS
PHILO	0.98	0.08	0.72	0.07	0.200	0.696	NS
PIPGLA	0.80	0.05	2.03	0.07	0.078	0.023	NS
PIPHIS	0.00	0.00	0.61	0.04	—	0.017	NS
PREMON	11.33	0.30	4.19	0.18	<0.001	0.002	NS
PSYBER	0.70	0.06	2.58	0.13	<0.001	0.030	NS
ROU	0.30	0.02	0.78	0.05	<0.001	0.182	NS
SLOB	0.55	0.05	1.89	0.10	0.001	0.055	NS
MIC	0.15	0.01	3.00	0.19	<0.001	0.017	NS
RUB	0.40	0.02	0.39	0.04	0.013	0.965	NS
ADEN	1.57	0.03	1.51	0.03	0.820	0.785	NS
ANAIL	1.75	0.03	1.85	0.04	0.298	0.738	NS
DW	2.28	0.03	3.17	0.04	0.071	0.007	NS
LC	2.93	0.02	2.92	0.02	0.548	0.963	NS
RC	2.75	0.04	1.81	0.04	0.235	0.005	NS
VC	2.30	0.04	1.69	0.03	0.039	0.045	NS
DEAD	80.13	1.07	109.19	1.64	0.050	0.018	NS

TABLE 3. Mean and standard deviation for each of four common snail species, *C. caracolla*, *P. acutangula*, *N. tridens*, and *G. nigrolineata*, on the Hurricane Recovery Plot (HRP) and the Bisley Grid (B). The range of density values for each species is shown in parentheses. Site-specific differences in the variance (Bartlett's test) and mean (t-test with unequal variances) of density were performed for each of the species.

Statistic	<i>C. caracolla</i>		<i>P. acutangula</i>		<i>N. tridens</i>		<i>G. nigrolineata</i>	
	HRP	B	HRP	B	HRP	B	HRP	B
Mean	14.33	8.92	0.40	0.39	15.83	32.61	3.50	1.64
Standard Deviation	11.68	7.92	0.67	0.60	12.32	22.15	2.70	1.71
Range	(1-55)	(0-27)	(0-3)	(0-2)	(1-59)	(6-107)	(0-10)	(0-6)
P (Bartlett's)	*		NS		***		**	
P (t-adjusted)	0.020		0.939		<0.001		0.001	

TABLE 4. Results from stepwise multiple regression assessing the degree to which a suite of habitat variables (Table 1) affect the density of *Caracolus caracolla*. The order of appearance of variables reflects their entry into the equation. Statistics include β , the standardized regression coefficient; t , test statistic; R^2 , the multiple coefficient of variation; ΔR^2 , the change in variation explained by the addition of a particular variable.

Location	Variable	Statistic				
		β	t	P -value	R^2	ΔR^2
El Verde	Apparency of <i>Heliconia caribaea</i>	0.378	3.015	0.005	0.387	0.387
	Apparency of <i>Philodendron</i> spp.	0.520	3.918	<0.001	0.518	0.131
	Apparency of <i>Ichnanthus pallens</i>	-0.263	-2.258	0.030	0.578	0.060
	Constant	12.165	8.545	<0.001	—	—
Bisley	Rock cover	0.608	3.911	<0.001	0.302	0.302
	Dead material cover	-0.359	-2.581	0.015	0.385	0.083
	Apparency of <i>Heliconia caribaea</i>	0.354	-2.320	0.027	0.474	0.089
	Constant	8.262	2.668	0.012	—	—
Combined	Rock cover	0.294	2.941	0.004	0.224	0.224
	Apparency of <i>Heliconia caribaea</i>	0.294	2.955	0.004	0.335	0.111
	Apparency of <i>Philodendron</i> spp.	0.298	2.985	0.004	0.383	0.048
	Apparency at 2 m	-0.212	-2.138	0.036	0.420	0.037
	Constant	7.733	3.332	0.001	—	—

15.83; Bisley, 32.61). The density of *P. acutangula* was low and similar at both sites (HRP, 0.40; Bisley, 0.39).

