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Geomorphology 13 (1995) 199–213

GEOMORPHOLOGY

Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico

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Received 31 August 1994; revised 14 November 1994; accepted 16 November 1994

Abstract

Relationships between landforms, soil nutrients, forest structure, and the relative importance of different disturbances were quantified in two subtropical wet steepland watersheds in Puerto Rico. Ridges had fewer landslides and treefall gaps, more above-ground biomass, older aged stands, and greater species richness than other landscape positions. Ridge soils had relatively low quantities of exchangeable bases but high soil organic matter, acidity and exchangeable iron. Valley sites had higher frequencies of disturbance, less biomass, younger aged stands, lower species richness and soils with more exchangeable bases. Soil N, P, and K were distributed relatively independently of geomorphic setting, but were significantly related to the composition and age of vegetation.

On a watershed basis, hurricanes were the dominant natural disturbance in the turnover of individuals, biomass, and forest canopy. However, turnover by the mortality of individuals that die without creating canopy openings was faster than the turnover by any natural disturbance. Only in riparian areas was forest turnover by treefall gaps faster than turnover by hurricanes. The same downslope mass transfer that links soil forming processes across the landscape also influences the distribution of landslides, treefall gaps, and the structure and composition of the forest. One consequence of these interactions is that the greatest above-ground biomass occurs on ridges where the soil nutrient pools are the smallest. Geomorphic stability, edaphic conditions, and biotic adaptations apparently override the importance of spatial variations in soil nutrients in the accumulation of above-ground biomass at this site.

1. Introduction

Tropical forests can be viewed on two levels of spatial organization: the geographic scale of 100's to 1000's of hectares, and the scale of landforms and patches that exist within this larger landscape (Webb et al., 1972). At the geographic scale, previous studies have demonstrated relationships between forest structure and the elevation, aspect, and climate of Caribbean mountain ranges (Shreve, 1914; Beard, 1949; Grubb and Tanner, 1976; Weaver and Murphy, 1990). At the scale of patches, recent research in tropical forest ecology has focused on biotic responses to spatially variable resources and the paradigms that the structure and diversity of tropical forests are related to either nutrient abundance or disturbances (Connell, 1978; Crow, 1980; Vitousek and Sanford, 1986; Denslow, 1987; Silver, 1994). While the importance of disturbances and soil nutrients are recognized, patch scale relationships between soil resources, forest composition, and the distribution of multiple disturbances are poorly documented or understood. This paper quantifies the distribution of soil nutrients, natural and anthropogenic disturbances, and vegetation structure at the scale of patches that exist within a landscape of relatively uniform aspect, elevation, climate, and bedrock geology.

SSDI 0169-555X(95)00021-6

We will show that the same processes that influence soil development also influence the distribution of disturbances, and the structure and composition of the forest. Moreover, that geomorphic processes, biotic adaptations, and nutrient cycling interact to override the importance of soil nutrients in the accumulation of above-ground biomass at this site.

2. Study area

2.1. Physiography and geomorphology

This study was conducted in two of the Bisley Experimental Watersheds of the Luquillo Experimental Forest (LEF) of Puerto Rico (Fig. 1). The Luquillo Mountains (18°18′N, 65°50′W) are the predominant physiographic feature in northeastern Puerto Rico and rise from sea level to an elevation of 1075 m over a distance of approximately 10 km. The Bisley watersheds 1 and 2 are on the windward side of the mountains, have a mean annual precipitation of approximately 3500 mm, and occur in the subtropical wet forest life zone (Scatena, 1989). These adjacent watersheds drain a total of 13 highly dissected hectares that are underlain by a Cretaceous age volcanoclastic sandstone of andesitic composition (Briggs and Aquilar-Cortes, 1980). When weathered the ferromagnesium-rich parent material produces a clayey, isohyperthermic, orthoxic, epiaquic pedon (Beinroth, 1982). In comparison to the soils from over 30 tropical montane forest pedons, the concentrations of exchangeable Ca, Mg, and K are intermediate in level at Bisley (Silver et al., 1994). Concentrations of exchangeable soil phosphorus at Bisley are slightly higher, while total soil nitrogen is slightly lower than in other tropical sites. Local variations in soil nutrient abundance have been related to soil series, microtopography, drainage, redox potential, soil aeration, the abundance of nitrate and carbon, and species-induced differences in the biological cycling of nutrients and soil organic matter (Bowden et al., 1992; Johnston, 1992; Lugo, 1992; McDowell et al., 1992).

Boulder lined perennial streams, amphitheater-shaped first order basins, steep slopes, and narrow drainage divides characterize the landscape (Fig. 2). The perennial drainage network is structurally controlled and fed by a dense network of variable source areas, intermittent channels, and leaf-filled swales (Scatena, 1989; Ahmad et al., 1993). Hillslopes typically have convex upper slopes and straight middle slopes. Over 50% of the study area has slopes greater than 45%. Lower slopes are concave in first-order valleys but often straight and nearly vertical where they join perennial channels. First-order valleys are filled with colluvium and physically similar to those described in other humid forest environments (Hack and Goodlett, 1960). Areas with greater than 20 percent stone rubble surfaces are common along perennial channels and near the outlets of first order valleys. Ridges are relatively well drained while concave lower slopes are poorly drained and have the greatest increases in soil-pore pressures following short-dura-

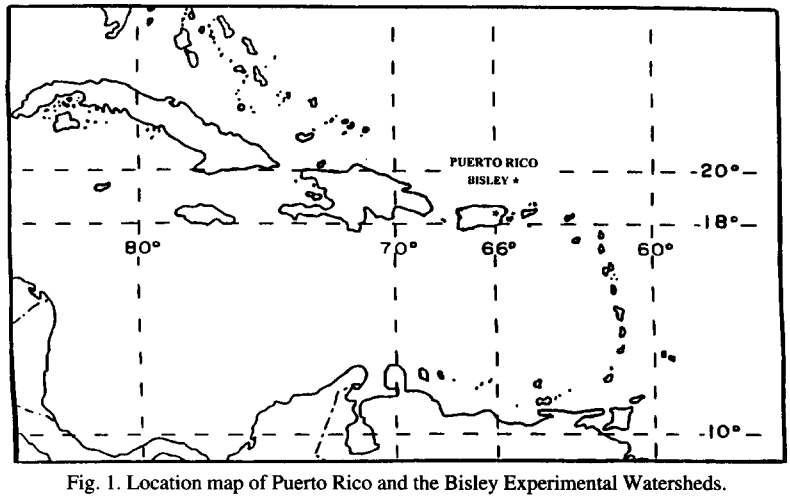

Fig. 1. Location map of Puerto Rico and the Bisley Experimental Watersheds.

