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Estimating soil turnover rate from tree uprooting during hurricanes in Puerto Rico

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ABSTRACT

Soil turnover by tree uprooting in primary and secondary forests on the island of Puerto Rico was measured in 42 study plots in the months immediately after the passage of a Category 3 hurricane. Trunk basal area explained 61% of the variability of mound volume and 53% of the variability of mound area. The proportion of uprooted trees, the number of uprooted trees, or the proportion of uprooted basal area explained 84–85% of the variation in hurricane-created mound area. These same variables explain 79–85% of the variation in mound volume. The study indicates that the soil turnover period from tree uprooting by Puerto Rican hurricanes is between 1600 and 4800 years. These rates are faster than soil turnover by landslides and background treefall in the same area and provide a useful age constraint on soil profile development and soil carbon sequestration in these dynamic landscapes.

1. Introduction

The uprooting of trees reallocates soil, biomass, carbon, and nutrients in forested watersheds (Gabet et al., 2003). Uprooting may be the most pervasive form of soil bioturbation (Mitchell, 1988). Uprooted trees bring buried nutrients, clasts and soil organic carbon to the surface, exposing them to atmospheric and surficial processes. Treethrow may increase mineral weathering processes and nutrient availability (Foster, 1988). By exposing material to aeration and erosion, it can influence the storage of carbon in soils, which globally contain 75% of the carbon in the terrestrial organic carbon pool and double the amount of carbon found in the atmosphere (Prentice, 2001). Thus, better quantitative estimates of bioturbation rates are needed to achieve an understanding of long-term terrestrial carbon dynamics (Gabet et al., 2003).

An element of this type of disturbance is mound-and-pit microtopography, which has interested scientists for at least 70 years (Lutz, 1940) because of its potential influence on soil formation, nutrient cycling, soil morphology, sediment movement, drainage patterns and forest ecology (Schaetzl et al., 1989). Mound-and-pit microtopography can influence species distributions (Putz et al., 1983), with some species favoring pits for establishment (Walker, 2000), while others favors mounds (Kabrick et al., 1997).

These processes have implications for forest soil development and forest management. Knowledge of uprooting susceptibility, such as by tree type or species, can yield informed decisions regarding reforestation and afforestation projects, including under the reducing emissions from deforestation in developing nations (REDD) structure of the proposed international climate treaty. Estimates of soil disturbance across a range of sites could complement existing literature on the proportion of trees uprooted by a hurricane or other disturbance event.

Reported mean areas of mounds and pits range from 1.5 m^2 for pits in Kentucky (Cremeans and Kalisz, 1988) to 16 m^2 for combined mound/pit complexes on Barro Colorado Island in Panama (Putz, 1983), with other estimates including 11.9 m^2 for “soil disturbance” from 22 freshly uprooted maple and beech trees in Michigan (Brewer and Merritt, 1978); an average of 2.5 m^2 for pits of various ages ($n = 73$) in a forested subalpine area of Colorado (Osterkamp et al., 2006); 8.8 m^2 of “exposed soil and rock” per uprooted tree in the Luquillo Experimental Forest in Puerto Rico (Zimmerman et al., 1994); and 4.7–8 m^2, depending on treefall

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type, for mounds in central New York forests (Beatty and Stone, 1986). These studies of mound formation, however, are applicable only to specific sites and are limited in applications beyond that forest stand.

Establishing the frequency of individual uprooting events, required when assessing soil turnover rate from uprooting, is especially challenging in tropical forests. While tree-ring cores can be used to estimate uprooting dates of many temperate species, tree-ring dating of tropical trees is limited and typically requires isotopic analysis (Evans and Schrag, 2004). However, an understanding of the return rate of catastrophic windthrow events, such as hurricanes, can help fill the knowledge gap about soil turnover processes in both tropical and temperate regions in the hurricane zone (Lugo, 2008). Furthermore, ongoing climate change may increase the frequency of uprooting events and soil turnover in hurricane-prone forests, as warming sea surface temperatures create conditions that increase wind velocity of hurricanes when other atmospheric factors do not intervene (Emanuel, 2005; IPCC, 2007).

This study quantifies the volume and area of soil uplifted by trees disturbed by the passage of Hurricane Georges over the Caribbean island of Puerto Rico, 21–22 September 1998. Our analyses focused on these questions: (1) How do the analyzed variables of individual trees and stands, landforms, and hurricane properties influence tree uprooting at the plot level? (2) How do these variables influence the quantity of soil uplifted by individual trees and at the plot level? (3) How does the rate of hurricane-induced soil turnover in Puerto Rico compare to other types of disturbance? To seek first-order principles that have applications at a variety of sites, more attention was given to finding broad similarities across heterogeneous sites than discerning small differences within or among sites or individual samples.

2. Material and methods

2.1. Study area

Puerto Rico is a 890,000-ha tropical island in the Greater Antilles chain of the West Indies, centered on approximately 18.5° North and 67° West. Approximately 60% of island area is classified (by Holdridge, 1967) as moist forest (1000–2000 mm rainfall annually), 25% as wet forest (2000–4000 mm), and 14% as dry forest (<1000 mm, Ewel and Whitmore, 1973). Extensive clearing for agriculture had reduced the island's forest cover to a low of about 12% by the late 1940s (Koenig, 1953). Since then, closed forest cover has increased to about 41.6% of island area (Helmer et al., 2002). Outside of protected areas, much of this closed forest is fragmented in sections ≤1 ha (Lugo and Helmer, 200 4).

2.2. Data collection and analysis

On 22–23 September 1998, Hurricane Georges passed over Puerto Rico with maximum sustained winds of 185 km h^{-1} and gusts up to 241 km h^{-1} (Bennett and Mojica, 1998). From 23 September through 20 December 1998, detailed measurements on 72 freshly uprooted mounds were taken in 42 plots of 500 m^2 in a variety of stands across the island (Lenart, 2003). Stands were selected island-wide to cover a diversity of forest types and a range of locations relative to the track of the hurricane (Fig. 1). Forests across the island of Puerto Rico were sampled for this paper, including stands in the Bisley and El Verde sections of the protected Luquillo Experimental Forest (LEF) of the Caribbean National Forest, state forests in the island's interior, and natural and managed forest stands on private and municipal land (Table 1). While individual stands were partially chosen because of their accessibility, plots within stands were sampled randomly. An additional 60 individual mounds were sampled outside of plots for potential comparison to the randomly sampled mounds.

The combined basal area of trees within each plot was assessed with a Bitterlich's Spiegel Relaskop. A hand-held clinometer was used to measure hillslope gradient at the plot scale. Aspect was taken using a Brunton compass corrected for local declination. Topographic categories of each plot were assigned as follows: *ridges* are local divides that receive no upland runoff; *slopes* are areas that both receive and transmit runoff; and *valleys* are low-gradient areas that concentrate runoff. Elevation values for sites were approximated to ±50 m using topographic maps. Forest types were assigned based on the Life Zone map in Ewel and Whitmore (1973). A map by the U.S. Global Change Research Program (2000) was used to derive precipitation during the 1998 hurricane event (using midpoint values for rainfall categories) and to determine whether the hurricane eye crossed a given plot.

