

Effects of Treefall Gaps on the Density of Land Snails in the Luquillo Experimental Forest of Puerto Rico¹

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ABSTRACT

The effect of disturbance on land snail density in a montane subtropical wet forest was evaluated during wet (March–April) and dry (June) seasons by collecting specimens from quadrats positioned along transects that bisected treefall gaps in the Luquillo Experimental Forest of Puerto Rico. Atmospheric and litter temperature, relative humidity, litter and soil moisture, slope, and substrate type also were measured in each quadrat to determine the effect of these environmental parameters on the spatial distribution of the land snails during two sampling periods in 1989. Of the 34 species of snail known from the forest, only five occurred with sufficient frequency to permit statistical analysis. The abundances of three species (*Austrosolenites alticola*, *Megalomastoma croceum*, and *Subulina octana*) were not significantly different in gap versus nongap areas. In contrast, *Nenia tridens* and *Caracolus caracolla* responded to patches created by treefalls. In particular, the abundance of *N. tridens* was significantly higher in gaps; whereas, that of *C. caracolla* was significantly higher in the surrounding undisturbed forest. Such differences in distribution may be attributable to factors related to diet and body water loss rates.

RESUMEN

Los efectos de disturbios naturales en la densidad de caracoles terrestres en un bosque tropical húmedo, durante las épocas de lluvia (marzo–abril) y sequía (junio), fueron examinados por medio de censos de individuos en cuadrantes localizados a lo largo de transectos atravesando claros en el Bosque Experimental de Luquillo en Puerto Rico. Las temperaturas atmosféricas y de la hojarasca, humedad relativa, humedad de la hojarasca y el suelo, pendiente y tipo de sustrato también fueron registrados en cada cuadrante para determinar el efecto de estos parámetros ambientales en la distribución espacial de caracoles terrestres durante dos muestreos en 1989. De las 34 especies de caracoles presentes en el bosque, solo cinco fueron lo suficientemente abundantes para permitirnos análisis estadístico. Las densidades de tres especies (*Austrosolenites alticola*, *Megalomastoma croceum*, y *Subulina octana*) no difirieron significativamente entre claros y el bosque circundante. Por otro lado, *Nenia tridens* y *Caracolus caracolla* respondieron a claros creados por la caída de árboles. *N. tridens* fue significativamente más abundante en claros mientras que *C. caracolla* fue significativamente más abundante en el bosque circundante. Estas diferencias en distribución pueden atribuirse a factores asociados con la dieta y la pérdida de agua en *N. tridens* y *C. caracolla*.

Key words: disturbance; gaps; land snails; Luquillo Experimental Forest; Puerto Rico; tabonuco forest; treefalls.

THE IMPORTANCE OF DISTURBANCE in structuring biological communities is widely recognized by ecologists (Pickett & White 1985, Platt & Strong 1989). Disturbances may increase species richness by lowering the densities of dominant species, thereby freeing resources for less competitive species and preventing competitive exclusion (Brokaw 1985, Denslow 1985). In addition, environmental heterogeneity created by disturbances may provide additional niche dimensions for resource partitioning among sympatric species.

In many forest ecosystems, treefalls represent important agents of landscape heterogeneity (Bro-

kaw & Scheiner 1989, Poulson & Platt 1989, Spies & Franklin 1989, Veblen 1989). Although the primary effect of a treefall is the opening of a space in the canopy, environmental conditions among and within treefall gaps vary as a function of gap size, shape, and age (Collins *et al.* 1985). Gap size determines the amount of light entering a gap and thereby affects soil moisture, substrate temperature, air temperature, and the subsequent establishment and success of new plants. Time since disturbance, on the other hand, determines successional patterns within gaps. Consequently, environmental heterogeneity is increased, not only as a result of environmental differences between the undisturbed matrix and disturbed gaps, but also as a result of environmental variability between and within gaps (Chazdon & Fetcher 1984, Fetcher *et al.* 1985, Denslow

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1987, Becker *et al.* 1988, Brandani *et al.* 1988, Lieberman *et al.* 1989).