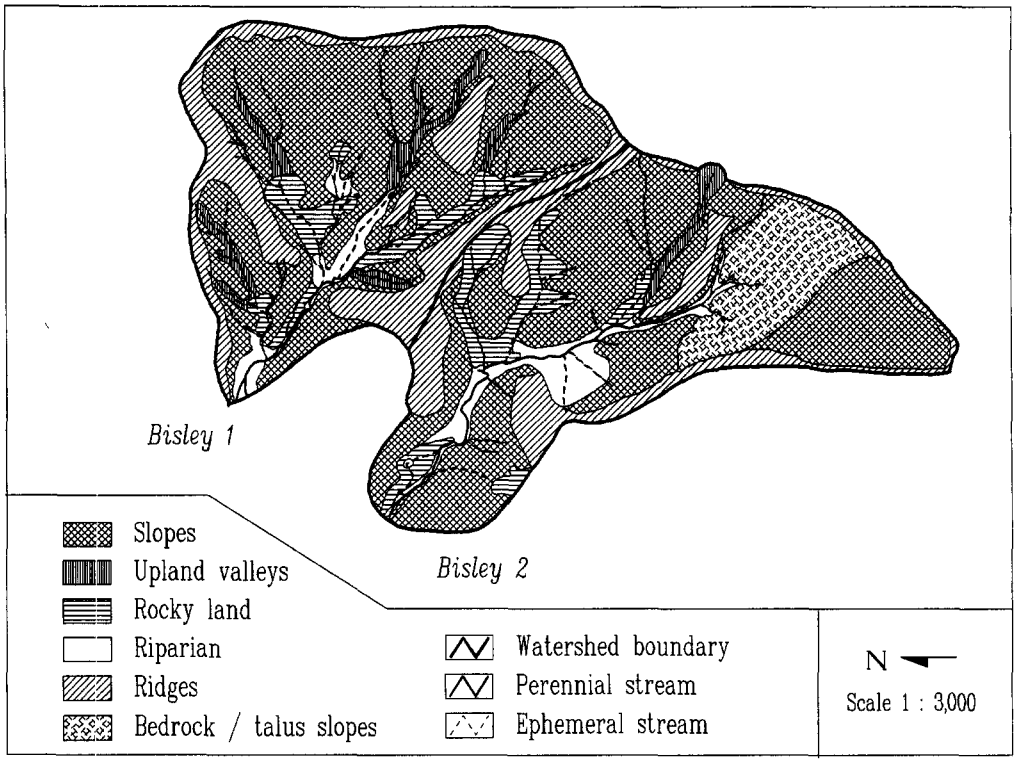

Fig. 2. Geomorphic map of Bisley watersheds 1 and 2, Luquillo Experimental Forest, Puerto Rico.

tion rainfalls (Larsen and Torres-Sanchez, 1992). In general, ridges, slopes, and colluvial valleys have traits of transport-limited landforms (i.e., thick soil profiles where sediment accumulation is faster than removal — Selby, 1982). Perennial stream channels, rocky land, and talus slopes are supply-limited landforms (i.e., fine sediments are virtually non-existent and sediment removal is faster than production).

2.2. *Vegetation and environmental history*

The study watersheds are covered with mature, secondary, tabonuco (*Dacryodes excelsa*) type forest vegetation. This forest type is part of the *Dacryodes–Sloanea* association of Puerto Rico and higher elevation islands of the Lesser Antilles (Beard, 1949; Crow and Grigal, 1979). A recent survey of the Bisley area identified 336 plant species, 255 genera, and 102 families (Chinea et al., 1994). Tabonuco is the dominant tree at the site and primarily occurs along ridges. Over 60% of the basal area of these tabonucos occur in unions of 2 to 24 trees which are connected by self and intraspecific root grafts (Basnet et al., 1993). Relationships between tree diameters and inter-tree distances suggests that individuals within these unions are not affected by inter-tree competition and indicate that the unions are maintained by non-competitive forces. These extensive root graft networks not only reduce the occurrence of windthrow in tabonuco's but also increase the accumulation of organic matter around the base of the trees and may create favorable conditions for nutrient retention and uptake.

The long-term (>50 yr) monitoring of permanent vegetation plots within the LEF has demonstrated stability in the composition of dominants and the integral role hurricanes play in the structure, composition, age, and development of these ecosystems (Crow, 1980, Weaver, 1986, Lugo and Rivera Batlle, 1987). Frequency analysis of hurricane tracks passing over the LEF since 1700 indicates that on the average a hurricane will pass directly over the watersheds once every 50 to 60 years (Scatena and Larsen, 1991). Since 1889, six hurricanes have passed over Puerto Rico and two directly over the study area. The most recent of these, Hurricane Hugo occurred in September 1989. The pre-

vious hurricane to pass directly over the watersheds was in 1932.

Although Pre-Columbian Indians and European settlers were active in the region, low population densities and the inaccessibility of the terrain limited anthropogenic disturbances in the watersheds until the early 1800's (Garcia-Montiel and Scatena, 1994). By the end of the 1800's the drainages had been selectively harvested for valuable timber species. In addition, bananas and root crops were planted along stream channels and some of the slopes were planted with a understory of coffee (*Coffea arabica*). Although the drainages remained forested, when the USDA Forest Service purchased the land in 1934, the commercial forest consisted of "mature and over mature tabonuco" that had been "exploited recklessly" and "severely damaged" by the 1932 hurricane (Gerhart, 1934). Since the mid 1940's the forest has been allowed to developed without human intervention. After nearly 50 years of forest development, the net effect of these human activities on the present forest is considered to be: (1) a depletion of valuable timber species; (2) an enrichment in canopy species used to provide coffee shade, namely *Inga vera*, *Inga fagifolia*, and *Guarea guidonia*, and (3) the immigration of subcanopy crop plants including bananas and coffee (Garcia-Montiel and Scatena, 1994).

