University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USDA National Wildlife Research Center - Staff Publications

U.S. Department of Agriculture: Animal and Plant Health Inspection Service

2013

Changes in abiotic influences on seed plants and ferns during 18 years of primary succession on Puerto Rican landslides

Lawrence R. Walker
University of Nevada Las Vegas, walker@unlv.nevada.edu

Aaron B. Shiels
USDA APHIS, National Wildlife Research Center, aaron.b.shiels@aphis.usda.gov

Peter J. Bellingham
Landcare Research

Ashley D. Sparrow
CSIRO Ecosystem Sciences

Ned Fetcher
Wilkes University

See next page for additional authors

Follow this and additional works at: https://digitalcommons.unl.edu/icwdm_usdanwrc

Authors

Lawrence R. Walker, Aaron B. Shiels, Peter J. Bellingham, Ashley D. Sparrow, Ned Fetcher, Fred H. Landau, and Deborah J. Lodge

Changes in abiotic influences on seed plants and ferns during 18 years of primary succession on Puerto Rican landslides

Lawrence R. Walker[1]*, Aaron B. Shiels[2], Peter J. Bellingham[3], Ashley D. Sparrow[4], Ned Fetcher[5], Fred H. Landau[1] and Deborah J. Lodge[6]

[1]*School of Life Sciences, University of Nevada Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154-4004, USA;* [2]*USDA APHIS, National Wildlife Research Center, Hawaii Field Station, PO Box 10880, Hilo, HI 96721, USA;* [3]*Landcare Research, PO Box 40, Lincoln 7640, New Zealand;* [4]*CSIRO Ecosystem Sciences, PO Box 2111, Alice Springs, NT 0871, Australia;* [5]*Institute for Environmental Science and Sustainability, Wilkes University, Wilkes-Barre, PA 18766, USA; and* [6]*Center for Forest Mycology Research, Northern Research Station, USDA Forest Service, PO Box 1377, Luquillo, PR 00773-1377, USA*

Summary

1. Abiotic variables are critical drivers of succession in most primary seres, but how their influence on biota changes over time is rarely examined. Landslides provide good model systems for examining abiotic influences because they are spatially and temporally heterogeneous habitats with distinct abiotic and biotic gradients and post-landslide erosion.

2. In an 18-year study on 6 Puerto Rican landslides, we used structural equation models to interpret the changing effects of abiotic influences (landslide dimensions, slope, aspect, elevation, parent material and related soil properties) on seed plants (density and diversity), tree fern density, scrambling fern cover, canopy openness and soil development (nitrogen, soil organic matter, pH and cation exchange capacity).

3. Seven years after landslide formation, catchment size (the landslide area above the point of measurement) was the key abiotic factor influencing plants. The larger the catchment the greater was the diversity and density of seed plants. Conversely, the smaller the catchment the greater was the density of tree ferns and the cover of scrambling ferns.

4. Eighteen years after landslide formation, landslide slope was the key abiotic influence. The greater the slope, the lower was the density and diversity of seed plants and the greater was the scrambling fern cover.

5. Aspect, particularly east-facing slopes exposed to wind disturbances, positively influenced tree fern densities at both 7 and 18 years and negatively influenced seed plants and scrambling ferns at 18 years. Soils were least developed, that is, had lowest soil nitrogen and organic matter concentrations, after 18 years on steep slopes (like seed plants); soils were most developed near landslide edges, on hurricane-exposed slopes (like tree ferns) and where there were high soil potassium concentrations.

6. *Synthesis.* Abiotic variables have important influences on plant succession on landslides and the relative influence of different abiotic variables changes with time. Improved predictability of temporal dynamics will rely not only on understanding the effects of initial disturbances and subsequent biological responses but also on the different and changing influences exerted by each abiotic variable.

Key-words: catchment, determinants of plant community diversity and structure, disturbance, diversity, erosion, hurricane, scrambling fern, slope, structural equation modelling, tree fern, tropical forest

*Correspondence author. E-mail: walker@unlv.nevada.edu

Introduction

Understanding successional trajectories following disturbances remains a challenge for ecologists because of the spatial heterogeneity of the disturbed surfaces and the temporal variability of ecosystem responses (Turner *et al.* 1998; Johnstone *et al.* 2010). The initial abiotic conditions and subsequent biotic responses are the variables most often studied, but a more comprehensive approach recognizes the shifting importance of both abiotic and biotic variables throughout succession (Bishop *et al.* 2010). Several approaches can identify key factors that drive succession. First, the examination of freshly denuded surfaces that undergo primary succession is ideal for determining the relative influence of abiotic variables because such surfaces lack the influence of a biological legacy (Platt & Connell 2003), which can obscure abiotic influences in secondary succession (Cramer & Hobbs 2007). Secondly, direct observations of change are generally more accurate than chronosequences that rely on assumptions about temporal dynamics (Walker *et al.* 2010a). Thirdly, the examination of gradients of disturbance severity, common in primary seres, provides another useful framework to understand the relative importance of abiotic vs. biotic influences (Turner 2010). Finally, the application of recent improvements in analytical models, combined with traditional long-term monitoring, can further elucidate the temporally variable influences of drivers of successional change. We used these four approaches to help interpret the role of abiotic variables on plant succession and soil development on landslides in Puerto Rico.

Landslides are excellent habitats in which to analyse multiple drivers of primary succession because they are numerous, spatially heterogeneous with distinct abiotic gradients, subject to post-landslide erosion and well studied (Sidle & Ochiai 2006; Restrepo *et al.* 2009; Shiels & Walker in press; Walker & Shiels 2013). Landslides in tropical, humid climates have additional advantages because succession occurs more rapidly than in most other primary seres (full canopy closure within 50–100 years; Guariguata 1990; Walker *et al.* 1996). Landslides are typically triggered by intense rainfall (Larsen & Simon 1993), earthquakes (Sidle & Ochiai 2006), volcanoes (Schuster 2001) and a variety of human activities such as road construction, urbanization and mining (Larsen & Parks 1997). The mountainous regions where landslides occur are often highly dissected, encompass multiple geological substrates and have a variety of slopes and aspects. Landslides contribute substantially to landscape heterogeneity (Geertsema & Pojar 2007; Elias & Dias 2009), in part through post-landslide erosion (Walker & Shiels 2008) and in part because of the distinct groups of organisms that colonize landslide scars. A number of studies have examined the role of abiotic (Fetcher *et al.* 1996; Shiels, Walker & Thompson 2006; Lepore *et al.* 2012) and biotic (Walker *et al.* 2010b) variables that drive plant succession on <10-year time-scales on tropical landslides, but there has been no direct examination of the importance of multiple abiotic variables on longer-term development of plant communities on landslides and associated changes in soil nutrients and soil organic content. Integrating short-term

mechanisms into an understanding of long-term dynamics (Hobbs & Suding 2009) is both useful to explain succession and soil development and desirable to restore ecosystem functions (Walker, Velázquez & Shiels 2009) and landscape heterogeneity (Dislich & Huth 2012).

A MODEL TO DETERMINE THE INFLUENCES OF ABIOTIC VARIABLES ON LANDSLIDE SUCCESSION

Based on previous studies of tropical landslides (particularly in Puerto Rico), we developed a series of hypotheses about a suite of abiotic factors that we predict may be responsible for plant succession (measurements taken in 1995 and 2006; Fig. 1) and related ecosystem variables measured only in 2006 (soil development, [not ;] foliar nutrients, canopy openness; Fig. S1). Evaluation of the relative contribution of each variable to 18 years of successional change was assessed with structural equation models (SEMs), which examine networks of causal relationships among factors (Grace 2006; Bellingham & Sparrow 2009). SEMs are particularly useful in situations where there is substantial prior knowledge about the system or the potential for variable biotic responses to abiotic conditions (Spitale, Petraglia & Tomaselli 2009). Abiotic predictor variables for landslide succession include both spatial features of landslides (area, length, distance to top and edge, catchment, slope, aspect) and soil conditions (parent material, particle size, and soil phosphorus [P] and potassium [K] concentrations). Catchment is the area (m^2) within a landslide above a given plot boundary from which sediments are likely to erode into the plot (Larsen, Torres-Sánchez & Concepción 1999). Catchment was mostly influenced by distance to edge and top of a landslide. We explain below our reasons for choosing each of these variables as important predictors for landslide succession.
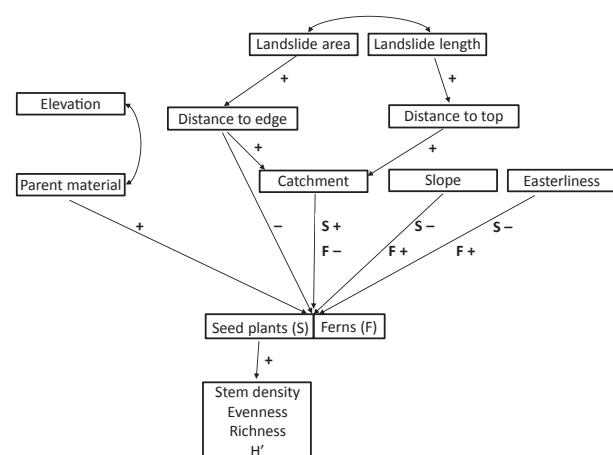
Fig. 1. Conceptual *a priori* models to test hypotheses for positive (+) or negative (−) relationships on Puerto Rican landslides between quantified environmental variables and seed plants (S) and ferns (F; tree ferns and scrambling ferns). Directions of hypothesized relationships ('+' or '−') were identical among both seed plants and ferns except as indicated. Models were tested for vegetation parameters in 1995 and 2006 (7 and 18 years after disturbance, respectively). Two-way arrows indicate correlation.