The effects of disturbance on biological communities are ubiquitous and may be critical parameters which constrain the design and management of reserves (Pickett & Thompson 1978, Foster 1980, Gilbert 1980, Hartshorn 1989). Although the role of disturbance in affecting spatial distribution of species is a recurrent theme in contemporary studies of plant ecology (Doyle 1982, Collins *et al.* 1985, Denslow 1987, Brandini *et al.* 1988, Platt & Strong 1989), the magnitude and pervasiveness of disturbance-related effects on animal populations is less well documented (Schemske & Brokaw 1981, Schowalter 1985, Wunderle *et al.* 1987, Crome & Richards 1988, Feinsinger *et al.* 1988, Levey 1988). Recent work concerning the impact of a large-scale, high intensity disturbance (Hurricane Hugo) on animal populations in the Caribbean is a notable exception (Askins & Ewert 1991; Covich *et al.* 1991; Lynch 1991; Reagan 1991; Waide 1991a, b; Will 1991; Willig & Camilo 1991; Woolbright 1991). Still, of those studies concerning animals, most are limited to vertebrates, which represent only 4 percent of all described animal species (Wilson 1988).

Land molluscs rank second in number of species in terrestrial ecosystems, being outnumbered only by arthropods (Russell-Hunter 1983). Land snails are important not only numerically, but also ecologically, because of their role in nutrient cycling as detritivores, herbivores, and carnivores (Purchon 1977). Despite their diversity and ecological importance, most of the published information on terrestrial molluscs concerns systematics; relatively little is known about terrestrial mollusc ecology. In addition, most of the ecological studies on terrestrial molluscs concern a few temperate zone species. Moreover, the low mobility and small home ranges of snails suggest that they would be likely candidates to reflect patch dynamics.

The objectives of this study were to determine and compare the effects of treefall gaps on snail species abundance in the tabonuco forest of Puerto Rico during two sampling periods, and to determine which of several environmental parameters play important roles in determining the spatial distribution of land snails. More specifically, the study evaluated whether particular species of land snail specialize in the use of gaps or undisturbed forest.

MATERIALS AND METHODS

STUDY SITE.—Research was conducted at El Verde Field Station in the northwestern corner of the Lu-

quillo Experimental Forest (LEF) of Puerto Rico (18°10'N, 65°30'W). The Field Station is located at an elevation of 500 m in the tabonuco forest (subtropical wet forest), which is the dominant life zone of the LEF, comprising about 70 percent of its area (Brown *et al.* 1983). The tabonuco forest is dominated by the hardwood tree, *Dacryodes excelsa*, which composes 35 percent of the forest canopy, and occurs at elevations below 600 m (Brown *et al.* 1983). Monthly temperatures at El Verde Field Station range from 21°C in January to 25°C in September (Brown *et al.* 1983). Annual rainfall averages 371.95 cm, with a standard error of 79.47 (McDowell & Estrada-Pinto 1988). Mean monthly rainfall shows some seasonality, with lower values from January to April (19.57 cm to 23.71 cm, respectively; hereafter referred to as the dry season) and higher values in the remaining months (45.99 cm to 35.01 cm from May to December; hereafter referred to as the wet season).

Data were collected during the periods of March 18–April 11 and June 1–15 of 1989, which occur within the dry and wet seasons, respectively, in the tabonuco forest. Nevertheless, rainfall patterns during the first half of 1989 did not follow the usual monthly precipitation regime. Total monthly rainfall for February (40.49 cm) was higher than average (monthly average = 21.81 cm); whereas, that for May (26.47 cm) was lower than average (average = 45.99 cm). To avoid confusion in referring to the drier month as the wet season sample and the wetter month as the dry season sample, we refer to these seasonal samples as the March and June sampling periods.

EXPERIMENTAL DESIGN.—Quadrats with an area of 8.0 m² (2 m × 4 m) were positioned along 13 transects set through treefall gaps in the tabonuco forest. Quadrat size was a compromise between two factors: larger quadrats would contain more snails; whereas, smaller quadrats could be positioned completely within light gaps. We chose the largest size quadrat that could be accommodated within a gap, given our experimental design. A gap was defined as “a hole in the forest, extending through all vertical levels, down to an average height of two m above ground” (Brokaw 1982). The edge of a gap was located at the innermost point reached by vegetation from the surrounding undisturbed area at any level (Brokaw 1982). The area of each gap was estimated as the area of an ellipse, $A = \pi \times L \times W/4$, where L and W represent length and width, respectively (Murray 1988).