3. Methods

3.1. Site characteristics and vegetation

Vegetation and site characteristics were measured in 83 permanent plots that were geographically referenced to a 1:500 scale topographic map of the area. These plots consisted of 10-m diameter circles that were established at the nodes of a 40×40 m grid that covered both watersheds. In 1988 and again 3 months after Hurricane Hugo, each stem within the plots that had a diameter at 1.3 m height (DBH) ≥ 2.5 cm was identified and measured. Species names follow Liogier and Martorell (1982) and Chinea et al. (1994).

The geomorphic setting of each plot was classified in the field into one of 4 groups: ridge, slope, upland valley, or riparian valley (Table 1). These landscape units follow those defined by Hack and Goodlett (1960). Ridges are local divides that receive no upland runoff, have gentle convex slopes, and are areas of divergent flow lines by runoff. Slopes receive runoff from upland areas and transmit runoff to valleys. Valleys are areas where flow lines converge and runoff concentrates. Two types of valleys were distinguished, upland and riparian valleys. Upland valleys included channeled and unchanneled colluvial valleys without perennial open channel flow. Riparian valleys were areas with perennial channels. Species areas curves for each topographic position were derived from the cumulative species and areas of permanent plots in each topographic zone that were randomly selected without replacement (Figs. 3 and 4).

Table 1
Drainage area by geomorphic setting in Bisley watersheds 1 and 2, Luquillo Experimental Forest, Puerto Rico

Geomorphic setting	Area (ha)
Ridges	2.2
Slopes	8.5
Valleys	2.3
Upland valleys	1.4
Riparian valleys	0.9
Total drainage area	13.0

The biomass of above-ground vegetation before and after Hurricane Hugo was calculated using allometric equations that were developed specifically for species in the watersheds (see Scatena et al., 1992 for additional details of equations and pre and post hurricane biomass estimates). The biomass prior to Hurricane Hugo was estimated by applying the allometric equations to the stand data from the 83 permanent plots. The amount of live biomass after Hurricane Hugo was determined by assessing damage to tagged individuals in the permanent plots, measuring accumulation in litter baskets, and by measuring all the downed wood in 59 transects ($40 \text{ m} \times 1 \text{ m}$) that were established between the permanent plots. Biomass was classified as dead only if it was severely broken and showed no signs of re-sprouting three months after the hurricane. Biomass damage in treefall gaps was estimated using the same allometric equations on the tree or trees that caused the gap and on snapped stems within the gap that had a DBH ≥ 10 cm and showed no signs of re-sprouting.

The relative ages of individual trees (Table 2) were estimated from species-specific annual diameter increments determined from repeated measurements in

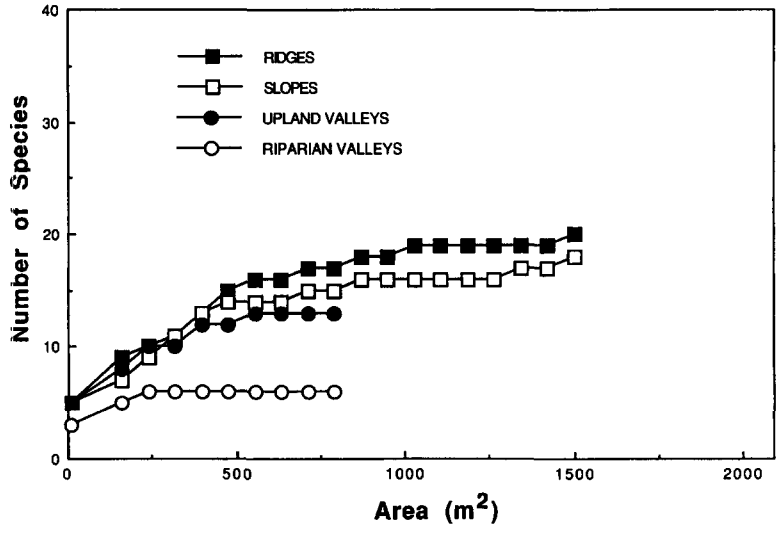

Fig. 3. Species area curves by geomorphic setting for stems ≥ 10 cm DBH in the Bisley watersheds, Luquillo Experimental Watersheds, Puerto Rico.

long-term growth plots that are located in nearby areas of the LEF (Crow and Weaver, 1977). Age groups used in comparison of soil properties were based on the estimated age of the oldest individual in each plot. These ages are considered approximate since they assume a constant growth rate and the original data was based on stems with DBH ≥ 10 cm. Nevertheless, they are used here for broad comparison since the original studies demonstrated that these rates are robust estimators of age, and they have been used in other studies that modeled the dynamics of the LEF forests (Crow and Weaver, 1977; Crow, 1980; Doyle, 1981; Hall et al., 1992).

3.2. *Extractable soil nutrient pools*

In June 1989 soil (0–60 cm) and forest floor were sampled at each vegetation plot in the 40 × 40 m grid. A detailed analysis of the field methods and extraction techniques that were used have been described else-

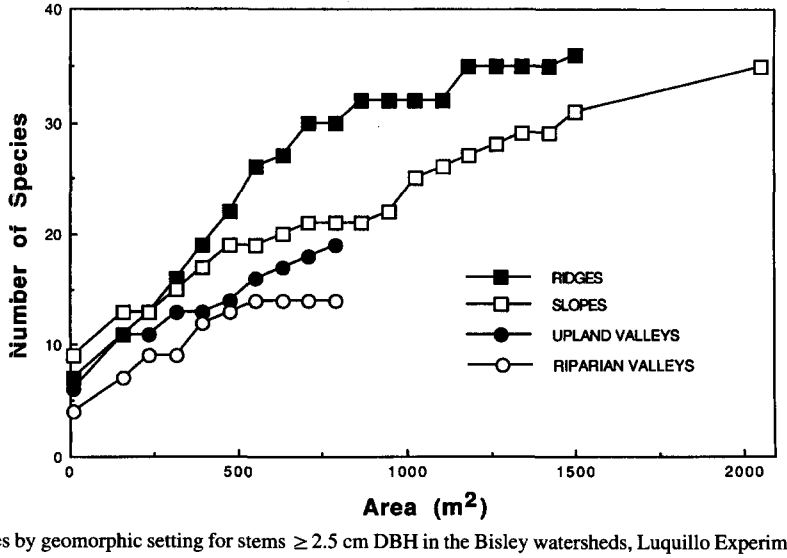

Fig. 4. Species area curves by geomorphic setting for stems ≥ 2.5 cm DBH in the Bisley watersheds, Luquillo Experimental Watersheds, Puerto Rico.

