CHAPTER 15

LONG-TERM MONITORING OF SNAILS IN THE LUQUILLO EXPERIMENTAL FOREST OF PUERTO RICO: HETEROGENEITY, SCALE, DISTURBANCE, AND RECOVERY

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INTRODUCTION

Global concern exists over losses of biodiversity, the erosion of habitat quantity and quality, and global warming. Stewardship of the land and wise management of natural resources requires enhanced understanding of ecological principles, especially in light of the pressing nature of these concerns. Ecology, as the study of the distribution and abundance of organisms (Krebs, 1985), has focused on the abiotic and biotic inter-relationships of species to identify critical determinants of population density and habitat association. However, most ecological studies have been conducted from a short-term perspective (1 to 3 years), even though underlying ecological processes likely integrate over substantially longer time frames. This is unfortunate for a variety of reasons.

Limitations of short-term studies

Short term-approaches limit the types of interactions and responses that are detectable in ecological research. For example, a plethora of short-term studies suggest that ants and rodents are strong competitors in desert systems of the southwestern United States, and carefully designed manipulation experiments have detailed the response of each taxon to removal of the other (Brown and Davidson, 1977; Brown *et al.*, 1979). Nonetheless, a long-term perspective on the interactions between ants and rodents suggests that they exhibit indirect mutualisms as a consequence of their differential use of resources and the asymmetric competitive interactions between desert plants based on seed size or life-history attributes (Davidson *et al.*, 1984, 1985). The depth of understanding about these interactions was only possible because of the long-term monitoring of animal and plant populations.

The pervasive role of disturbance in molding attributes of communities and ecosystems has become a paradigm in ecology (Levin and Paine, 1974; Mooney and Gordon, 1983; Pickett and White, 1985). The frequency, intensity, scale, and pattern of disturbances are critical characteristics that affect system response. Short-term perspectives inherently are incapable of assessing the impact of important natural disturbances, especially those that are infrequent and severe (e.g. fire, hurricanes, floods), on the structure and function of ecosystems. Secondary succession may require decades before recovery is attained in relation to population, community, or ecosystem properties (West *et al.*, 1981). Moreover, researchers without historical information about past disturbance events may erroneously attribute contemporary structure or function to current conditions, rather than to the original causative agents.

Finally, human activity has had a long and controversial history of causing or accelerating changes in natural communities and ecosystems (Schlesinger *et al.*, 1990; Schulze and Mooney, 1993; Solomon and Shugart, 1993). Global warming, desertification, pollution, and habitat destruction are contemporary ecological problems that are anthropogenic in nature. The absence of long-term data from a variety of locations reduces effectiveness in detecting deleterious impacts early and contributes to the controversy surrounding the inability to distinguish between natural variation over time and space and ecological aberrations induced by human activities.

Design of long-term monitoring strategies

Despite consensus recognizing the need for long-term ecological data collection (Franklin *et al.*, 1990; Magnuson, 1990; Swanson and Sparks, 1990), little agreement characterizes spatial approaches for estimating population- and community-level parameters. This is not surprising, given the multitude of questions that field research addresses and the close correspondence between hypothesis testing and the practical aspects of experimental design (Lacher and Willig, 1994; Willig, 1994). Still, long-term monitoring can be enhanced by modifying the spatial context of sampling so as to increase the number of questions to which the data may be applied in a rigorous fashion. In particular, we advocate a methodology that facilitates detection of spatial and temporal variation in ecological attributes of populations and communities. It is especially appropriate for studying disturbance-mediated ecosystems, areas historically subjected to a diversity of land-use practices, or areas that encompass appreciable spatial heterogeneity.

TERRESTRIAL SNAILS

In terrestrial ecosystems, land mollusks rank second in species richness; only arthropods have more species (Russell-Hunter, 1983). Land snails are important not only from a numerical perspective, but also because of their role in nutrient cycling as litter feeders and herbivores (Mason, 1970). Despite their high diversity and ecological importance, most published information concerning terrestrial mollusks focuses on systematic or taxonomic questions; their ecology is less well understood than that of other invertebrates or vertebrates, especially in tropical or subtropical ecosystems.

The terrestrial snail fauna of the tabonuco forest in Puerto Rico includes 34 species (Alvarez, 1991; Garrison and Willig, 1996). Heatwole and Heatwole (1978) provided a broad overview of the camaenid tree snails at the island's Luquillo Experimental Forest (LEF), with emphasis on the most abundant species, *Caracolus caracolla*. More recent research evaluated the response of snail populations and communities to tree-fall gaps scattered throughout an otherwise undisturbed forest matrix (Alvarez, 1991; Alvarez and Willig, 1993) and as the response of common snail species to an infrequent but severe disturbance – in this case, Hurricane Hugo (Willig and Camilo, 1991; Secrest *et al.*, 1996). A monographic treatment (Cary, 1992) of the biology of *C. caracolla* included analyses of demographic parameters, home-range size and fidelity, habitat associations, and spatial distribution. In general, spatial heterogeneity characterizes the distribution of snail populations, with disturbance having a profound effect on population and community organization.

STUDY SITE

The 11,330-ha Luquillo Experimental Forest is in the northeastern corner of Puerto Rico (18°10'N, 65°30' W) (Figure 15.1). The LEF is a UNESCO Man and the Biosphere preserve and as a consequence of elevational changes in climate, soil, and vegetational structure and composition, may be categorized into four distinct life zones: tabonuco forest, colorado forest, dwarf forest, and palm forest (Brown *et al.*, 1983). The tabonuco forest (subtropical wet forest) is the largest and most intensively studied life zone (see Odum and Pigeon, 1970a,b,c; Walker *et al.*, 1991; Reagan and Waide, 1996) occurring at elevations below 650 m on well-drained mountain slopes. It is the location of much of the research activity associated with the Luquillo Mountains Long-Term Ecological site, funded by the National Science Foundation (Franklin *et al.*, 1990; Waide and Lugo, 1992). The forest harbors >150 species of trees, the most common of which are *Dacryodes excelsa* (tabonuco), *Cecropia schreberiana* (trumpet tree), *Didymopanax morototoni* (matchwood), *Sloanea berteriana* (motillo), and *Prestoea montana* (sierra palm). Mean monthly temperature is relatively constant (21°C in January to 25°C in September), whereas precipitation is seasonal and substantial – 15.57 to 23.71 cm from January to April and 45.99 to 35.01 cm from May to December.

Like most of the islands of the Caribbean, Puerto Rico is subject to frequent disturbances such as hurricanes (wind speeds > 110 km/h) and tropical storms (wind speeds between 70 and 110 km/h). Hurricane Hugo, which occurred on 18 September 1989, was a severe (category 4 hurricane) disturbance. The eye of the storm passed within 10 km of the forest (Figure 15.1), triggering > 200 landslides and initiating thousands of tree falls (Brokaw and Grear, 1991; Scatena and Larsen, 1991; Walker, 1991). Susceptibility to damage from the hurricane

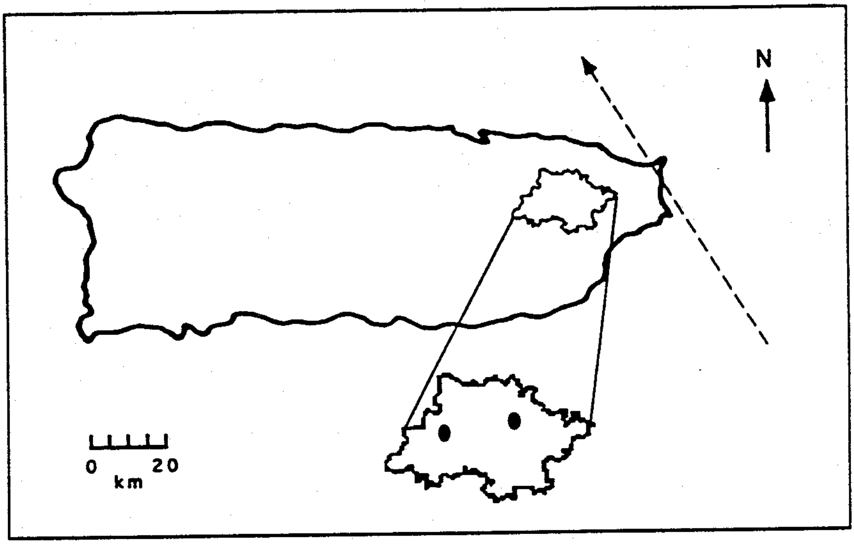

Figure 15.1 Luquillo Experimental Forest, coincident with the Caribbean National Forest, in the northeastern corner of Puerto Rico in the Luquillo Mountains. The location and proximity of the two tabonuco forest study sites – El Verde to the west and Bisley to the east – are shown by the two dark ovals. The approximate path of the eye of Hurricane Hugo is designated by the dashed line intersecting the far northeastern corner of the island

and subsequent recovery differed among trees in a species-specific fashion (Zimmerman *et al.*, 1994). In addition to the flora, the abundance and distribution of faunal elements were drastically altered by Hurricane Hugo (Waide, 1991a,b; Willig and Camilo, 1991; Woolbright, 1991; Gannon and Willig, 1994).

Long-term monitoring of snail populations in the tabonuco forest was conducted at two sites: El Verde Field Station and Bisley watersheds. Differences between the sites are related to topography, previous land-use history, and degree of exposure to Hurricane Hugo. The forest at Bisley occupies steep slopes and deep valleys, whereas changes in terrain are more gradual at El Verde. The tabonuco forest at Bisley was more drastically affected by Hurricane Hugo than was the forest at El Verde (Boose *et al.*, 1994). At El Verde (Walker, 1991), tree damage included moderate defoliation (56%), mortality (7%), uprooting (9%), and trunk snapping (11%). In contrast, defoliation (100%) and mortality (50%) of trees was much more extensive and severe at Bisley (Walker *et al.*, 1992).