Transects were established so that the center of

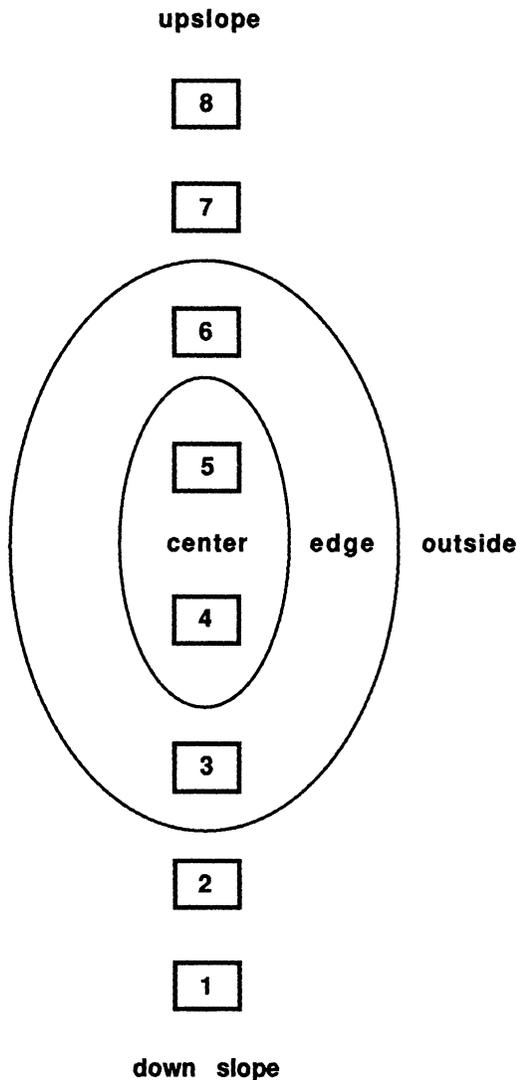


FIGURE 1. Location of quadrats (1–8) along transects through treefall gaps. Quadrats 3 to 6 were located within the gap; 1, 2, 7, and 8 were in the surrounding undisturbed forest.

a gap was at the middle of a transect. Eight quadrats were sampled along each of the transects (Fig. 1): two were located at the gap center (4 and 5), two at the gap edge (3 and 6), two outside the gap at 10.0 m from the edge of the gap (2 and 7), and two at 20.0 m from the edge of the gap (1 and 8). Because of the small size of most gaps, quadrats 3, 4, 5, and 6 were adjacent, except in transect H where they were 2 m apart. Transects were aligned with the prevailing slope gradient, with quadrat 1 located down slope.

Each quadrat was searched thoroughly for land snails (≥ 5 mm) present within or above the litter, but beneath a height of 2.0 m. Specimens were identified based upon descriptions and the key by Velez (pers. comm.).

Abiotic variables were measured for each quadrat including atmospheric and litter temperature, relative humidity, litter and soil moisture, slope, and substrate type. However, these were measured only in June, except for litter and soil moisture, which were recorded in March also.

Land snails are restricted primarily to humid terrestrial habitats because they lose water through their skins (Russell-Hunter 1983). Temperature affects the rate of water loss of snails (Heatwole & Heatwole 1978), ultimately influencing snail distribution. For example, five species of land snail (*Sphincterochila*) in Israel replace each other along a climatic gradient, extending from mesic Mediterranean habitats (1000 mm rain per year) to arid zones (70 mm rain per year), primarily because of differences in their resistance to desiccation (Arad *et al.* 1989). Measurements of litter (under litter surface) and atmospheric temperature (1 m from the ground) were taken in the left and right halves of each quadrat at about 1 m from the center of the quadrat. The mean litter and air temperatures were then used to characterize each quadrat. Humidity also affects the rate of water loss in snails (Heatwole & Heatwole 1978). Atmospheric relative humidity (1 m from the ground) was measured at 1 m to the left and right of the quadrat center utilizing a Taylor Mason's hygrometer, and a mean value was calculated for each quadrat. In addition, the percent litter and soil moisture of a quadrat were estimated from each subquadrat as,

$$\frac{[(\text{wet weight} - \text{dry weight})/\text{wet weight}]100}{}$$

where wet weight corresponds to a subsample (20 g) removed from the litter and soil samples, and dry weight is the weight of the subsamples after being oven dried at 65°C for 24 hr.

Substrate type is important to snails as it is related to the availability of food and shelter. Rocks provide shelter (Dillon 1980); whereas, plants provide food either in the form of litter (Karlin 1961) or live tissue (Barnes 1980). For each quadrat, a score was assigned for each of several parameters related to substrate availability. The parameters measured were amount of dead wood, area covered by dead wood, area covered by rock, and palm tree material abundance. Amount of dead wood and palm tree material abundance was scored on a scale from 1 to 5, based upon visual inspection of the

quadrat, with 1 designating none; 2, little; 3, moderate; 4, considerable; and 5, abundant quantities of material. Similarly, area covered by dead wood or rock was scored from 0 to 10, with 0 representing 0 percent; 1, 1 to 10 percent; 2, 11 to 20 percent; 3, 21 to 30 percent; 4, 31 to 40 percent; 5, 41 to 50 percent; 6, 51 to 60 percent; 7, 61 to 70 percent; 8, 71 to 80 percent; 9, 81 to 90 percent; and 10, 90 to 100 percent of the quadrat. In addition, the numbers of shrubs, trees, and palms were recorded, as well as the particular substrate from which land snails were collected.

