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The Effect of Hurricane Hugo on Six Invertebrate Species in the Luquillo Experimental Forest of Puerto Rico[1]

Michael R. Willig and **Gerardo R. Camilo**

Ecology Program, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409-3131, U.S.A.

ABSTRACT

Although the importance of disturbance regimes in affecting ecosystem structure and function is becoming an accepted paradigm in ecology, the consequences of catastrophic events are poorly understood. On 18 September 1989 Hurricane Hugo struck Puerto Rico, with the center of the hurricane passing within ten kilometers of the Luquillo Experimental Forest. This provided a rare opportunity to document direct and indirect effects of a natural disturbance of high intensity, large scale, but low frequency on selected aspects of animal ecology. The densities and spatial distributions of six species of common invertebrates (four snails, *Caracolus caracolla, Polydontes acutangula, Nenia tridens,* and *Gaeotis nigrolineata,* and two walking sticks, *Lamponius portoricensis* and *Agamemnon iphimedeia*) in the tabonuco rain forest were estimated before and after the hurricane. Circular quadrats (radius = 5 m; area = 78.54 m^2) were established at each of 40 points in the Bisley watersheds. Numbers of individuals of each species were counted during nighttime surveys and densities were compared before and after the hurricane via paired t-tests. Both species of walking stick and three of the four species of snail exhibited statistically significant reductions in density after the hurricane. Densities of *N. tridens, G. nigrolineata,* and *A. iphimedeia* were reduced to the point that no specimens were detected in posthurricane surveys. In fact, all species of invertebrates were so rare after the hurricane that comparisons of spatial distribution were only possible for *C. caracolla,* and its distribution was significantly less clumped after Hurricane Hugo (G-test). At the Bisley watersheds, all size categories of *C. caracolla* suffered similar reductions in density; no significant alteration in size distribution was detected after the hurricane (G-test).

RESUMEN

Aunque la importancia de los regímenes de disturbio en el mantenimiento de la estructura y funcionamiento de ecosistemas es un paradigma aceptado hoy en día en ecología, las consecuencias de eventos catastróficos son poco entendidas. El 18 de septiembre de 1989, el huracán Hugo atravesó por Puerto Rico, pasando el ojo del huracán a menos de diez kilómetros del Bosque Experimental de Luquillo. Esto nos proveyó la rara oportunidad de documentar los efectos, tanto directos como indirectos, de un disturbio natural de gran escala e intensidad, pero baja frecuencia, en varios aspectos de la ecología animal del área. Las densidades y distribuciones espaciales de seis especies de consumidores invertebrados (cuatro caracoles, *Caracolus caracolla, Polydontes acutangula, Nenia tridens* y *Gaeotis nigrolineata,* y dos caballitos de palo, *Lamponius portoricensis* y *Agamemnon iphimedeia*), del bosque de tabonuco, fueron estimadas antes y despues del huracán. Se establecieron cuadratines circulares (radio = 5 m; área = 78.54 m^2) en 40 puntos de la vertiente de Bisley. Los números de especímenes observados de cada taxón durante los censos nocturnos fueron comparados mediante pruebas de t pareadas. Ambas especies de caballitos de palo y tres de las cuatro especies de caracoles exhibieron reducciones estadísticas significativas de sus respectivas densidades despues del huracán. Las densidades de *N. tridens, G. nigrolineata* y *A. iphimedeia* fueron reducidas de tal forma que no se detectaron especímenes de estas especies despues del huracán. De hecho, las densidades de todas las especies de invertebrados estudiados fueron tan bajas después del huracán, que tan solo las distribuciones espaciales de *C. caracolla* se pudieron comparar antes y despues de Hugo, y estas sufrieron una reducción significativa en dispersión (prueba de G). En las vertientes de Bisley, donde los efectos del huracán fueron más severos, todas las categorías de tamaños de *C. caracolla* sufrieron disminuciones equivalentes en densidad; no se detectó diferencias significativas entre la estructuración de las clases de tamaños antes y después del huracán (prueba de G).