METHODS

The abundance, composition, and diversity of snail species in the tabonuco forest were assessed at a variety of spatial scales. These included two large and three small areas: a 16-ha grid (Hurricane Recovery Plot, or HRP) at El Verde (Figure 15.2), a 13-ha grid in the Bisley watersheds (Figure 15.3), and three

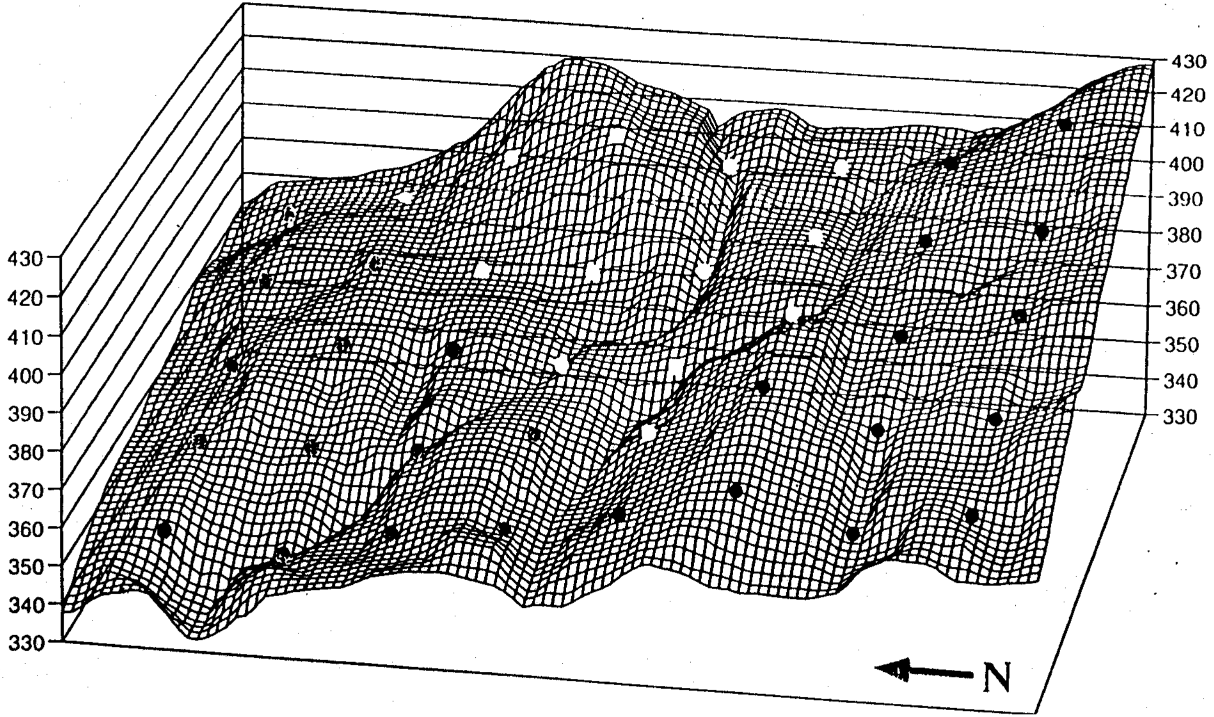

Figure 15.2 Elevational relief map of the 16-ha El Verde Hurricane Recovery Plot. Circles illustrate the location and proximity (60-m spacing) of circular quadrats (r = 3 m) where snail surveys were conducted. Shading of circles (dark = little damage, forest cover > 80%; gray = intermediate damage, forest cover between 80% and 50%; white = severe damage, forest cover < 50%) indicates degree of disturbance based on historical land use. Vertical axis represents elevation in meters

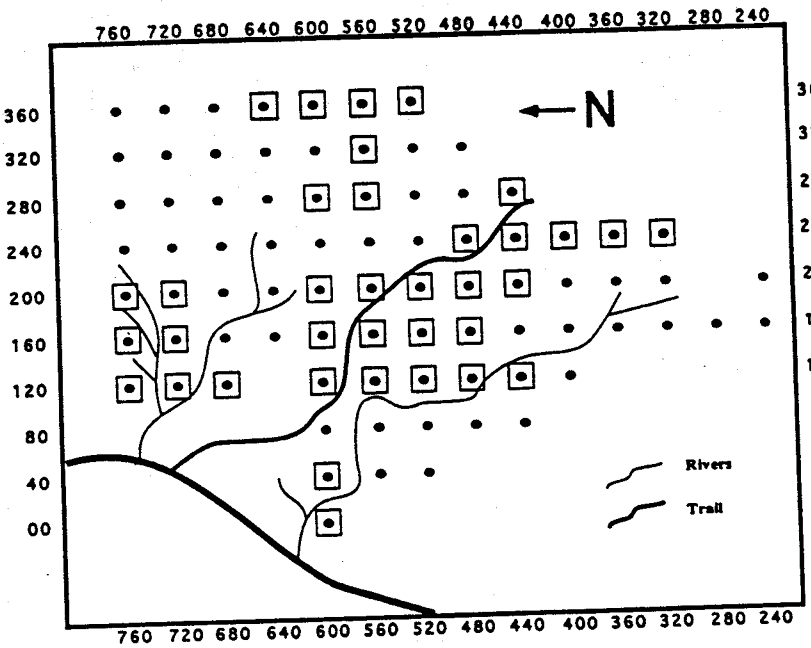

Figure 15.3 Diagrammatic representation of the 13-ha grid at Bisley watersheds (after Willig and Camilo, 1991). Dots represent circular quadrats (r = 5 m) with 40-m spacing; those enclosed by a square were surveyed for snails. Numbers around border are the coordinate system for the grid

small grids totaling 324 m^2 at El Verde. Sampling schemes and temporal extents of study differed among the areas. as detailed below. In general, sampling occurred between 19:30 and 03:00 h and involved visual examination of all available surfaces (e.g. vegetation, litter, rock, soil) for the presence of snails. For the most part, survey methodologies were adapted from those of Willig and Camilo (1991) for the two large grids and from those of Cary (1992) for the three small grids; consequently, only salient features of design and sampling are described here. Unless otherwise stated, all statistical analyses were performed using SPSS (SPSS Inc., 1990). We considered significance to occur if $p \leq 0.05$, but because of small sample sizes, we also recognized situations as approaching significance if $0.10 \geq p > 0.05$.

Hurricane Recovery Plot

Forty regularly spaced points were selected from the HRP so that the linear distance between adjacent points along rows or columns was 60 m (Figure 15.2). Circular plots (r = 3 m) were established at each point and seasonally sampled (March and July or August) from the wet season of 1991 to the dry season of 1995. The plots were classified as severely damaged (< 50%; 13), moderately damaged (50 to 80%; 14), or little damaged (> 80%; 13) based on a reconstruction of natural and anthropogenic disturbance assessed from aerial photographs and US Forest Service records.

Population analysis

Although estimates of the number of individuals of each species at each point during each sampling period consistently were calculated as the minimum number known to be alive (MNKA), the number of nights upon which the estimates were based differed among time periods. On any night that the HRP was sampled, each point was surveyed by a minimum of two people for at least 20 min. No snails were removed from circular plots, and snails were replaced as close as possible to the point of capture within the plot.

For each common species of snail, comparisons of mean density among damage classes were achieved by one-way analysis of variance (ANOVA) within sampling periods. Variances were heteroscedastic for most species (Bartlett-Box F-test); as a consequence, *a posteriori* tests were conducted based on the Games and Howell method (Sokal and Rohlf, 1981).

Community analyses

Temporal changes in the proportional representation of snail species in the community at El Verde were assessed through a Heterogeneity G-test followed by *a posteriori* comparisons of years within seasons based on unplanned tests of homogeneity of replicates (Sokal and Rohlf, 1981). In all cases, the MNKA of each common snail species (*Gaeotis nigrolineata, Caracolus caracolla, Cepolis squamosa, Nenia tridens, Oleacina playa* and *O. glabra* as a group, and *Polydontes acutangula*) for each circular plot were pooled from all 40 points on the Hurricane Recovery Plot prior to analysis. Differences in community organization among areas with different land-use histories were assessed using discriminant function analysis (DFA) based on Wilks' lambda (SPSS, 1990). For each time period separately, the MNKA of each common species within each circular plot was transformed into a percent by dividing the sum of the MNKA of all species at all points. Thereafter, all possible pair-wise comparisons of land-use categories were conducted based on F-tests (SPSS, 1990). Finally, species richness, evenness, and diversity (Shannon-Weiner index of diversity, see Magurran, 1988) were estimated for pooled quadrats within land-use categories for each time period based on MNKA of each snail species. Confidence intervals for species diversity and species evenness were based on recommendations of Pielou (1974) and Magurran (1988).

Trajectories of secondary succession based on snail species composition were visualized using principal components analysis (PCA) based on the correlation matrix (SPSS, 1990). In particular, each circular plot during each time period was characterized by the transformed MNKA of each species (see approach defined for DFA above). To some extent, this minimized the effect of differences in short-term weather conditions on the activity and apparent numbers of snails detected on different days. Although all data were combined in the PCA, mean (± SE) scores for each principal component axis were calculated separately for each of three land-use categories during each of eight time periods. Recovery in the aftermath of Hurricane Hugo was visualized for each land-use category by constructing trajectories (sequential connection of centroids over time) based on relative snail species composition during wet and dry seasons separately.

Bisley watersheds

Forty points were selected from the grid at Bisley based upon accessibility during night-time surveys. These were the same points examined by Willig and Camilo (1991) in assessing the immediate impact of Hurricane Hugo on invertebrates in the tabonuco forest. The distance between adjacent points along rows or columns was 40 m (Figure 15.3). Circular plots (r = 5 m) were established at each point and sampled during the wet season, immediately prior to Hurricane Hugo (June through August 1989), one year after the storm (July through August 1990), and five years later (July through August 1994). As at the HRP, although estimates of the number of individuals of each species at each point during each sampling period consistently were calculated as MNKA, the number of nights upon which the estimates were based differed among time periods. On any night that it was sampled, each point was surveyed by a minimum of two people for at least 20 min. No snails were removed from circular plots and snails were replaced as close as possible to the point of capture within the plot.

Small grids at El Verde

Several capture-recapture methods were used to estimate densities of two common snails, *C. caracolla* and *N. tridens*, on each of the three small grids (T1, T2, and T3) at El Verde (located near the western edge of the HRP). Seasonal surveys for *C. caracolla* were conducted from the wet season of 1990 to the dry season of 1995 and for *N. tridens* from the dry season of 1992 to the dry season of 1995. Each small grid was divided into 36 quadrats (9 m^2) that served as reference areas while surveying snails. Upon capture, individual snails were provided with a unique alphanumeric mark and subsequently released in the quadrat of discovery as close to the point of capture as possible. The T1 and T2 grids evinced moderate disturbance and canopy openness as a consequence of Hurricane Hugo; T3 was relatively unaffected by the storm (Cary, 1992).