The size of a disturbance (area, length) and position of measurement (catchment) are critical variables influencing succession both on landslides (Walker *et al.* 1996; Myster, Thomlinson & Larsen 1997; Walker & Shiels 2008) and in other types of gaps (Dietze & Clark 2008). Many landslides have vertical gradients from steep, nutrient-poor slip faces at the top (Elias & Dias 2009), to central chutes with moderate soil nutrient concentrations (Velázquez & Gómez-Sal 2007), to deposition zones where nutrient-rich sediments accumulate (Guariguata 1990; Cruden & Varnes 1996). A large catchment therefore generally implies a position near the base of a large landslide, often in the fertile deposition zone. Plots closer to the landslide edge have smaller catchments than plots towards the centre of the landslide. Edge and centre plots may differ in abiotic (e.g. soil nutrients, soil temperatures, canopy openness; Myster & Fernández 1995; Fetcher *et al.* 1996) and biotic (e.g. seed rain number and diversity; Walker & Neris 1993; Myster & Fernández 1995) conditions. We hypothesized that landslide area and length positively affect catchment and that larger catchments (plots located near the base and centre of a landslide) would have more positive effects on seed plant density and diversity (as proxies for succession; Fig. 1) and soil development and foliar nutrients (Fig. S1A) than smaller ones.

Slope can influence short-term landslide succession (Walker *et al.* 1996; Wilcke *et al.* 2003; Sidle & Ochiai 2006; Shiels *et al.* 2008), particularly by its association with post-landslide erosion (Walker & Shiels 2008). We hypothesized that slope would negatively affect seed plant development (Fig. 1). We also hypothesized that foliar nutrients (nitrogen [N] and P concentrations; Fig. S1A) would respond favourably to increased catchment and negatively to increased slope because of the more fertile soils found in the lower, flatter zones of landslides (Guariguata 1990). Aspect may also influence plant succession on landslides, particularly when disturbances come from a consistent direction. In Puerto Rico, the dominant weather patterns come from north-easterly trade winds and south-easterly hurricanes (Scatena & Larsen 1991; Larsen & Torres-Sánchez 1998). We therefore hypothesized that easterliness (east-facing aspect) is negatively associated with seed plant density and diversity and soil development in Puerto Rico, but positively associated with scrambling fern cover, due to potential wind damage (Boose, Foster & Fluet 1994; Cordero, Fetcher & Voltzow 2007). However, moisture-bearing winds may instead accelerate forest recovery (Crk *et al.* 2009).

The effects of abiotic influences on tree fern density, scrambling fern cover and canopy openness were also included in our SEM models. Based on studies examining these response variables (Dalling & Tanner 1995; Shiels *et al.* 2008; Walker *et al.* 2010b), we hypothesized that ferns (tree fern density and scrambling fern cover; Fig. 1) and canopy openness (Fig. S1B) would be negatively affected by catchment and positively affected by steep slopes and easterliness. Although both tree ferns and scrambling ferns colonize open areas, they tend to be displaced by seed plants in the lower zones of landslides with the largest catchment and least

canopy openness and tend to be most abundant on steeper, less fertile substrates (Negishi *et al.* 2006). Reduced competition may also make ferns more likely to dominate wind-damaged slopes.

The parent material from which landslide soils are derived can have a large influence on nutrient accumulation (Zarin & Johnson 1995) and plant succession (Shiels *et al.* 2008; Walker & Shiels 2008). For example, in the mountains of north-eastern Puerto Rico, soils are either of volcaniclastic or of dioritic origin (Larsen, Torres-Sánchez & Concepción 1999; Shiels & Walker in press). Soils derived from volcaniclastic parent material are less erosive (Walker & Shiels 2008), have lower sand and higher clay content (Guariguata 1990; Shiels *et al.* 2008) and higher soil P (Shiels 2006) than dioritic soils. The main source of K in Puerto Rico is from sea salt aerosols deposited via rain (McDowell *et al.* 1990); K is then retained (particularly in clay-rich soils) against high leaching rates by plants and soil organisms (Lodge 1987; Silver *et al.* 1994). Clay content, N, P and soil organic matter (SOM) were positively correlated with plant growth on several landslides in Jamaica (Dalling & Tanner 1995) and Puerto Rico (Fetcher *et al.* 1996; Shiels, Walker & Thompson 2006; Shiels *et al.* 2008). Soil conditions also vary within landslides, with highest concentrations of nutrients and associated soil organisms in lower than upper zones (Li *et al.* 2005). Based on the above studies, we hypothesized that parent material, through its positive influence on clay and soil P, and aerosol-driven K, will have a positive effect on soil N concentration, SOM and cation exchange capacity (CEC) and a negative effect on soil pH (Fig. S1A).

Tests of our predictions about landslide succession were based on data from direct sampling (1–3 times per year) of six Puerto Rican landslides over an 18-year period. Because most other studies of landslide succession have focussed on biotic influences and responses (Shiels & Walker in press; Walker & Shiels 2013), in this study we emphasized the differential effects of abiotic influences on plant functional groups and related ecosystem parameters. Most of our predictions about the roles of specific abiotic variables were verified, but we found unexpected temporal variation in the influences of abiotic variables on landslide succession.

Materials and methods

STUDY AREA

The study was conducted on 6 landslides located between 370–650 m a.s.l. in the Luquillo Experimental Forest (LEF) in eastern Puerto Rico (18°15–19′ N, 65°47–50′ W). The landslides, formed in 1987–1988, reflected the variation in area, elevation, slope, aspect and parent material among landslides in the LEF (Table S1), but they were all characterized by freshly exposed mineral soil surfaces with < 2% plant cover when the study began in 1988. The landslides all occurred in the subtropical wet forest zone (Ewel & Whitmore 1973), where surrounding mature forest is 20–25 m tall and dominated by *Dacryodes excelsa* (tabonuco) and *Prestoea acuminata* var. *montana* (sierra palm). Mean annual precipitation is 3455 mm, and mean monthly

temperatures range between 21 and 25° C (Brown *et al.* 1983). The most powerful hurricanes to affect the LEF during our study were Hurricanes Hugo (1989), Hortense (1996) and Georges (1998). The soils in the Río Espíritu Santo drainage (around the research station El Verde in the north-western part of the LEF; landslides ES1, ES2, ES5, ES10) are a complex of upland Ultisols and Oxisols (Zarzal-Cristal complex; Soil Survey Staff 1995) of volcanic origin and are mostly well-drained clays and silty clay loams. Soils in the upper Río Blanco drainage (in the south-eastern part of the LEF; landslides RB2, RB9) are poorly drained quartz diorite (Seiders 1971). The dioritic soils can be *c.* threefold lower in N, sandier and more erosive than the volcaniclastic soils (Shiels *et al.* 2008; Walker & Shiels 2008). These 6 landslides are the subset of 16 landslides further described by Myster & Walker (1997) that were both large enough and stable enough to include in this 18-year data set. Taxonomic nomenclature follows Liogier (1985–1997) and Proctor (1989).

STUDY DESIGN

On each landslide, 3–6 transects were positioned perpendicular to the long, down-hill axis of the landslide at 10-m intervals starting 10 m from the top of the slip-face (at the forest/landslide boundary). At random intervals along each transect, we placed between two and nine rectangular 2 × 5 m permanent plots on the exposed soil that were oriented with the long side along the down-hill axis. The numbers of transects and plots depended on the width and length of the landslide but were designed to maximize the sampled area (between 15 and 24 plots per landslide). The plots and transects thus represented a range of habitats including the steep slip-face at the top of each slide, the chute or central zone and the landslide edges. The deposition zone near the bottom of each slide was not included because most were missing due to river erosion and removal from roadways.

Vegetation measurements began in June 1988 for ES1, October 1988 for ES2 and January 1989 for the remainder of the landslides (each date was 6–13 months after landslide formation) and were repeated every 4–7 months for 18 years (36 total measurements; 1988–2006) on ES1 and ES2. On the remaining 4 landslides, vegetation measurements were less frequent over the same 18-year period (every 4–7 months from 1988–1992, annually from 1992 to 1997, in 1999, and in 2006). During the first 2 years, care was taken not to introduce mycorrhizae, seeds or organic soil into the landslide plots by cleaning our boots prior to sampling. At each sampling date, we counted and identified stems of all seed plants and tree ferns (exclusively *Cyathea arborea* (L.) Sm.; a single-trunked species that does not have a creeping rhizome; henceforth 'tree ferns') that were ≥ 1 m tall and rooted in each plot. We also estimated the combined cover (in 6 classes: < 1%, 1–5%, 6–25%, 26–50%, 51–75% and > 75%) of scrambling ferns *Gleichenella pectinata* (Willd.) Ching (formerly *Dicranopteris pectinata*) and *Sticherus bifidus* (Willd.) Ching (formerly *Gleichenia bifida*) (henceforth 'scrambling ferns') in a 1 × 2 m subplot within the lower edge of each larger plot.

SEM MODELS

We used structural equation modelling (SEM; AMOS version 18.0.0; AMOS Development Corporation 2009) to examine the likely direct and indirect drivers (i.e. environmental variables) of plant and soil development on all six landslides. Before analysis, abiotic drivers and abiotic and biotic response variables were log-transformed as required to meet assumptions of normality. We present standardized path coefficients for three SEMs: (i) a 1995 model that represented vegetation

development 7 years after landslide disturbance, (ii) a 2006 model that represented vegetation and soil development 18 years after landslide disturbance and (iii) a 1995–2006 difference model that represented the 11-year change in vegetation from 1995 to 2006 and measured biotic predictors of succession. We examined the 2006 model in two ways: (i) using variables measured in both 1995 and 2006 (results in text) and (ii) using variables measured only in 2006 (results in appendices). Our selection of abiotic predictor variables and associated hypotheses are justified in the Introduction. Area was total landslide area in m^2; length was maximum distance in metres from top to bottom; distance to top of the landslide was from the base of each plot; distance to edge of the landslide was from the midpoint of the bottom of each plot. Catchment was the estimate of the area in m^2 of the landslide surface above each plot that could erode into the plot; this value was similar for plots among transects but reduced by edge effects (see Larsen, Torres-Sánchez & Concepción 1999 and Walker & Shiels 2008 for relative merits of various catchment estimates). Elevation (m a.s.l.) was taken at the lowest transect on each landslide. Slope was the average for the entire landslide. Aspect (easterliness) was calculated using the sine of the radian to adjust aspect of each landslide along an east-west gradient (high values to the east) that represented influence from the hurricanes and trade winds, which arrive mostly from the east in Puerto Rico. Parent material was either volcaniclastic (assigned a value of one) or dioritic (value of zero). Further soil analyses were made on each landslide from five surface soil samples (0–10 cm) taken on 8–12 August 2006 from the corners and centre of each plot and pooled for analysis. Percent sand and clay were determined by the hydrometer method (Sheldrick & Wang 1993); available P (Olsen) and available K (Mehlich III) were also analysed (Gavlek *et al.* 2003).