Table 2
Importance value, above-ground biomass, and estimated age by species in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico, prior to Hurricane Hugo in September 1989

Species	IV	Basal area	Density	Frequency	Biomass	Age (yr)		
		(m^2/ha)	(stems/ha)	(%)	(Mg/ha)	Average	Median	Maximum
Dacryodes excelsa	63.0	12.6	214	56	103.1	45	75	302
Sloanea berteriana	53.6	4.0	382	67	25.2	11	17	141
Prestoea montana	28.2	2.3	123	54	6.8	NA	NA	NA
Guarea guidonia	15.2	3.5	31	14	24.0	47	49	108
Ocotea leucoxylon	13.9	0.9	77	25	4.4	11	17	75
Inga fagifolia	11.9	0.8	47	26	4.9	17	23	88
Cyathea sp.	11.4	0.3	63	25	0.7	NA	NA	NA
Psychotria berteriana	8.5	0.1	51	19	0.3	NA	NA	NA
Casearia arborea	8.4	0.4	45	17	0.6	NA	NA	NA
Didymopanax morototoni	8.0	2.1	11	6	3.9	NA	NA	NA
Guarea glabra	7.7	0.1	43	18	0.3	9	12	33
Alchorneopsis floribunda	7.0	1.4	13	9	6.2	NA	NA	NA
Cecropia peltata	5.9	0.9	18	9	3.1	NA	NA	NA
Musa sp.	5.6	0.3	42	8	0.7	NA	NA	NA
Buchenavia capitata	5.1	1.2	8	5	10.4	48	56	120
Alchornea latifolia	4.6	0.4	16	10	1.9	61	37	83
Calophyllum brasiliense	4.6	0.1	28	10	0.2	NA	NA	NA
Manilkara bidentata	4.7	0.5	19	8	2.1	18	23	95
Meliosma herbertii	4.6	0.2	27	9	0.9	NA	NA	NA
Total	300.0	36.7	1480		225.6	29	14	302

Importance value (IV) is the sum of relative basal area, density and frequency of stems ≥ 2.5 cm DBH.
Age of individuals was estimated from Crow and Weaver (1977).
NA = not available.

where (Silver et al., 1994). All soil nutrient analyses reported here were done at the International Institute of Tropical Forestry on air-dried soils (Tables 3 and 4). Chemical extractions for exchangeable Ca, Mg, Na, and Al were made with 1 N KCl. Extractions for exchangeable K and available P, Mn, and Fe follow a modified Olsen's method (Hunter, 1982). A Beckman plasma emission spectrometer (Spectra Span V) was used to analyze the soil extracts. Nitrogen was analyzed with a Kjeldahl process (Bremner and Mulvaney, 1982). Soil pH was measured in a 1:1 water:soil solution with a combination electrode. Soil organic matter was determined by the Walkley–Black method (Nelson and Sommers, 1982). Nutrient pool size per unit area was calculated from the product of bulk density, soil volume to 60 cm depth, and nutrient concentration. Pearson correlation coefficients and ANOVA's were used to determine relationships between nutrient pool size, topographic variables, and vegetation (SAS, 1988).

3.3. Disturbance regimes and ecosystem turnover

During the 2 years prior to Hurricane Hugo, the entire 13 ha was surveyed monthly for treefall gaps, landslides, and other canopy-opening disturbances. At each disturbance the following data were collected: (1) type of disturbance; (2) geographic location; (3) area of canopy disturbed (Brokaw, 1985 and N.V.L. Brokaw, pers. commun.); (4) geomorphic setting; (5) slope and aspect; (6) number, species, and size of woody debris created by the disturbance that was not resprouting; (7) the type of tree failure, i.e., stem snap or root failure.

The relative effectiveness of different disturbance types were ascertained by comparing their turnover periods for forest canopy, individual stems, and above-ground biomass. Turnover periods were calculated as the ratio of total watershed area, pre-hurricane biomass, or number of stems to the total annual flux of those quantities (Bolin and Rodhe, 1973). For example, the

Table 3
Mean and standard error for Bisley soil to 60 cm depth

Group	SOM[a]	N[a]	P[b]	K[c]	Ca[c]	Mg[c]	Na[c]	Fe[c]	Mn[c]	pH	AC[c]	BAS/SOM
Entire drainage	170	8.5	45.4	0.42	1.83	1.37	0.29	3.33	0.572	5.0	3.6	217
($n=83$)	9	0.3	2.7	0.03	0.37	0.24	0.02	0.30	0.063	0.0	0.2	50
Geomorphic setting												
Ridge	210a	9.0a	42.0a	0.39ab	0.88a	0.76a	0.31a	4.74a	0.29a	4.8a	4.0a	122a
($n=22$)	23	0.7	4.8	0.04	0.28	0.26	0.03	0.76	0.09	0.1	0.3	66
Slope	163a	7.7a	39.8a	0.44a	1.56a	1.51ab	0.29a	2.83ab	0.52ab	5.0ab	3.2ab	218b
($n=40$)	11	0.5	3.8	0.05	0.40	0.44	0.03	0.31	0.09	0.1	0.2	76
Upland valley	143ab	7.0ab	47.1a	0.36b	3.18a	1.93b	0.31a	2.68b	0.97b	5.2bc	3.7bc	365c
($n=12$)	18	0.7	5.6	0.04	1.93	0.75	0.05	0.72	0.16	0.1	0.5	221
Riparian valley	131b	7.2b	71.7a	0.48a	3.33b	1.59b	0.24a	2.65b	0.91ab	5.4c	3.8c	266b
($n=9$)	9	1.0	10.3	0.04	0.64	0.35	0.47	0.40	0.20	0.1	1.2	43
R^2	0.11	0.06	0.17	0.04	0.19	0.12	0.02	0.11	0.28	0.2	0.054	0.187
F	3.28	1.69	5.45	1.05	6.25	3.55	0.44	3.30	10.06	7.15	1.53	6.070
P	*0.03*	0.17	**0.002**	0.38	***0.0006***	*0.018*	0.72	0.24	***0.0001***	***0.0003***	0.21	***0.0009***