Program CAPTURE (Otis *et al.*, 1978) was used to estimate population density of snails on each grid during each seasonal survey. The heterogeneity model (M_h) was chosen as the estimation algorithm because it allows capture probabilities to differ among individuals (Otis *et al.*, 1978; White *et al.*, 1982)

Table 15.1 List of snail species captured in the Luquillo Experimental Forest (El Verde and Bisley watersheds) from 1990 to 1995

Alcadia alta	*Nenia tridens*
Alcadia striata	*Obeliscus terebraster*
Austroselenites alticola	*Oleacina glabra*
Caracolus caracolla	*Oleacina playa*
Caracolus marginella	*Platysuccinea portoricensis*
Cepolis squamosa	*Polydontes acutangula*
Gaeotis nigrolineata	*Sublina octana*
Megalomastoma croceum	*Vaginulus occidentalis*

and has been shown to be the most appropriate approach for estimating snail density in the tabonuco forest at El Verde (Cary, 1992).

RESULTS AND DISCUSSION

Sixteen snail species were captured at either Bisley or El Verde (Table 15.1). Considerable spatial and temporal variation in density characterized most species. Because of methodological differences among sites, density estimates were derived from different sized sampling units (HRP at El Verde, 28.27 m^2; grid at Bisley, 78.54 m^2; small grids at El Verde, 324 m^2). Still, all densities are reported as numbers of individuals/ha to facilitate direct comparisons. Moreover, in accord with the recommendations of Otis *et al.* (1978), a boundary strip was added to the size of each of the small grids (total area, 374.68 m^2) in the estimation of ecological density.

Temporal change and disturbance at the population level

Large-scale sampling

Trends in population density of each snail species at the El Verde HRP (Figures 15.4 and 15.5) suggested individualistic rather than uniform responses to the disturbance created by Hurricane Hugo. Two species, *Alcadia striata* and *C. squamosa*, showed asymptotic declines in density, whereas *N. tridens* and *Platysuccinea portoricensis* essentially increased in density. *G. nigrolineata* increased from the wet season of 1991 to the dry season of 1993, but decreased thereafter. Conversely, *P. acutangula* decreased from the wet season of 1991 to the dry season of 1993, but increased thereafter. Because of low densities or sporadic detection in surveys, it was difficult to discern any trends in population density for the other snail species.

Compared to El Verde, surveys at Bisley were less frequent, restricted to the wet season, and only focused on the two common snails, *C. caracolla* and *N. tridens*. Nonetheless, Bisley is the only area in the LEF for which extensive data on snail abundance exist prior to Hurricane Hugo, and both species clearly

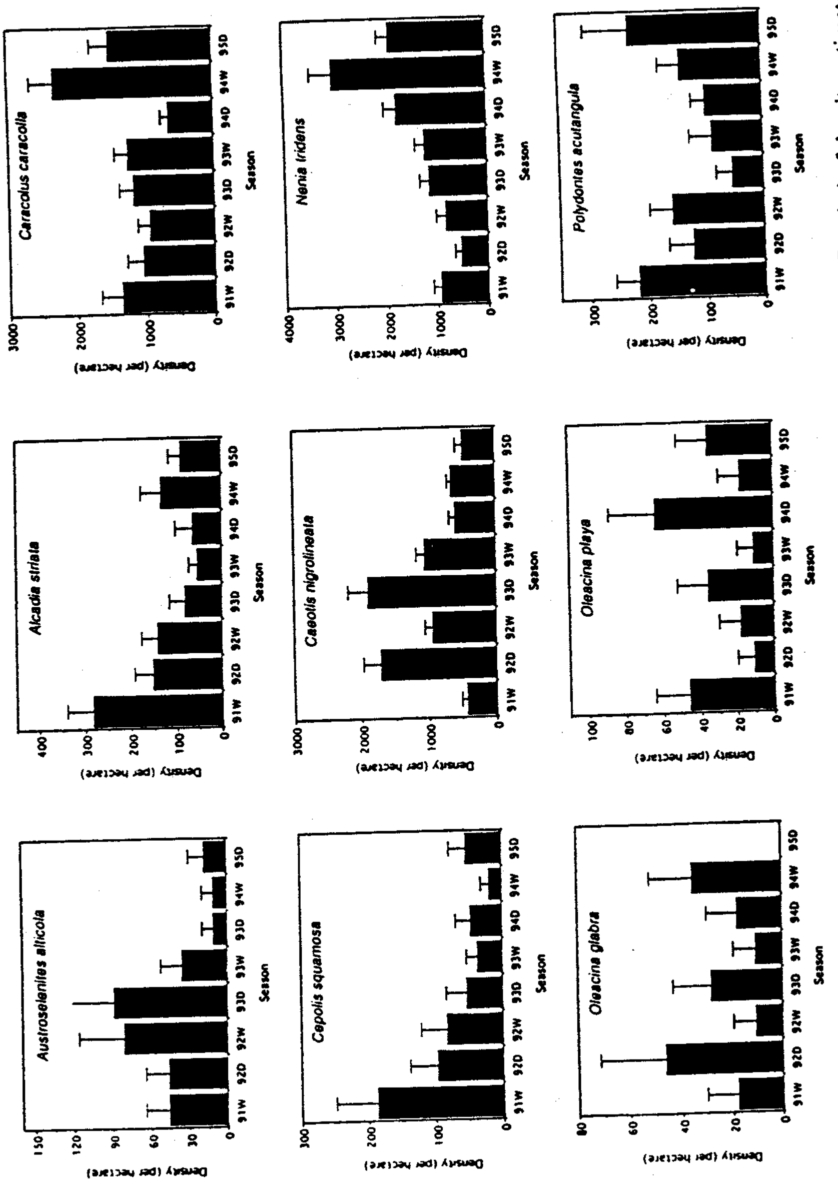

Figure 15.4 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons; W = wet, D = dry) of density estimates (mean ± SE) for 9 common snails at El Verde Hurricane Recovery Plot

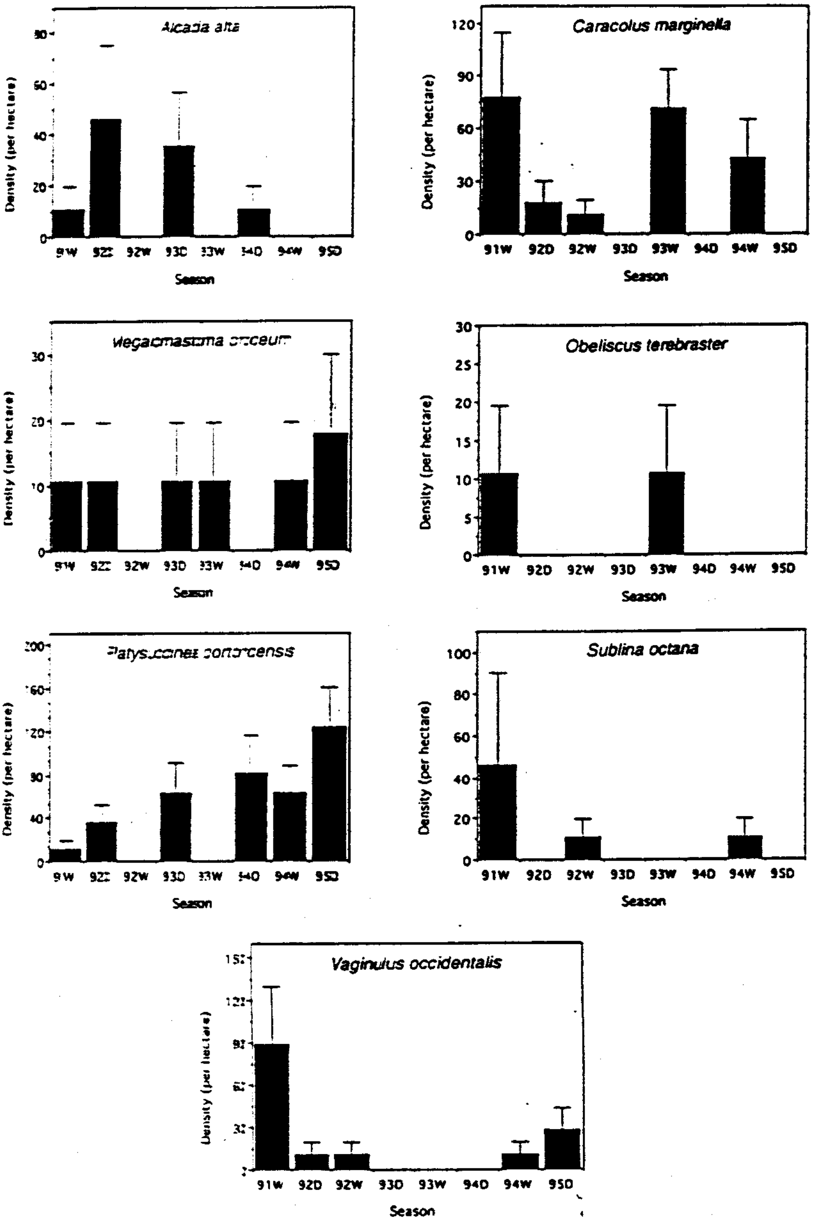

Figure 15.5 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons: W = wet, D = dry) of density estimates (mean ± SE) for 7 less common snails at El Verde Hurricane Recovery Plot

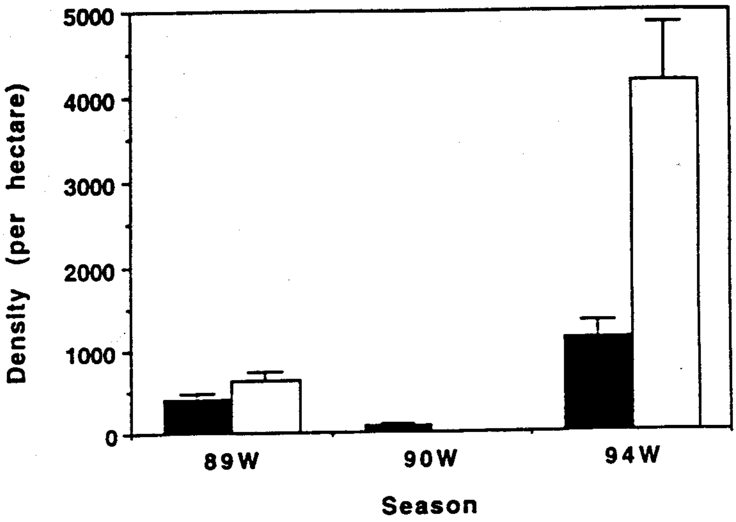

Figure 15.6 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons; W = wet, D = dry) of density estimates (mean ± SE) for common snails (*Caracolus caracolla*, shaded bars; *Nenia tridens*, unshaded bars) on the 13-ha grid at Bisley watersheds

suffered significant reductions in density in the aftermath of Hurricane Hugo (Willig and Camilo, 1991). Yet when compared to pre-hurricane estimates, each species currently enjoys elevated densities – *N. tridens* a six-fold and *C. caracolla* a three-fold increase in average numbers (Figure 15.6).