HABITAT ASSOCIATIONS.—The combined regression equation for *C. caracolla* accounted for 38.7 percent of the variation in snail density among points, regardless of site (the dummy variable was not significant, $P = 0.322$). Significant habitat variables included rock cover, apparency of *Heliconia caribaea*, apparency of *Philodendron* spp., and plant apparency at 2 m (Table 4). The standardized coefficients for the first three variables were positive and equivalent in magnitude (0.294, 0.294, and 0.298, respectively), whereas the standardized coefficient for plant apparency at 2 m was negative and slight-

ly smaller (-0.212). The consequence of combining data for the HRP and Bisley involved only a slight reduction in R^2 compared to regression equations tailored to each site separately. The significant variables in the combined analyses were a composite of those appearing in each of the separate analyses.

For *N. tridens*, slope and elevation were significant in the combined analysis, accounting for 28.8 percent of the variation in snail density (Table 5). Again, the dummy variable was not significant ($P = 0.330$); habitat associations were not different between sites. The standardized coefficient for slope was positive (0.342), whereas the standardized coefficient for elevation was negative (-0.328). The R^2 from the combined analysis was

TABLE 5. Results from stepwise multiple regression assessing the degree to which a suite of habitat variables (Table 1) affects the density of *Nenia tridens*. The order of appearance of variables reflects their entry into the equation. Statistics include β , the standardized regression coefficient; t , test statistic; R^2 , the multiple coefficient of variation; ΔR^2 , the change in variation explained by the addition of a particular variable.

Location	Variable	Statistic				
		β	t	P -value	R^2	ΔR^2
El Verde	Elevation	-0.338	-2.216	0.033	0.114	0.114
	Constant	107.778	2.595	0.013	—	—
Bisley	Rock cover	0.491	3.557	0.001	0.168	0.168
	Litter cover	-0.462	-3.317	0.002	0.325	0.157
	Apparency at 3 m	-0.335	-2.474	0.019	0.434	0.109
	Constant	61.342	5.059	<0.001	—	—
Combined	Slope	0.342	3.321	0.001	0.189	0.189
	Elevation	-0.328	-3.187	0.002	0.288	0.099
	Constant	72.927	3.649	<0.001	—	—

TABLE 6. Results from stepwise multiple regression assessing the degree to which a suite of habitat variables (Table 1) affects the density of *Gaeotis nigrolineata*. The order of appearance of variables reflects their entry into the equation. Statistics include β , the standardized regression coefficient; t , test statistic; R^2 , the multiple coefficient of variation; ΔR^2 , the change in variation explained by the addition of a particular variable.

Location	Variable	Statistic				
		β	t	P -value	R^2	ΔR^2
El Verde	Apparency at 0 m	-0.025	-2.515	0.016	0.143	0.143
	Apparency of <i>Prestoea montana</i>	0.081	2.558	0.015	0.272	0.129
	Constant	5.000	5.559	<0.001	—	—
Bisley	Apparency at 1 m	-0.117	-2.414	0.021	0.146	0.146
	Constant	2.600	5.424	<0.001	—	—
Combined	Apparency of <i>Prestoea montana</i>	0.070	3.010	0.004	0.215	0.215
	Apparency at 0 m	-0.014	-2.852	0.006	0.269	0.054
	Apparency at 1 m	-0.121	-2.398	0.019	0.311	0.042
	Apparency of <i>Piper glabrescens</i>	-0.218	-2.081	0.041	0.338	0.027
	Constant	4.510	6.847	<0.001	—	—

approximately twice that at El Verde but only half that at Bisley.

The apparencies of *P. montana* and *P. glabrescens*, along with apparency at 0 and 1 m, significantly accounted for 33.8 percent of the variation in density of *G. nigrolineata*. Again, the dummy variable was not significant and habitat associations were equivalent at both sites (Table 6). A number of the significant variables from the site-specific analyses (apparency at 0 and 1 m, as well as apparency of *P. montana*) appear in the regression equation for the combined data as well. The combined analysis (33.8%) accounted for more of the variation in density than did site-specific analyses (El Verde, 27.2%; Bisley, 14.6%).

For the combined data, the only habitat characteristic to account for a significant proportion of the variation in density of *P. acutangula* was the apparency at 2 m (Table 7). Little of the variation (< 16.0%) in density was explained by site-specific or combined models.

Bonferonni's sequential adjustment of significances from simple correlation analyses confirmed the overall relationship between snail density and habitat characteristics (*C. caracolla*, *N. tridens*, and *G. nigrolineata* were significant; *P. acutangula*, was not significant) for the combined data (Table 8). Rock cover and apparency of *H. caribaea* were most strongly and positively correlated with density of *C. caracolla*. Slope (positive), elevation (negative), and apparency of *P. glabrescens* (positive) were most strongly correlated with density of *N. tridens*. Apparency of *P. montana* was strongly and positively associated with density of *G. nigrolineata*.

DISCUSSION

TEMPORAL COMPARISONS.—Long-term demographic trends of snails at El Verde (Willig *et al.*, in press) and Bisley (Secret 1995, Willig *et al.*, in press) appear in detail elsewhere. The salient comparisons with regard to this study briefly are summarized to

TABLE 7. Results from stepwise multiple regression assessing the degree to which a suite of habitat variables (Table 1) affects the density of *Polydortes acutangula*. The order of appearance of variables reflects their entry into the equation. Statistics include β , the standardized regression coefficient; t , test statistic; R^2 , the multiple coefficient of variation; ΔR^2 , the change in variation explained by the addition of a particular variable.

Location	Variable	Statistic				
		β	t	P -value	R^2	ΔR^2
El Verde	Apparency at 2 m	-0.060	-2.569	0.014	0.148	0.148
	Constant	0.727	4.503	<0.001	—	—
Bisley	Rock cover	0.186	2.534	0.016	0.159	0.159
	Constant	0.053	0.328	0.745	—	—
Combined	Apparency at 2 m	-0.031	-2.534	0.013	0.080	0.080
	Constant	0.604	5.573	<0.001	—	—

TABLE 8. Correlations between density and each of 31 habitat descriptors (Table 1; El Verde and Bisley combined) are shown for *C. caracolla*, *P. acutangula*, *N. tridens*, and *G. nigrolineata*. The significance of P-values is assessed via Bonferonni's sequential adjustment (*, significant; NS, not significant) in order to maintain an overall error rate of 5%.

Variables	<i>C. caracolla</i>			<i>P. acutangula</i>			<i>N. tridens</i>			<i>G. nigrolineata</i>		
	<i>r</i>	<i>P</i> -value	Bonferonni's sequential adjustment	<i>r</i>	<i>P</i> -value	Bonferonni's sequential adjustment	<i>r</i>	<i>P</i> -value	Bonferonni's sequential adjustment	<i>r</i>	<i>P</i> -value	Bonferonni's sequential adjustment
SLOPE	-0.073	0.529	NS	-0.038	0.743	NS	0.435	<0.001	*	-0.226	0.050	NS
ELEV	-0.082	0.483	NS	-0.141	0.223	NS	-0.425	<0.001	*	0.192	0.096	NS
HT1	-0.313	0.006	NS	-0.028	0.810	NS	-0.004	0.976	NS	-0.311	0.006	NS
HT2	-0.088	0.449	NS	0.056	0.633	NS	0.086	0.458	NS	-0.162	0.162	NS
HT3	0.005	0.963	NS	-0.050	0.671	NS	-0.029	0.807	NS	-0.335	0.003	NS
HT4	-0.170	0.143	NS	-0.151	0.194	NS	-0.080	0.491	NS	-0.156	0.178	NS
HT5	-0.184	0.113	NS	-0.283	0.013	NS	-0.146	0.207	NS	-0.159	0.170	NS
HT6	-0.191	0.098	NS	-0.282	0.013	NS	-0.062	0.594	NS	-0.052	0.659	NS
HT7	-0.130	0.262	NS	-0.243	0.035	NS	-0.109	0.351	NS	-0.048	0.681	NS
CASARB	-0.148	0.202	NS	-0.170	0.142	NS	-0.141	0.225	NS	0.029	0.802	NS
CECSCH	0.078	0.506	NS	-0.052	0.656	NS	0.091	0.433	NS	-0.136	0.241	NS
DIDMOR	-0.097	0.404	NS	-0.015	0.896	NS	-0.057	0.623	NS	-0.082	0.481	NS
HELCAR	0.468	<0.001	*	-0.022	0.851	NS	-0.080	0.493	NS	0.120	0.303	NS
ICHPAL	-0.060	0.605	NS	-0.079	0.496	NS	-0.182	0.116	NS	-0.125	0.283	NS
PALRIP	-0.191	0.099	NS	-0.185	0.109	NS	-0.127	0.273	NS	-0.030	0.794	NS
PHILO	0.351	0.002	NS	-0.102	0.381	NS	-0.131	0.260	NS	-0.027	0.814	NS
PIPGLA	0.034	0.769	NS	0.104	0.369	NS	0.414	0.000	*	-0.289	0.011	NS
PIPHIS	-0.130	0.262	NS	0.006	0.956	NS	0.228	0.048	NS	-0.029	0.802	NS
PREMON	0.138	0.235	NS	-0.055	0.634	NS	-0.159	0.172	NS	0.379	0.001	*
PSYBER	-0.254	0.027	NS	-0.102	0.383	NS	0.124	0.286	NS	-0.063	0.578	NS
ROU	-0.239	0.037	NS	-0.110	0.345	NS	-0.080	0.490	NS	-0.141	0.224	NS
SLOB	-0.194	0.093	NS	-0.182	0.115	NS	-0.101	0.383	NS	-0.166	0.153	NS
MIC	-0.028	0.808	NS	-0.133	0.251	NS	0.081	0.486	NS	0.008	0.943	NS
RUB	-0.089	0.447	NS	-0.096	0.409	NS	-0.171	0.140	NS	0.033	0.777	NS
ADEN	0.194	0.093	NS	0.087	0.453	NS	0.034	0.770	NS	-0.113	0.331	NS
ANAIL	-0.072	0.539	NS	0.056	0.633	NS	-0.105	0.369	NS	-0.021	0.859	NS
DW	0.057	0.622	NS	-0.043	0.711	NS	0.180	0.119	NS	-0.194	0.094	NS
LC	-0.028	0.812	NS	0.038	0.746	NS	-0.071	0.540	NS	-0.123	0.289	NS
RC	0.473	<0.001	*	0.264	0.021	NS	0.018	0.879	NS	0.165	0.154	NS
VC	0.276	0.016	NS	-0.038	0.748	NS	-0.174	0.134	NS	0.038	0.745	NS
DEAD	-0.335	0.003	NS	-0.058	0.616	NS	-0.033	0.780	NS	-0.304	0.008	NS

provide context for the discussion that follows. All four snail species suffered significant reductions in abundance in the aftermath of Hurricane Hugo (Willig & Camilo 1991) and all subsequently attained densities (per 78.25 m² sampling unit) at least twice as great as pre-hurricane levels. From 1989 (pre-hurricane) to 1994, *C. caracolla* increased three-fold (3.1 to 8.9), *N. tridens* increased seven-fold (4.9 to 32.6), *P. acutangula* doubled (0.2 to 0.4), and *G. nigrolineata* increased six-fold (0.6 to 3.5). Although absolute measures of spatial variability (variance) were greater in 1994 than before the hurricane, relative spatial variability (coefficient of variation) decreased in response to the hurricane for all species (*C. caracolla*, from 1.0 to 0.8; *N. tridens*, from 1.1 to 0.5; *P. acutangula*, from 1.0 to 0.8; *G. nigrolineata*, from 0.6 to 0.4). At least at Bisley, where severe hurricane damage was documented, the long-term (5 yr) response of common snail populations was to increase and become more homogeneously distributed throughout the landscape. The direct effects of Hurricane Hugo, along with the subsequent changes in microclimate at the soil-litter interface, apparently caused significant mortality in snails. Nonetheless, large inputs of litter as a consequence of the hurricane, followed by appreciable increases in the development of the understory, provided increased amounts of shelter and food for snails. Similarly, as the canopy regenerated, many individual plants in the understory were unable to survive, renewing inputs of substrate and food for species like snails that feed on detritus.