Slope angle is related to the availability of shelter and food (Heatwole & Heatwole 1978, Dillon 1980). Steep slopes do not permit the accumulation of rocks and litter which otherwise might provide shelter or food to the snails. The slope angle at the center of each quadrat was measured using a Peco Abney Level.

STATISTICAL ANALYSIS.—For each snail species, the mean numbers of individuals in the undisturbed forest (quadrats 1, 2, 7, and 8) and gap sites (quadrats 3, 4, 5, and 6) were compared statistically by a repeated measures (time) one-way (habitat) analysis of variance (ANOVA), via SPSSX statistical procedure MANOVA (SPSS Inc. 1988), to determine if spatial (gap versus undisturbed forest) or temporal (March versus June) differences exist. Tests of significance in a repeated measures experimental design can be based on either multivariate criteria or averaged univariate F tests, of which the latter are more powerful (SPSS Inc. 1988). However, to use the univariate approach, the variance-covariance matrices must satisfy two assumptions. The variances of all the transformed variables for a particular within-subject effect should be equal and their covariances equal to zero. The variance-covariance matrices of transformed variables should be equal across all levels of each between-subjects factor. The multivariate approach only assumes that all measurements on a subject follow a multivariate normal distribution and no assumption is made about the characteristics of the variance-covariance matrices.

In this study, the within-subject factor (time) in all repeated measures comparisons had only two levels, and therefore, the multivariate and univariate results for the time effect were identical (*i.e.*, a single transformed variable, $S_1 - S_2$, constitutes the data). The second assumption was satisfied for all tests involving habitat or quadrat effects, except for those involving *N. tridens* and *S. octana* (Box's M test, $P \leq 0.01$). However, only two levels for the habitat effect exist for each taxon. Hence, a *t*-test was per-

formed, with the *t* statistic converted to an *F* statistic. Consequently, only univariate results are reported for all repeated measures comparisons. Because considerable heterogeneity exists among gaps, and we were only able to locate and sample 13 gaps in the vicinity of El Verde, we recognize four levels of significance (very highly significant, $P \leq 0.001$; highly significant, $0.001 < P \leq 0.01$; significant, $0.05 \geq P > 0.01$; approaching significance, $0.05 < P \leq 0.10$; Sokal & Rohlf 1981, Yoccoz 1991) in order to compensate for the effects of these constraints on statistical power.

The mean litter moisture and soil moisture of each of the eight quadrats along the transects were compared by separate repeated measures (time) one-way (quadrat) ANOVAs, including a priori contrasts, to determine if spatial or temporal effects exist on each of these environmental parameters. Mean comparisons among the eight quadrat types during June were achieved via one-way ANOVA on atmospheric temperature, litter temperature, and relative humidity, separately, using SPSSX statistical procedure ONEWAY (SPSS Inc. 1988).

The relationship between population density of each of the five common species and each of the environmental parameters was analyzed statistically using the nonparametric Spearman rank correlation coefficient via SPSSX statistical procedure NONPAR CORR (SPSS Inc. 1988). For March, the environmental parameters included litter moisture, soil moisture, and slope. For June, the environmental variables were litter temperature, air temperature, relative humidity, litter moisture, soil moisture, slope, amount of dead wood, area covered by wood, area covered by rock, and tree, shrub, and palm tree density.

A direct discriminant function analysis of quadrats was performed via SPSSX statistical procedure FACTOR (SPSS Inc. 1988). Quadrat position along the transect defined groups, and the 12 environmental parameters measured during June constituted dependent variables.