Response variables used in the SEMs included three vegetation variables related to plant succession (seed plants, tree fern density, scrambling fern cover) and three related ecosystem parameters (foliar nutrients, canopy openness, and soil development). Seed plants (Table S2) included mostly trees (*n* = 41 species), but also one shrub, one vine and one herb. 'Seed plants' was used as a latent variable (i.e. a variable not measured directly but estimated from several variables predicted to comprise the latent variable) in the SEMs to account for the following four variables that were highly correlated: (i) stem density, (ii) species diversity (Shannon's Index; H′), (iii) species richness (S) and (iv) species evenness (E = H′/lnS). Tree ferns are dispersed by spores and do not reproduce vegetatively; therefore, stem densities were measured annually from 1995 to 1999 (except 1998) and 2006 in all plots on all the landslides (except ES2, where counts were only made in 1995 and 2006). Scrambling ferns rarely reproduce by spores, but do spread vegetatively through rhizome branching and indeterminate leaf growth, so estimates of scrambling fern cover were made at the same time as seed plant stem counts at each sampling date. Foliar nutrients of live and senesced tree fern leaves were measured once in August 2006 as a latent variable that included the highly correlated P and N concentrations (Kjeldahl analysis; Alpkem Corporation 1992). No other plant species were sufficiently common and widespread to obtain samples for foliar nutrient analyses. Canopy openness was determined from hemispherical photographs taken at 1.5 m off the ground at the centre of each plot on 8–12 August 2006 with a Nikon Fisheye Converter Lens (FC–E8; 0.21×) and a Nikon Cool Pix 950 digital camera. The images were analysed using Gap Light Analyser Version 2 software (Frazer, Canham & Lertzman 1999) to obtain per cent canopy openness.

'Soil development' was a latent variable (sampled as described above) because it included the following highly correlated variables: (i) pH, (ii) percent SOM (determined by combustion), (iii) CEC (Ross 1995) and (iv) total Kjeldahl N. Soil N concentrations were deter-

mined from samples taken in 2000 because detection levels used in 2006 were not sufficient in 31% of the samples to record low values (comparisons of values from plots with data from both years were significantly positively related; $R^2 = 0.74$).

SEM variables were measured at various spatial scales (landslide, transect or plot). Landslide-level measurements included area, length, elevation, slope, aspect and parent material; transect-level measurements included distance to the top, distance to the base, leaf N and P concentrations and litter N and P concentrations; plot-level measurements included sand, clay, soil K, soil P, catchment, seed plant characteristics (stem density, evenness, richness, H′), soil development factors (N, SOM, CEC, pH), tree fern stem density, scrambling fern cover and canopy openness. Significance ($P \leq 0.05$) was adjusted using the appropriate degrees of freedom for measurements at landslide (d.f. = 5), transect (d.f. = 23) and plot and subplot (both d.f. = 107) levels.

FINE-SCALE TEMPORAL PATTERNS

On the two landslides with the most frequent observations (ES1: four transects; ES2: five transects; 1988–2006), we examined additional variables not included in the SEM models: the development of canopy height, changes in total stem densities, densities of the 3 most abundant seed plants and diversity of seed plants ≥ 1 m tall. For tree ferns on ES-1 between 1991 and 1995, we assessed height growth, leaf number, leaf production and leaf longevity on the largest individual ≥ 1 m tall in each plot that had tree ferns ($n = 18$ plots). Tree fern heights were measured from a nail inserted into the trunk within 50 cm of the ground to the base of the lowest expanding leaf. Tree fern leaf number, production and turnover were monitored by placing colour-coded tags on each new leaf during each visit.

Results

PATTERNS OF SUCCESSION ACROSS SIX LANDSLIDES

None of our SEMs were significantly different from the conceptual *a priori* model after deleting all non-significant paths. When highly significant standardized path coefficients ($P \leq 0.001$) were selected for 1995 plus 2006 vegetation measurements (Table 1) and soil development, foliar nutrients and canopy openness in 2006 (Table S3), only 2 of 18 coefficients deviated from the expected direction of response. This outcome suggests the validity of using SEMs to highlight which variables are most relevant for prediction of plant succession and soil development, when there is a substantial preliminary data base and results are cautiously interpreted within both local and landscape contexts.

In the 1995 SEM model (7 years after landslide formation), catchment size had the strongest and positive influence on seed plants (Fig. 2a; standardized path coefficient = 0.93; $P < 0.001$; greater density and diversity of seed plants on larger catchments). The most critical influences on catchment size were landslide length and distance from each plot to the top of the landslide. Parent material also positively influenced seed plants ($P < 0.001$; greater density and diversity of seed plants on volcaniclastic than on dioritic parent material). Slope (range: 20–33°) had a slightly negative effect on seed plants ($P = 0.001$; the less the slope the greater the density

Table 1. Summary of highly significant ($P \leq 0.001$) standardized path coefficients from 2 structural equation models showing multivariate relationships for 7 and 18 years after landslide occurrences in Puerto Rico. Bold font indicates the observation that did not follow the hypothesized direction of response

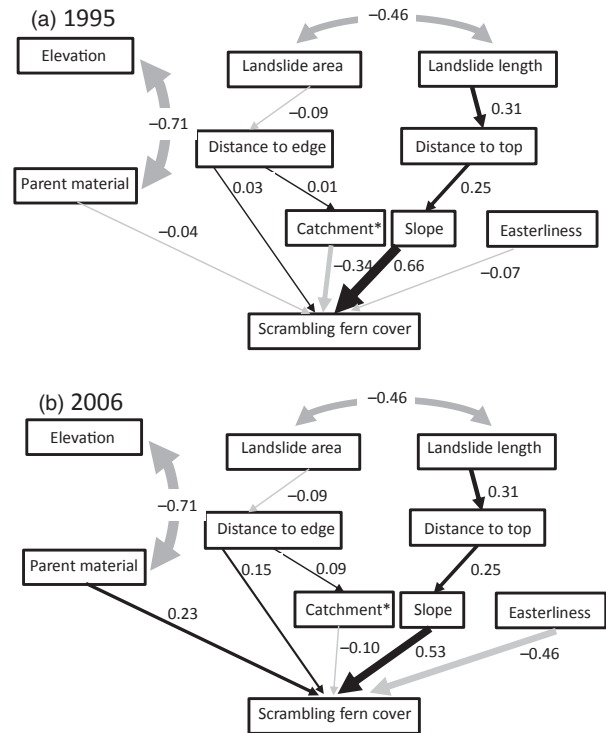| Response variable	Year	Parent material	Catchment	Slope	Aspect (Easterliness)
Seed plants	7	+0.29	+0.93	−0.20	
	18			−0.81	
Tree ferns	7		−0.41		+0.41
	18				
Scrambling ferns	7		−0.34	+0.66	
	18	+0.23		+0.53	**−0.46**
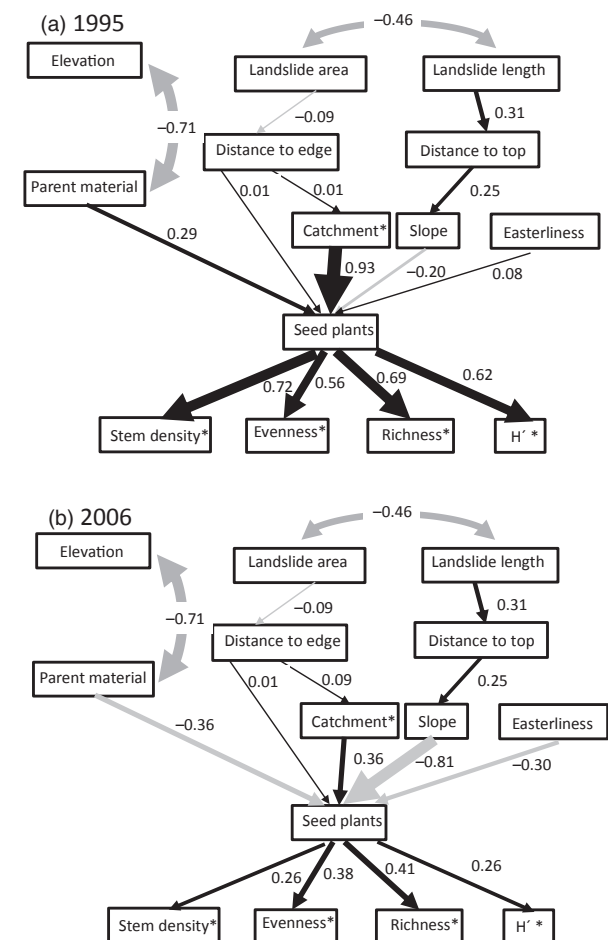
Fig. 2. Structural equation models (SEMs) showing multivariate relationships (a) in 1995 (7 years after disturbance) and (b) in 2006 (18 years after disturbance) on Puerto Rican landslides among quantified environmental variables and seed plants >1 m tall and component variables of seed plants (density, evenness, richness and Shannon index of diversity [H′]). Two-way arrows indicate correlation. Thickness of arrows is proportional to the standardized path coefficients shown on each arrow. Positive relationships are shown in black, negative relationships in grey. Asterisks denote values that were log-transformed before model fitting. Both the 1995 model ($\chi^2 = 3711.12$; d.f. = 83; $P < 0.001$; AIC = 3815.12) and the 2006 model ($\chi^2 = 1426.03$; d.f. = 81; $P < 0.001$; AIC = 1534.03) were not significantly different from the conceptual *a priori* model (Fig. 1) after deleting all non-significant paths.
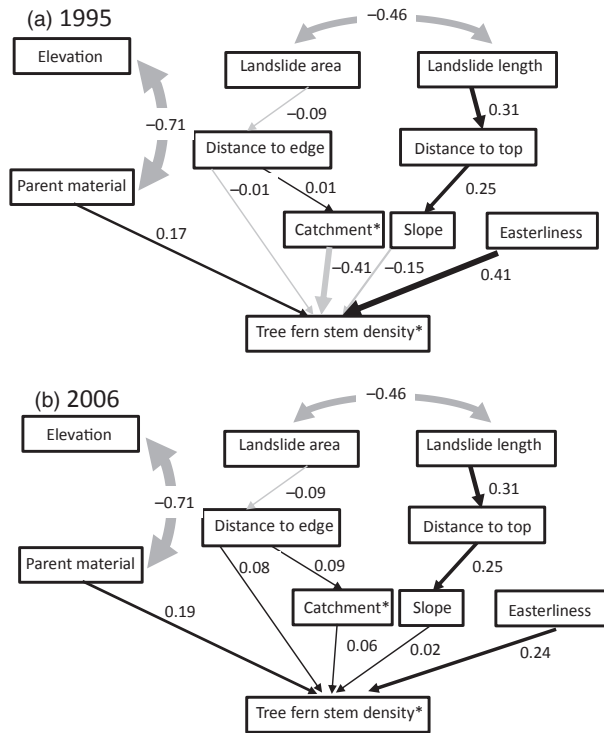
Fig. 3. Structural equation models (SEMs) showing multivariate relationships (a) in 1995 (7 years after disturbance) and (b) in 2006 (18 years after disturbance) on Puerto Rican landslides among quantified environmental variables and tree fern stem density (ferns > 1 m tall). Two-way arrows indicate correlation. Thickness of arrows is proportional to the standardized path coefficients shown on each arrow. Positive relationships are shown in black, negative relationships in grey. Asterisks denote values that were log-transformed before model fitting. Both the 1995 model ($\chi^2 = 3711.12$; d.f. = 83; $P < 0.001$; AIC = 3815.12) and the 2006 model ($\chi^2 = 1426.03$; d.f. = 81; $P < 0.001$; AIC = 1534.03) were not significantly different from the conceptual *a priori* model (Fig. 1) after deleting all non-significant paths.