Small-scale sampling

Considerable temporal and spatial variation characterized estimates of density for *C. caracolla* and *N. tridens* (Figure 15.7) on the small grids at El Verde. Temporal differences likely reflected trajectories of recovery from the impact of Hurricane Hugo. Similarly, spatial differences among small grids reflected topographic variation and differential damage sustained from Hurricane Hugo. In general, the population density of *C. caracolla* gradually increased or remained more or less constant, but that for *N. tridens* initially decreased (dry season of 1992 to wet season of 1993), then increased on each of the three small grids to attain highest density in the wet season of 1994.

The effect of disturbance at the population level

Temporal patterns of population density for *C. caracolla* and *N. tridens* were similar on large and small grids, even though density estimates were quite different (Figures 15.4, 15.6, and 15.7). Differences in historical land use at El

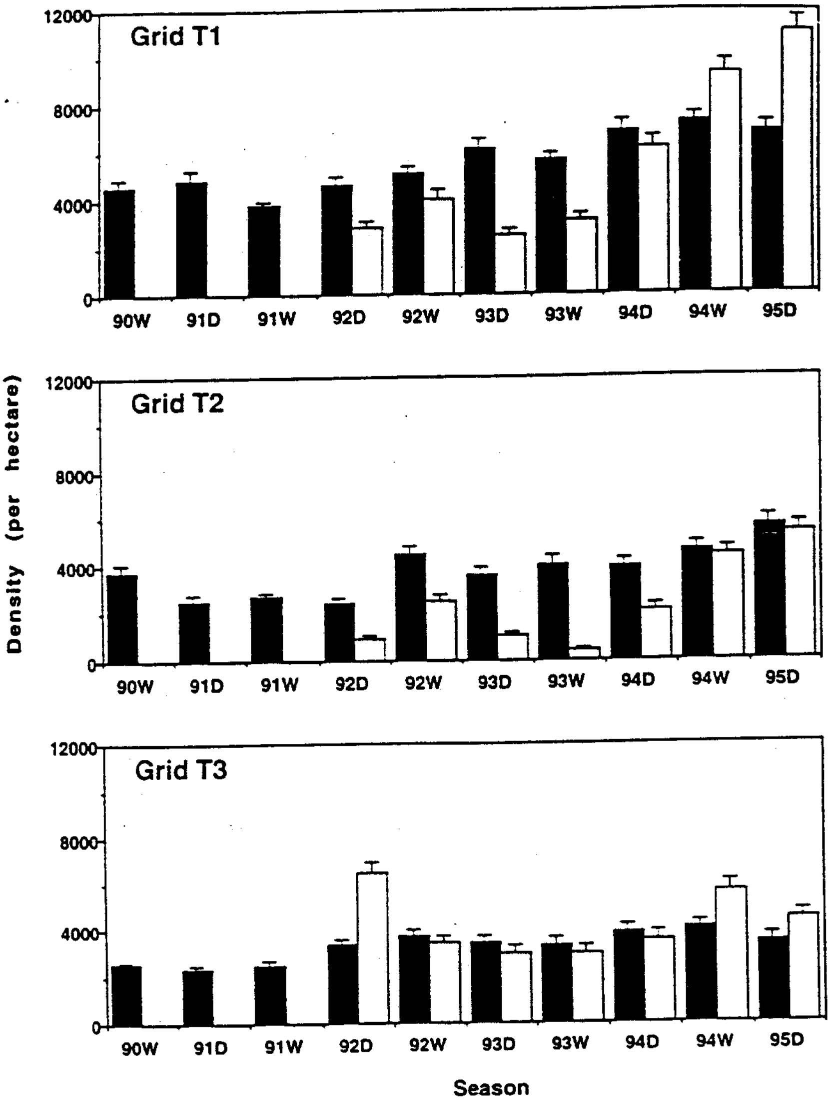

Figure 15.7 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons; W = wet, D = dry) of density estimates (mean ± SE) for *Caracolus caracolla* (shaded, 90W to 94W) and *Nenia tridens* (unshaded, 92D to 94W) at each of three small grids (T1 and T2, disturbed; T3, undisturbed) at El Verde

Table 15.2 Results of one-way analysis of variance to detect mean differences in density among categories of land use on the Hurricane Recovery Plot El Verde (* = significant, $p \leq 0.05$; @ = approaches significant, $0.10 \geq p$ 0.05; ANOVAs that at least approached significance were generally heterocedastic, and the Games and Howell method was used to make *a posteriori* comparisons; all pair-wise contrasts were not significant (NS))

	Time Periods and Seasons							
Species	*1991 wet*	*1992 dry*	*1992 wet*	*1993 dry*	*1993 wet*	*1994 dry*	*1994 wet*	*1995 dry*
Alcadia alta	NS	NS	*	NS	NS	NS	NS	NS
Alcadia striata	@	@	*	NS	NS	NS	*	*
Austroselenites alticola	NS	@	NS	NS	NS	NS	NS	NS
Caracolus caracolla	NS	NS	NS	NS	NS	NS	NS	NS
Caracolus marginella	NS	NS	NS	NS	NS	NS	NS	NS
Cepolis squamosa	NS	NS	NS	NS	NS	NS	NS	NS
Gaeotis nigrolineata	NS	NS	*	NS	NS	NS	NS	@
Megalomasoma croceum	NS	NS	NS	NS	NS	NS	NS	NS
Nenia tridens	@	NS	*	*	*	*	*	NS
Obeliscus terebraster	NS	NS	NS	NS	NS	NS	NS	NS
Oleacina glabra	NS	NS	NS	NS	NS	NS	NS	NS
Oleacina playa	NS	NS	NS	NS	NS	NS	NS	NS
Platysuccinea portoricensis	NS	NS	NS	NS	NS	NS	@	*
Polydontes acutangula	NS	@	NS	NS	*	NS	NS	*
Sublina octana	NS	NS	NS	NS	NS	NS	NS	NS
Vaginulus occidentalis	NS	NS	NS	NS	NS	NS	NS	NS

Verde had no detectable or pervasive effect on the abundance of most snail species (Table 15.2), including the common species (Figures 15.8 through 15.12). At any one time period, land-use-specific differences in abundance were at most detected for four (*Alcadia alta*, *A. striata*, *G. nigrolineata*, and *N. tridens*) of 16 species based on ANOVA (wet season of 1992). Only *N. tridens* consistently exhibited mean differences in density among land-use categories, with higher densities in quadrats suffering moderate disturbance (Figure 15.11). High spatial variation among sites within land-use categories, perhaps as a consequence of previous disturbance or topography, coupled with relatively small sample sizes (13 or 14), may have severely reduced the power of statistical tests to detect true mean differences.

Temporal change and disturbance at the community level

Sample size ($n > 3$) requirements (Sokal and Rohlf, 1981) necessitated pooling data for some species to conduct reliable G-tests. Consequently, temporal comparisons of relative species composition were conducted using eight taxonomic categories: *C. caracolla*, *C. squamosa*, *G. nigrolineata*, *N. tridens*, *P. acutangula*, *Alcadia* spp., *Oleacina* spp., and all other species (Figure 15.13).

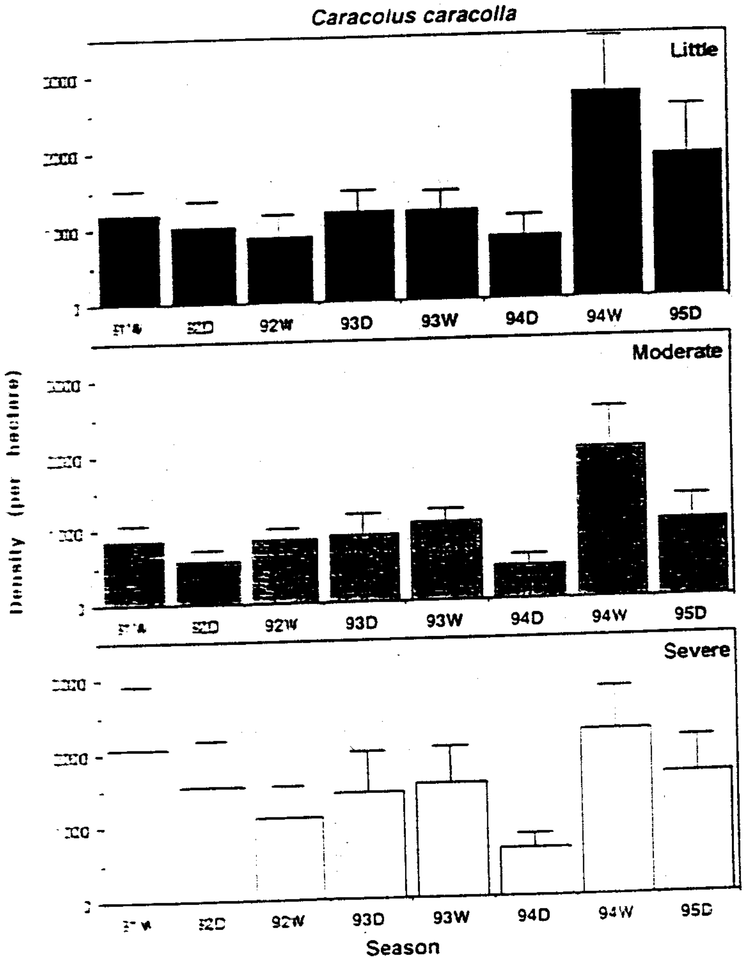

Figure 15.3 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons: W = wet, D = dry) of density estimates (mean ± SE) for *Caracolus caracolla* on the Hurricane Recovery Plot at El Verde. Separate estimates appear for each of the three levels of disturbance (canopy openness) related to historical land-use categories, as indicated by shading (dark = little damage, forest cover > 80%; gray = intermediate damage, forest cover between 80% and 50%; white = severe damage, forest cover < 50%)