Standing trees >10 cm dbh and uprooted trees of any size within each plot were noted as standing live, standing dead, snapped or uprooted, and classified as a needleleaf (typically *Pinus caribaea* or *Casuarina equisetifolia*), palm (*Prestoea montana*) or broadleaf tree (hundreds of species thrive in Puerto Rico). Tree diameter at breast height (1.3 m), bole length, slope of the fallen bole, ground slope, and treefall direction were measured on each fallen tree. Trunk area (i.e., trunk basal area) as derived from diameter at breast height [$BA = \Pi\,(1/2\ d)^2$], was used to represent tree size because values could be summed when more than one bole formed a single mound/pit complex. Mounds and pits were

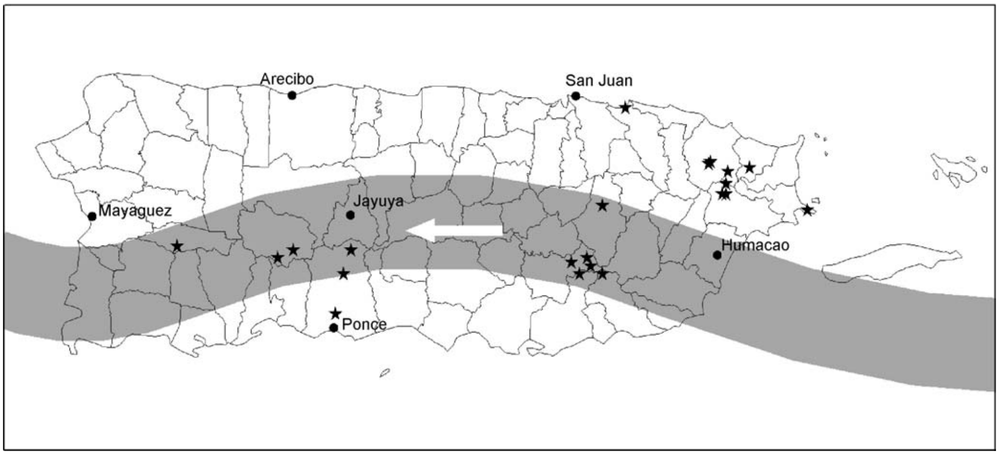

Fig. 1. Path of 1998 Hurricane Georges across Puerto Rico; Xs indicate approximate locations of the 21 sites from which 42 plots were sampled in this study.

Table 1
Characteristic features of the 42 plots assessed in Puerto Rico.

	Number of plots
Location	
Within hurricane eye band	16
Outside hurricane eye band	26
Hurricane rainfall totals	
<130 mm	10
130–250 mm	16
251–380 mm	5
381–510 mm	7
>510 mm	4
Topographic setting of plots	
Slope	23
Valley	12
Ridge	7
Elevation of plots	
0–199 m	7
200–399 m	13
400–599 m	5
600–799 m	11
800–1000 m	6
Aspect of plots	
North (316–45°)	9
East (46–135°)	9
South (136–225°)	12
West (226–315°)	12
Forest type of plots	
Dry	4
Moist	7
Wet	27
Rain	4
Dominant tree type in plots	
Broadleaf (>60%)	27
Needleleaf (>60%)	5
Palm (>40%)	10
Predominant grain size of soil	
Clay	31
Loam	4
Sand	7
Land ownership	
Federal	20
State (including airports)	16
Private	6

classified as ellipses, half-ellipses, triangles, or rectangles for measuring and calculation purposes. Mound area was multiplied by approximate mound thickness (equivalent to pit depth) to compute volume. *Mound* here refers to the disturbed soil, roots, and rocks uplifted by a fallen tree (Fig. 2). The proportions of roots and clasts in the mound were estimated visually. Dominant particle sizes (clay, silt or loam, sand) and apparent organic matter content (low, medium, high) were classified informally in the field using tactile and visual assessments (Watts and Halliwell, 1996). Soil bulk density was measured on a subsample of mounds to test whether it was comparable to surrounding soil.

2.3. Statistical analyses

Analyses were conducted on related data sets: (1) the set of 42 plots, from which uprooting proportion and soil disturbance were estimated; and (2) the set of 72 mounds (containing 79 trees) from the plots, from which means for individual uprooted trees were estimated and linear regressions predicting soil disturbance for individual mounds were developed. An expanded set included the 72 plot-based mounds and an additional 60 mounds (containing 73 trees), with the latter used to refine linear regressions predicting soil disturbance for individual mounds (Lenart, 2003).

Fig. 2. A typical mound resulting from the uprooting of a tree in Puerto Rico during Hurricane Georges in 1998.

Data were analyzed using JMP computer software (Sall and Lehman, 1996). Simple and multiple linear regression models employed the method of ordinary least squares; a value of $\alpha = 0.05$ was used to determine statistical significance of all tests. Data were log- or square-root-transformed as necessary to meet assumptions of parametric tests, i.e., Gaussian (normal) distribution. In cases where an abundance of zero values for data points made a normal distribution impossible even with transformations, zero values initially were excluded to estimate means, then weighted in later. An example of this approach is described in the next section.

2.3.1. Uprooting proportion

To estimate the mean proportion ($\bar{P}$) of uprooted trees in plots, we calculated the mean of the logit values ($\ln[P_u/(1-P_u)]$) of the proportion of uprooted trees in the 25 plots with uproots (P_u); logits were used to obtain a normal distribution and hence a valid mean (Sall and Lehman, 1996) (Table 3). We then backtransformed the mean logit to a mean proportion ($\hat{P}$) and calculated the weighted mean (including the influence of plots with no uproots) as

$$\bar{P} = \frac{\hat{P} * N_u}{N_u + N_x} \tag{1}$$

where N_u and N_x are the number of plots with and without uprooted trees, respectively.

Variables tested for influence on uprooting proportion at the plot level were: number of trees; stand basal area ($\mathrm{m}^2\,\mathrm{ha}^{-1}$);

proportion of palm trees in plot; proportion of needleleaf trees in plot; topography (slopes, ridges, or valleys); slope of the plot-scale landscape (°); predominant soil type (clay, silt/loam, or sand); elevation (m); forest type (dry, moist, wet, or rain forest); whether the hurricane eye went over the plot; and estimated rainfall during the hurricane. We also compared the direction of treefall with aspect and dominant wind force direction from the hurricane.

2.3.2. Soil disturbance

Multiple linear regression was used to evaluate relationships between soil disturbance and tree and site properties. Variables tested for influence on mound volume, area and depth were: topography; tree type; treefall direction (°); aspect (0–360°); tree-trunk inclination (0–90°); local ground slope (0–90°); forest basal area (m^2 ha^{-1}); trunk area of the uprooted tree(s) (cm^2, converted from dbh); number of trees in the mound; height of the tallest tree in mound (m); predominant soil grain (clay, silt/loam, or sand); soil organic matter level (low, medium, or high); fraction of clasts; fraction of roots; and number of days between the hurricane's passage and field measurements.