Fig. 4. Structural equation models showing multivariate relationships (a) in 1995 (7 years after disturbance) and (b) in 2006 (18 years after disturbance) on Puerto Rican landslides among quantified environmental variables and scrambling fern cover. Two-way arrows indicate correlation. Thickness of arrows is proportional to the standardized path coefficients shown on each arrow. Positive relationships are shown in black, negative relationships in grey. Asterisks denote values that were log-transformed before model fitting. Both the 1995 model ($\chi^2 = 3711.12$; d.f. = 83; $P < 0.001$; AIC = 3815.12) and the 2006 model ($\chi^2 = 1426.03$; d.f. = 81; $P < 0.001$; AIC = 1534.03) were not significantly different from the conceptual *a priori* model (Fig. 1) after deleting all non-significant paths.

and diversity of seed plants). Tree fern density (Fig. 3a) was negatively affected by catchment size ($P < 0.001$; more tree ferns at the tops than bottoms of landslides) and positively by easterliness ($P < 0.001$; more tree ferns on east-facing landslides). In addition, tree fern density was positively affected by parent material ($P = 0.024$; more tree ferns on volcaniclastic soils than on dioritic soils) and negatively affected by slope ($P = 0.048$). Scrambling fern cover (Fig. 4a) was also negatively influenced by catchment ($P < 0.001$) but positively by slope ($P < 0.001$; more scrambling fern cover on steeper slopes), while easterliness had no strong influence ($P = 0.30$).

In the 2006 SEM model (18 years after landslide disturbance), only slope had a strongly significant ($P \leq 0.001$) and negative influence on seed plant density and diversity, and its standardized path coefficient was much greater (-0.81) than in 1995 (Figs 2a and b). Catchment size still had a positive influence on seed plant density and diversity in 2006 ($P = 0.018$), but its standardized path coefficient (0.36) was much less than in 1995. By 2006, the effect of parent material was the opposite of that in 1995 ($P = 0.017$; Figs 2a and b; greater density and diversity of seed plants on dioritic

than volcaniclastic parent material). Easterliness also had a negative influence on seed plants in 2006 ($P = 0.041$; greater density and diversity on westerly or leeward aspects). Although both easterliness and parent material still influenced tree fern stem density in 2006 ($P = 0.009$ and 0.040, respectively, Fig. 3b), their influences were weaker than in 1995. Scrambling fern cover in 2006 (Fig. 4b) was positively affected by slope ($P < 0.001$; higher cover on steeper slopes), negatively affected by easterliness ($P < 0.001$; lower cover on east-facing than on west-facing landslides) and positively affected by parent material ($P < 0.001$; higher cover on volcaniclastic soils). Slope and distance to edge both had strong negative influences on foliar nutrient concentrations ($P < 0.001$; Fig. S2A; lower leaf and litter N concentrations but higher leaf and litter P concentrations on steep slopes and in plots near landslide edges in 2006). Easterliness has a weakly negative influence on foliar nutrients ($P = 0.036$; higher values on leeward west-facing slopes). Canopy openness (Fig. S2B) was positively affected by slope ($P < 0.001$; the steeper the slope the more open the canopy) and distance to edge ($P = 0.022$) but negatively affected by catchment size ($P = 0.002$).

Soil development in 2006 (Fig. S3; total N, SOM, pH, CEC) was positively associated with available soil K and easterliness (both $P < 0.001$) and catchment size ($P = 0.014$) and negatively influenced by slope and distance to edge (both $P < 0.001$; less soil development on steep plots in the centre of landslides).

In the difference model (Fig. S4), both 1995 seed plant characteristics (-0.87) and 1995 tree fern densities (-0.37) were negatively correlated with the changes in seed plants during the 11-year period between 1995 and 2006. Changes in seed plant characteristics included increases in stem density, evenness, richness and H′. Plots with high seed plant density or diversity and high tree fern density in 1995 experienced fewer changes in seed plant characteristics between 1995 and 2006 than plots with low values in 1995.

When the six landslides were compared for soil and foliar measurements, all measured parameters differed significantly ($P < 0.05$) among landslides except soil P concentration, clay and sand, suggesting high soil substrate heterogeneity across the landscape (Table S1). Among those parameters that did differ among landslides, ES1 had the highest absolute values for soil N concentration, soil K concentration, SOM, CEC and pH, as well as for leaf and litter N concentrations. Leaf and litter P concentrations were highest on RB2, and canopy openness was highest on ES10. Either RB2 or ES10 had the lowest values for most other parameters.

FINE-SCALE TEMPORAL PATTERNS

When 2 landslides (ES1 and ES2) were assessed for 20 years, canopy height developed rapidly after landslide formation in 1987, and it continued to increase during the course of the study on ES1 to about 16 m in 2008 (Fig. 5a), whereas canopy height appeared to be stabilizing at about 8 m on ES2 (Fig. 5b). Successive hurricanes caused only minor fluctuations in these overall trends. Seed plant woody stem densities also varied by landslide, with several peaks between hurricanes on ES1 (Fig. 5c) and only one peak on ES2 (Fig. 5d). Seed plant diversity (H′) remained fairly stable on both landslides, with slight post-hurricane increases on ES1 (Fig. 5e) but no obvious increases on ES2 (Fig. 5f), probably due to large variation among transects. A closer examination of the three most abundant woody stems on each landslide indicated high mortality of *Cecropia schreberiana* from damage sustained during Hurricane Hugo (1989) on ES1 (Fig. 5g), pronounced increases of *Piper glabrescens* and less pronounced increases of *Psychotria berteriana* following Hurricanes Hugo and Georges (1998). On ES2 (Fig. 5h), stem density of both *Cecropia schreberiana* and *Psychotria berteriana* peaked within several years of landslide formation while density of *Prestoea acuminata* var. *montana* increased slowly during the study period.

Tree ferns (*Cyathea arborea*) colonized both ES1 and ES2 landslides with stem densities ranging from 0.06 to 0.72 stems m^{-2} in 1996. On ES1, tree fern stem densities peaked in 1992 (4 years after landslide formation) at 0.82 stems m^{-2} (Fig. S5) and had > 50% cover from 1990 to 1994 before

thinning dramatically (e.g. 157 stems in 1992 and only 8 in 2006; data not shown). A similar decline occurred on ES2 between 1995 (7 years after landslide formation; 49 stems) and 2006 (8 stems). On ES1 between 1991 and 1995, measured tree ferns grew vertically at 92.7 ± 9.5 cm year^{-1} (range: 16–150), had 7.3 ± 0.3 leaves (range: 1–21) at each measurement date and produced 13.2 ± 0.3 leaves year^{-1} (range: 11–21). The rapid turnover resulted from the short leaf life spans of tree ferns; 50% of tree fern leaves lived only 3–7 months and few survived > 7 months, while some leaves died after only 2 months (L. Walker, personal observation).

Discussion

During primary succession, abiotic variables associated with the initial conditions after a disturbance do not exert constant influences on the development of vegetation. Instead, our study shows that the relative influence of different abiotic variables on successional processes changes with time. The net result is a spatially and temporally variable pattern of resources for colonists of landslides (Rebertus & Veblen 1993) and strong linkages between abiotic drivers and biotic responses during the first two decades of plant succession and soil development (Restrepo *et al.* 2009).