ALTHOUGH THE ROLE OF DISTURBANCE in affecting the structure and function of ecological systems is a contemporary paradigm in ecology (Pickett & White 1985, Coffin & Laurenroth 1989), few empirical studies have documented the effect of disturbance regimes on terrestrial animal populations. Similarly, few research efforts have been directed toward understanding the role of consumers during recovery from disturbance events. The impact of natural disturbances of large scale and high intensity, but low frequency (*i.e.,* disasters), on invertebrate species is more poorly understood than that on other animal taxa. Nonetheless, disasters may play a critical role

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in shaping ecosystems if their impact is sufficiently pervasive and frequent to be a primary factor to which constituent populations respond. In such a context, current population and community attributes may be a legacy of past disturbance events.

Disturbances have effects that are both direct and indirect. For example, the high winds and elevated levels of precipitation associated with hurricanes may have devastating effects on the biota that are manifested by immediate mortality and morbidity. These are effects that are most frequently detected for producer populations. Tree death due to uprooting, stem breaks, and leaf loss, are clear direct effects of disturbance (Walker 1991). Subsequent alterations in microhabitat structure, microclimatic regime, or biotic associations (*e.g.*, competition, predation, mutualism) caused by unequal survivorship or susceptibility to the disturbance constitute indirect effects and can exacerbate or mitigate the direct effects. In practice, separation of direct and indirect effects may be difficult in the absence of immediate postdisturbance research.

In the Luquillo Experimental Forest (LEF), the most common herbivores are invertebrates, specifically phytophagous insects (Martorell 1945) and gastropods (Van Der Schalie 1948). The endemic Puerto Rican walking stick, *Lamponius portoricensis* (Rehn), is found associated with the vegetation of light gaps throughout the tabonuco rain forest of the LEF (Willig *et al.* 1986). This species may be a keystone taxon because it can reach and sustain large population densities within light gaps, where it potentially plays an important role in nutrient turnover (Willig *et al.* 1986, Sandlin Smith 1989). A second species of walking stick commonly found throughout the LEF is *Agamemnon iphimedeia* Moxey, but other than taxonomic, and to a lesser extent, systematic considerations (Van Den Bussche *et al.* 1988), little is known about this insect. Both of these insects are wingless, consequently their dispersal is cursorial.

Snails are another major component of the invertebrate fauna of the Puerto Rican rain forests (Van Der Schalie 1948). The tree-snails of the family Camaenidae are the most dominant gastropods in the LEF (Heatwole & Heatwole 1978). The most abundant camaenid species in the tabonuco rain forest are *Caracolus caracolla* (L.) and *Polydontes acutangula* (Burrow). Other land snails that are common include *Gaeotis nigrolineata* Shuttleworth and *Nenia tridens* (Schweigger) (Alvarez 1991). Diets of the camaenids are diverse and include wood, bark, seeds, leaves, diatoms, algae, and detritus (Heatwole & Heatwole 1978). A recent investigation concerning the light gap dynamics of snails in the tabonuco rain forest revealed that *C. caracolla* tended to avoid gaps; whereas, the slug, *Nenia tridens,* was found in higher densities within these gaps, often in association with dead leaves of the sierra palm, *Prestoea montana* (Alvarez 1991).

STUDY SITE

Puerto Rico, as the easternmost island of the Greater Antilles, is subjected to climatic disturbances such as hurricanes (wind speed >110 km/hr) and tropical storms (wind speed between 70 and 110 km/hr) with relatively high frequency. The Luquillo Experimental Forest, located in the northeast corner of Puerto Rico, was severely affected by Hurricane Hugo because the eye of the storm passed within 10 km of the site (Scatena & Larsen 1991). Over 200 landslides (Scatena & Larsen 1991) and thousands of tipped-over and snapped-off trees (Brokaw & Grear 1991, Walker 1991) occurred throughout the forest. Cyclonic winds emanated from the north and east; thus, most north- and east-facing slopes were almost completely defoliated by the hurricane. The Bisley watersheds (see Fig. 1, Scatena 1989) were among the sites most devastated by Hurricane Hugo because they are located on the northeast side of the forest, and because they face northward. Tree mortality was extremely high within these watersheds, that, when added to the defoliation produced by the winds, resulted in a major and pervasive alteration in the structure of the forest. Moreover, the loss of the canopy was accompanied by a dramatic change in the microclimatic regime of the forest floor and understory, where insolation approached 100 percent during subsequent months.

The Bisley watersheds are part of the Luquillo Experimental Forest Long-Term Ecological Research project which has, as a unifying theme, the role of disturbance on ecological structure and function (Franklin *et al.* 1990). The watersheds are part of the Rio Mameyes drainage system. The elevation ranges from 265 m to 455 m, with mean annual precipitation of 3500 mm (Lugo 1986).

The invertebrate fauna of the tabonuco forest is diverse and constitutes critical links in the food web of the forest. Four species of walking stick and 24 species of terrestrial snail are documented from the forest (Table 1), but only two of the former (*L. portoricensis* and *A. iphimedeia*) and four of the latter (*C. caracolla, P. acutangula, N. tridens,* and *G. nigrolineata*) occurred with sufficient frequency at Bisley to be included in the assessment of hurricane effects on the invertebrate fauna.

TABLE 1. *Taxonomic listing of walking sticks and land snails documented to occur in the tabonuco forest of Puerto Rico (Alvarez 1991).*

Walking sticks	
Lamponius portoricensis	*Agamemnon iphimedeia*
Diapherodes achaeles	*Pseudobacteria yersiniana*
Land snails	
Alcadia alta	*Nenia tridens*
Alcadia striata	*Nesovitrea subhyalina*
Austroselenites alticola	*Obeliscus terebraster*
Caracolus caracolla	*Oleacina glabra*
Cepolis squamosa	*Oleacina playa*
Chondropoma riisei	*Oleacina interrupta*
Gaeotis nigrolineata	*Opeas pumilum*
Guppya gundlachi	*Platysuccinea portoricensis*
Habroconus ernsti	*Polydontes acutangula*
Lamellaxis gracilis	*Striatura meridionalis*
Lamellaxis micra	*Subulina octana*
Megalomastoma croceum	*Vaginulus occidentalis*

METHODS

The densities and spatial distributions of six invertebrate species, four snails and two walking sticks, were estimated during the summers immediately before (28 July 1989 to 21 August 1989) and after (19 July 1990 to 20 August 1990) Hurricane Hugo. Circular quadrats (radius = 5 m; area = 78.54 m^2) were established at each of 40 points in the Bisley watersheds (Fig. 1), and the numbers of specimens of each taxon were counted during nighttime surveys. Care was taken to visually scan all vegetation (dead and living), as well as litter, rocks, and exposed soil surfaces during the surveys. In practice, snails or walking sticks active above 5 m from the ground were probably underestimated in the surveys; however, more detailed work in the tabonuco forest at El Verde Field Station (see map, Scatena & Larsen 1991) before the hurricane revealed few specimens occurring above that height. The survey of each quadrat was accomplished by two people on most nights, although up to four individuals participated on some occasions. At least 60 min was required to confidently locate all individuals of all 6 taxa within a particular quadrat.

Each of the same 40 points was surveyed before and after Hurricane Hugo; data were thus logically paired and appropriately analyzed by a paired *t*-test (Sokal & Rohlf 1981) to evaluate the effects of Hurricane Hugo on density of each species separately. Observed spatial distributions were compared to random distributions (Poisson) by Chi-square Goodness of Fit Tests (Sokal & Rohlf 1981) for each species during the pre-Hugo period, and for *C. caracolla* during the post-Hugo period. Low frequencies of occurrence prevented statistical analyses of the other five invertebrate species after Hurricane Hugo (most quadrats did not contain any individuals). Spatial distributions of *C. caracolla* before and after the hurricane were compared by a *G*-test (Sokal & Rohlf 1981). Individuals were measured from the lip to the distalmost portion of the shell and categorized into 9 arbitrary size classes (25 mm $\leq Y_1 <$ 30 mm; 30 mm $\leq Y_2 <$ 35 mm; 35 mm $\leq Y_3 <$ 40 mm; 40 mm $\leq Y_4 <$ 45 mm; 45 mm $\leq Y_5 <$ 50 mm; 50 mm $\leq Y_6 <$ 55 mm; 55 mm $\leq Y_7 <$ 60 mm; 60 mm $\leq Y_8 <$ 65 mm; 65 mm $\leq Y_9$). The size-frequency distributions of *C. caracolla* before and after the hurricane were compared with a *G*-test.

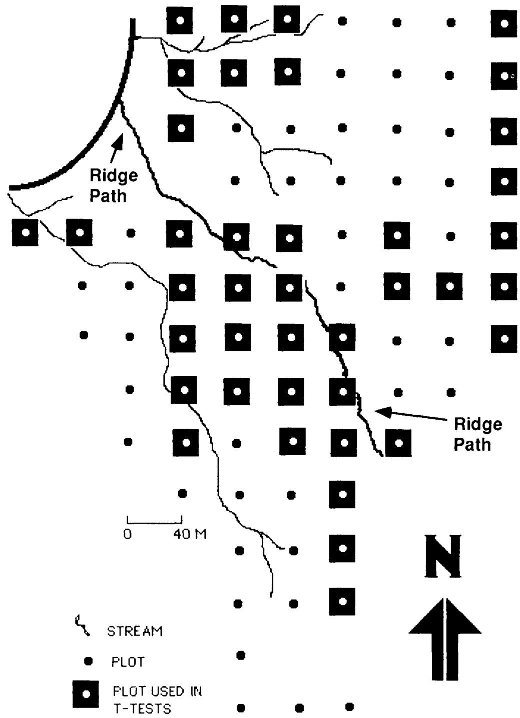

FIGURE 1. Schematic representation of the study area showing the location of the 40 quadrats (solid squares containing the open circles) within the Bisley watersheds which were surveyed for invertebrates before and after the impact of Hurricane Hugo. See general map in Scatena and Larsen (1991).

RESULTS

Hurricane Hugo had a dramatic effect on the invertebrate fauna in the Luquillo Experimental For-

TABLE 2. *Comparison of mean numbers of each invertebrate taxon (mean, $\bar{Y}$; standard deviation S) before and after Hurricane Hugo via a paired* t*-test (df = 39) based upon 40 sites within the Bisley watersheds of the Luquillo Experimental Forest.*

Taxon	$\bar{Y}$(S) Before	$\bar{Y}$(S) After	Paired t-test t	Paired t-test P
Caracolus caracolla	3.1 (3.05)	0.7 (1.05)	−4.918	≪0.001
Polydontes acutangula	0.2 (0.67)	0.0 (0.16)	−1.404	0.168
Nenia tridens	4.9 (5.55)	0.0 (0.00)	−5.570	≪0.001
Gaeotis nigrolineata	0.6 (1.12)	0.0 (0.00)	−3.148	0.003
Lamponius portoricensis	2.9 (3.25)	0.1 (0.27)	−5.431	≪0.001
Agamemnon iphemedeia	0.5 (1.39)	0.0 (0.00)	−2.184	0.035

est. Both species of walking sticks and three of the four species of snails exhibited statistically significant reductions in density in response to the hurricane (Table 2). All taxa suffered population reductions to less than 25 percent of their original pre-Hugo densities. In fact, three of the species (*N. tridens, G. nigrolineata,* and *A. iphimedeia*) were absent from all quadrats after the hurricane. Moreover, the only species not to show a significant reduction in density (*P. acutangula*) was rare before hurricane (average density 0.2 specimens per quadrat) and absent in all but one quadrat after the hurricane.

All species exhibited significantly clumped (underdispersed) spatial distributions before the hurricane (Table 3). Only the posthurricane data for *C. caracolla* was amenable to statistical analysis, and it, too, suggested a clumped spatial distribution. Nonetheless, a comparison of spatial distributions of *C. caracolla* revealed a significant reduction in underdispersion after Hurricane Hugo (Fig. 2). Such rarefaction is probably the result of a pervasive loss of microhabitats favorable to the persistence of snails. All size categories of *C. caracolla* suffered reductions in density after Hurricane Hugo (Fig. 3a). Moreover, these reductions were homogeneously experienced by all size classes (Fig. 3b), as no significant alteration in size distribution was detected after the hurricane.

DISCUSSION

The response of invertebrate populations to natural disturbances is poorly documented, yet "residual" species which survive the direct effects of system-level catastrophies can have a major role during recovery by modifying the rate and pathway of subsequent secondary succession (see Edwards & Schwartz 1981 and Andersen & MacMahon 1985). Fortunately, anthropogenic disturbances of high intensity and large scale, such as clearcutting, may provide insight into the complexities and mechanisms of response by invertebrates. Populations of chewing phytophagous insects remained at low levels after clearcutting a watershed, even though subsequent host plant availability was high (Schowalter *et al.* 1981). These authors suggested that the lower

TABLE 3. *Descriptive statistics for densities of invertebrates per circular quadrat (78.54 m²) in the Bisley watersheds of the Luquillo Experimental Forest. Chi-square Goodness of Fit Tests together with the coefficient of dispersion indicate that each species exhibits a significantly clumped spatial distribution (Cc* = Caracolus caracolla, *Nt* = Nenia tridens, *Gn* = Gaeotis nigrolineata, *Lp* = Lamponius portoricensis, *Ai* = Agamemnon iphemedeia).

Statistic	Cc Before	Cc After	Nt before	Gn before	Lp before	Ai before
Mean	2.952	0.739	4.881	0.524	2.762	0.452
Variance	9.120	1.019	29.181	1.182	10.186	1.815
Coefficient of dispersion	3.894	1.379	5.978	2.256	3.688	4.015
Chi-square	35.977	6.784	211.123	6.427	51.832	12.345
Degrees of freedom	4	2	2	2	5	2
Significance	***	*	***	*	***	*

* 0.05 > P > 0.01.
*** 0.001 > P.

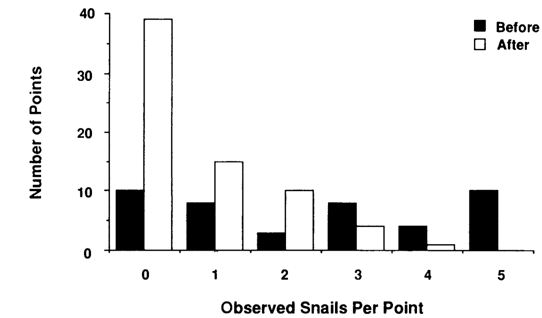

FIGURE 2. A comparison of the frequency distribution of *Caracolus caracolla* before and after Hurricane Hugo at the Bisley watersheds of the Luquillo Experimental Forest via a *G*-test ($G = 24.23$, df = 3, $P \ll 0.001$) indicates a significant change in spatial distribution.

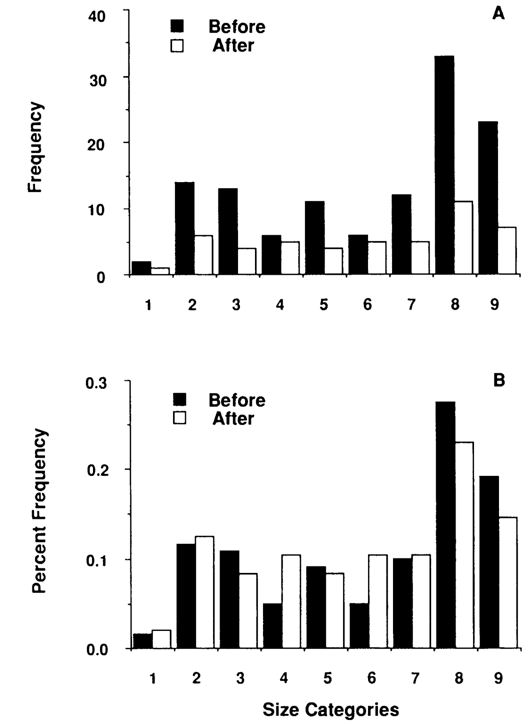

FIGURE 3. Comparison of size frequency distributions of *Caracolus caracolla* before and after Hurricane Hugo in the Bisley watersheds of the Luquillo Experimental Forest. Figure 3a represents the absolute observed frequency distributions, whereas Figure 3b represents the relative observed frequency distributions. No significant shift in size distribution occurred in response to Hurricane Hugo (*G*-test: $G = 1.90$, df = 7, $0.995 < P < 0.975$). Size categories, in mm, are: $25 \leq Y_1 < 30$; $30 \leq Y_2 < 35$; $35 \leq Y_3 < 40$; $40 \leq Y_4 < 45$; $45 \leq Y_5 < 50$; $50 \leq Y_6 < 55$; $55 \leq Y_7 < 60$; $60 \leq Y_8 < 65$; $65 \leq Y_9$.

densities of such chewing phytophagous insects resulted from indirect and secondary effects of logging. Increased predation pressure after clearcutting, rather than a reduction in potential food supply, was hypothesized to have reduced insect numbers. In contrast, a dramatic increase in piercing-sucking herbivorous insects (*e.g.,* aphids) followed logging at the same site (Schowalter *et al.* 1981). A concomitant increase in numbers of aphid-tending ants (*Formica* sp.) paralleled the increased density of their food source. Clearly, the demographic response of insects to clearcutting cannot be predicted with confidence based upon the response of their food supply, because alterations in other biotic interactions, or in the habitat characteristics which affect them, may overwhelm food-based considerations.

Distinctions between direct and indirect effects of Hurricane Hugo are not possible for invertebrates because an intervening period of ten months occurred between the arrival of Hugo and the post-Hugo surveys at the Bisley watersheds. Severe winds such as those experienced during Hugo could certainly dislodge snails and walking sticks from their substrate while moderate flooding could transport individuals appreciable distances. In concert, these direct effects of the Hurricane undoubtedly contributed to the observed reductions in invertebrate density. Subsequent modification of the composition and structure of microhabitats, with attendant changes in microclimatic conditions, could further intensify increases in mortality or reductions in reproductive activity. Increased temperature and reduced humidity (see Heatwole & Heatwole 1978) at the level of the forest floor would increase mortality rates for those individuals surviving the direct effects of Hurricane Hugo. These abiotic factors also could have a secondary effect on invertebrates by reducing the abundance of their vital resources or modifying the density and abundance of species with which snails or walking sticks interact.

Walking sticks are chewing, phytophagous insects and, even though host plant availability was high during the time of the posthurricane population surveys (*Piper* spp., *Urera baccifera,* and *Dendropanax arboreus* were more apparent after [M. Willig, pers. obs.] than before [Willig *et al.* 1986] the hurricane), densities of these insects were unusually low ten months following the hurricane. Younger instars, particularly eggs, would be most susceptible to the effects of flooding and subsequent desiccation following the hurricane. Although a diapause of two years in the egg stadium has been reported for temperate species, this is not the case for tropical species (Bedford 1978) and our observations on *Lamponius* indicate that the egg stadium only persists for 60 to 80 days. Comparable data are lacking for *Agamemnon,* but because *Agamemnon* and *Lamponius* are in the same tribe (Hesperophasmatini) they most likely have similar developmental rates (Bradley & Galil 1977). Hence, an extended diapause most likely does not account for the failure of these species to increase in density within nine months of Hugo's impact.

As in the scenario for walking sticks, the indirect effects of Hurricane Hugo on snails would be most associated with changes in microclimatic conditions at or near the forest floor. Eggs and early growth stages of snails would be particularly vulnerable to elevated temperatures and reduced humidity (Heatwole & Heatwole 1978). Moreover, *P. acutangula* and *G. nigrolineata* are unable to retract their entire foot inside the shell during times of physiological stress. The shell of *P. acutangula* is too small to accommodate all soft tissues; whereas, *G. nigrolineata* contains a small internal shell, with the bulk of the soft tissues in direct contact with the external environment. Potential secondary consequences of these same microclimatic conditions include a reduction in the abundance of algae, diatoms, and fungi—important food resources for *C. caracola* and *N. tridens.*

Although this research cannot distinguish between direct or indirect effects of Hurricane Hugo on snails and walking sticks, it clearly demonstrates that these taxa are among the most severely affected by the hurricane (compare with Covich *et al.* 1991, Reagan 1991, Waide 1991, and Woolbright 1991). Recovery of these taxa is most likely linked with reestablishment of microclimatic conditions similar to those enjoyed before Hurricane Hugo and limited by the recruitment abilities of each species. Populations of species may avoid local extinction during less severe or pervasive disturbances by recruitment from surrounding sites. Within the context of community ecology and biogeography, this phenomenon is known as the rescue effect (Brown & Kodric-Brown 1977) or mass effect (Schmida & Wilson 1985). Such a mechanism is ineffective after disasters such as Hurricane Hugo. The scale of the hurricane's effect and the low mobility of both snails (Heatwole & Heatwole 1978) and walking sticks (Willig *et al.* 1986) result in low recruitment into affected habitats.

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LITERATURE CITED

Alvarez, J. 1991. The population and community level response of snails to light gaps in the tabonuco rain forest of Puerto Rico. M.S. thesis, Texas Tech University, Lubbock, Texas.

Andersen, D. C., and J. A. MacMahon. 1985. The effects of catastrophic disturbance: the residual mammals at Mount St. Helens. J. Mammal. 66: 581–589.

Bedford, G. O. 1978. Biology and ecology of the Phasmatodea. Annu. Rev. Entomol. 23: 125–149.

Bradley, J. C., and B. S. Galil. 1977. The taxonomic arrangement of the Phasmatodea with keys to the subfamilies and tribes. Proc. Entomol. Soc. Wash. 79: 176–208.

Brokaw, N. V. L., and J. S. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. Biotropica 23: 386–392.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration and extinction. Ecology 58: 445–449.

Coffin, D. P., and W. K. Laurenroth. 1989. Disturbance and gap dynamics in a semiarid grassland: a landscape-level approach. Landscape Ecol. 3: 19–27.

Covich, A. P., T. A. Crowl, S. L. Johnson, D. Varza, and D. L. Certain. 1991. Post-Hurricane Hugo increases in atyid shrimp abundances in a Puerto Rican montane stream. Biotropica 23:

Edwards, J. S., and L. M. Schwartz. 1981. Mount St. Helens ash: a natural insecticide. Can. J. Zool. 59: 714–715.

FRANKLIN, J. F., C. S. BLEDSOE, AND J. T. CALLAHAN. 1990. Contributions of the long-term ecological research program. BioScience 40: 509–523.

HEATWOLE, H., AND A. HEATWOLE. 1978. Ecology of the Puerto Rican camaenid tree-snails. Malacologia 17: 241–315.

LUGO, A. E. 1986. Water and the ecosystems of the Luquillo Experimental Forest. U.S. For. Serv. Gen. Tech. Rep. 50-63. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana.

MARTORELL, L. F. 1945. A survey of the forest insects of Puerto Rico. Parts I & II. J. Agric. Univ. P. R. 29: 69–608.

PICKETT, S. T. A., AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York.

REAGAN, D. P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain forest. Biotropica 23: 468–474.

SANDLIN SMITH, E. 1989. Foraging ecology of a neotropical folivore, *Lamponius portoricensis* Rehn (Phasmatodea: Phasmatidae). M.S. thesis, Texas Tech University, Lubbock, Texas.

SCATENA, F. N. 1989. An introduction to the physiography and history of the Bisley experimental watersheds in the Luquillo Mountains of Puerto Rico. U.S. For. Serv. Gen. Tech. Rep. SO-72. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana.

———, AND M. C. LARSEN. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23: 317–323.

SCHMIDA, A., AND M. V. WILSON. 1985. Biological determinants of species diversity. J. Biogeogr. 12: 1–20.

SCHOWALTER, T. D., J. W. WEBB, AND D. A. CROSSLEY, JR. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology 62: 1010–1019.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman & Co., New York, New York.

VAN DEN BUSSCHE, R. A., M. R. WILLIG, R. K. CHESSER, AND R. B. WAIDE. 1988. Genetic variation and systematics of four taxa of neotropical walking sticks (Phasmatodea: Phasmatidae). Proc. Entomol. Soc. Wash. 90: 422–427.

VAN DER SCHALIE, H. 1948. The land and fresh-water mollusks of Puerto Rico. Misc. Publ. Mus. Zool. Univ. Mich., No. 70.

WAIDE, R. B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 475–480.

WALKER, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 379–385.

WILLIG, M. R., R. W. GARRISON, AND A. J. BAUMAN. 1986. Population dynamics and natural history of a neotropical walking stick, *Lamponius portoricensis* Rehn (Phasmatodea: Phasmatidae). Texas J. Sci. 38: 121–137.

WOOLBRIGHT, L. L. 1991. The impact of Hurricane Hugo on forest frogs in Puerto Rico. Biotropica 23: 455–461.