Mounds and pits were analyzed separately (Table 2), except in one case: to make the results comparable to a study from Panama by Putz (1983) that reported mound/pit area, Puerto Rican mound areas were doubled to approximate mound and pit area (Lenart, 2003). Our study design called for measuring pits only if they were deemed capable of trapping sediment, so some pits went unmeasured (Lenart, 2003). Mound area was considered a robust proxy of pit area after comparisons of a subsample of paired 10-cm cores from mounds showed no difference between the bulk density of the soil they contained and that of nearby undisturbed soil.

Plot-level results were used to model the area and volume of soil uplifted (i.e., combined mound area and volume) with simple and multiple linear regressions using these explanatory variables independently: (1) number of uproots; (2) proportion of uproots; and (3) proportion of the stand basal area uprooted. The mean area of soil uplifted per plot was estimated by natural log transformation of the per-ha extrapolation for plots with uproots ($n = 25$), and then weighting the resulting mean to include all 42 plots.

2.3.3. Soil turnover period

The mean annual soil turnover rate of uprooting by hurricanes was calculated by pairing data from this study with estimated hurricane return rates. Let T = measured soil turnover (m^2 ha^{-1}) in plots from one or more individual disturbance events. The annual soil turnover rate R is estimated by dividing T by the disturbance return interval (I, year):

$$R = \frac{T}{I} \tag{2}$$

giving R in units of m^2 ha^{-1} $year^{-1}$. This is converted to an annual landscape proportion (L) by normalizing m^2 as a proportion of ha (10^4 m^2 ha^{-1}).

$$L = R/10^4\ \text{year}^{-1} \tag{3}$$

To calculate the soil turnover period (S), the number of years required for soil turnover of a defined amount of land, S is estimated as

$$S = \frac{1}{L} \tag{4}$$

giving the soil turnover period in units of year.

Soil turnover period can be defined as the quantity of an ecosystem reservoir divided by the mean annual flux (Scatena, 1995), analogous to turnover times of geomorphic processes as well as disturbance events such as fire rotation (Agee, 1993). Because it includes both time and area, the soil turnover period is, like the fire rotation, a scale-independent metric that allows comparison areas among sites (Falk et al., 2007). Turnover calculations generate a mean turnover period for a landscape L as a whole; soil at specific points may be turned over more or less than once. Hence, the soil turnover period is equivalent to the mean residence time for the top layer of soil before disturbance by uprooting.

3. Results

Of 42 study plots, approximately 40% did not include uprooted trees, two included landslides, and one showed evidence of recent surface fire. No pattern was discernable to explain why no trees uprooted in some plots, most of which were adjacent to plots in similar forest types with uproots. The eye of Hurricane Georges passed over about 40% of the plots, generally bringing higher rainfall (Fig. 1). About 64% of the plots were in subtropical wet forest and 64% contained predominantly broadleaf evergreen trees, while clay was the predominant substrate (Table 1).

Table 2
Descriptive statistics for 72 mounds and 45 pits measured in 42 plots (diameter at breast height given for 79 individual uprooted trees within mounds).

Category	Mean	95% C.I.	Median	Range	Transformation formula used (NT = not transformed)	*n*
Treefall direction (°)	228.5	214.2–242.6	240	10–360	NT	72
Tree-trunk inclination (°)	+1.5	−2.8 to +5.8	0	−35 to +57	NT[a]	72
Slope of ground (°)	−20.1	−16.9 to −23.3	−20.0	−63 to 0	NT[a]	72
Trunk area (of trees(s) in mound at breast ht, m^2)	0.037	0.029–0.047	0.038	0.002–0.349	Ln(Trunk area of tree(s) in mound, cm^2)	72
Diameter at breast height of uprooted trees (cm)	20.3	18.0–22.9	20.4	5.1–65.5	Ln(tree diameter at breast height, cm)	79
Height of uprooted trees (m)	11.3	9.9–12.8	12.0	2.5–27.0	Ln(Height of tallest tree in mound)	72
Mound thickness (m)	0.33	0.28–0.38	0.35	0.05–1.10	Ln(Mound thickness, m)	72
Mound area (m^2)	0.91	0.68–1.20	0.84	0.05–15.90	Ln(Mound area, m^2)	72
Mound volume (m^3)	0.292	0.202–0.422	0.340	0.002–4.502	Ln(Mound vol, m^3)	72
Soil alone in typical mound (m^3)	0.193	0.134–0.279	0.248	0.002–3.598	Ln(Soil only in mound, cm^3)	72
Proportion of soil in mound (%)	65.9	61.9–70.0	70.0	0–100	Soil fraction[a]	72
Proportion of roots in mound (%)	29.0	25.4–32.6	30.0	0–100	Root fraction[a]	
Proportion of clasts in mound (%)	4.6	2.4–6.9	0	0–50	Ln(Fraction of clasts + 1)[a]	72
Pit depth (m)	0.29	0.24–0.34	0.25	0.05–0.90	Pit depth[a,b]	45
Pit area (m^2)	0.86	0.63–1.19	0.98	0.071–8.254	Ln(Pit area, m^2)[b]	45
Pit volume (m^3)	0.20	0.134–0.298	0.251	0.008–2.513	Ln(Pit volume, m^3)[b]	45

[a] Data for these variables not normally distributed (Shapiro-Wilk W test, $p < 0.05$).

[b] Plots with zero values were excluded, as described in Methods.

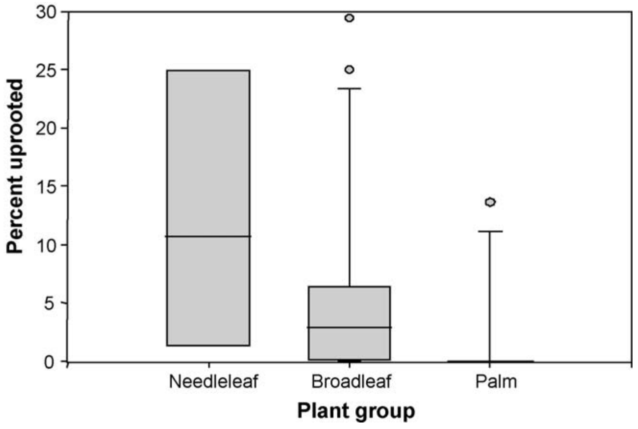

Fig. 3. Proportion of trees uprooted in plots in Puerto Rico in 1998, comparing needleleaf (NL), evergreen broadleaf (BL) and palms (P). The 95% confidence intervals and outliers are shown.