ABIOTIC INFLUENCES

Catchment size and slope were the most substantial abiotic influences of plant succession, although aspect and parent material were also important (Table 1). The effects of each of these influences differed according to plant life-form and changed with time. The influence of catchment size was most pronounced after 7 years (1995) and of slope after 18 years (2006). Catchment size, which incorporates the distance from each plot to the landslide top and edge, influences the colonization of seed plants in that plot (Walker & Neris 1993; Shiels *et al.* 2008). Catchment size was positively associated with seed plant biomass, as demonstrated on a landslide in Nicaragua (Velázquez & Gómez-Sal 2008), because large catchments generally include the flattest, most stable regions of a landslide and small catchments are relatively more influenced by steep, unstable regions of a landslide than are large catchments (Guariguata 1990; Walker *et al.* 1996; Myster, Thomlinson & Larsen 1997). Small catchments in our study and elsewhere (Dalling 1994; Negishi *et al.* 2006) supported tree ferns and scrambling ferns. However, these patterns are not universal, as various life-forms were found in multiple landslide microhabitats in New Zealand (Mark *et al.* 1964), including woody seed plants on the uppermost, steepest slopes. The sharp decline in the influence of catchment size on all life-forms on Puerto Rican landslides between 7 and 18 years after landslide formation highlights how its influence is strongest during the earliest stages (< 7 years) of colonization and is ameliorated by biotic factors as succession proceeds.

Slope had a strong positive influence on scrambling fern cover 7 years after landslide formation, and this was still the
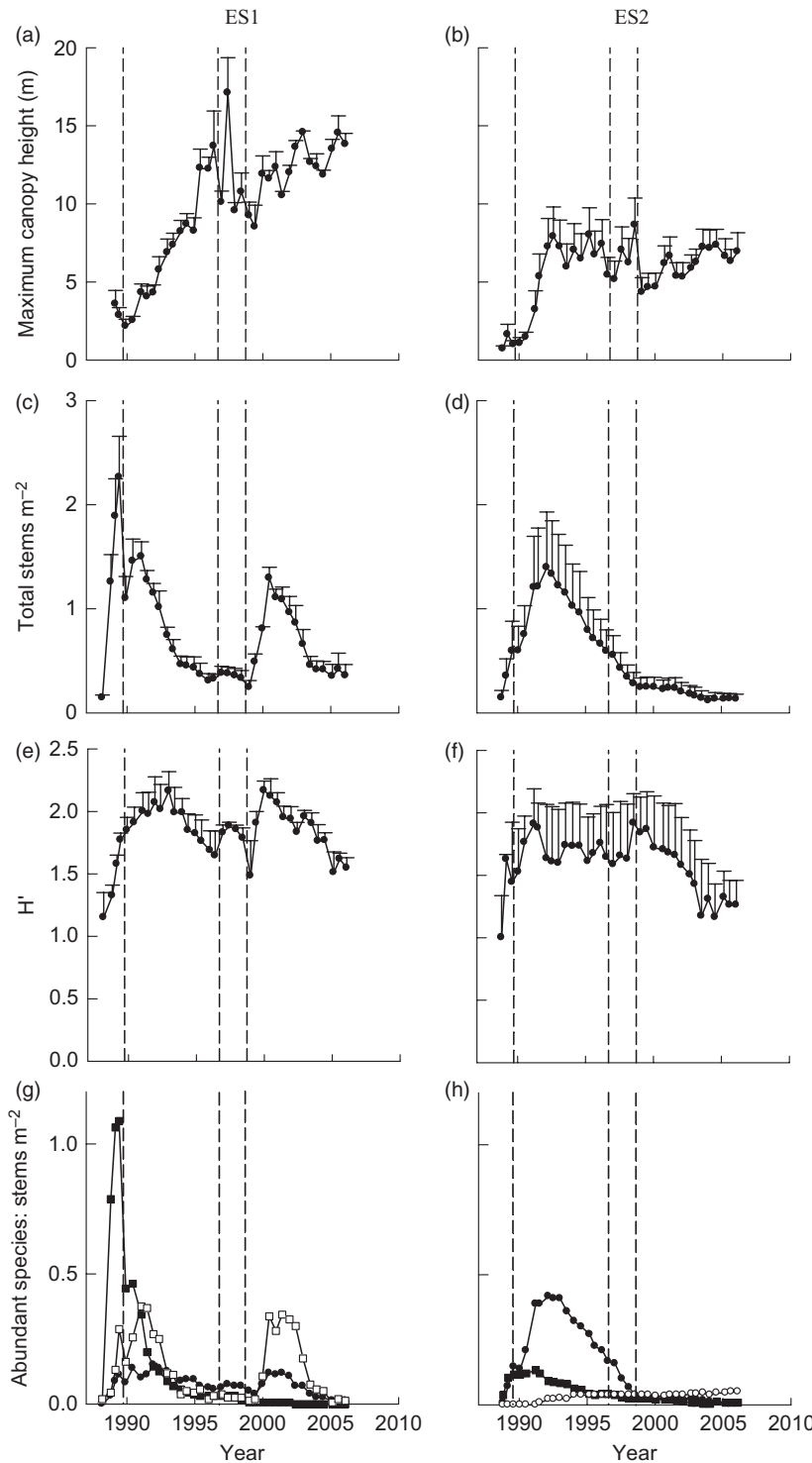
Fig. 5. Fine-scale temporal patterns of seed plants ≥ 1 m tall on landslide ES1 (left column) and landslide ES2 (right column). Maximum canopy height (m) for (a) ES1 and (b) ES2; total seed plant stem density (stems m^{-2}) for (c) ES1 and (d) ES2; Shannon diversity index (H') for (e) ES1 and (f) ES2; and seed plant density for the three most abundant species on (g) ES1 and (h) ES2. In g and h, filled squares = *Cecropia schreberiana*, filled circles = *Psychotria berteriana*, open squares = *Piper glabrescens*, and open circles = *Prestoea acuminata* var. *montana*. Mean + SE for transects ($n = 4$ transects for ES1 and $n = 5$ transects for ES2) for all graphs except (g) and (h) where transect totals were used. The following hurricanes are indicated by vertical dashed lines from left to right: 18 September 1989 (Hugo), 22 September 1996 (Hortense) and 21 September 1998 (Georges).

case after 18 years. Slope had a strong negative influence on seed plants after 18 years, which suggests that there is a negative correlation between plant size (ground-covering ferns vs. taller tree ferns and trees) and slope (Walker & Shiels 2013). Canopy openness was also greatest on steep slopes at the centre and top portions of landslides after 18 years, probably reflecting patterns of seed plant colonization or growth. While the effect of slope on scrambling ferns was fairly constant, its effect – on seed plants (as measured by standardized path coefficients in SEMs) – increased fourfold during our study, while the influence of catchment decreased threefold. Walker *et al.* (1996) proposed that colonization of landslides by seed plants and scrambling ferns reflected both substrate stability (inversely related to slope) and nutrient availability, but subsequent studies have indicated that duration of slope stability (e.g. the influence of post-landslide erosion; Lundgren 1978; Walker & Shiels 2008) and the form and availability of nutrients (e.g., soil vs. leaves; Shiels, Walker &

Thompson 2006; Shiels *et al.* 2008) are also important, particularly in early succession. Evidence for a link between slope and nutrients was found in our study, where flatter slopes were associated with tree fern leaves containing high concentrations of N. Our landslide-level data on slope did not account for plot-level variation within each landslide, and we did not sample the full range of slopes because most landslides lacked deposition zones. Nevertheless, slope clearly had an influence on landslide succession that was dynamic and dependent on differential biotic responses to slope stability and accumulations or losses of soil and nutrients.

The aspect of landslides in the LEF relates to the greater prevalence of moisture-bearing trade winds that come from the north-east. Episodic hurricanes and smaller storms embedded in the trade winds (e.g. tropical waves and depressions) also come primarily from the east and north-east (Larsen & Torres-Sánchez 1998) but sometimes from the north-west (Boose, Foster & Fluet 1994). We expected that seed plants would respond negatively to more exposure to these easterly weather systems because most of the seed plants that colonize landslides are pioneers with high relative growth rates and low wood density (Chave *et al.* 2009) that are prone to damage and mortality during storms (Curran *et al.* 2008). Consistent with this explanation, seed plants were more negatively associated with easterliness in 2006 than in 1995, possibly because of the effects of Hurricanes Hortense and George (see Fig. 5). We expected that scrambling ferns would respond positively to more exposure to hurricanes, given their low stature and pioneer status on landslides and other frequently disturbed habitats (Walker & Sharpe 2010). Their unexpected negative response to easterliness after 18 years may be due to shading by tree ferns. Finally, we did not have clear expectations for tree fern responses to aspect. Tree ferns are also common pioneers on disturbed surfaces, but they have large leaf surfaces and an erect growth form, leading to potentially adverse effects of hurricanes (Bellingham, Tanner & Healey 1995). Tree ferns were most dense on east-facing slopes after 7 years, but that relationship became less clear after 18 years, perhaps due in part to the hurricanes during our study period. Our results contrast with Myster, Thomlinson & Larsen (1997), who found higher structural complexity on LEF landslides facing south-east, but their five aspect categories focussed on north-west–south-east comparisons, and they pooled tree ferns and *Cecropia* trees in their structural complexity categories, making direct comparisons with our study difficult. Our results also contrast with Crk *et al.* (2009), who suggest that forest recovery is fastest on north-west to north-east-facing slopes in the LEF, due to moisture-bearing north-east trade winds. This moisture source may have favoured the early dominance by tree ferns on east-facing slopes. Hence, because landslide aspect results in different impacts from both moisture and hurricane regimes in the LEF, it is a significant abiotic influence comparable to catchment and slope, even when applied to plot-level plant characteristics. The influence of aspect changes with time, and this change is likely to be commensurate with periods of frequent tropical disturbances.

Parent material had a highly significant effect on seed plants 7 years after landslide formation, that is, higher density on the clay-rich and more fertile, volcaniclastic soils than on the less fertile, dioritic soils. This result supports several studies that show the importance of parent material for plant composition in Puerto Rico, at least for the early stages of primary succession (Myster, Thomlinson & Larsen 1997; Shiels 2006; Shiels *et al.* 2008; Walker & Shiels 2008). However, after 18 years, seed plants were slightly less dense and diverse on volcaniclastic than on dioritic soils. In contrast, ferns, unaffected by parent material after 7 years, were slightly (tree ferns) to strongly (scrambling ferns) more dense on volcaniclastic soils. This changing influence of parent material may reflect early and vigorous colonization of fertile soils by seed plants, followed by self-thinning and competitive dominance and a more gradual colonization of ferns on fertile soils.