RESULTS

The gaps used in the study ranged in area from 14.0 to 53.0 m². A total of 16 species of land snails (*Alcadia alta*, *Alcadia striata*, *Austrosolenites alticola*, *Caracolus caracolla*, *Cepolis squamosa*, *Gaeotis nigrolineata*, *Lamellaxis gracilis*, *Megalomastoma croceum*, *Nenia tridens*, *Obeliscus terebraster*, *Oleacina glabra*, *Oleacina playa*, *Platysuccinea portoricensis*, *Polydotes acutangula*, *Subulina octana*, and *Vaginulus occidentalis*) was identified from the

TABLE 1. *Distribution and habitat associations of the five most common land snail species in the tabonuco forest during the March and June sampling periods.*

Species	Number of individuals											
	March		June		Litter or top soil		Rock		Live plant material		Dead plant material	
	For-est	Gap	For-est	Gap	March	June	March	June	March	June	March	June
<i>Austrosolenites alticola</i>	14	16	9	14	28	20	1	2	0	0	1	0
<i>Caracolus caracolla</i>	56	23	58	32	42	19	1	2	25	40	11	28
<i>Megalomastoma croceum</i>	107	57	61	22	162	80	0	0	0	0	0	1
<i>Nenia tridens</i>	36	123	71	221	6	5	1	0	24	79	126	207
<i>Subulina octana</i>	20	10	13	13	30	25	0	1	0	0	0	0

quadrat surveys. Of these 16 species, the five most common were *A. alticola*, *C. caracolla*, *N. tridens*, *M. croceum*, and *S. octana* (Table 1). These species accounted for 91 percent and 92 percent of the snails collected during March and June, respectively.

Densities of about 2/3 of the species were too low to permit statistical analysis and, as a result, tests to detect spatial or temporal differences in species abundance were performed only on the five most common species. No significant differences related to habitat or time were detected for *A. alticola* or *S. octana* (Tables 2–3). However, in the case of *C. caracolla*, the habitat effect approached significance with $P = 0.08$. *Megalomastoma croceum* was found to be significantly more abundant in March than in June ($P \leq 0.05$), but no significance was found for either the habitat or interaction effects. *Nenia tridens* was significantly more abundant in gaps than in the forest ($P \leq 0.05$), and in June than in March ($P \leq 0.001$).

Soil moisture was consistently higher in March than in June ($P = 0.001$), and within gaps than in the surrounding forest ($P = 0.035$). No significant differences among quadrats were found for litter moisture, atmospheric temperature, litter temperature, or relative humidity in June. Descriptive statistics of abiotic parameters for each quadrat type, as well as details of the statistical analyses, appear in Alvarez (1991).

In March, abundance of *A. alticola* was correlated with soil moisture ($r = -0.20$, $N = 104$), slope ($r = 0.20$, $N = 104$), and area covered by rock ($r = -0.29$, $N = 104$). In June, abundance of *A. alticola* was again positively correlated with slope ($r = 0.24$, $N = 104$), but not with soil moisture or area covered by rock. Instead, it showed a significant relationship with both litter ($r = -0.24$, $N = 104$) and atmospheric ($r = -0.20$, $N = 104$) temperatures. In the case of *C. caracolla*, a significant negative relationship with soil moisture ($r =$

TABLE 2. *Number of individuals per 32.0 m² (mean \pm standard error) of A. alticola, C. caracolla, M. croceum, N. tridens, and S. octana in gap (quadrats 1, 2, 7, and 8) and undisturbed forest (quadrats 3–6) sites during the March and June sampling periods (N = 13).*

Species	Sample	Habitat	
		Forest	Gap
<i>Austrosolenites alticola</i>	March	1.1 \pm 0.4	1.2 \pm 0.6
	June	0.7 \pm 0.4	1.1 \pm 0.4
<i>Caracolus caracolla</i>	March	4.3 \pm 0.8	1.8 \pm 0.5
	June	4.5 \pm 1.6	2.5 \pm 0.8
<i>Megalomastoma croceum</i>	March	8.2 \pm 4.6	4.4 \pm 2.4
	June	4.7 \pm 2.2	1.7 \pm 1.2
<i>Nenia tridens</i>	March	2.8 \pm 0.5	9.5 \pm 2.9
	June	5.5 \pm 1.3	17.0 \pm 4.9
<i>Subulina octana</i>	March	1.5 \pm 1.1	0.8 \pm 0.7
	June	1.0 \pm 0.5	1.0 \pm 0.8

TABLE 3. Results of repeated measures (season) one-way (habitat) ANOVA for number of individuals of *A. alticola*, *C. caracolla*, *M. croceum*, *N. tridens*, and *S. octana*.