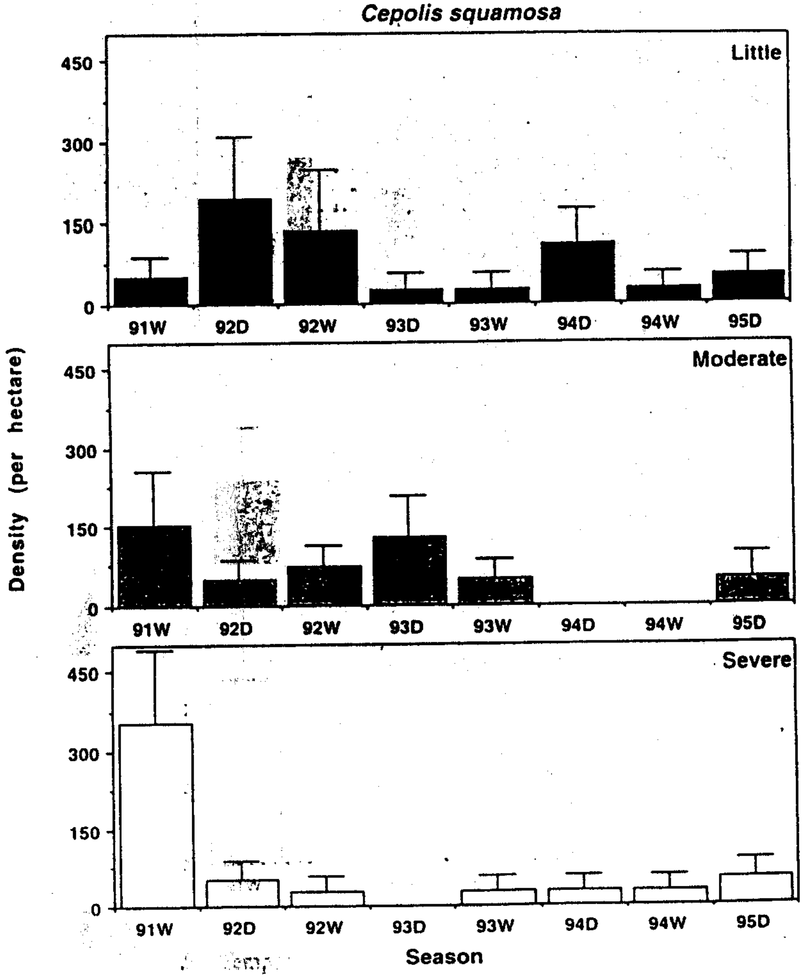

Figure 15.9 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons; W = wet, D = dry) of density estimates (mean ± SE) for *Cepolis squamosa* on the Hurricane Recovery Plot at El Verde. Separate estimates appear for each of the three levels of disturbance (canopy openness) related to historical land-use categories, as indicated by shading (dark = little damage, forest cover > 80%; gray = intermediate damage, forest cover between 80% and 50%; white = severe damage, forest cover < 50%)

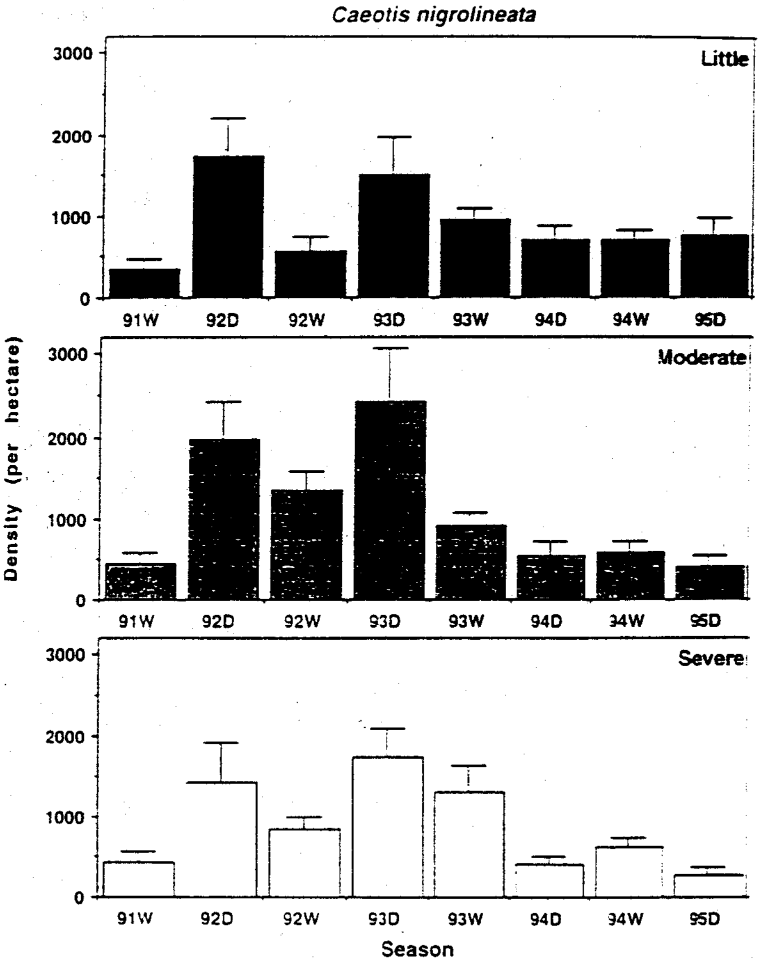

Figure 15.10 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons; with W = wet, D = dry) of density estimates (mean ± SE) for *Gaeotis nigrolineata* on the Hurricane Recovery Plot at El Verde. Separate estimates appear for each of the three levels of disturbance (canopy openness) related to historical land-use categories, as indicated by shading (dark = little damage, forest cover > 80%; gray = intermediate damage, forest cover between 80% and 50%; white = severe damage, forest cover < 50%)

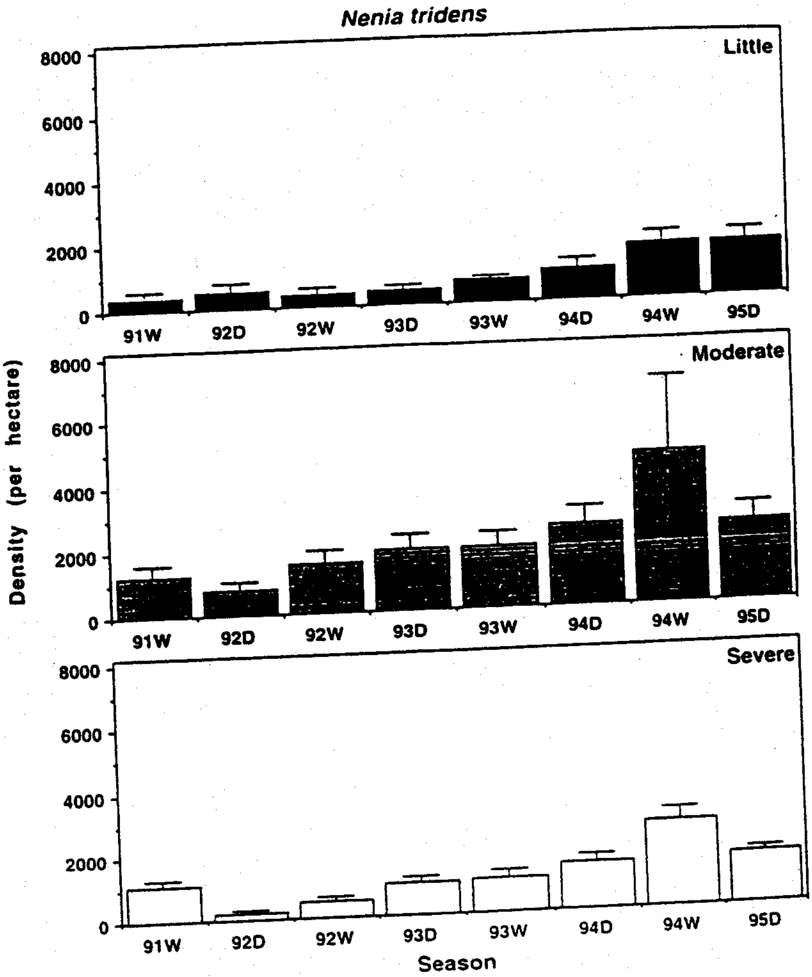

Figure 15.11 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons; with W = wet, D = dry) of density estimates (mean ± SE) for *Nenia tridens* on the Hurricane Recovery Plot at El Verde . Separate estimates appear for each of the three levels of disturbance (canopy openness) related to historical land-use categories, as indicated by shading (dark = little damage, forest cover > 80%; gray = intermediate damage, forest cover between 80% and 50%; white = severe damage, forest cover < 50%)

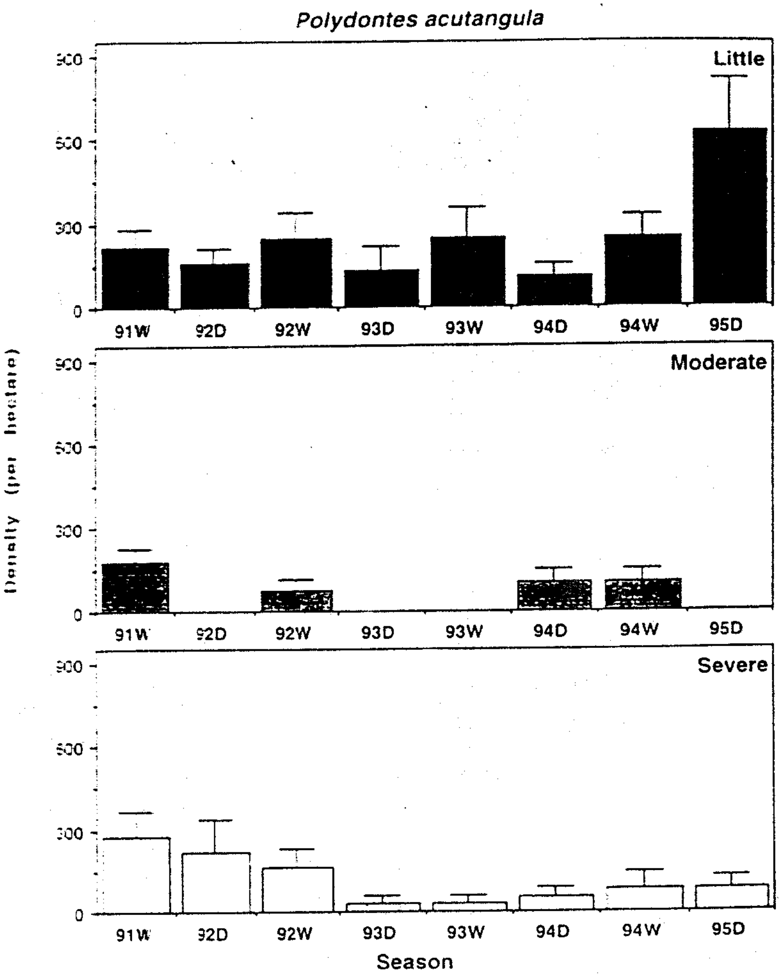

Figure 15.12 Temporal sequence (numbers on the abscissa refer to years, letters refer to seasons; with W = wet, D = dry) of density estimates (mean ± SE) for *Polydontes acutangula* on the Hurricane Recovery Plot at El Verde. Separate estimates appear for each of the three levels of disturbance (canopy openness) related to historical land-use categories, as indicated by shading (dark = little damage, forest cover > 80%; gray = intermediate damage, forest cover between 80% and 50%; white = severe damage, forest cover < 50%)

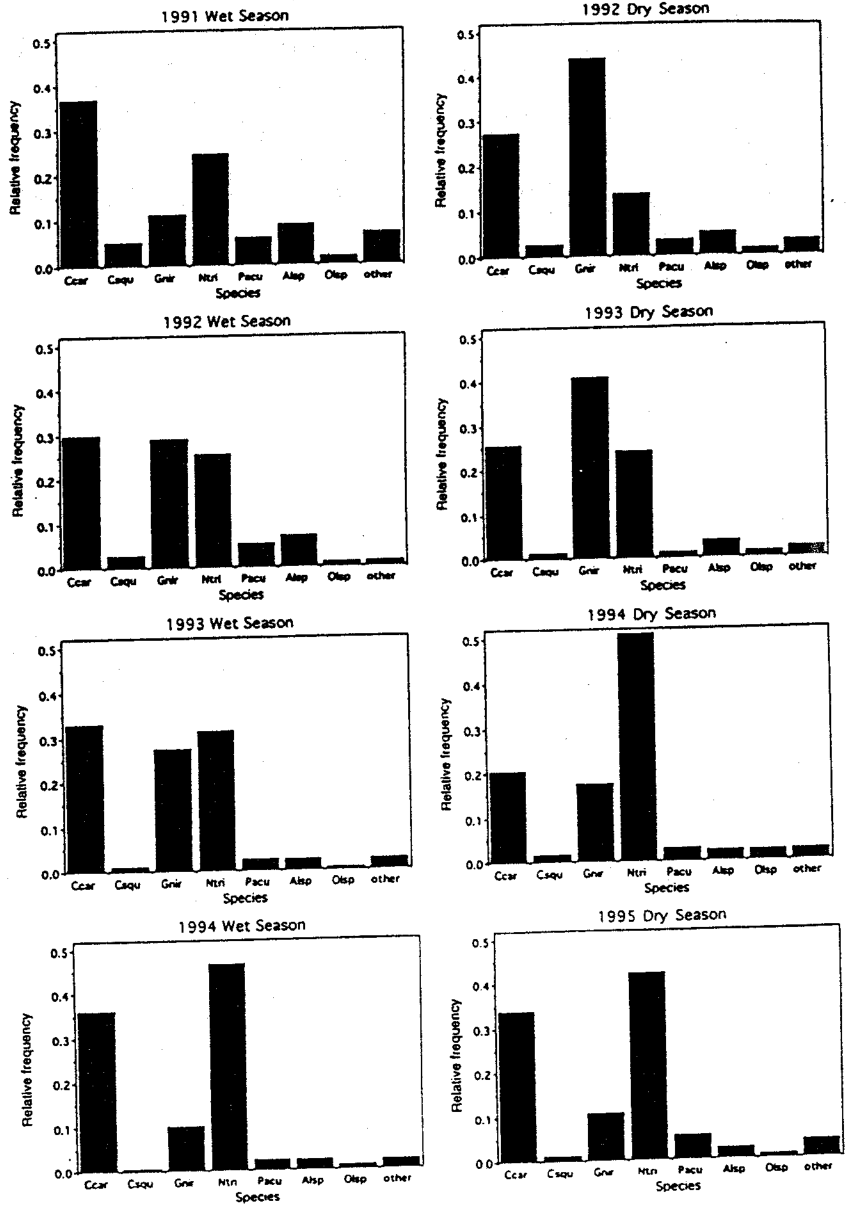

Figure 15.13 Temporal changes in snail species composition on the Hurricane Recovery Plot at El Verde. Species were pooled into categories to meet the requirements of G-tests of independence (Sokal and Rohlf, 1981). Abbreviations are: Ccar = *Caracolus caracolla*, Csqu = *Cepolis squamosa*, Gnir = *Gaeotis nigrolineata*, Ntri = *Nenia tridens*, Pacu = *Polydontes acutangula*, Alsp = *Alcadia alta* and *A. striata*, Olsp = *Oleacina glabra* and *O. playa*, and other = all other snail taxa

Table 15.3 Results of discriminant function analysis of land-use categories (little disturbance = forest cover > 80%; moderate disturbance = forest cover between 80% and 50%; severe disturbance = forest cover < 50%) on the Hurricane Recovery Plot at El Verde, based on the relative density of snail species (disturbance categories classified by historical land use that share the same letter were statistically indistinguishable using pair-wise F-tests ($p > 0.05$))

		Significance		*Pair-wise comparisons*		
Year	*Season*	*DF-1*	*DF-2*	*little*	*moderate*	*severe*
1991	Wet	0.027	0.251	A	B	B
1992	Dry	0.093	0.374	A	A	B
1992	Wet	0.030	0.604	A	B	A
1993	Dry	0.034	0.519	A	B	B
1993	Wet	0.006	0.214	A	B	B
1994	Dry	0.011	0.050	A	B	A
1994	Wet	0.018	0.585	A	B	B
1995	Dry	0.002	0.282	A	B	B

Taxonomic composition was significantly heterogeneous among all eight time periods (Heterogeneity G = 631.6, DF = 42, $p < 0.001$), with fluctuations in relative abundance of *C. caracolla*, *N. tridens*, and *G. nigrolineata* making an appreciable contribution to temporal differences. Moreover, all possible pair-wise comparisons of the four years were significant within the wet ($p < 0.001$) and dry ($p < 0.001$) seasons. Although *C. caracolla* and *N. tridens* dominated the snail community in density two years after Hurricane Hugo (1991), *C. squamosa*, *G. nigrolineata*, *P. acutangula*, and *Alcadia* spp. each represented at least 5% of the individuals in the community (Figure 15.13). Over time, *N. tridens* became more dominant (Figure 15.13), while *P. acutangula* (Figure 15.12), *Alcadia* spp., and especially *C. squamosa* (Fig 15.9) became uncommon, particularly in areas that were most disturbed as a consequence of previous land use.

Seven of eight DFAs that examined differences in snail species composition among land-use categories were significant ($p < 0.034$), with the analysis approaching significance ($p = 0.093$) in the dry season of 1992 (Table 15.3, Figure 15.14). Based on pair-wise F-tests, the severe damage category differed from the little damage category during most time periods, with exceptions occurring in the wet season of 1992 and dry season of 1994. The difference between severe damage and little damage categories approached significance ($p = 0.100$) during the latter time period. Clearly, spatial heterogeneity in the local assembly of snail species was affected by differences in levels of disturbance related to pre-Hugo land use.

In general, temporal variation in snail species composition (PC1 versus PC2 and PC1 versus PC3) was greatest in the severe-damage category, intermediate in the moderate-damage category, and least in the little-damage category (Figure

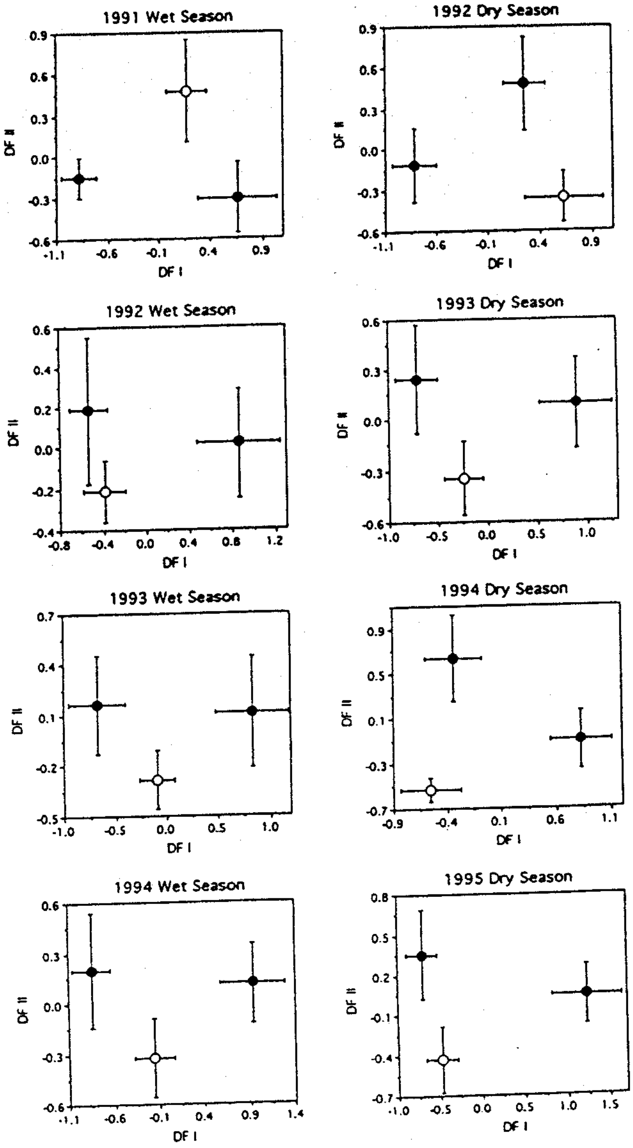

Figure 15.14 Diagrammatic representation of differences in snail species composition among historical land-use categories representing different levels of disturbance (dark circle = little damage, forest cover > 80%; gray circle = moderate damage, forest cover between 80% and 50%; white circle = severe damage, forest cover < 50%) for points on the Hurricane Recovery Plot at El Verde, based on discriminant function analysis of relative species densities. Horizontal and vertical bars passing through group centroids represent the standard errors for DF I and DF II, respectively. Severely damaged sites, identified from 1936 aerial photographs, generally were statistically distinguishable from sites with little damage

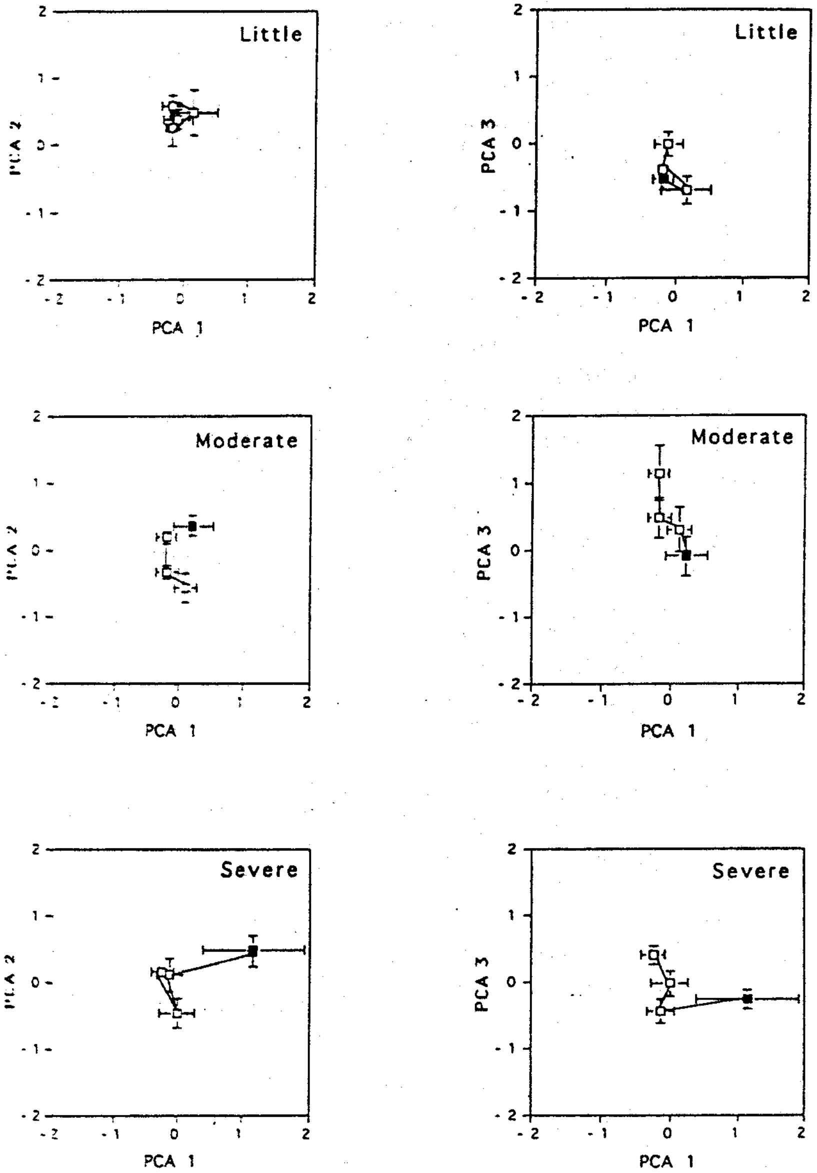

Figure 15.15 Trajectories of recovery for historical land-use categories representing different levels of disturbance (little damage, forest cover > 80%; moderate damage, forest cover between 80% and 50%; severe damage, forest cover < 50%) are based on principal components analysis of relative snail species densities in the wet season on the Hurricane Recovery Plot at El Verde. The wet season of 1991 is illustrated as a shaded square; unshaded squares represent subsequent years and are connected in temporal sequence by lines, thereby defining a trajectory. Horizontal and vertical bars passing through group centroids represent the SE of PC scores

15.15). To some extent, PC1 reflected recovery from disturbance, with the largest displacement along PC1 occurring between the first two sampling periods (1990 and 1991) for severely damaged quadrats. All other temporal variation was minor in comparison. After the first year, all categories followed similar trajectories with respect to PC3, moving in a negative-to-positive direction.

Biodiversity estimates varied considerably over time and differed among land-use categories within time periods (Figure 15.16). With the exception of the 1991 wet season, species diversity was always significantly highest in little disturbed areas compared to areas of moderate or severe disturbance. In addition, areas with little disturbance exhibited the statistically highest species evenness during all time periods. The higher diversity in least disturbed areas was primarily a consequence of the more even distribution of individuals among species than a product of high species richness. In fact, areas with relatively intact canopies (> 80% cover) rarely exhibited the highest number of snail species. More specifically, overlap among 95% confidence intervals of species diversity for land-use categories was rare, occurring only slightly in the dry season of 1992. Similarly, overlap among 95% confidence intervals of species evenness for land-use categories occurred twice – between severe and moderate categories during the dry season of 1992 and 1993.

Disturbance, recovery, and spatial heterogeneity

Land snails of the Luquillo Experimental Forest clearly are affected by frequent, small-scale disturbances such as tree falls (Alvarez and Willig, 1993) in addition to infrequent, large-scale disturbances such as hurricanes (Willig and Camilo, 1991). Response to tree falls was species-specific. Three snail species (*Austroselenites alticola*, *Sublina octana*, and *Megalomastoma croceum*) had indistinguishable densities in light gaps and in surrounding forest, whereas *C. caracolla* and *N. tridens* evinced statistically lower and higher densities, respectively, in tree-fall gaps (Alvarez, 1991; Alvarez and Willig, 1993). In contrast, the short-term response of all monitored snail species at Bisley (*C. caracolla*, *G. nigrolineata*, *N. tridens*, and *P. acutangula*) to Hurricane Hugo was similar: drastic reductions in density (Willig and Camilo, 1991). Five years later, both *C. caracolla* and *N. tridens* exhibited densities that were even higher than those they enjoyed prior to the hurricane (Figure 15.6). This is likely a consequence of the massive input of litter that resulted from the hurricane and the relatively rapid, albeit partial, regeneration of forest canopy.

At the community level, previous land use imparted significant spatial heterogeneity to the tabonuco forest in relation to snail species composition (Table 15.3, Figure 15.14), evenness, and diversity (Figure 15.16). Areas with severe reductions in canopy (based on 1936 aerial photographs) support assemblages of snails that are distinct from those in areas which were relatively undisturbed at that same time. Such differences remain after 60 years and despite a more recent hurricane. At the population level, the legacy of land use is less

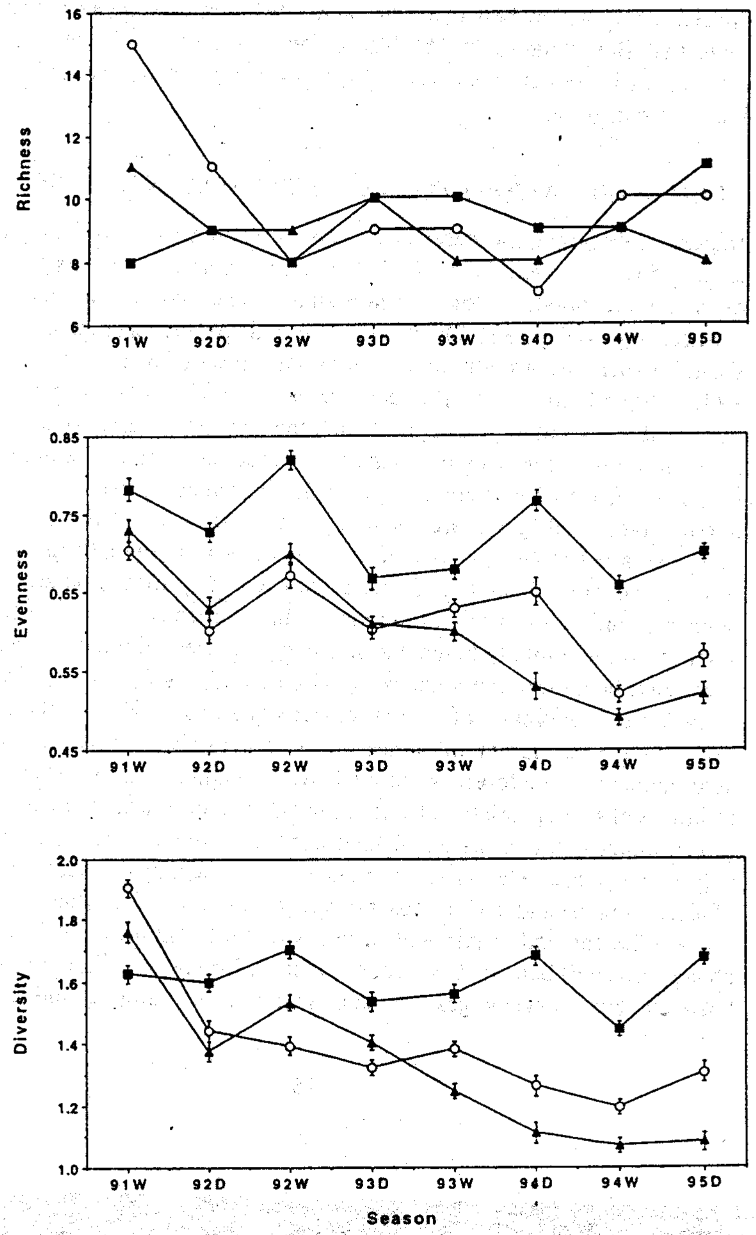

Figure 15.16 Temporal patterns of biodiversity (species richness, diversity, and evenness) with respect to historical land-use categories representing different levels of disturbance (dark squares = little damage, forest cover > 80%; gray triangles = moderate damage, forest cover between 80% and 50%; unshaded circles = severe damage, forest cover < 50%) for snails on the Hurricane Recovery Plot at El Verde. Vertical bars represent 95% confidence intervals for parameters (Pielou, 1974; Magurran, 1988)

apparent. Most snail species did not exhibit significant differences among land-use categories at any time since 1991. Lack of significance for a particular species could be a result of at least three factors: the pattern of damage from Hurricane Hugo may have mitigated the effects of previous land use, species may have been too rare before the hurricane to detect a demographic effect, or power may have been too low to detect an effect for particular levels of variability within land-use categories. Only two species (*N. tridens* and *A. striata*) at least approached significance during a majority of the sampling periods.

In relation to recovery by the snail community as revealed by PCA analysis, most of the changes likely occurred within 3 years of Hurricane Hugo's strike on the tabonuco forest. Areas of the forest that historically experienced little or moderate disturbance did not evince the magnitude of temporal variation in species composition between 1991 and 1992 that was apparent for severely disturbed sites (Figure 15.15). Thereafter (1992 to 1995), few appreciable differences in trajectories based on species composition were evident among land-use categories.

RECOMMENDATIONS FOR LONG-TERM MONITORING

Important demographic parameters may be estimated from data gathered on small grids. For example, on T1, T2, and T3, rigorous estimates of population density were obtained for common snails based upon mark and recapture methodologies (Figure 15.7); other demographic parameters such as home range, spatial dispersion, growth, and survivorship may be estimated as well (Cary, 1992). Nonetheless, the inference space to which these estimates apply is restricted to the small grids upon which they are based. Extrapolation to other areas of the forest may be tenuous or unreliable because of the high degree of spatial heterogeneity characteristic of the tabonuco forest. From a practical perspective, small grids are ideal for obtaining detailed data, but may not comprise a sufficient quantity of heterogeneity to allow extrapolation to the forest in general. If small grids are to be used, they should be apportioned to landscape units in a stratified random fashion. Because of their reduced area, small grids are unlikely to include sufficient numbers of uncommon species to permit application of mark and recapture methodologies with confidence.

In contrast, estimates of population density from the HRP or the Bisley grid apply to a much larger inference space that likely comprises much of the heterogeneity of the forest. Variation in density among sampling units provides estimates of spatial variation. Density may then be correlated to other categorical (e.g. damage classes, historical land uses, gap versus matrix) or continuous (e.g. slope, aspect, elevation, litter cover, shrub density) variables with a goal of discerning the underlying causes of spatial variation in snail species. Although the MNKA method is efficient in terms of time and effort, it is sensitive to changes in snail behavior. As a consequence, it may be difficult to distinguish between behavioral changes associated with reduced humidity and soil moisture during the dry season or during any particular sampling period) from actual changes in density as a consequence of increased or decreased natality. Moreover, density estimates derived from MNKA are underestimates of true population density. They are equivalent to indices of density rather than measures of ecological density *per se*. In fact, density of *C. caracolla* or *N. tridens* was consistently much higher based on mark and recapture methods than on MNKA methods (compare Figures 15.4 and 15.7).

If estimates of true ecological density for common species are important goals of long-term monitoring and less concern surrounds other demographic parameters, we suggest a hybrid approach that includes the advantages of large-scale sampling as well as the benefits of mark and recapture approaches. More specifically, we recommend multiple surveys (≥ 4) of quadrats dispersed on a large grid in a regular or stratified random manner. We also recommend application of mark and recapture protocols to each sampling quadrat rather than the use of MNKA techniques. Only uncommon taxa should continue to be surveyed by MNKA techniques. This hybrid approach would likely result in a modest increase in time and effort compared to using a universal application of MNKA approach to sampling large grids. The data gathered based on mark and recapture techniques easily can be converted to MNKA estimates for use in community analyses that require equivalent data for all taxa.

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REFERENCES

Alvarez, J. (1991). The effects of treefall gaps on a tropical land snail community. M.S. thesis. Texas Tech University, Lubbock, TX

Alvarez, J. and Willig, M.R. (1993). Efects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, **25**, 100–10

Boose, R.R., Foster, D.R. and Fluet, M. (1994). Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs*, **64**, 369–400

Brokaw, N.V.L. and Grear, J.S. (1991). Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica*, **23**, 386–92

Brown, J.H. and Davidson, D.W. (1977). Competition between seed-eating rodents and ants in desert ecosystems. *Science*, **196**, 880–2

Brown, J.H., Davidson, D.W. and Reichman, O.J. (1979). An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist*, **19**, 1129–43

Brown, S., Lugo, A.E., Silander, S. and Liegel, L. (1983). *Research History and Opportunities in the Luquillo Experimental Forest*. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA

Cary, J.F., Jr. (1992). Habitat selection, home range, and population dynamics of *Caracolus caracolla* in the Luquillo Experimental Forest of Puerto Rico. M.S. thesis. Texas Tech University, Lubbock, TX

Davidson, D.W., Inouye, R.S. and Brown, J.H. (1984). Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology*, **65**, 1780–6

Davidson, D.W., Samson, D.A. and Inouye, R.S. (1985). Granivory in the Chihuahuan Desert: interactions within and between trophic levels. *Ecology*, **66**, 486–502

Franklin, J.F., Bledsoe, C.S. and Callahan, J.T. (1990). Contributions of the long-term ecological research program. *Bioscience*, **40**, 509–23

Gannon, M.R. and Willig, M.R. (1994). The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, **26**, 320–31

Garrison, R.W. and Willig, M.R. (1996). Terrestrial invertebrates. In Reagan D.P. and Waide, R.B. (eds.) *A Tropical Foodweb*. University of Chicago Press, Chicago, IL

Heatwole, H. and Heatwole, A. (1978). Ecology of the Puerto Rican camaenid tree-snails. *Malacol.*, **17**, 241–315

Krebs, C.J. (1985). *Ecology: The Experimental Analysis of Distribution and Abundance*. Harper and Row, San Francisco, CA

Lacher, T.E., Jr. and Willig, M.R. (1994). Univariate and multivariate approaches to the analysis of ecotoxicological data. In Kendall R.J. and Lacher, T.E. Jr., (eds) *Wildlife Toxicology and Population Modeling*. Lewis Publishers, Boca Raton, FL, pp.425-37

Levin, S.A., and Paine, R.T. (1974). Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences*, **71**, 2744–7

Magnuson, J.J. (1990). Long-term ecological research and the invisible present. *Bioscience*, **40**, 495–501

Magurran, A.E. (1988). *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, NJ

Mason, C.F. (1970). Snail populations, beech litter production, and the role of snails in litter decomposition. *Oecologia*, **5**, 215–93

Mooney, H.A. and Gordon, M. (1983). *Disturbance and Ecosystems*. Springer-Verlag, New York

Odum, H.T. and Pigeon, R.F. (1970a). *A Tropical Rain Forest. Book 1.* US Atomic Energy Commission, NTIS, Oak Ridge, TE

Odum, H.T. and Pigeon, R.F. (1970b). *A Tropical Rain Forest. Book 2.* US Atomic Energy Commission, NTIS, Oak Ridge, TE

Odum, H.T. and Pigeon, R.F. (1970c). *A Tropical Rain Forest. Book 3.* US Atomic Energy Commission, NTIS, Oak Ridge, TE

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, **62**, 1–135

Pickett, S.T.A. and White, P.S. (1985). *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, San Diego, CA

Pielou, E.C. (1974). *Population and Community Ecology.* Gordon and Breach Science Publishers, New York

Reagan, D.P. and Waide, R.B. (eds) (1996). *A Tropical Foodweb.* University of Chicago Press, Chicago, IL

Russell-Hunter, W.D. (1983). Overview: planetary distribution of and the ecological constraints upon the mollusca. In Russell-Hunter, W.D. (ed.) *The Mollusca, Volume 6, Ecology.* Academic Press, Orlando, FL, pp.1–27

Scatena, F.N. and Larsen, M.C. (1991). Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, **23**, 317–23

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. and Whitford, W.G. (1990). Biological feedbacks in global desertification. *Science*, **247**, 1043–8

Schulze, E.D. and Mooney, H.A. (1993). *Design and Execution of Experiments on CO_2 Enrichment.* Commission of the European Communities, Brussels

Secrest, M.F., Willig, M.R. and Peppers, L.L. (1996). The legacy of disturbance on habitat associations of terrestrial snails in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*,

Sokal, R.R. and Rohlf, F.J. (1981). *Biometry.* W. H. Freeman and Company, San Francisco, CA

Solomon, A.M. and Shugart, H.H. (1993). *Vegetation Dynamics and Global Change.* Chapman and Hall, New York

SPSS Inc. (1990). *SPSS Advanced Statistics User's Guide.* SPSS Inc., Chicago, IL

Swanson, F.J. and Sparks, R.E. (1990). Long-term ecological research and the invisible place. *Bioscience*, **40**, 502–8

Waide, R.B. (1991a). The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **23**, 475–80

Waide, R.B. (1991b). Summary of response of animal populations to hurricanes in the Caribbean. *Biotropica*, **23**, 508–12

Waide, R.B. and Lugo, A.E. (1992). A research perspective on disturbance and recovery of a tropical montane forest. In Goldammer, J.G. (ed.) *Tropical Forests in Transition.* Birkhauser Verlag, Basel, pp.173–90

Walker, L.R. (1991). Tree damage and recovery from Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **23**, 379–85

Walker, L.R., Browkaw, N.V.L., Lodge, D.J. and Waide, R.B. (1991). Special issue: ecosystem, plant, and animal responses to hurricanes in the Caribbean. *Biotropica*, **23**, 313-521

Walker, L.R., Voltzow, J., Ackerman, J.D., Fernandez, D.S. and Fetcher, N. (1992). Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. *Ecology*, **73**, 691–4

West, D.C., Shugart, H.H. and Botkin, D.B. (1981). *Forest Succession: Concepts and Application*. Springer-Verlag, New York

White, G.C., Anderson, D.R., Burnham, K.P. and Otis, D.L. (1982). *Capture–recapture and Removal Methods for Sampling Closed Populations*. LA 8787-NERP. Los Alamos National Laboratory, Los Alamos, NM

Willig, M.R. (1994). Experimental design, statistical analysis, and demographic models. In Kendall R.J. and Lacher, T.E. Jr., (eds) *Wildlife Toxicology and Population Modeling*. Lewis Publishers, Boca Raton, FL, pp.489–95

Willig, M.R. and Camilo, G.R. (1991). The effect of Hurricane Hugo on six invertebrate species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, **23**, 455–61

Woolbright, L.L. (1991). The impact of Hurricane Hugo on forest frogs in Puerto Rico. *Biotropica*, **23**, 462–7

Zimmerman, J.K., Everham, E.M., Waide, R.B., Lodge, D.J., Taylor, C.M. and Brokaw, N.V. (1994). Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology*, **82**, 911–22