SOIL DEVELOPMENT

The strongest drivers of soil development (as measured after 18 years by soil N concentration, SOM, pH and CEC) were slope, soil-available K concentration, distance to edge and aspect. There was less soil development on steep slopes, probably due to the prevalence of post-landslide erosion, a common feature on landslides (Walker & Shiels 2008) and a major concern of landslide risk assessment (Espizua & Bengochea 2002). Soil development was least furthest from landslide edges; hence, the proximity of forested edges is important not only for plant colonization of landslides (Walker & Neris 1993) but also for soil development. Leaf litter fall, sloughing of fertile soil from the edges, root growth and vegetative expansion can all influence landslide soils (Shiels & Walker in press).

The positive effect of easterliness on soil development may be related to the vegetative response to aspect (denser tree ferns after 7 years but lower scrambling fern cover after 18 years on east-facing slopes). Tree fern litter decomposes more rapidly than some other early successional species (Shiels 2006), but scrambling fern litter is relatively slow to decompose (Maheswaran & Gunatilleke 1988; Russell, Raich & Vitousek 1998). In addition, east-facing (windward) slopes likely receive more inputs of aerosol K, Ca, Mg and Na (McDowell *et al.* 1990) and maybe N (Asbury *et al.* 1994), thereby potentially increasing soil development directly, or perhaps indirectly by increasing tree fern densities (Vitousek *et al.* 1995; Richardson & Walker 2010).

BIOTIC INFLUENCES

Succession is influenced by a combination of abiotic and biotic factors, even in primary seres following severe disturbances such as landslides. Although our focus here is on the often overlooked changes in abiotic influences, we also found evidence of the importance of biotic influences on succession. The primary influences on the changes in seed plant characteristics between 7 and 18 years after disturbance were seed

plant characteristics and tree fern stem densities from 1995. These influences were both negative, indicating that where densities of seed plants or tree ferns were highest at 7 years, least change occurred in the subsequent 11-year interval; most change occurred where 7-year densities were lowest. Competition by early landslide colonists, including thicket-forming forbs, can inhibit woody plant colonists for several decades (Walker *et al.* 2010b). Tree ferns can successfully inhibit landslide succession because of their capacity to monopolize nutrients (Tanner 1985; Richardson & Walker 2010) and produce copious leaf litter. Leaf turnover rates of the tree ferns recorded on ES1 are higher than any previously reported for tree ferns (Walker & Aplet 1994). Interestingly, scrambling ferns often inhibit succession as well (Slocum *et al.* 2004), but did not emerge as important biotic drivers in our model. With the diverse array of potential landslide colonists representing several life-forms (Table S1), life cycles and competitive abilities, many successional trajectories are possible. These trajectories are also influenced by both the broader abiotic gradients discussed in this paper (e.g. aspect) and the local physical conditions determined by the severity of the disturbance (e.g. SOM), although we suspect that succession is not the result of a temporally hierarchical set of responses (Myster, Thomlinson & Larsen 1997), but rather develops from the simultaneous interaction of all abiotic and biotic variables.

FINE-SCALE TEMPORAL PATTERNS

Species-specific responses on two intensively monitored landslides (ES1 and ES2) that share the same age, elevation and general location (0.8 km apart) show inconsistent responses by the same suite of colonizing species. These inconsistencies are not only apparent in terms of different successional trajectories on each landslide, but also in terms of the effects of subsequent disturbances caused by three hurricanes. Plant canopies on ES1 reached double the height of those on ES2, but stem densities and species diversity were more similar in magnitude between the two landslides. The taller vegetation on ES1 was more affected by hurricanes than on ES2, particularly with the dramatic loss of its dominant *Cecropia schreberiana* cover during Hurricane Hugo in 1989 (cf. Brokaw 1998). Differential responses among landslide colonists to multiple abiotic drivers (e.g., landslides and hurricanes) therefore increase spatial heterogeneity at landscape scales.

Species diversity is often but not always (Hughes *et al.* 2007) altered by disturbance. A typical response is an initial loss of species (Hooper *et al.* 2005), sometimes followed by a rapid recovery to pre-disturbance levels of diversity. Recovery rates can be related to life histories, with fast-growing, pioneer species responding more rapidly than mature forest species (Fetcher *et al.* 1996; Shiels *et al.* 2010). Recovery rates can also be influenced by the nature of the disturbance. Landslide diversity in this study increased most rapidly as the bare surfaces were colonized, but also responded positively, although not as rapidly, to subsequent hurricane disturbances. Differences in hurricane responses between ES1 and ES2 suggest that higher hurricane-induced mortality on ES1 was followed by post-hurricane increases in diversity, whereas hurricane effects on ES2 were relatively muted. A similarly muted response was found following Hurricane George for forest understorey species in the LEF (Royo *et al.* 2011). Large variations in species diversity (and stem density) among plots on ES2 obscured any consistent patterns of plant responses to hurricanes. Scrambling ferns continued to dominate the uppermost transect on ES2, in contrast to the development of 5- to 8-m-tall trees on the remaining transects. Despite their physical proximity, similar soil type and similar elevation, ES1 and ES2 had distinct patterns of stem density and diversity responses to the initial landslide and subsequent hurricanes.

Conclusions

We investigated the relatively unexplored importance of abiotic influences for 18 years after initial landslide disturbances. We found expected responses of life-forms to catchment and slope (more seed plants than ferns in large catchments with flat slopes) and related responses of soil development and foliar nutrients (enhanced on flatter slopes and on plots closer to landslide edges) and canopy openness (reduced on flatter slopes). The dynamic nature of biotic influences and responses in succession is well-established (Dietze & Clark 2008), but the role of abiotic influences can also change with time. We found that the importance of relatively stable abiotic conditions such as catchment size, slope, aspect and parent material changed during succession. Shifts in biotic responses, including specific life-form affinities to topographic features, have long-term influences on successional trajectories and landscape-level patterns of spatial heterogeneity. Biotic influences were also important in our study, as shown by the influence of the plant communities in 1995 on those that developed during the 1995–2006 interval. Our study provides evidence that abiotic influences on succession do not exert constant influences, but instead can change in their relative influence and importance based on changing responses of the biota. Projections for increased hurricane intensity and frequency may mean more landslides and/or slower landslide recovery in the future (Bender *et al.* 2010), so it is critical to further our understanding of biotic responses to abiotic disturbances. Our results point to the necessity of an adaptive approach to landslide stabilization efforts, because biotic responses to abiotic variables change over time.

Acknowledgements

References

Alpkem Corporation (1992) *The Flow Solution Operation Manual*. Alpkem Corporation, Wilsonville, Oregon, USA.

AMOS Development Corporation (2009) *IBM Corporation*. Armonk, New York, USA.

Asbury, C.E., McDowell, W.H., Trinidad-Pizarro, R. & Berrios, S. (1994) Solute deposition from cloud water to the canopy of a Puerto Rican montane forest. *Atmospheric Environment*, **28**, 1773–1780.

Bellingham, P.J. & Sparrow, A.D. (2009) Multi-stemmed trees in montane rain forests: their frequency and demography in relation to elevation, soil nutrients and disturbance. *Journal of Ecology*, **97**, 472–483.

Bellingham, P.J., Tanner, E.V.J. & Healey, J.R. (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology*, **76**, 2562–2580.

Bender, M.A., Knutson, T.R., Tuleya, R.E., Sirutis, J.J., Vecchi, G.A., Garner, S.T. & Held, I.M. (2010) Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science*, **327**, 454–458.

Bishop, J.G., O'Hara, N.B., Titus, J.H., Apple, J.L., Gill, R.A. & Wynn, L. (2010) N-P co-limitation of primary production and response of arthropods to N and P in early primary succession on Mount St. Helens volcano. *PLoS ONE*, **5**, e13598.

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

Brokaw, N.V.L. (1998) *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. *Botanical Review*, **64**, 91–120.

Brown, S., Lugo, A.E., Silander, S. & Liegel, L. (1983) Research history and opportunities in the Luquillo Experimental Forest. United States Forest Service, General Technical Report SO–44, Washington, DC, USA.

Chave, J., Coomes, D., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Cordero, R.A., Fetcher, N. & Voltzow, J. (2007) Effects of wind on the allometry of two species of plants in an elfin cloud forest. *Biotropica*, **39**, 177–185.

Cramer, V.A. & Hobbs, R.J. (eds) (2007) *Old Fields: Dynamics and Restoration of Abandoned Farmland*. Island Press, Washington, DC, USA.

Crk, T., Uriarte, M., Corsi, F. & Flynn, D. (2009) Forest recovery in a tropical landscape: what is the relative importance of biophysical, socioeconomic, and landscape variables? *Landscape Ecology*, **24**, 629–642.

Cruden, D.M. & Varnes, D.J. (1996) Landslide types and processes. *Landslides: Investigation and Mitigation* (eds A.K. Turner & R.L. Schuster), pp. 36–75. Special Report 247, Transportation Research Board, National Research Council, National Academy Press, Washington, DC, USA.

Curran, T.J., Gersbach, L.N., Edwards, W. & Krockenberger, A.K. (2008) Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest species of North Queensland, Australia. *Austral Ecology*, **33**, 442–450.

Dalling, J.W. (1994) Vegetation colonization of landslides in the Blue Mountains, Jamaica. *Biotropica*, **26**, 392–399.

Dalling, J.W. & Tanner, E.V.J. (1995) An experimental study of regeneration on landslides in montane rain forest in Jamaica. *Journal of Ecology*, **83**, 55–64.

Dietze, M.C. & Clark, J.S. (2008) Changing the gap dynamics paradigm: vegetation regeneration control on forest response to disturbance. *Ecological Monographs*, **78**, 331–347.

Dislich, C. & Huth, A. (2012) Modelling the impact of shallow landslides on forest structure in tropical montane forests. *Ecological Modelling*, **239**, 40–53.

Elias, R.B. & Dias, E. (2009) Effects of landslides on the mountain vegetation of Flores Island, Azores. *Journal of Vegetation Science*, **20**, 706–717.