[a]Mg ha^{-1}, [b]kg ha^{-1}, [c]cmol kg^{-1}.
Relationships that are significant at the 0.05 level are in italics, **0.01** in bold, and ***0.001*** in bold and italics.
SOM = soil organic matter plus forest floor, AC = exchangeable acidity for 0–10 cm, BAS/SOM = (K + Ca + Mg + Na)/SOM, in cmol per kg of SOM.
Means with the same letters are not different at the 0.05 level by Duncan's multiple range test for the 0–10 cm depth only.
R^2, F, P refer to ANOVA results for the entire 0–60 cm profile. See text for details.

turnover of above-ground biomass by slope failures was calculated by dividing the pre-hurricane above-ground biomass by the total above-ground biomass in failures per year. The rates of non-catastrophic mortality (i.e., mortality of individuals that die without creating canopy openings) were based on the mortality of tagged individuals in long-term plots within the LEF that were repeatedly measured during the previous inter-hurricane period (Crow, 1980, Lugo and Scatena, 1995).

4. Results

4.1. Closed forest composition and structure

Immediately prior to Hurricane Hugo, tabonuco, *Sloanea berteriana*, and *Prestoea montana* together comprised 60, 51, 49, and 57% of the above-ground biomass, basal area, stem density, and importance value, respectively (Table 2). Biomass, basal area, stem density, and species richness all decreased from ridges to valleys (Table 5). Species–area curves for stems ≥ 10 cm DBH, indicate that the rate of encountering new species rapidly declines in areas smaller than 500 m^2 in riparian zones but requires over 1000 m^2 to stabilize on ridges and slopes (Fig. 3). When all stems ≥ 2.5 cm are considered (Fig. 4) many more species occur in all geomorphic units and the total number of species encountered only stabilizes in riparian areas larger than 500 m^2. This suggests that the distribution of adult trees across the watersheds is being influenced by processes that occur after seedling establishment and is not solely related to seed dispersal.

4.2. Extractable soil nutrient pools

Soil acidity, and the sizes of the soil organic matter and exchangeable nutrients pools were correlated with geomorphic setting, the estimated age of the oldest tree in a plot, and the composition of vegetation in the plot (Tables 3 and 4). Age and the composition of vegetation, which were also correlated with geomorphic setting, explained between 1 and 23% of the variance in nutrient pool size and were significantly correlated to eight soil properties. Geomorphic setting alone explained from 2 to 28 percent of the variance in extractable nutrient pools, was significant for seven soil

Table 4
Mean and standard error for Bisley soil to 60 cm depth

Group	SOM[a]	N[a]	P[b]	K[c]	Ca[c]	Mg[c]	Na[c]	Fe[c]	Mn[c]	pH	AC[c]	BAS/SOM
Age group												
> 120 yr	203a	9.0a	40.7a	4.4a	0.53a	0.46a	0.29a	4.91a	0.29a	4.8a	4.1a	53a
(n=22)	16	0.6	4.7	0.68	0.08	0.07	0.04	0.83	0.09	0.0	0.3	7
60–120 yr	184a	8.4a	46.7ab	4.1a	1.36ab	1.55b	0.27a	3.28b	0.53ab	5.0b	3.8b	204b
(n=33)	18	0.5	4.2	0.51	0.39	0.49	0.03	0.42	0.08	0.1	0.3	84
< 60 yr	135b	6.8a	44.9b	4.2a	2.25b	1.56b	0.31a	2.30b	0.778b	5.1b	3.2c	261b
(n=28)	12	0.6	5.1	0.35	0.40	0.29	0.04	0.30	0.126	0.1	0.4	68
R^2	0.15	0.11	0.01	0.001	0.23	0.16	0.005	0.14	0.17	0.13	0.06	0.23
F	6.67	4.54	0.45	0.18	11.11	7.06	0.51	6.03	7.85	5.65	2.35	11.01
P	**0.002**	**0.014**	0.64	0.84	***0.0001***	**0.002**	0.60	**0.004**	***0.0008***	**0.005**	0.6	***0.0001***
Vegetation group												
Dominated by	177a	8.5a	44.4a	0.48a	1.11a	0.94a	0.29a	3.52a	0.57a	4.9a	3.7a	66a
Dacryodes (n=34)	12	0.5	4.5	0.06	0.19	0.16	0.03	0.60	0.10	0.0	0.3	8
Not dominated by	166a	7.7a	47.2a	0.39a	2.23b	1.60b	0.29a	3.23b	0.54b	5.0b	3.7b	280b
Dacryodes (n=43)	14	0.4	3.8	0.03	0.66	0.43	0.03	0.31	0.80	0.1	0.3	72
R^2	0.12	0.09	0.13	0.03	0.13	0.14	0.022	0.10	0.12	0.10	0.01	0.17
F	4.91	3.48	5.72	1.03	5.72	6.18	0.86	4.30	5.10	4.27	0.50	7.71
P	**0.009**	*0.036*	**0.005**	0.36	**0.005**	**0.003**	0.427	*0.02*	**0.008**	*0.018*	0.61	***0.0009***

[a]Mg ha^{-1}, [b]kg ha^{-1}, [c]cmol kg^{-1}.
Relationships that are significant at the 0.05 level are in italics, **0.01** in bold, and ***0.001*** in bold and italics.
SOM = soil organic matter plus forest floor, AC = exchangeable acidity for 0–10 cm, BAS/SOM = (K + Ca + Mg + Na) / SOM, in cmol per kg of SOM.
Means with the same letters are not different at the 0.05 level by Duncan's multiple range test for the 0–10 cm depth only.
R^2, F, P refer to ANOVA results for the entire 0–60 cm profile.
Age groups are based on age of oldest tree in plot. Vegetation group dominated by Dacroydes were plots where *Dacroydes excelsa* had the greatest biomass of all species in the plot.

Table 5
Above-ground biomass, basal area, stem density, tree species per plot, and the average and median estimated age for stems with DBH ≥ 2.5 cm by geomorphic setting in the Bisley watersheds, Luquillo Experimental Forest, Puerto Rico, prior to Hurricane Hugo (September 1989)

Topographic zone	Biomass (Mg/ha)	Basal area (m^2/ha)	Stem density (stems/ha)	Species per 78 m^2 plot	Age (yr) Avg —Median
Ridges [22]	312.1a	54.2a	1772a	6.8a	32a —14a
	(57.3)	(7.9)	(133)	(0.43)	
Slopes [40]	185.5b	33.4b	1547ab	5.8ab	24a —13a
	(31.2)	(4.6)	(155)	(0.37)	
Upland valley [12]	121.4b	21.3b	1157bc	5.5ab	22a —14a
	(33.1)	(4.0)	(123)	(0.70)	
Riparian valley [9]	119.1b	20.9b	778c	3.8b	29a —18a
	(63.2)	(9.5)	(177)	(0.5)	
Total area [83]	221.3	36.7	1480	5.9	28 —14
	(25.6)	(3.5)	(78)	(0.25)	

Means with the same letter are not significantly different at the 0.05 level according to Tukey's range test.
Number of sample plots in brackets and standard error of the mean in parentheses.

Table 6
Characteristics of treefall gaps between August 1987 and August 1989 in the Bisley watersheds of the Luquillo Experimental Forest, Puerto Rico

Landscape position	Rate of formation (gaps ha^{-1} yr^{-1})	Affected trees per gap number	Canopy opening per gap (m^2)	Above-ground biomass per gap (Mg/gap)
Ridges	0.9	1.8 (0.85, 7)	55 (45, 4)	1.37 (0.10, 4)
Slopes and upland valleys	0.5	2.0 (0.48, 12)	57 (21, 6)	1.99 (1.11, 6)
Riparian valleys	1.7	1.4 (0.61, 13)	104 (65, 9)	1.81 (0.45, 9)
Total drainage area	0.8	1.8 (0.40, 32)	76 (22, 19)	1.78 (0.38, 19)

Standard error and sample size are in parentheses.
Data for trees with DBH ≥ 10 cm.

properties, and was a more robust estimator than simple topographic variables (i.e., distance to ridge top or valley bottom, slope, or the product of slope and slope length). In general, soils on ridges and under older age stands had relatively high levels of soil organic matter, acidity, and exchangeable iron but low levels of exchangeable bases and a small ratio of exchangeable bases per mass of soil organic matter. Lower landscape position soils had more exchangeable bases and less soil organic matter. Soil nutrients that are primarily cycled by biotic processes, like N, P, and K (Jenny, 1980; Silver et al., 1994) were distributed relatively independently of geomorphic setting (Table 3), but were significantly related to either the estimated age of the oldest tree within a plot, or the composition of vegetation within a plot (Table 4). A notable exception is when the entire 0–60 cm pool of P is considered. When only the 0–10 cm pool is considered, P was correlated with the age of vegetation but was not correlated with geomorphic position or forest composition (Tables 3 and 4). The correlation with geomorphic position for the entire 0–60 cm pool is apparently due to a blocking of phosphate adsorption site by organic anions in surface soils (Fox, 1982), and an increase in P adsorption in the subsurface riparian areas that do not have high concentrations of iron. These process interact to increase the relative size of the P pool in subsurface riparian soils compared to ridges or older sites that have high soil organic matter in their surface soils.

4.3. Disturbances

Hurricanes, treefall gaps, and slope failures were the dominant natural disturbances observed in the study area. Catastrophic droughts, fires, or pest out-breaks are not known to have occurred in historic times. The frequency of treefall gaps (Table 6) and slope failures (Table 7) varied systematically with geomorphic setting and increased toward lower landscape positions. All of the slope failures were shallow earth-slides (sensu Varnes, 1976). The median area of failures reported here (175 m^2) is comparable to the median area (161 m^2) of 215 failures measured in the LEF (Larsen and Torres-Sanchez, 1992). The average canopy turnover period by landslides on the volcanoclastic sandstone of the LEF for the period between 1936 and

Table 7
Characteristics of slope failures between August 1987 and December 1989 in the Bisley watersheds, Luquillo Experimental Forest, Puerto Rico

Geomorphic setting	Rate of formation (slides ha^{-1} yr^{-1})	Mean number of affected trees (no./slide)	Median canopy opening (m^2/slide)	Aboveground biomass per slide (Mg/slide)
Ridges [0]	0	0	0	0
Slopes and upland valleys [5]	0.05	6	200 (50)	1.8
Riparian valleys [4]	0.16	4	145 (120)	1.1
Total watershed [9]	0.04	5	175 (56)	1.5

Sample size in brackets and standard error of the mean in parentheses.
Rate of slide formation includes both hurricane and non-hurricane slides and a 57 year recurrence of hurricane slides.
Data are for trees with DBH ≥ 10 cm.

Table 8
Estimated forest turnover period, in years for disturbance regime and geomorphic setting for the Bisley watersheds, Luquillo Experimental Forest, Puerto Rico, for the period from 1932 to 1989

	Canopy area			Biomass				Stems > 10 cm DBH			
	G	H	S	G	H	S	B	G	H	S	B
Ridges	200	57	∞	250	110	∞	80	430	380	∞	75
Slopes	350	57	980	185	95	2000	50	560	190	2070	55
Riparian valleys	60	57	430	40	105	680	30	110	145	400	50
All drainage area	165	57	1300	150	105	3350	55	380	220	3300	55

G = Treefall gaps, H = Hurricane, S = Slope failure, B = background or non-catastrophic mortality.
Slope failures include those associated with hurricane and non-hurricane events.
Biomass and stem turnover periods are based on pre-hurricane above-ground biomass and stem density.

1987 was estimated as 1250 years (Guariguata, 1990) compared to the 1300 estimate reported here (Table 8).

During the 2 years prior to Hurricane Hugo, 21 treefall gaps occurred within the 13 ha study area. The average canopy opening of these gaps was 76 m^2 (Table 6) and is comparable to the 60 to 100 m^2 openings expected from canopy trees of this size that have crown diameters ranging from 8.8 to 11.3 m. The largest fallen tree in each gap averaged 46.8 cm DBH ($SE = 3.8$, $n = 21$) and had diameters among the 4.4% largest stems in the watersheds. The average rate of gap formation across the pre-hurricane forest (0.8 gaps $ha^{-1}\ yr^{-1}$ in Table 6) was slightly lower than the 0.97 to 1.0 range reported for other neotropical forests (Brokaw, 1985; Hartshorn, 1990). The percentage of uproots in treefall gaps (47%) is greater than reported for most lowland neotropical forests, but is within the range reported for all forests (Putz, 1983). The lower rate of gap formation in the Bisley forest is expected considering that these forests are also subject to periodic thinning by hurricanes. The greater fraction of uproots in the Bisley forest is probably a reflection of the steeply sloping topography and high rainfall of the area.

The forest's response to Hurricane Hugo varied, albeit complexly, by tree size class, species, and geomorphic setting. At the scale of the Luquillo Mountains, hurricane damage was very uneven and influenced by regional physiographic features, regional wind velocity gradients, and localized wind shielding (Boose et al., 1994). At the scale of the Bisley watersheds, which was within the most heavily damaged area of the forest (Boose et al., 1994) only 3% of the stems ≥ 2.5 cm had more than 50% of their leaves intact. Nearly 77% of all stems were found standing and nearly half remained vertical. However, 38% were so severely damaged that only their bole remained vertical, or at least 75% of their bole was lying on the ground. For those individuals where at least 75% of the original bole was lying on the ground, uprooting was the most common type of damage and uprooting with crowns intact the most common classification. Uproots were twice as likely to have fallen with intact crowns than without.

Of the four dominant species in the forest, all but *S. berteriana* had increases in relative density and biomass following the hurricane. The dominant species in the forest, tabonuco, was the least likely to have fallen by root failure and had the greatest relative increase in dominance following the hurricane. Not a single tabonuco tree in a root grafted union was uprooted (Basnet et al., 1992). Vegetation in riparian valleys and slopes suffered the greatest hurricane impacts, as measured by percent of stem breaks and uprooted stems per plot (Table 9). However, the net effect of the hurricane on the Bisley forest, which was close to the storm's eye and had a relatively uniform aspect, was a relatively even spatial distribution in the fraction of pre-hurricane biomass lying on the ground, and in the hurricane induced turnover of forest canopy and biomass (Table 8). Additional information on the impacts of the hurricane on Bisley and the LEF can be found elsewhere (Walker et al., 1991; Basnet et al., 1992; Boose et al., 1994).

4.4. Forest age and turnover

Before and after Hurricane Hugo, the largest tree in the watersheds was a 100 cm DBH tabonuco that was estimated to be over 300 years old. All common species had irregular age and diameter distributions. In other parts of the LEF, irregularities in diameter and age distributions have been related to past hurricanes (Weaver, 1986; Lugo and Rivera Batlle, 1987). Half

Table 9
Hurricane impact by geomorphic setting in the Bisley watersheds of the Luquillo Experimental Forest, Puerto Rico

Geomorphic setting and number of plots	Uproots (%)	Breaks (%)	Lying biomass (Mg/ha)	Fraction of pre-hurricane biomass lying on ground (%)
Ridges [22]	8.0 (2.6)	5.9 (5.7)	157	50
Slopes [40]	22.3 (5.2)	4.1 (2.0)	107	42
Upland valley [12]	9.4 (3.4)	6.6 (3.5)	90	26
Riparian valley [9]	24.5 (11.9)	14.0 (6.3)	64	46
Entire drainage area [83]	15.9 (2.8)	6.5 (1.4)	111	50

Shown are average percent of uprooted and bole snapped individuals per plot, above-ground biomass of trees with DBH stems ≥ 2.5 cm on the forest floor, and percent of pre-hurricane biomass that was vigorously regenerating three months after Hurricane Hugo.
Standard error of the mean in parentheses.

the population prior to Hurricane Hugo was estimated to be younger than 14 years old and the median age of all woody stems did not vary with geomorphic setting (Table 5). However, distinct differences in the age distributions in different geomorphic position did occur. In riparian sites, no stem was estimated to be older than 125 years and less than 40 stems/ha were older than 80 years. On ridges, over 170 stems/ha were older than 80 years and 4% of the stems were older than 125 years. A significantly higher number of large trees (>30 cm DBH) on ridges compared to slopes and valleys was also demonstrated by Basnet (1992).

Turnover periods in the Bisley forests vary with disturbance regime, topography, and the forest component considered (Table 8). From the 1932 hurricane through 1989, Hurricane Hugo was the dominant natural disturbance in removing individuals, biomass, or canopy from the Bisley forest. Only along riparian margins was forest turnover by treefall gaps faster than turnover by hurricanes. However, turnover by non-catastrophic processes was faster than any physically induced disturbance and similar to estimates reported in other tropical forests (Putz and Milton, 1982; Lieberman et al., 1985; Hartshorn, 1990). Most of this mortality is from individuals that are subcanopy trees or have crowns that are gradually replaced as the tree dies standing without producing large canopy openings (Crow, 1980).

5. Discussion

Our results demonstrate that the Bisley forest is highly dynamic and affected by different types of disturbances and ecological processes that operate on different spatial and temporal scales. We view these watersheds as a mosaic of landforms that are set within the physiographic setting of the Luquillo Mountains. This regional landscape provides the geologic structure, climate, and broad environmental gradients within which the different forest types of the Luquillo Mountains develop. At the watershed scale, both disturbance frequency and properties of soil and vegetation are strongly interrelated and correlated with local landforms. Because soil catenas and disturbances are fundamental to understanding this ecosystem they are discussed first and then related to the spatial distribution of vegetation.

5.1. The soil catena and disturbances

The pedons of ridges and riparian valleys in the Bisley watersheds can be viewed as end-members of a soil sequence that is physically and genetically related to the transport of water, soil, and nutrients from upper to lower landscape positions. In lower catena positions, this downslope transfer results in saturated, occasionally anaerobic soils where denitrification, hydrolysis, and the reduction and removal of iron from the pedon are common (Bowden et al., 1992; McDowell et al., 1992; Silver et al., 1994). These biogeochemical processes interact within these lower catena pedons to increase the number of available exchange sites (Jenny, 1980; Fox, 1982) and produce pedons that have relatively high quantities of exchangeable bases per unit of soil organic matter (Tables 3 and 4). In addition to affecting soil nutrient pools, the concentration of subsurface water in these lower catena areas also increases

soil pore pressures and the occurrence of slope failures (Larsen and Torres-Sanchez, 1992) and treefall uproots. Apparently, nutrient and water input from upslope areas, impeded drainage, high soil pore pressures, and occasional flooding interact to produce a geomorphically unstable, high stress environment with relatively nutrient-rich soils and a high frequency of treefalls and gaps.

In the upper sections of the catena, soils are comparatively well drained. This downslope flow of water not only leaches and transports base cations to lower landscape positions but also results in lower soil pore pressures and fewer slope failures. Since these upper catena positions are the most geomorphically stable they have also had the greatest opportunity for soil acidification through the removal of bases, the formation of iron–organic matter complexes that block mineral exchange sites, and the accumulation of soil organic matter. Apparently, the interaction of these physical and biogeochemical processes results in relatively stable landforms where vegetation is able to accumulate considerable biomass even though they are growing on relatively nutrient-poor soils.

The spatial distribution of soil nutrients and natural disturbances also influenced the distribution of anthropogenic disturbance in the forest. Moreover, coffee was apparently planted on slopes rather than on acidic ridges or manganese-rich valleys because it is very susceptible to manganese toxicity and is sensitive to low nutrient abundance when soil pH is less than 4.8 (Abruna et al., 1965; Garcia-Montiel and Scatena, 1994). Valley sites were apparently preferred for bananas and root crops because of their deep, relatively nutrient-rich soils and open forest canopies (Young, 1976). Likewise, the geomorphically stable well drained ridge-tops dominated by hardwoods were preferred for trails and timber harvesting, while forested slopes without valuable hardwoods were used to supply wood for charcoal production (Garcia-Montiel and Scatena, 1994).

5.2. The distribution ecosystem processes and the pattern of vegetation.

Hurricanes are the dominant natural disturbance with respect to the turnover of individuals, biomass and forest canopy in the Bisley Forest (Table 8). However, the effectiveness of a disturbance in modifying the geomorphic landscape or the structure and composition of the forest is not only related to it's magnitude and frequency, but also to the destructive and restorative conditions that occur between disturbances (Wolman and Gerson, 1978; Scatena, 1995). Our observations following Hurricane Hugo and the monitoring of stand development following the 1932 hurricane (Crow, 1980; Weaver, 1986), indicate that during inter-hurricane periods, slope failures, treefall gaps, competition, and natural senescence continually modify the forest and result in an increase in the dominance of a few species and individuals. The spatial distribution of environmental conditions and disturbance frequency that are associated with the soil catena play an important role in shaping the forest during these inter-hurricane periods. Moreover, the drainage and geomorphic stability of the upper catena allows for the development of older, larger and more diverse forest stands, even though these same conditions promote soil leaching and acidification. Likewise, the geomorphic instability and edaphic conditions that characterize lower catena positions result in faster forest turnover by disturbances and younger, less diverse stands growing on nutrient-rich soils. Apparently geomorphic stability, favorable edaphic conditions, biotic adaptations like root grafted tabonucos (Basnet et al., 1993), life history strategies (Zimmerman et al., 1994), and the biotic cycling of certain nutrients (Silver et al., 1994) interact to override the importance of spatial variations in soil nutrients in the accumulation of above-ground biomass at this site.

The vegetation mosaic that results from this interplay of periodic hurricanes, frequent local disturbances, and geomorphic setting is an irregular-aged assemblage comprised of hurricane survivors and post-hurricane regeneration. Comparison of the age of vegetation (Table 2) and the turnover periods induced by disturbances (Table 8) indicates that the length of time needed for any natural disturbance to turnover stems in the forest (220 to 3300 yr) is considerably longer than either the average or median age of trees in the forest (29 to 14 yr). In addition, the oldest individuals of a species are considerably older than the average or median age of that species (Table 2). This type of highly skewed age distribution pattern is typical of a situation in which removal of individuals is caused by different processes (Bolin and Rodhe, 1973). In this forest the pattern results because there is continual turn-

over among younger class sizes and ages while individuals that survive the recruitment and establishment phases live for a relatively long period until they are removed by senescence or a natural disturbance. On ridges and other stable landscape positions, background mortality and the periodic thinning by hurricanes dominate forest turnover and result in populations that have a conspicuous size and age class dominance which is related to past hurricanes (Weaver, 1986; Lugo and Rivera Batlle, 1987). In contrast, riparian valleys and other geomorphically unstable areas with a high frequency of small scale disturbances, have relatively young populations, a low diversity of mature adults, and are in a continual state of succession.

Many of the current theories in tropical forest ecology are based upon the premise that the structure and diversity of tropical forests are related to either nutrient abundance or disturbances. At this site, soil nutrient abundance and disturbance are interrelated. Moreover, the same drainage conditions and downslope mass movement that link soil forming processes across the landscape also influences the distribution of landslides, treefall gaps, and the age, structure and composition of the forest. These interactions underscore the problems associated with viewing vegetation patterns solely in terms of disturbance, soil nutrients, or biotic processes. Over short time periods and in localized areas, forest structure and development are responding to recent disturbances and local environmental conditions. When longer time frames (graded time sensu Schumm and Lichty, 1965) and the scale of the catena or watershed are considered, both the distribution of soils and vegetation are correlated with landforms. However, these landforms are not environmental variables themselves but surrogates for an array of geomorphic and pedologic processes that are influence by the landforms themselves. Over even longer time periods (cyclic time sensu Schumm and Lichty, 1965), the same geomorphic processes and mass transport that influence the distribution of soils, disturbances, and vegetation are also responsible for eroding and sculpturing the landforms themselves. Deciphering the interactions of biota and landforms over various temporal and spatial scales is fundamental to understanding and managing these complex ecosystems. The approach used in this study is applicable to understanding natural and human induced dynamics of other forests.

Acknowledgements

This research was performed under grant BSR-8811902 from the National Science Foundation to the Center for Energy and Environment Research (University of Puerto Rico) and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the Forest Service (U.S. Department of Agriculture). Special thanks to Olga Ramos of the IITF-GIS lab for producing Figs. 1 and 2 from our original maps and to the outside support provided to students and collaborators whose work made this synthesis possible, including support from the A.H. Mellon Foundation to A.J. Johnson, W.L. Silver, and D. Garcia-Montiel.

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