Source	df	Significance level				
		<i>Austrosolenites alticola</i>	<i>Caracolus caracolla</i>	<i>Megalomastoma croceum</i>	<i>Nenia tridens</i>	<i>Subulina octana</i>
Habitat	1	0.649	0.080	0.376	0.029	0.718
Within	24					
Time	1	0.303	0.493	0.040	0.001	0.722
Habitat × Time	1	0.656	0.662	0.771	0.092	0.376
Within	24					

−0.20, $N = 104$) was detected during March, but no significant correlations were found in June. Number of *M. croceum* was correlated with both amount of dead wood ($r = -0.20$, $N = 104$) and area covered by wood ($r = -0.22$, $N = 104$) in June, but with none of the variables measured in March. Abundance of *N. tridens* was correlated with litter moisture ($r = 0.31$, $N = 104$) in March, and amount of dead wood ($r = 0.25$, $N = 104$) and area covered by wood ($r = 0.19$, $N = 104$) in June. No significant correlations between abiotic parameters and abundance of *S. octana* were detected in either March or June.

Land snails were collected from four major substrate types: litter or top soil, rock, live plants, and dead plant material (Table 1). Live and dead plant material included leaves, branches, and stems. The five common species of snail did not use these substrate categories in the same manner during March (G -test of independence, $G = 456.4$, $df = 12$, $P \leq 0.05$) or June (G -test of independence, $G = 473.6$, $df = 12$, $P \leq 0.05$). Pairwise unplanned tests of the homogeneity of replicates revealed that *A. alticola*, *M. croceum*, and *S. octana* did not differ significantly among themselves in habitat use, but that they each differed significantly from *C. caracolla* and *N. tridens*. In addition, significant differences in habitat use were found between *C. caracolla* and *N. tridens*. *Austrosolenites alticola*, *M. croceum*, and *S. octana* could be referred to as “forest floor specialists,” as they were collected more often (over 85% of the time) in the litter and top soil during both sampling periods. *Nenia tridens* was highly associated with dead plant material, being collected from this substrate 80 percent and 71 percent of the time, during March and June, respectively. In contrast, *C. caracolla* shows a seasonal change in substrate selection; 53 percent of the individuals were collected from the litter or top soil in March; whereas, 45 percent were collected from live plant material in June.

First and second discriminant functions (Fig. 2) derived from the environmental parameters measured in June account for 71.5 and 13.7 percent of the variance among quadrats, respectively. The loading matrix of correlations between predictor variables and discriminant functions suggests that quadrats outside the gap (1, 2, 7, and 8) can be separated from those inside the gap (3, 4, 5, and 6) on the basis of amount of dead wood and area covered by wood. The quadrats inside the gap had a larger quantity of dead wood (mean = 3.27), and greater area covered by wood (mean = 3.38) than did quadrats outside the gap (mean amount of dead wood and mean area covered by wood are 1.98 and 0.98, respectively).

DISCUSSION

Tropical storms have been recurrent events in the Caribbean for long periods of time. Presumably, sufficient evolutionary time has passed for organisms, particularly those that are sessile or with low mobility, to adapt to disturbance-generated patches, provided that sufficient environmental differences exist between the undisturbed matrix and patches. For example, in the tabonuco forest, tree species diversity and species abundance are maintained by hurricanes (Doyle 1982), the underlying disturbance agents in this ecosystem.

The magnitude of effect produced by hurricanes depends upon their proximity to particular site. For example, Hurricane Hugo passed within 10 km of our study site, and caused severe and pervasive damage (see special issue of *Biotropica* which details ecosystem, plant, and animal responses to hurricanes in the Caribbean; Walker *et al.* 1991). In particular, *C. caracolla*, *N. tridens*, and *G. nigrolineata* each significantly decreased in density by at least 75 percent as a consequence of Hurricane Hugo (Willig & Camilo 1991). Although not significantly, the density of *P. acutangula* decreased to the point

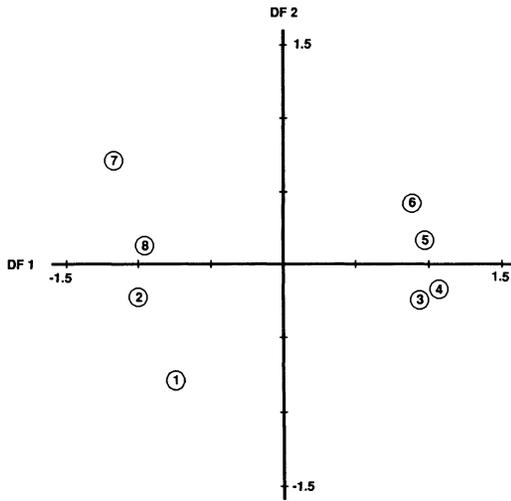


FIGURE 2. Plot of the eight quadrat centroids on the first two discriminant functions derived from 12 environmental parameters measured in June.

where no individuals occurred in the surveys. Population reductions were attributed to microclimatic shifts as well as to direct effects of flooding and wind damage on mortality. Hurricanes which pass more distant from a site may still modify habitat structure via the production of treefalls or landslides. In fact, many light gaps represent direct effects of distant hurricanes, with subsequent microclimatic changes and substrate alteration acting as indirect effects. Together they probably represent a profound force affecting the density and spatial distributions of snails.