Espizua, L. & Bengochea, J. (2002) Landslide hazard and risk zonation mapping in the Rio Grande Basin, Central Andes of Mendoza, Argentina. *Mountain Research Development*, **22**, 177–185.

Ewel, J.J. & Whitmore, J.L. (1973) *The Ecological Life Zones of Puerto Rico and the Virgin Islands*. U.S. Forest Service Research Paper ITF-18. Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Fetcher, N., Haines, B.L., Cordero, R.A., Lodge, D.J., Walker, L.R., Fernandez, D.S. & Lawrence, W.F. (1996) Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology*, **84**, 331–341.

Frazer, G.W., Canham, C.D. & Lertzman, K.P. (1999) *Gap Light Analyzer (GLA), version 2.0: Imaging Software to Extract Canopy Software and Gap Light Transmission Indices from True-Color Fisheye Photographs, Users' Manual and Program Documentation*. Simon Fraser University, Burneby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York, USA.

Gavlek, R.G., Horneck, D.A., Miller, R.O. & Kotuby-Amacher, J. (2003) *Plant, Soil and Water Reference Methods for the Western Regions*, 2nd edn. WREP–125. University of Alaska, Fairbanks, Alaska, USA.

Geertsema, M. & Pojar, J.J. (2007) Influence of landslides on biophysical diversity – a perspective from British Columbia. *Geomorphology*, **89**, 55–59.

Grace, J.B. (2006) *Structure Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge.

Guariguata, M.R. (1990) Landslide disturbance and forest regeneration in the Upper Luquillo Mountains. *Journal of Ecology*, **78**, 814–832.

Hobbs, R.J. & Suding, K.N. (eds) (2009) *New Models for Ecosystem Dynamics and Restoration*. Island Press, Washington, DC, USA.

Hooper, D.U., Chapin, F.S. III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Hughes, A.R., Byrnes, J.E., Kimbro, D.L. & Stachowicz, J.J. (2007) Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters*, **10**, 849–864.

Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S. III & Mack, M.C. (2010) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, **16**, 1281–1295.

Larsen, M.C. & Parks, J.E. (1997) How wide is a road? The association of roads and mass-wasting in a forested montane environment. *Earth Surface Processes and Landforms*, **22**, 835–848.

Larsen, M.C. & Simon, A. (1993) A rainfall intensity-duration threshold for landslides in a humid-tropical environment, Puerto Rico. *Geografiske Annaler*, **75A**, 13–23.

Larsen, M.C. & Torres-Sánchez, A.J. (1998) The frequency and distribution of recent landslides in three montane tropical regions of Puerto Rico. *Geomorphology*, **24**, 309–331.

Larsen, M.C., Torres-Sánchez, A.J. & Concepción, I.M. (1999) Slopewash, surface runoff, and fine-litter transport in forest and landslide scars in humid-tropical steeplands, Luquillo Experimental Forest, Puerto Rico. *Earth Surface Processes and Landforms*, **24**, 481–502.

Lepore, C., Kamal, S.A., Shanahan, P. & Bras, R.L. (2012) Rainfall-induced landslide susceptibility zonation of Puerto Rico. *Environmental Earth Sciences*, **66**, 1667–1681.

Li, Y., Ruan, H., Zou, X. & Myster, R.W. (2005) Response of major soil decomposers to landslide disturbance in a Puerto Rican rainforest. *Soil Science*, **170**, 202–211.

Liogier, H.A. (1985–1997) *Descriptive Flora of Puerto Rico and Adjacent Islands*. Vol. 1–5. Editorial de la Universidad de Puerto Rico, Río Piedras, Puerto Rico.

Lodge, D.J. (1987) Nutrient concentrations, percentage moisture and density of field-collected fungal mycelia. *Soil Biology and Biochemistry*, **19**, 727–733.

Lundgren, L. (1978) Studies of soil and vegetation development on fresh landslide scars in the Mgeta Valley, Western Ulugura Mountains, Tanzania. *Geografiska Annaler*, **60A**, 91–127.

Maheswaran, J. & Gunatilleke, I.A.U.N. (1988) Litter decomposition in a lowland rain forest and a deforested area in Sri Lanka. *Biotropica*, **20**, 90–99.

Mark, A.F., Scott, G.A.M., Sanderson, F.R. & James, P.W. (1964) Forest succession on landslides above Lake Thomson, Fiordland. *New Zealand Journal of Botany*, **2**, 60–89.

McDowell, W.H., Gines-Sanchez, C., Asbury, C.E. & Ramos-Perez, C.R. (1990) Influence of seasalt aerosols and long range transport on precipitation chemistry at El Verde, Puerto Rico. *Atmospheric Environment*, **24A**, 2813–2821.

Myster, R.W. & Fernández, D.S. (1995) Spatial gradients and patch structure on two Puerto Rican landslides. *Biotropica*, **27**, 149–159.

Myster, R.W., Thomlinson, J.R. & Larsen, M.C. (1997) Predicting landslide vegetation in patches on landscape gradients in Puerto Rico. *Landscape Ecology*, **12**, 299–307.

Myster, R.W. & Walker, L.R. (1997) Plant succession pathways on Puerto Rican landslides. *Journal of Tropical Ecology*, **13**, 165–173.

Negishi, J.N., Sidle, R.C., Noguchi, S., Nik, A.R. & Stanforth, R. (2006) Ecological roles of roadside fern (*Dicranopteris currani*) on logging road

recovery in Peninsular Malaysia: preliminary results. *Forest Ecology and Management*, **224**, 176–186.

Platt, W.J. & Connell, J.H. (2003) Natural disturbances and directional replacement of species. *Ecological Monographs*, **73**, 507–522.

Proctor, G.R. (1989) *Ferns of Puerto Rico and the Virgin Islands*. Memoirs of the New York Botanical Garden, **53**, New York, NY, USA.

Rebertus, A.J. & Veblen, T.T. (1993) Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. *Journal of Vegetation Science*, **4**, 641–654.

Restrepo, C., Walker, L.R., Shiels, A.B., Bussmann, R.W., Claessens, L., Fisch, S., *et al.* (2009) Landsliding and its multiscale influence on mountainscapes. *BioScience*, **59**, 685–698.

Richardson, S.J. & Walker, L.R. (2010) Nutrient ecology of ferns. *Fern Ecology* (eds K. Mehltreter, L.R. Walker & J.M. Sharpe), pp. 111–139. Cambridge University Press, Cambridge.

Ross, D. (1995) Recommended soil tests for determining soil cation exchange capacity. *Recommended Soil Testing Procedures for the Northeastern United States* (eds J.T. Sims & A. Wolf), pp. 62–69. Northeastern Regional Bulletin # 493. Agricultural Experimental Station, University of Delaware, Newark, Delaware, USA.

Royo, A.E., Heartsill Scalley, T., Moya, S. & Scatena, F.N. (2011) Non-arborescent vegetation trajectories following repeated hurricane disturbance: ephemeral versus enduring responses. *Ecosphere*, **2**: art77, http://dx.doi.org/10.1890/ES11-00118.1.

Russell, A.E., Raich, J.W. & Vitousek, P.M. (1998) The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawaii. *Journal of Ecology*, **86**, 765–779.

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

Schuster, R.L. (2001) Landslides: effects on the natural environment. *Engineering Geology and the Environment* (eds A.K. Turner & R.L. Schuster), pp. 12–35. Special Report 247, Transportation Research Board, National Research Council. National Academy Press, Washington, DC, USA.

Seiders, V.M. (1971) *Geologic Map of the El Yunque Quadrangle, Puerto Rico*. United States Geologic Survey Map I-658. United States Government Printing Office, Washington, DC, USA.

Sheldrick, B.H. & Wang, C. (1993) Particle size distribution. *Soil Sampling Methods of Analysis* (ed. M.R. Carter), pp. 507–509. Lewis Publishers, Boca Raton, FL, USA.

Shiels, A.B. (2006) Leaf litter decomposition and substrate chemistry of early successional species on landslides in Puerto Rico. *Biotropica*, **38**, 348–353.

Shiels, A.B. & Walker, L.R. (in press) Landslides cause spatial and temporal gradients at multiple scales in the Luquillo Mountains of Puerto Rico. *Ecological Gradient Analyses in a Tropical Landscape: Ecological Bulletin no. 54*, John Wiley & Sons, New York.

Shiels, A.B., Walker, L.R. & Thompson, D.B. (2006) Organic matter inputs create variable resource patches on Puerto Rican landslides. *Plant Ecology*, **184**, 223–236.

Shiels, A.B., West, C.A., Weiss, L., Klawinski, P.D. & Walker, L.R. (2008) Soil factors predict initial plant colonization on Puerto Rican landslides. *Plant Ecology*, **195**, 165–178.

Shiels, A.B., Zimmerman, J.K., Garcia-Montiel, D.C., Jonckheere, I., Holm, J., Horton, D. & Brokaw, N. (2010) Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology*, **98**, 659–673.

Sidle, R.C. & Ochiai, H. (2006) *Landslides: Processes, Prediction, and Land Use*. American Geophysical Union, Washington, DC, USA.

Silver, W., Scatena, F.N., Johnson, A.H., Siccama, T.G. & Sánchez, M.J. (1994) Nutrient availability in a montane wet tropical forest: spatial patterns and methodological considerations. *Plant and Soil*, **164**, 129–145.

Slocum, M.G., Aide, T.M., Zimmerman, J.K. & Navarro, L. (2004) Natural regeneration of subtropical montane forest after clearing fern thickets in the Dominican Republic. *Journal of Tropical Ecology*, **20**, 483–486.

Soil Survey Staff (1995) *Order 1 Soil Surveys of Luquillo Long-Term Ecological Research Grid, Puerto Rico*. United States Department of Agriculture, National Resource Conservation Service, Washington, DC, USA.

Spitale, D., Petraglia, A. & Tomaselli, M. (2009) Structural equation modeling detects unexpected differences between bryophyte and vascular plant richness along multiple environmental gradients. *Journal of Biogeography*, **36**, 745–755.