3.1. Uprooting proportion

The mean proportion of uproots was 4.2%, while the mean proportion of snaps was 14.3%, and the mean proportion of downed trees (uproots plus snaps) was 20.5% (values are not additive because of transformations applied). The proportion of uprooted trees was uncorrelated with the proportion of snapped trees ($r = 0.095$, $n = 42$). Rainfall during the hurricane was strongly positively correlated with distance to the hurricane eye ($r = 0.91$); therefore, these two variables could not be considered independent. Needleleaf trees tended to uproot more frequently than broadleaf trees ($p = 0.0403$) and palms (0.0494) (Fig. 3).

Poisson regressions identified a suite of variables that influenced the proportion of uproots at a site. Uprooting proportion was higher in plots exposed to the hurricane eye and its eye wall – which often contains the strongest winds and most intense precipitation of a hurricane (Aguado and Burt, 1999) ($p < 0.0001$). Ground slope (in degrees) had a positive influence on the proportion of uproots ($p = 0.039$), as did elevation ($p < 0.0001$), and rainfall during the storm ($p < 0.0001$). Stand basal area exerted a negative influence ($p = 0.039$), i.e., uprooting proportion decreased as stand basal area increased. Uprooting rates were highest on ridges ($p < 0.0001$) and higher on slopes ($p = 0.001$) than in valleys. When uprooting by forest life zone was tested, uprooting proportion was higher in moist forests ($p < 0.0001$) and lower in rain forests ($p < 0.0001$) than in wet forests. When soil type was tested, uprooting proportion was lowest in silty or loamy soils ($p < 0.0001$), and lower in clay soils ($p = 0.001$) than in sandy soils. The proportion of needleleaf trees on the plots had a positive influence on their uprooting proportion ($p < 0.0001$, range of 0–100% needleleaf trees per plot). The proportion of palms had no influence ($p = 0.848$, range 0–72% palm trees per plot).

3.2. Soil disturbance

3.2.1. Mound area

Trunk basal area alone explained 44% of the variability in area of individual mounds within plots ($n = 72$), and 53% of the area of individual mounds in the larger data set ($n = 131$) (F-test, $p < 0.0001$) (Fig. 4a). For the full data set, the MLR model with the best fit of significant variables (adjusted $r^2 = 0.591$) also included parameters accounting for the tendency for mounds of palms to be smaller than needleleaf or broadleaf trees ($p = 0.0042$), and for mounds formed within the hurricane eye to be smaller than those formed outside of it ($p < 0.0001$).

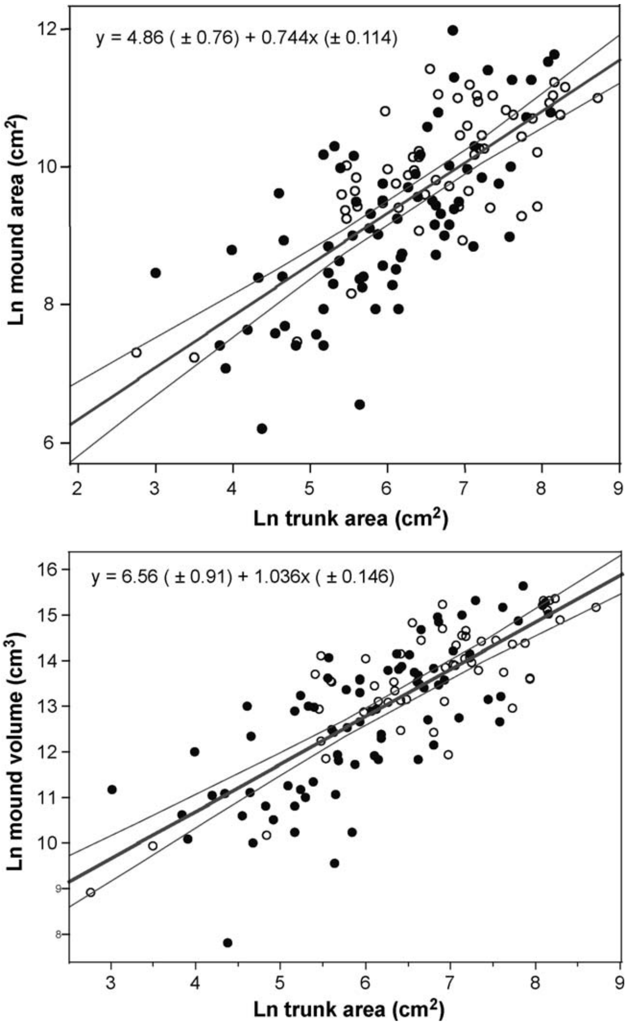

Fig. 4. Results of simple linear regression models using trunk area to predict mound volume and area from trees in Puerto Rican forests uprooted from Hurricane Georges. Area (a) and volume (b) of 72 plot-based mounds (filled circles) and 60 opportunistically measured mounds (open circles). Variables are log-transformed. Dashed line is the 95% confidence interval. Equations posted in the figures relate to the full data set. Equations for plots-only values for *a* and *b*, respectively, are: $y = 4.80\ (\pm 1.19) + 0.728x\ (\pm 0.198)$, and $y = 6.28\ (\pm 1.43) + 1.068x\ (\pm 0.238)$.

In plots, the proportion of uprooted trees, number of uprooted trees, or proportion of stand basal area uprooted explained 84–85% of the variation in combined mound area (m^2 of soil per ha^{-1}) in simple linear regression models (Table 4).

Mound soil bulk density did not differ from that of nearby soil ($p = 0.885$, subsample paired test, $n = 9$ pairs), indicating that measured mound volumes fairly represented initial pit volume for freshly uprooted trees. When the freshly uprooted trees in this study (with mound areas doubled to approximate mound/pit area) are plotted with the estimated coordinates for 88 recognizable points for the BCI trees (extracted from Putz, 1983, Fig. 1b), there is no difference between the resulting regression equation and the regression equation reported by Putz (1983) for BCI trees alone (Table 5).

3.2.2. Mound volume

Trunk basal area explained 53% of the variability in volume of individual mounds within plots ($n = 72$), and 61% of the volume of individual mounds in the larger data set ($n = 132$) (F-test, $p < 0.0001$) (Fig. 4b). While several additional variables were

Table 3
Variables involving continuous measurements in the 42 plots. NT = not transformed.

Category	Mean	95% C.I.	Median	Range	Transformation, if used	n
Basal area of site (m^2/ha)	24.5	22.3–26.7	23.9	11.8–42.4	NT (relascope values corrected for bias based on a subsample of seven measured plots)	42
Trees per plot (per ha)	41.1 (822)	34.9–47.4 (698–948)	39.0 (780)	7–94 (140–1880)	NT	42
Mean diameter (cm) of trees per plot[a]	22.1	19.7–24.4	20.1	13.0–57.1	Conversion from mean trunk area	42
Number of uproots (per ha)	35.8	26.3–46.8	35.7	20–200	Square root of number of uproots[b]	42[b]
Proportion of uproots (%)	4.16	3.13–6.90	7.05	1.5–29.41	Ln[%uproots/(100 – %uproots)][b]	25[b] 42
Proportion of snaps (%)	14.29	9.15–21.51	16.21	1.33–91.67	Ln[%snaps/(100 – %snaps)][b]	25[b] 42
Proportion felled (%) (uproots + snaps)	20.52	13.89–29.05	20.59	1.33–91.67	Ln[(%uproots + snaps)/(100 – %uproots + snaps)][b]	25[b] 42
Area of earth uplifted per site (m^2/ha)	36.0	21.0–61.7	43.6	0–344.9	Ln(Mound area, m^2)[b]	25[b] 42
Volume of earth uplifted per site (m^3/ha)	11.7	5.9–23.4	15.5	0–139.0	Ln(Mound volume, m^3)[b]	25[b] 42

[a] Mean diameter of tree was calculated by dividing site basal area by tree density.
[b] Plots with zero values were initially excluded and weighted in later, as described in Section 2. Because of this, values of snapped and uprooted trees do not sum to describe the proportion of felled trees.

statistically significant in multiple linear regression models, no combination in a variety of models tested explained more than 66% of the variability in mound volume. Mounds in silt/loam had the largest volume (MLR, $p = 0.0030$), followed by mounds in sand (MLR, $p = 0.0414$). Mounds in clay had the smallest volume for a given tree size. In the best-fitting MLR model of mound volume ($r^2 = 0.656$), mounds from needleleaf trees were larger than those from broadleaf trees ($p = 0.0010$), mounds on ridges were smaller than those on slopes ($p = 0.0264$), and mounds in silt/loam were larger than those in clay ($p = 0.0061$), while mound volume increased with trunk area ($p < 0.0001$).

For plot-level uprooting data, the proportion of uprooted trees, number of uprooted trees, or proportion of stand basal area of uprooted trees in the plot independently predicted 79–85% of the variation in mound volume (m^2 of soil ha^{-1}) using simple linear regression models (Table 4).

3.2.3. Other variables

Mean direction of tree uprooting was 225.6° ($C.I._{0.95} = 214.2$–242.7), aligned with the strongest wind vectors of Hurricane Georges as it moved west and significantly different from mean plot aspect (182.5°, $C.I._{0.95} = 165.0$–$200.0°$, Wilcoxon $W = 5132$, $p = 0.012$). The direction of uprooting conformed to expectations that the most powerful winds responsible for the majority of windthrow occur where the vector of wind velocity is augmented by storm movement (Aguado and Burt, 1999).

3.3. Soil turnover rate and period

Puerto Rico has an island-wide hurricane return rate of once per decade ($I = 10$ year) based on the period 1851–1996 (Elsner and Kara, 1999). Using the mean plot measured soil turnover ($T = 36.0\ m^2\ ha^{-1}$, Table 3) and Eqs. (2)–(4), we calculated the mean annual soil turnover rate ($R = 3.60\ m^2\ ha^{-1}\ year^{-1}$), which gives landscape proportion $L = 0.000360$. Eq. (4) yields an estimated mean soil turnover cycle for Puerto Rico of 2777 year ($C.I._{0.95} = 1620$–4792 year) from hurricanes alone.

4. Discussion

4.1. Uprooting proportion

The proportion of uprooting was highly variable among the plots and supported other studies that indicate complex non-linear relationships between hurricane wind velocity and damage (Everham and Brokaw, 1996; Scatena et al., 2004). In general the proportion of uproots was greater in plots exposed to the hurricane eye than in plots away from the storm center.

Palms have a well-documented tendency to shed fronds early in a hurricane, which may help account for relatively low uprooting rates compared to other tree types [e.g., <1% (Frangi and Lugo, 1991), and 1.5% (Zimmerman et al., 1994; and this study)]. Our findings that the needleleaf trees considered here (*Casuarina equisetifolia, Pinus caribaea*) are more susceptible to uprooting than

Table 4
Simple linear regression coefficients predicting soil disturbance at the plot level. All logit formulas are for cases where plots without uproots are included, as described in Methods. All intercepts and slopes are significantly different from zero ($p < 0.0001$) (r^2 = coefficient of determination).

Response variable (y)	Intercept (95% confidence interval)	Slope (95% confidence interval)	Explanatory variable (x)	r^2
$\ln[(\text{Mound vol in } m^3\ ha^{-1} + 1) \times 10^6]$	13.92 (13.51–14.32)	0.38 (0.32–0.45)	SqRt (#uproots ha^{-1})	0.79
$\ln[(\text{Mound area in } m^2\ ha^{-1} + 1) \times 10^4]$	9.48 (9.07–9.88)	0.48 (0.14–0.54)	SqRt (#uproots ha^{-1})	0.85
$\ln[(\text{Mound vol in } m^3\ ha^{-1} + 1) \times 10^6]$	20.38 (19.60–21.17)	1.42 (1.19–1.64)	Logit (%uprooted trees)	0.80
$\ln[(\text{Mound area in } m^2\ ha^{-1} + 1) \times 10^4]$	17.53 (16.78–18.29)	1.77 (1.55–1.98)	Logit (%uprooted trees)	0.84
$\ln[(\text{Mound vol in } m^3\ ha^{-1} + 1) \times 10^6]$	19.46 (18.90–20.01)	1.20 (1.04–1.36)	Logit (% Stand Basal Area uprooted)	0.85
$\ln[(\text{Mound area in } m^2\ ha^{-1} + 1) \times 10^4]$	16.16 (15.47–16.84)	1.43 (1.23–1.63)	Logit (% Stand Basal Area uprooted)	0.84

Table 5
Simple linear regression equations comparing results from this study with Putz (1983) using tree diameter to predict area of soil disturbed by uprooted trees.

Response (y)	Intercept (95% confidence interval)	Slope (95% confidence interval)	Predictor (x)	r^2	n
Log_{10} (Mound/pit area, m^2), BCI trees alone (Putz, 1983)	1.35 (not given)	1.51 (not given)	Log_{10} (diameter largest tree, m)	0.68 (S.E. = 0.11)	94
Log_{10} (Mound/pit area, m^2), BCI trees from Putz (1983) plus PR mounds from this study (doubled to approximate mound/pit area)	1.34 (1.25–1.43)	1.49 (1.33–1.65)	Log_{10} (diameter largest tree, m)	0.61	211

both palms and broadleaf trees is tentative given the small sample size ($n = 6$ plots with 6 or more needleleaf trees), and consistent with previous wind damage studies (reviewed by Everham and Brokaw, 1996). Our study found uprooting rates were highest on ridges and lowest in valleys. This is the reverse of patterns of tree damage during Hurricane Hugo reported by Scatena and Lugo (1995) and Basnet et al. (1992), both of which included snapped trees in their tallies. Also, both earlier studies were confined to the tabonuco forest, whose dominant species (*Dacroydes excelsa*) prefers ridges (Scatena and Lugo, 1995), and is largely resistant to uprooting due to widespread root grafting among individuals (Basnet et al., 1993). Other studies of wind damage have found that topography has an inconsistent influence on treefall (Everham and Brokaw, 1996).

4.2. Soil disturbance

The mean mound thickness in this study of 0.33 m (Table 2, $\text{C.I.}_{0.95} = 0.28–0.38$ m) approximates the vertical distribution of roots, which are concentrated in the top 0.24–0.40 m in Puerto Rican soils (Brown et al., 1983). Simon et al. (1990) suggested that high root density contributed to high shear strength in the upper 0.25 m of LEF soils, and found minimum shear strength at 0.50 m, which is the mean depth of landslides.

The area and volume of the mounds increase with trunk area (Fig. 4). This pattern is consistent with the scaling of root biomass with stem diameter (Enquist and Niklas, 2002), and indicates that a tree's potential contribution to soil disturbance increases as it becomes larger. Using the regression equation for mound volume based on trees ranging from 4.5 to 67 cm in diameter (Fig. 4b), a Tree 40 cm in diameter would lift about 84 times more soil than a Tree 4 cm in diameter. Although growth rates for individuals vary widely, these sizes correspond roughly to 100-year-old and 10-year-old trees, respectively, based on average annual growth increments for these forests (Crow and Weaver, 1977).

The quantity of soil disturbed by an individual tree is correlated with tree size (with trunk area as calculated from diameter used here) to a degree that renders other factors relatively unimportant. Because of this, the regression equation from the full set of 132 mounds can be used for most purposes rather than the plots-only data set; it yields the same equations while its 95% confidence interval is narrower than the intervals for the smaller plots-only data set (not shown), indicating that it provides a more precise estimate of the relationship. Additionally, the dependence of mound size on tree size indicates that literature reports of mean mound size should be considered site-specific if tree diameter is not considered explicitly. In this study, mound area averaged about 0.9 m^2, so the combined mound/pit complex averaged about 1.8 m^2 (using the doubling technique described in Section 2.3.2). This compares to an average of 8.8 m^2 of "exposed soil and rock" per tree uprooted by Hurricane Hugo in the El Verde section of the LEF (Zimmerman et al., 1994), and about 16 m^2 of mound/pit area created by the "average uprooted tree" in the old forest on Barro Colorado Island (BCI) in Panama (Putz, 1983, $n = 94$). These differences in mean mound/pit areas among studies typically can be accounted for by differences in tree size, where reported. In fact, the regression equation using tree diameter to predict mound area in this study was indistinguishable from the results for Barro Colorado Island in Panama (Putz, 1983; Table 5 and Fig. 5) suggesting that these relationships may hold across a variety of sites. A comparison between estimated values and measured values from sites in Colorado further supports this premise (Lenart, 2003). However, pits areas in podzols measured by Peterson (2000) averaged 22% larger than predicted by equations developed in this study, which may relate to the high organic content typical of podzols. Soils with the highest soil organic matter in this study, silt/loams, tended to yield larger pits and mounds when tree size was held constant. This points to a need for more precise comparisons among soil types—ideally, continuous measurements of soil grain size and carbon content—in future studies to refine predictions.

At the plot scale, models using the proportion of uproots to predict soil disturbance were not improved by including mean trunk area, stand basal area or the number of trees in a stand. This may seem surprising given the importance of tree size to mound size at the scale of the individual tree. In fact, the uprooted trees on our plots were generally similar in size and relatively small in diameter. Stands had an average mean basal area of 24.5 $m^2\ ha^{-1}$ compared to 35–85 $m^2\ ha^{-1}$ within the LEF (Brown et al., 1983) and 9 $m^2\ ha^{-1}$ and 13 $m^2\ ha^{-1}$ for moist and wet forest respectively outside the LEF boundaries (Franco et al., 1997). In addition, Hurricane Hugo already had thinned out many of the mid-size LEF trees (25–45 cm dbh) which are most vulnerable to uprooting (Everham and Brokaw, 1996).

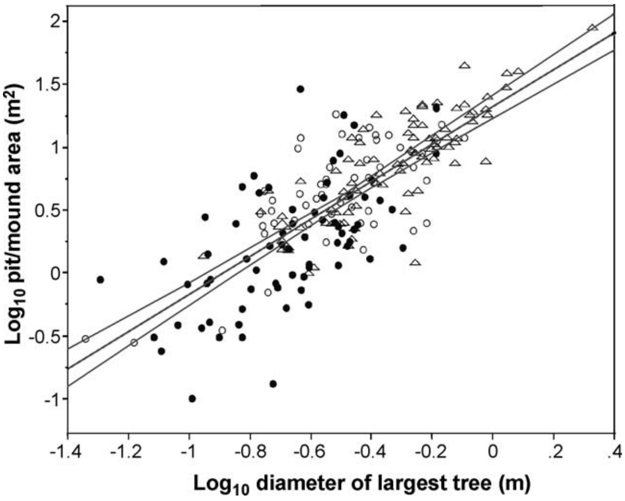

Fig. 5. Linear regression of log tree diameter for the largest tree predicts log mound/pit area for individual uproots, estimated as described in Section 2. Mounds measured from plot samples (filled circles) and non-plot samples (open circles) from this study, compared to Barro Colorado Island (Putz, 1983; triangles). Data from this study were re-plotted in log 10 based on largest tree in mound for comparison with Putz (1983). Equations and confidence intervals are given in Table 5.

4.3. Soil turnover period

We compared the mean soil turnover period calculated from Hurricane Georges to estimates based on hurricane damage from Hurricane Hugo in 1989. Scatena and Lugo (1995) observed a mean uprooting rate of 15.9% (±2.8% S.E.) in LEF from that event. Using the mound area equation in Table 4 and an estimated 60-year return interval to that specific location for an event of similar magnitude and proximity (Scatena and Larsen, 1991) yields an estimated soil turnover period of 2300 year, well within the confidence interval of the present study's estimate of 2777 year ($\text{C.I.}_{0.95}$ = 1620–4792 year). Nevertheless these estimates should be considered conservative because they do not consider damage from less frequent stronger hurricanes or distant hurricanes that can also impact the site.

To consider how soil turnover from episodic hurricane uprooting in Puerto Rico compares to individual gap-forming events and landslides, we considered reported values for these processes in similar Puerto Rican forests. In a 13-ha study area of the LEF's Bisley section during the 2 years before Hurricane Hugo struck, the mean diameter of gap-forming trees was 46.8 cm, which was among the largest 5% of standing trees (Scatena and Lugo, 1995). Putting this value into the mound area equation from this study (Fig. 4a) and using reported frequency of these events, the estimated mean soil turnover period from background uprooting is 4478 year. To estimate turnover from landslides, we used the Larsen (1997) estimate of 0.5–2% per century for two adjacent Puerto Rican watersheds, giving a soil turnover period from landslides of 5000–20,000 years in mountainous areas. Similarly, Guariguata (1990) reported that 0.08–0.3% of LEF slopes were disturbed by landslides per century, for a soil turnover period of 3300–125,000 years. The lower estimate corresponds to an independent estimate of mean stem turnover period from slope failure of 3300 years for trees >10 cm dbh over a 57-year period in the LEF (Scatena and Lugo, 1995). Although landslides are treated here as a separate process, most landslides in Puerto Rico also occur during hurricanes (Larsen, 1997), which may help explain the similarity in lower estimates of turnover period.

These results indicate that physical turnover of soils in Puerto Rican forests may be dominated by uprooting events during episodic hurricanes. Uprooting from individual gap-forming events (i.e., background uprooting) also becomes important during intervals between hurricanes. Landslides are most likely to occur on slopes greater than 30° (Simon et al., 1990), and may be a competing force on these steep slopes; in flatter parts of the watershed, landslides will be less common or even rare. Valleys may be inundated locally by floods, but turnover from this factor was not calculated in this study. Hurricanes appear to be the dominant forces in overturning soil in valleys and on ridges, with background uprooting acting as a secondary influence. The importance of hurricane-caused versus background uprooting may fluctuate from decade to decade, depending on hurricane return rate as it relates to climate variability and change and the size of the trees available for uprooting. Overall, however, hurricanes appear to be the driving force on soil turnover in Puerto Rico. This may well hold throughout the Caribbean, and perhaps in other tropical forests within the hurricane zone.

Soil turnover rates in Puerto Rico could change if the frequency of intense hurricanes in the Atlantic changes as climate change raises the sea surface temperatures as expected (Emanuel, 2005; IPCC, 2007). Because of the importance of hurricanes and other tropical cyclones to soil turnover periods, anthropogenically forced trends affecting oceanic and atmospheric processes could join natural climate variability in having major influences on forest dynamics in many regions.

4.4. Implications for forest dynamics

Forests are affected by a variety of disturbances and individual uprooting events that influence the rate of tree and soil turnover, which in turn has important implications for soil development and carbon storage. Globally, high forest turnover rates correlate with high net primary productivity (Stephenson and Van Mantgem, 2005). Phillips et al. (2004) found that tree turnover rates were positively correlated with increasing soil fertility. Because decomposing wood is a major source of soil carbon (e.g., Zalamea et al., 2007), increases in tree turnover rate, including from increased hurricane intensity, could increase soil carbon at some sites, although this might involve temporal variability and a possible overall decline in aboveground biomass (*sensu* Sanford et al., 1991).

In the context of reforestation and afforestation projects under the proposed REDD structure of the successor to the 1997 U.N. Kyoto Protocol, changes in soil carbon as well as changes in aboveground carbon turnover could have implications for land managers if they receive funding based on the amount of carbon sequestered. Studies of tree damage from hurricanes also suggest the need to consider tree type, species, and successional states in addition to wind velocity, wind direction, and soil characteristics when attempting to gain an understanding of forest dynamics. A REDD project in Chiapas, Mexico, which falls in the hurricane zone, encourages farmers to plant mahogany and cedar (Tracey N. Osborne, University of California-Berkeley, personal communication). Species selection could affect vulnerability; for example, West Indian mahogany (*Swietenia mahogani*) was among the most resistant to damage from hurricane winds, while Honduras mahogany (*Swietenia macrophylla*) was among the least resistant (Merry et al., 2009). Similarly, native species may be more resistant to windthrow than exotic plantation species in hurricane-prone areas, comparable to findings by Basnet et al. (1993) that native tabonuco (*Dacroydes excelsa)* in Puerto Rico had evolved wind-hardy adaptations such as root grafting.

The ecological and management implications of more intense hurricanes include the potential for more rapid soil turnover in hurricane-prone forests, changes in forest stature and structure, species composition, carbon and nutrient dynamics, and microtopography. Other variables that control the degree of tree toppling include root growth and decay, a ‘‘domino effect'' of other falling trees, movement of carbon-rich soil by erosion following tree-toppling events, and a broad array of bioturbation processes by invertebrates and burrowing mammals (Gabet et al., 2003). A related 2-year study on a subsample of uprooted Puerto Rico trees suggested that roughly one-third of the soil eroding from the mound falls into the pit (Lenart, 2003). Soil carbon studies of pit-and-mound topography would be useful for evaluating what proportion of carbon in mounds and pits decays because of exposure to the atmosphere. The fact that soil carbon accumulates under forest after conversion from grasslands and decreases upon deforestation (Silver et al., 2000) suggests that the input of soil organic matter from decaying tree boles more than compensates for the loss of soil carbon from aeration or erosion from uprooting. Still, it would be useful to quantify in more detail these processes and others that relate to soil carbon dynamics, especially given that soil carbon potentially could have a future economic value under REDD. The soil turnover rate estimated here suggests belowground soil carbon pools will remain intact on the scale of thousands of years even in these dynamic landscapes.

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References

Agee, J.K., 1993. Fire Ecology of the Pacific Northwest. Island Press, Washington, DC.

Aguado, E., Burt, J.E., 1999. Understanding Weather and Climate. Prentice Hall, Upper Saddle River, NJ.

Basnet, K., Likens, G.E., Scatena, F.N., Lugo, A.E., 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. J. Trop. Ecol. 8, 47–55.

Basnet, K., Scatena, F.N., Likens, G.E., Lugo, A.E., 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in Luquillo Experimental Forest, Puerto Rico. Biotropica 25, 28–35.

Beatty, S.W., Stone, E.L., 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. 16, 539–548.

Bennett, S.P., Mojica, R., 1998. Hurricane Georges Preliminary Storm Report. National Weather Service, Carolina, Puerto Rico, p. 15.

Brewer, R., Merritt, P.G., 1978. Wind throw and tree replacement in a climax beech-maple forest. Oikos 30, 149–152.

Brown, S., Lugo, A.E., Silander, S., Liegel, L., 1983. Research History and Opportunities in the Luquillo Experimental Forest. Southern Forest Exp. Stn., New Orleans, LA, U.S. Department of Agriculture Forest Service General Technical Report SO-44.

Cremeans, D.W., Kalisz, P.J., 1988. Distribution and characteristics of windthrow microtopography on the Cumberland Plateau of Kentucky. Soil Sci. Soc. Am. J. 52, 816–821.

Crow, T.R., Weaver, P.L., 1977. Tree growth in a moist tropical forest of Puerto Rico. Río Piedras, Puerto Rico. USDA Forest Service. Forest Service Research Paper ITF-22.

Elsner, J.B., Kara, A.B., 1999. Hurricanes of the North Atlantic. Oxford University Press, Oxford, England.

Emanuel, K., 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436, 686–688.

Enquist, B.J., Niklas, K.J., 2002. Global allocation rules for patterns of biomass partitioning in seed plants. Science 295, 1517–1520.

Evans, M.N., Schrag, D.P., 2004. A stable isotope-based approach to tropical dendrochronology. Geochim. Cosmochim. Acta 68 (16), 3295–3305.

Everham III, E.M., Brokaw, N.V.L., 1996. Forest damage and recovery from catastrophic wind. Botan. Rev. 62, 113–185.

Ewel, J.J., Whitmore, J.L., 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Rio Piedras, Puerto Rico: Institute of Tropical Forestry. Forest Service Research Paper ITF-18.

Falk, D.A., Miller, C., McKenzie, D.M., Black, A.E., 2007. Cross-scale analysis of fire regimes. Ecosystems 10, 809–823.

Foster, D.R., 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire, USA. J. Ecol. 76, 105–134.

Franco, P.A., Weaver, P.L., Eggen-McIntosh, S., 1997. Forest Resources of Puerto Rico, 1990. USDA For. Serv. Resour. Bull. SRS-22.

Frangi, J.L., Lugo, A.E., 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. Biotropica 23, 324–335.

Gabet, E.J., Reichman, O.J., Seabloom, E.W., 2003. The effects of bioturbation on soil processes and sediment transport. Annu. Rev. Earth Planet. Sci. 31, 249–273.

Guariguata, M.R., 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. J. Ecol. 78 (3), 814–832.

Helmer, E.H., Ramos, O., Del, M., López, T., Quiñones, M., Diaz, W., 2002. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. Caribbean J. Sci. 38 (3–4), 165–183.

Holdridge, L.R., 1967. Life Zone Ecology. Trop. Sci. Center, San Jose, Costa Rica.

IPCC, 2007. Climate Change 2007: The Physical Science Basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Aberyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel of Climate Change. Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA, p. 996.

Kabrick, J.M., Clayton, M.K., Mcbratney, A.B., Mcsweeney, K., 1997. Cradle-knoll patterns and characteristics on drumlins in northeastern Wisconsin. Am. J. Soil Sci. Soc. 61, 595–603.

Koenig, N., 1953. A Comprehensive Agricultural Program for Puerto Rico. USDA Forest Service, Washington, DC.

Larsen, M.C., 1997. Tropical geomorphology and geomorphic work: a study of geomorphic processes and sediment and water budgets in montane humid-tropical forested and developed watersheds. Ph.D. Dissertation. University of Colorado.

Lenart, M.T., 2003. A comparative study of soil disturbance from uprooted trees, and mound and pit decay in Puerto Rico and Colorado. Ph.D. Dissertation. School of Natural Resources, University of Arizona, 176 pp.

Lugo, A.E., 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. Aust. Ecol. 33 (4), 368–398.

Lugo, A.E., Helmer, E., 2004. Emerging forests on abandoned land: Puerto Rico's new forests. For. Eco. Manage. 190 (2–3), 145–161.

Lutz, H.J., 1940. Disturbance of forest soil resulting from the uprooting of trees. Bull. Yale Univ. Sch. 45 .

Merry, K., Bettinger, P., Hepinstall, J., 2009. Physical and biological responses of forests to tropical cyclones affecting the United States Atlantic Ocean and Gulf of Mexico coasts. Am. J. Env. Sci. 5 (1), 784–800.

Mitchell, P., 1988. The influence of vegetation, animals and micro-organisms on soil processes. In: Viles, H.A. (Ed.), Biogeomorphology. Basil Blackwell Ltd, Oxford, UK, pp. 43–82.

Osterkamp, W.R., Toy, T.J., Lenart, M.T., 2006. Development of partial rock veneers by root throw in a subalpine setting. Earth Surf. Process. Landforms 31, 1–14.

Peterson, C.J., 2000. Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. For. Eco. Manage. 135, 237–252.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Silva, J.N.M., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C.A., Saldias, M., Torres Lezama, A., Vinceti, B., 2004. Pattern and process in Amazon tree turnover, 1976–2001. Philos. Trans. R. Soc. Lond. B 359, 381–407.

Prentice, I.C., 2001. The Carbon Cycle and Atmospheric Carbon Dioxide Climate Change 2001: The Scientific Basis IPCC. Cambridge University Press, Cambridge, UK, pp. 183–237.

Putz, F.E., 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64, 1069–1074.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., Aiello, A., 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Can. J. For. Res. 13, 1011–1020.

Sall, J., Lehman, A., 1996. JMP Start Statistics: A Guide to Statistics and Data Analysis Using JMP and JMP IN Software. Duxbury Press, Belmont, CA.

Sanford Jr., R.L., Parton, W.J., Ojima, D.S., Lodge, D.J., 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modeling. Biotropica 23 (4a), 364–372.

Scatena, F.N., 1995. Relative scales of time and effectiveness of watershed processes in a tropical montane rain forest of Puerto Rico. Natural and Anthropogenic Influences in Fluvial Geomorphology. Geophys. Monogr. 89, 103–111.

Scatena, F.N., Larsen, M.C., 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23, 317–323.

Scatena, F.N., Lugo, A.E., 1995. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. Geomorphology 13, 199–213.

Scatena, F.N., Planos-Gutierrez, E.O., Schellekens, J., 2004. Natural disturbances and the hydrology of humid tropical forests. In: Bonell, M., Bruijnzeel, L.A. (Eds.), Forests, Water and People in the Humid Tropics. International Hydrology Series. Cambridge University Press, pp. 489–513.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., Small, T.W., 1989. Tree uprooting: review of impacts on forest ecology. Vegetation 79, 165–179.

Silver, W.L., Ostertag, R., Lugo, A.E., 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restor. Ecol. 8 (4), 394–407.

Simon, A., Larsen, M.C., Hupp, C.R., 1990. The role of soil processes in determining mechanisms of slope failure and hillslope development in a humid-tropical forest, eastern Puerto Rico. Geomorphology 3, 263–286.

Stephenson, J.L, Van Mantgem, P.J., 2005. Forest turnover rates follow global and regional patterns of productivity. Ecol. Lett. 8, 524–531.

U.S. Global Change Research National Assessment Synthesis Team, 2000. Path of Hurricane Georges in Relation to Puerto Rico with Precipitation Totals, map, pp. 82 of climate change assessment retrieved in 2003 from the following U.S. Global Change Research Program website: http://www.grcio.org/NationalAssessment/overpdf/12Is.pdf.

Walker, L.R., 2000. Seedling and sapling dynamics of treefall pits in Puerto Rico. Biotropica 32, 262–275.

Watts, S., Halliwell, L., 1996. Essential Environmental Sciences: Methods and Techniques. Routledge Publishers, London, 279.

Zalamea, M., Gonzalez, G., Ping, C.-L., Michaelson, G., 2007. Soil organic matter dynamics under decaying wood in a subtropical wet forest: effect of tree species and decay stage. Plant Soil 296, 173–185.

Zimmerman, J.K., Everham Iii, E.M., Waide, R.B., Lodge, D.J., Taylor, C.M., Brokaw, N.V.L., 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. J. Ecol. 82, 911–922.