In addition to physiognomic differences between gaps and the surrounding forest (which allow their detection), major physical differences between quadrats in gaps and the undisturbed tabonuco forest included amount of dead wood, area covered by wood, and soil moisture, all of which were higher in gaps than in the surrounding forest. Such increased soil moisture in gaps has been reported for other tropical and temperate forests (citations in Collins *et al.* 1985 and Becker *et al.* 1988), and has been attributed to greater through fall (Collins *et al.* 1985), reduced root density (Geiger 1965 cited by Becker *et al.* 1988), and lower transpiration rates (Denslow 1987) in gaps.

Although several studies (Wunderle *et al.* 1987, Crome & Richards 1988, Levey 1988, Schemske & Brokaw 1981) have shown that other animals can differentiate between undisturbed forest and patches, this is the first study examining the response of snails to forest heterogeneity caused by treefall

gaps. Some species of land snails are able to respond to patches created by treefalls in the tabonuco forest, but such response is not ubiquitous. In particular, *N. tridens* is more abundant within gaps; whereas, *C. caracolla* is more abundant within the surrounding undisturbed forest. The large percentage (80% and 71% in March and June, respectively) of *N. tridens* collected from dead plant material, other than litter (Table 1), suggests that dead plant material serves either as a direct food source for *N. tridens* or for organisms on which they feed, particularly algae (de Jesus, pers. comm.) and fungi. Van der Schalie (1948) also reported large numbers of *N. tridens* in areas abundant with algae covered tree trunks. Hence, the abundance of *N. tridens* may be higher in gaps because they contain more dead plant material than does the undisturbed forest. This hypothesis is supported by the significant positive correlations between both the amount of dead wood and area covered by wood, and numbers of *N. tridens*.

In contrast, *C. caracolla* may be more abundant in the undisturbed forest because it suffers increased water loss in gaps compared to undisturbed forest. This idea is consistent with the contention of Heatwole and Heatwole (1978) that differences in behavior and mortality between lowland and upland populations and different age groups of *C. caracolla* are primarily attributable to evaporative water loss. For example, Heatwole and Heatwole (1978) reported that in the cool and wet montane forest (elevation = 400–650 m), a larger proportion of adult *C. caracolla* occupied tree trunks than in the hotter and drier lowland forest (elevation below 30 m), where adult snails tended to occupy the leaf litter and other less exposed habitats. In addition, juveniles occupied less exposed microhabitats than did adults in both forests, and juvenile mortality was higher in the lowlands than in the montane forest.

Differences in water loss rates between snails from xeric and mesic habitats have been known to result from differences in shell aperture area, shell thickness, and epiphragm thickness (see Riddle 1983 and Arad *et al.* 1989, and references therein). In general, species from xeric habitats have a smaller shell aperture, greater shell thickness, and greater epiphragm thickness than do their counterparts from mesic areas. *N. tridens* (height = 25–30 mm; width = 5 mm) has a smaller shell aperture area (25 mm² approx. in adults) than does *C. caracolla* (450 mm² approx. in adults; height = 20–25 mm; width = 55–65 mm), possibly allowing it to remain active in gaps for longer periods without any substantial

loss of body water. As a result, *N. tridens* is able to exploit resources within the gap microhabitat that may be inhospitable to *C. caracolla*.

Megalomastoma croceum, *A. altiloca*, and *S. octana* are found almost entirely on litter or top soil, which provide cover against water loss and are distributed in a relatively homogeneous manner throughout the forest. Because no major environmental differences were detected between the undisturbed forest and gaps at the level of the forest floor, except for soil moisture, and because the densities of none of the three species were highly correlated with soil moisture, these "forest floor specialists" would not be expected to respond differentially to gaps.

Differences in species abundance could be the result of demographic or behavioral responses to disturbance or season. Demographic effects occur when actual densities are modified as a consequence of the effects of treatment factors on birth and death rates. On the other hand, behavioral responses could produce the appearance of density differences by altering snail activity or microhabitat association. For example, burrowing in the soil to avoid desiccation would appear as a density reduction within the limits of field methodologies. Behavioral and demographic responses to treatment factors cannot be distinguished herein.

Why do land snails in the tabonuco forest not exhibit the population heterogeneity expected of organisms in disturbance mosaics? Two major explanations exist which are not necessarily mutually exclusive. Variation among gaps may be so great, and environmental differences between undisturbed forest and gaps insufficient from the perspective of most snail taxa as to prevent the differential use of these two microhabitats. The response of animals to disturbance mosaics may be complex, varying within and between forests according to taxonomic groups and geographic region, hence impeding a uniform animal response to disturbance.

Although the most conspicuous environmental change in treefall gaps is the increase in light, other physical parameters have been reported to differ between gaps and undisturbed forest, such as air temperature, soil temperature, relative humidity, and soil moisture (Fetcher *et al.* 1985, Denslow 1987, Becker *et al.* 1988). However, the magnitude of such differences depends on factors such as gap size, height of adjacent canopy, gap shape, and gap age (Collins *et al.* 1985, Denslow 1987) as well as the legacy of previous disturbance that is reflected in the composition and stereogeometry of the surrounding matrix (Lieberman *et al.* 1989). In par-

ticular, environmental differences between gaps and undisturbed forest are known to decrease as gap size decreases and gap age increases. Moreover, these environmental factors may be modified even further by topography, as well as by daily and seasonal variation in the position of the sun (Collins *et al.* 1985). In the tabonuco forest, treefall gaps may be too small in size and topographically heterogeneous to develop detectable environmental differences from the surrounding undisturbed forest. In fact, average gap area in the tabonuco forest is smaller (29 m²) compared to Panama (86 m²), Venezuela (160 m²), Mexico (200 m²), Ivory Coast (208 m²), Costa Rica (336 m²), and French Guiana (628 m²) (Brokaw 1985, Vitousek & Denslow 1986).

Data from other studies on the effects of disturbance on animal communities suggests that animal species do not respond in a uniform fashion to disturbances. For example, Crome and Richards (1988) reported that 75 percent (9 of 12) of the bat species in a Queensland rain forest distinguished between gaps and the undisturbed forest. However, in the Panamanian, Puerto Rican, and Costa Rican rain forests, 16 percent (5 of 31), 33 percent (4 of 12) and 45 percent (19 of 42) of the bird species, respectively, were either gap or forest specialists (Wunderle *et al.* 1987, Levey 1988, Schemske & Brokaw 1981).

Time had no major effect on the environmental variables measured except for soil moisture. Rainfall data show an unusual extension of the dry season with a continuous decrease in mean daily rainfall from March (mean = 8.97 mm) to June (mean = 8.39 mm) of 1989; this is a plausible explanation of why soil moisture was higher in March than in June. Only *M. croceum* and *N. tridens* seemed to be affected by this extension of the dry season, although in different ways. While numbers of *M. croceum* decreased from March to June, those of *N. tridens* increased. *Megalomastoma croceum* is known to burrow deep into the soil during the dry season, resuming activity whenever sufficient moisture is available (Van Der Schalie 1948). Because sampling during June represented only an extension of the dry season during the course of this research, further study is necessary to determine if seasonal effects exist during more typical years in the tabonuco forest.

In a different context, Lieberman *et al.* (1989) questioned the utility of the "gaps vs nongaps" paradigm, and suggested that a "canopy closure continuum" would better serve as a leitmotif for future research. Our results suggest that both approaches may be reasonable, depending upon the

target species and the critical factors which regulate their local density. Moreover, the "gaps vs nongaps" dichotomy could be considered a special case of the continuum model. Certain critical environmental parameters may persist at high or low levels within gaps for a sufficiently long time after gap establishment (e.g., abundance of dead wood) to produce clear-cut distinctions from the surrounding matrix, regardless of dynamic history or legacy of previous disturbance which is reflected in the heterogeneity of the matrix. Species which respond to these attributes would appear as gap specialists or forest specialists. In contrast, other taxa may respond to gaps, but only in the sense that gaps represent one of a number of sources of the critical resource which affects them. Total abandonment of a gap-based approach would neither provide resolution of these differences, nor facilitate an appreciation of the role of disturbance in structuring the abundance and distribution of organisms. Future research should

focus on the manner in which species abundances respond to the continuum of resource quantities as well as to the gap versus nongap dichotomy.

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