Tanner, E.V.J. (1985) Leaf demography and growth of the tree fern *Cyathea pubescens* in Jamaica. *Botanical Journal of the Linnean Society*, **87**, 213–227.

Turner, M.G. (2010) Disturbance and landscape dynamics in a changing world. *Ecology*, **91**, 2833–2849.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems*, **1**, 511–523.

Velázquez, E. & Gómez-Sal, A. (2007) Environmental control of early succession in a landslide on a dry tropical ecosystem (Casita Volcano, Nicaragua). *Biotropica*, **39**, 601–609.

Velázquez, E. & Gómez-Sal, A. (2008) Landslide early succession in a neotropical dry forest. *Plant Ecology*, **199**, 295–308.

Vitousek, P.M., Gerrish, G., Turner, D.R., Walker, L.R. & Mueller-Dombois, D. (1995) Litterfall and nutrient cycling in four Hawaiian montane rain forests. *Journal of Tropical Ecology*, **11**, 189–203.

Walker, L.R. & Aplet, G.H. (1994) Growth and fertilization of Hawaiian tree ferns. *Biotropica*, **26**, 378–383.

Walker, L.R. & Neris, L.E. (1993) Posthurricane seed rain dynamics in Puerto Rico. *Biotropica*, **25**, 408–418.

Walker, L.R. & Sharpe, J. (2010) Ferns, disturbance and succession. *Fern Ecology* (eds K. Mehltreter, L.R. Walker & J.M. Sharpe), pp. 177–219. Cambridge University Press, Cambridge.

Walker, L.R. & Shiels, A.B. (2008) Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides. *Plant and Soil*, **313**, 205–216.

Walker, L.R. & Shiels, A.B. (2013) *Landslide Ecology*. Cambridge University Press, Cambridge.

Walker, L.R., Velázquez, E. & Shiels, A.B. (2009) Applying lessons from ecological succession to the restoration of landslides. *Plant and Soil*, **324**, 157–168.

Walker, L.R., Zarin, D.J., Fetcher, N., Myster, R.M. & Johnson, A.H. (1996) Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica*, **28**, 566–576.

Walker, L.R., Wardle, D.A., Bardgett, R.D. & Clarkson, B.D. (2010a) The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology*, **98**, 725–736.

Walker, L.R., Landau, F.H., Velázquez, E., Shiels, A.B. & Sparrow, A.D. (2010b) Early successional woody plants facilitate and ferns inhibit forest development on Puerto Rican landslides. *Journal of Ecology*, **98**, 625–635.

Wilcke, W., Valladarez, H., Stoyan, R., Yasin, S., Valarezo, C. & Zech, W. (2003) Soil properties on a chronosequence of landslides in montane rain forest, Ecuador. *Catena*, **53**, 79–95.

Zarin, D.J. & Johnson, A.H. (1995) Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. *Soil Science Society of America Journal*, **59**, 1444–1452.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Characteristics of the six landslides in Puerto Rico.

Table S2. Species > 1 m tall found on the six landslides.

Table S3. Summary of highly significant standardized path coefficients.

Figure S1. Conceptual *a priori* methods to test hypotheses.

Figure S2. Structural equation models for foliar nutrients and canopy openness.

Figure S3. Structural equation model for soil development.

Figure S4. Structural equation model for differences between 1995 and 2006 measurements.

Figure S5. *Cyathea arborea* tree fern density during 18 years of succession.

Supporting Information

Table S1. Characteristics of six landslides formed between 1987–1988 in the Luquillo Experimental Forest, Puerto Rico. Data were used in the SEM models. Soil parameters and leaf and litter nutrients (for the tree fern *Cyathea arborea*) are from 2006 (mean ± S.E. where appropriate). $n = 3$–5 (transects for plant nutrients) to 11–24 (plots for soils and canopy openness).

		ES1	ES2	ES5	ES10	RB2	RB9	F	P
Geography	Area (m)	2100	1550	2510	2420	1700[*]	1750		
	Elevation (m a.s.l.)	370	370	530	590	650	600		
	Slope (degrees)	22	30	33	25	29	20		
	Aspect (degrees)	336	49	330	270	164	100		
Soils	Parent material[†]	V	V	V	V	D	D		
	Total N (%)[‡]	0.5 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.4 ± 0.0	4.0	0.002
	Olsen P (mg kg^{-1})	3.8 ± 0.2	4.4 ± 0.4	4.1 ± 0.5	5.0 ± 0.6	3.4 ± 0.4	3.9 ± 0.3	1.5	0.204
	Mehlich K (mg kg^{-1})	68.6 ± 6.1	65.2 ± 3.8	55.1 ± 5.6	63.5 ± 4.0	49.0 ± 3.4	45.6 ± 6.7	3.3	0.008
	SOM (%)	6.5 ± 0.4	5.7 ± 0.3	4.1 ± 0.1	5.8 ± 0.3	1.9 ± 0.1	4.2 ± 0.4	40.9	< 0.001
	CEC (meq 100 g^{-1})	15.1 ± 0.4	14.7 ± 0.4	12.1 ± 0.5	8.0 ± 0.4	7.1 ± 0.5	7.7 ± 0.6	48.1	< 0.001
	pH	5.5 ± 0.0	5.1 ± 0.0	5.0 ± 0.0	4.6 ± 0.0	4.8 ± 0.0	4.9 ± 0.0	72.7	< 0.001
	Clay (%)	8.6 ± 0.8	10.8 ± 0.9	9.7 ± 1.0	7.7 ± 0.7	9.9 ± 0.9	8.5 ± + 1.3	1.4	0.232
	Sand (%)	61.3 ± 1.7	63.7 ± 2.3	64.1 ± 1.1	62.6 ± 1.6	61.8 ± 1.3	60.9 ± 1.3	0.5	0.791
Plants	Leaf N (mg g^{-1})[‡]	24.7 ± 1.1	13.3 ± 1.2	15.5 ± 1.0	11.0 ± 0.0	12.7 ± 0.1	12.8 ± 1.3	14.3	< 0.001
	Litter N (mg g^{-1})	17.0 ± 1.3	7.7 ± 0.7	12.0 ± 1.2	7.4 ± 0.4	9.8 ± 0.8	8.1 ± 0.8	13.3	< 0.001
	Leaf P (mg g^{-1})	2.4 ± 0.4	1.0 ± 0.1	1.3 ± 0.3	0.6 ± 0. 0	4.4 ± 0.4	1.7 ± 0.1	38.7	< 0.001

Litter P(mg g^{-1})	1.3 ± 0.0	0.6 ± 0.1	0.8 ± 0.1	0.4 ± 0.0	2.8 ± 0.4	1.1 ± 0.1	26.9	< 0.001
Canopy openness (%)	10.1 ± 0.3	12.0 ± 1.3	11.7 ± 1.5	28.5 ± 3.3	25.7 ± 1.9	12.1 ± 1.3	19.0	< 0.001

8   [*] Area of freshly eroded surface within a 25,000 m^2 landslide formed in 1977.

[†] V = volcaniclastic; D = dioritic

[‡] A MANOVA was performed for both foliar chemistry (all variables were log-transformed; Pillai-Bartlett = 2.197, numerator d.f. = 20, denominator. d.f. = 70, $P < 0.001$) and soil chemistry (only total N required log-transformation; Pillai-Bartlett = 1.837, numerator d.f. =

12   40, denominator d.f. = 505, $P < 0.001$). Canopy openness required log-transformation prior to one-way ANOVA (R Development Core Team (2010) R: A Language and Environment for Statistical Computing. The R Foundation for Statistical Computing, Vienna, Austria).

Table S2. Species ≥ 1 m tall found on the six landslides during the 18 – year study, ranked by decreasing number of stems (*n* = 44). All species were trees except *Pinzona coriacea* (vine), *Urera baccifera* (shrub) and *Phytolacca icosandra* (herb).

Species	Family	No. Stems	No. Plots	No. of Landslides
Miconia racemosa (Aubl.) DC.	Melastomataceae	55	11	5
Prestoea acuminata var. *montana* (Wiild.) H.E.	Arecaceae	29	10	2
Cyrilla racemiflora L.	Cyrillaceae	27	8	2
Psychotria brachiata Sw.	Rubiaceae	21	10	2
Clidemia cymosa (Wendl. ex Spreng.) Alain	Melastomataceae	19	6	3
Psychotria berteriana DC.	Rubiaceae	18	8	4
Swietenia macrophylla King	Meliaceae	15	8	1
Chromolaena odorata (L.) King & H. Rob.	Asteraceae	13	6	2
Syzygium jambos (L.) Alston	Myrtaceae	13	5	1
Tabebuia heterophylla (DC.) Britton	Bignoniaceae	13	7	4
Piper hispidum Sw.	Piperaceae	11	3	1
Inga laurina (Sw.) Wiild. ex L.	Fabaceae	8	4	2
Pinzona coriaceae Mart. & Zucc.	Dilleniaceae	6	4	2
Inga vera Willd. ex L.	Fabaceae	5	4	1
Miconia prasina (Sw.) DC.	Melastomataceae	5	4	3
Miconia tetandra (Sw.) D. Don	Melastomataceae	5	4	3
Casearia sylvestris Sw.	Flacourtiaceae	4	3	2
Cecropia schreberiana Miq.	Cecropiaceae	4	2	2
Matayba domingensis (DC.) Radlk.	Sapindaceae	4	3	2
Mecranium amygdalinum f. *latifolia* Cogniaux. C.A.	Melastomataceae	3	2	1

Miconia mirabilis (Aubl.) L.O. Williams	Melastomataceae	3	3	3
Palicourea riparia Benth.	Rubiaceae	3	2	2
Clusia rosea Jacq.	Clusiaceae	2	2	1
Eugenia domingensis Berg	Myrtaceae	2	2	1
Myrcia deflexa (Poir.) DC.	Myrtaceae	2	1	1
Myrcia splendens (Sw.) DC.	Myrtaceae	2	2	1
Piper glabrescens (Miq.) C. DC.	Piperaceae	2	1	1
Schefflera morototoni (Aubl.) