NOTES

Changes in the herbaceous and vine communities at the Bisley Experimental Watersheds, Puerto Rico, following Hurricane Hugo

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Abstract: While herbaceous species and vines constitute a minor portion of the biomass in tropical closed forest ecosystems, they account for a substantial portion of the diversity of these ecosystems and become more conspicuous after natural disturbances. This study describes the changes in abundance and diversity of the herbs and vines during 5 years following Hurricane Hugo at the Bisley Experimental Watersheds, Puerto Rico. The cover of herbs, ferns, and vine species was sampled within a 5-m^2 area in 25 randomly chosen circular permanent plots within the 13 ha of these watersheds. Sampling was done 12, 18, 36, 48, and 60 months after the hurricane. One year after the hurricane the overall mean herbaceous cover in the watersheds was 55%. Four years later, the cover and species richness of herbs and vines, but not ferns, had been significantly reduced. The only change in species diversity (H') was a significant increase in ferns. These changes are explained in terms of the extent and spatial variability of the hurricane damage, as well as changes in the tree component of this ecosystem.

Résumé : Bien que les espèces herbacées et les plantes grimpantes constituent une faible proportion de la biomasse des écosystèmes forestiers tropicaux fermés, elles représentent une partie substantielle de leur diversité et deviennent plus apparentes à la suite de perturbations naturelles. Cette étude décrit les changements dans l'abondance et la diversité des herbes et des plantes grimpantes survenus durant les cinq années qui ont suivi le passage de l'ouragan Hugo dans les bassins hydrographiques expérimentaux Bisley, à Porto Rico. Le recouvrement des herbes, des fougères et des plantes grimpantes a été déterminé sur une superficie de 5 m^2, dans 25 places échantillons circulaires permanentes choisies au hasard dans les 13 ha d'étendue de ces bassins. L'échantillonnage a été fait 12, 18, 36, 48 et 60 mois après le passage de l'ouragan. Un an après l'ouragan, le recouvrement herbacé moyen total, dans les bassins, était de 55%. Quatre ans plus tard, le recouvrement et la richesse en espèces avaient diminué de façon significative chez les herbes et les plantes grimpantes, mais non pas chez les fougères. Le seul changement dans la diversité spécifique (H') concernait son augmentation significative chez les fougères. Ces changements s'expliquent par l'étendue et la variabilité spatiale des dommages causés par l'ouragan et par des changements de la composante arborée de cet écosystème.

[Traduit par la Rédaction]

Introduction

Although herbaceous species constitute a minor component of the biomass of mature closed tropical forests these species may account for more than two fifths of the richness of these ecosystems (Gentry and Dodson 1987). More over, these plants increase in abundance after disturbance events such as tree falls (Brokaw 1985; Smith 1987) or logging. However, little is known about the changes in community attributes of the herbaceous layer of tropical forests following natural or anthropogenic disturbances.

Although infrequent, hurricanes may affect extensive areas in the tropics. An average of five severe (type A) hurricanes have passed over Puerto Rico every century since the early 1700s, and about every 50–60 years one crosses over some part of the Luquillo Mountains of Puerto Rico (Scatena and Larsen 1991). Several studies have reported the damaging effects of these storms on the structure of the woody components of tropical forest ecosystems (e.g., Basnet et al. 1992; Brokaw and Walker 1991; Whitmore 1984), but little has been documented about changes in the herbaceous community as a consequence of these storms (Walker et al. 1996).

In September 1989, Hurricane Hugo damaged a large portion of the Luquillo Experimental Forest in eastern Puerto

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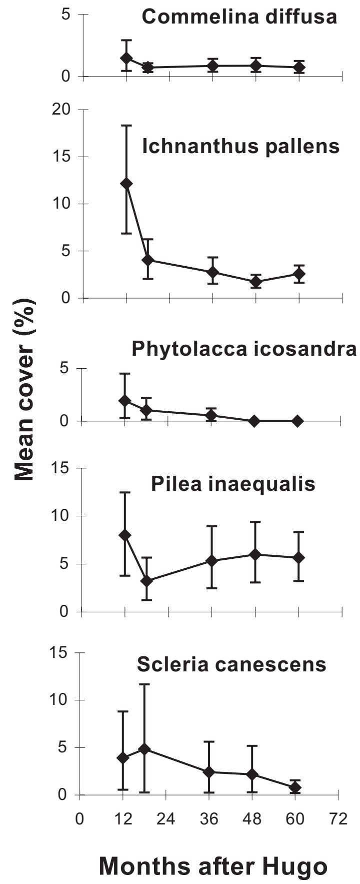
Table 1. Mean cover values by life form for five sampling periods after Hurricane Hugo.

	Months after Hugo				
Life form	12	18	36	48	60
All species	55.3*a*	37.0*ab*	42.7*ab*	35.8*b*	32.7*b*
Vines	9.5*a*	2.8*b*	3.9*ab*	3.2*b*	2.7*b*
Herbs	34.6*a*	22.9*ab*	21.0*ab*	17.1*b*	14.5*b*
Ferns	11.1*a*	11.6*a*	17.6*a*	15.5*a*	15.5*a*

Note: Values with different letters within a row are significantly different based on nonoverlapping bootstrapped 95% confidence intervals.

Fig. 1. Mean cover values for the most frequent herb species over 60 months after Hurricane Hugo. Values are bootstrapped estimates; error bars are the bootstrapped 95% confidence intervals.



Rico, reducing the pre-hurricane standing biomass by 50% (Scatena et al. 1993). This article reports on the first long-term comprehensive observations on the abundance and diversity of the herbs and vines occurring on a tropical watershed after an intense hurricane.

Study area

The USDA International Institute of Tropical Forestry administers three watersheds within the Bisley area in the northeastern section of the Luquillo Experimental Forest (LEF) in Puerto Rico (18°18′N, 65°50′W) for long-term ecological studies. Two of these watersheds are similar in size, topography, and other environmental characteristics (Scatena 1989). These two experimental watersheds each have been marked with a 40 × 40 m grid for long-term studies.

The Bisley Experimental Watersheds (BEW) are located within the Subtropical Wet Forest life zone (sensu Holdridge; Ewel and Whitmore 1973) and are dominated by the tabonuco forest type. The elevation in these watersheds ranges from 260 to 450 m, and their combined total area is approximately 13 ha. The climate is dominated by the trade winds from the northeast, which bring an average of about 3500 mm of rainfall annually. The watersheds are underlain by tuffaceous sandstones, and their soils are well weathered, highly leached, clayey Ultisols that form well defined soil catenas with acid soils on ridges and higher extractable soil nutrients in valleys (Silver et al. 1994).

Methods

Vegetation sampling

Twenty-five grid points were chosen randomly from the 88 grid points already established at the watersheds. At each point, five 1-m^2 quadrats were located at random within a permanent circular plot (5 m diameter) and the percent cover (vertical projection) of ground-rooted herb, fern, and vine species within these quadrats was estimated visually. In most cases herbaceous cover was estimated while looking down over the center of each quadrat, but in some cases where herbaceous species grew above eye level, a cord with a weight was used to delineate the sides of the quadrat. Tree-like ferns were not included in this study. Most vines were herbaceous, but a few woody vines still growing near ground level were included. Congeneric species of seven genera could not be accurately distinguished in the field and were lumped at the genus level (e.g., mountain fern (*Dennstaedtia obtusifolia* (Willd.) Moore) and lacy mountain fern (*Dennstaedia bipinnata* (Cav.) Maxon), and two species named pegapalma (*Marcgravia rectiflora* Triana & Planch., and *Marcgravia sintenisii* Urban)); six other taxa were only identified at the genus level and two only at the family level, for a total of 61 taxa. Nomenclature follows Chinea et al. (1993) and Liogier and Martorell (1982).

Permanent markers were located at two diagonal corners of each quadrat such that future sampling would measure the same areas. Sampling was done at 12, 18, 36, 48 and 60 months after Hurricane Hugo.

Analyses

Species cover estimates of the five quadrats were averaged for each grid point. These mean cover estimates were used to calculate the mean cover of the most frequent species (i.e., present in ≥10 grid points at either the first or the last sampling date), three life forms (herbs, ferns, and vines), and all species combined for the study area at every sampling date. As the mean cover values for the plots were far from normally distributed, the mean cover values and 95% confidence intervals for the study area were calculated by a bootstrapping procedure (Mooney and Duval 1993). These bootstrapped means were obtained by averaging the means of 1000 randomly chosen (with replacement) sets of the original 25 cover estimates (per species or life form). Confidence intervals at the 95% level were obtained from the 2.5% cut-off values of the bootstrapped probability distributions. Significant differences were inferred from nonoverlapping confidence intervals.

Changes in species richness and diversity (i.e., the Shanon–Weaver index) were also compared among sampling dates and by life forms. Repeated measures analysis of variance, using only the anniversary sampling dates (i.e., 12, 36, 48, and 60 months), was used to test for trends in species richness and diversity over time. Significance levels were set at $\alpha = 0.05$ for all analyses.

Fig. 2. Mean cover values for the most frequent vine species over 60 months after Hurricane Hugo. Values are bootstrapped estimates; error bars are the bootstrapped 95% confidence intervals. Note different scales on the *y* axes.

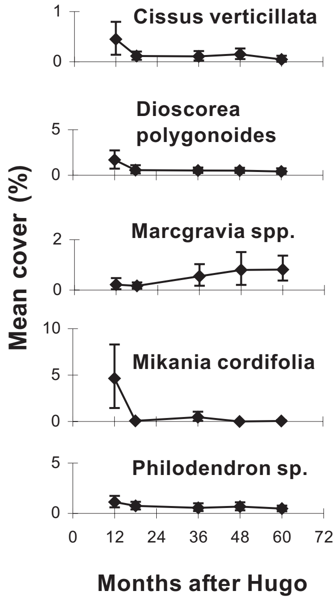


Fig. 3. Mean cover values for the most frequent fern species over 60 months after Hurricane Hugo. Values are bootstrapped estimates; error bars are the bootstrapped 95% confidence intervals.

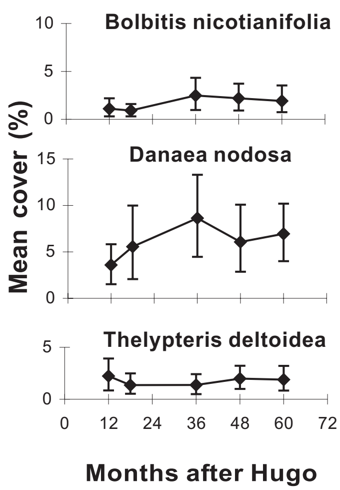


Fig. 4. Changes in species richness and diversity (Shannon index) by life form over 60 months after Hurricane Hugo. Error bars are standard errors. Values within bars indicate the number of months after the hurricane.

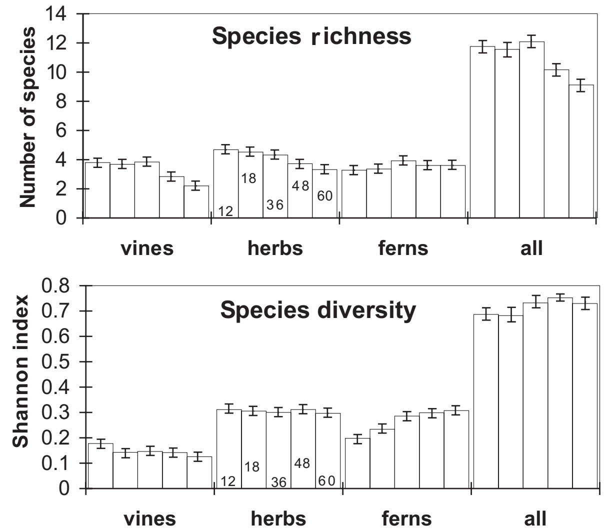


Table 2. Repeated measures analysis of trends in species richness and diversity for various components of the herbaceous community at the Bisley Watersheds.

			Species richness		Species diversity (H')	
Life form	Model	df	F	$p>F$	F	$p>F$
All species	Time	3	16.37	<0.001	1.83	0.149
Ferns	Time	3	2.65	0.055	21.95	<0.001
Herbs	Time	3	9.21	<0.001	0.28	0.837
Vines	Time	3	11.33	<0.001	1.94	0.131

Results

Changes in abundance

Compared with the cover measured 12 months after the hurricane, significant reductions were detected after 48 months for all species combined, as well as for the vines and herbs (Table 1). There was no significant change in mean cover of ferns during the 5-year period. Vine cover significantly decreased from 12 to 18 months after the hurricane. However, this change may have been confounded by seasonal rather than hurricane related trends since this sampling date corresponds to the middle of the mild dry season at this site.

Among the most frequent species, significant cover reductions were only observed in two herbs, carrucillo (*Ichnanthus pallens* (Sw.) Muntro) and southern poke-weed (*Phytolacca icosandra* L.; Fig. 1), and in one vine, guaco (*Mikania cordifolia* (L.f.) Willd.; Fig. 2). These observations suggest that the peak abundance of these frequent species may have been reached before the first 18 months after the hurricane. *Mikania cordifolia* and *P. icosandra* nearly disappeared from the watersheds during the study period. However, *I. pallens* remained as the fourth most abundant and the most frequent herb at the last sampling date. Among the most frequent taxa, the only ones that increased their mean cover during the study period were one woody climber taxon, *Marcgravia* spp. (Fig. 2), and two species of ferns, large knobbly fern (*Danaea nodosa* (L.) J.E. Smith) and ravine fern (*Bolbitis nicotianifolia* (Sw.) Alst.; Fig. 3) but these changes could not be distinguished from random variation at the 5% confidence level.

Changes in species diversity

Sixty-one taxa were found during the study period of which 21 were ferns or fern allies, 19 were herb species, and 21 were vine species. Nineteen of the 61 taxa disappeared from the plots (6 ferns, 4 herbs, and 8 vines), while 9 of the

61 taxa (5 ferns, 2 herbs, and 1 vine) were recruited in the plots after the initial sampling date. The mean species richness for all life forms combined decreased significantly during the study period but no significant change in diversity was detected (Fig. 4, Table 2). Mean fern species richness did not change significantly. However, mean fern species diversity increased significantly, while the mean diversity of the other species categories did not. The contrasting trends of species richness and diversity observed in this study indicate that evenness increased throughout the study period.

Diversity was very similar for ferns and herbs, and much lower for vines throughout the study period. The very low diversity values for vines resulted from high dominance of a few species.

Discussion

A comparison of the results of this study with another study documenting changes in the understory vegetation after Hurricane Hugo at the El Verde site (Walker et al. 1996), located just a few miles west of the BEW, suggests that the impact of this type of disturbance on the abundance of the herb and vine components of this ecosystem depends on the severity of the disturbance. Since the eye of the hurricane passed much closer to the BEW, damage was higher there than at El Verde (i.e., about twice the percentage of snapped trunks and four times the percentage of uprooted trees; Brokaw and Walker 1991). Vines reached maximum cover 12 months after the hurricane and then declined at BEW, while at El Verde, vines declined during the first 18 months and slowly recovered afterwards. Also, maximum fern cover was reached between 1 and 2 years later at BEW (i.e., 36 months after the hurricane) than at El Verde (i.e., 12–23 months after the hurricane; Walker et al. 1996). Disturbance types more severe than Hurricane Hugo at BEW, like clear-cutting (Byer and Weaver 1977) and landslides (Guariguata 1990), further extend the period of dominance by herbs, ferns, and vines.

Differences in the pattern of diversity change among life forms were detected at BEW. While herbs and vines showed a significant decrease in richness during the 5 years, no significant change was detected for ferns. However, ferns were the only life form showing a significant change in diversity. These contrasting trends of species richness and diversity indicate that evenness increased throughout the study period within each life form and for all species combined.

The above results are not in agreement with those of Smith (1987) and Dirzo et al. (1992) in studies of changes in the herbaceous community after the creation of canopy gaps. In our study, maximum species richness was achieved during the first year after the hurricane while Smith (1987) found a significant increase in species richness through 2 years of an experimentally created gap. Meanwhile, in Dirzo et al.'s (1992) study mean richness decreased along a gradient of gap ages, but this change was not significant. However, they detected a significant decrease in diversity, which they attributed to a decrease in evenness. Even though they were studying the same disturbance type, the results of Smith's and Dirzo et al.'s studies are inconsistent. Therefore, it is difficult to propose any patterns of diversity change of the herbaceous components of tropical forests after disturbances that remove the canopy.

However, increase in herbaceous species richness in the very early stages of secondary succession followed by a reduction in richness through the middle stages was also described by Whittaker (1975) in the Brookhaven National Laboratory oak–pine forest, New York. He attributed the initial high herbaceous species richness to higher microhabitat variability and to less intense chemical effects of leaf litter on the soil than at later successional stages. Both of these factors may have also affected the herbaceous community at Bisley. Hurricane Hugo eliminated the leaves of the forest canopy and deposited a large amount of litter on the forest floor (Scatena et al. 1996). It is likely that the high amounts of litter and woody debris superimposed on the topoedaphic environmental variability already present at the site increased microhabitat variability during the early stages of ecosystem recovery, thus providing for higher species richness initially with a later reduction in this parameter as the tree component of this ecosystem recovered.

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