HABITAT ASSOCIATIONS.—The lack of significance for the dummy variable in multiple regression analyses (Tables 5–7) suggests that differences within sites that lead to differential abundance of snails are consistent with and sufficient to account for the differences between sites in the density of snails. This is corroborated for each of the three species that exhibited significant habitat associations and differed significantly in density between sites (*C. caracolla*, *N. tridens*, and *P. acutangula*). Sites within El Verde or Bisley that exhibited high apparency of *Heliconia* or *Philodendron*, were rocky, and had little subcanopy development at 2 m, supported high densities of *C. caracolla* (Table 4). Similarly, the site (HRP) with higher density of *C. caracolla* (Table 3) had the higher apparency of both plant species, lower subcanopy development at 2 m, and higher rock cover (Table 2). In another study of habitat selection by *C. caracolla* in the tabonuco forest at El Verde, Cary (1992) found that snail density was highest at points with high apparency

of *Philodendron* or other vines and *Heliconia*. His result was true for the HRP in the dry season of 1991 (2 yr after Hurricane Hugo), as well as for an analysis at a finer spatial scale (*i.e.*, variation among 36 9-m² quadrats within each of three 324-m² grids). Within both El Verde and Bisley, points with steep slopes but low elevation had high densities of *N. tridens* (Table 5). As expected, the site with higher slope and lower elevation (Bisley; Table 2) supported higher densities of *N. tridens* (Table 3). Finally, *G. nigrolineata* was most abundant at points within sites that had high apparency of *Prestoea montana*, low apparency of *Piper glabrescens*, and low foliar development at ground level and at 1 m (Table 6). In an analogous fashion, the site (HRP) with the higher apparency of *Prestoea montana*, lower apparency of *Piper glabrescens*, and lower foliar development at ground and 1 m (Table 2) had the higher density of *G. nigrolineata*. The only snail species (*P. acutangula*) for which significant habitat associations were not detectable in multiple regression analyses had statistically indistinguishable densities at Bisley and on the HRP (Table 3).

SCALE EFFECTS.—Hurricane Hugo had a drastic effect on the density and distribution of animals in general (Waide 1991b), and snails in particular (Willig & Camilo 1991), in tabonuco forest. The legacy of the hurricane's impact is still detectable at El Verde (Willig *et al.*, in press.) where significant differences in density persist among sites that experienced different degrees of damage as a result of tree mortality, and trajectories of recovery from the effect of Hurricane Hugo are dependent on previous landuse history. At a larger geographic scale, significant differences in the mean and variability of snail densities exist between El Verde and Bisley (Table 3).

We designed our analyses to assess if these site-specific differences in abiotic, floral, and faunal components, arising at least in part from Hurricane Hugo and persisting to the present, were of sufficient magnitude to alter patterns of habitat association in four common snail species. For all four species of invertebrates, habitat associations were not significantly affected by site-specific differences beyond those related to the magnitude of the 31 habitat characteristics. Differences between sites in the density of each snail species are explicable in terms of differences related to habitat characteristics. To a large extent, consistent patterns of habitat association may occur because the association between habitat characteristics at Bisley is similar to the association between habitat characteristics at El

Verde. Either the hurricane did not alter the correlation between habitat characteristics in a significant fashion, or recovery has progressed to the point that any initial differences in the pattern of correlation between habitat characteristics is no longer detectable.

These results pertain to questions that revolve around the scale dependence of ecological processes. We have shown that differences in snail density between locations in the tabonuco forest that suffered differential damage from Hurricane Hugo are explicable in terms of the same factors that account for microspatial differences within each location. Insight derived from research conducted at a single location (e.g., El Verde) adequately accounts for patterns of variation at another site (e.g., Bisley), even though differences in the extent and severity of damage are well-documented. We hypothesize that proximate cues and ultimate consequences of habitat selection remain consistent throughout tabonuco forest because the structure of the correlation among habitat variables was not differentially affected by Hurricane Hugo. Radical changes in the way in which animals respond to differences in the biotic or abiotic environment may require an

equally radical disruption of the correlation of habitat characteristics.

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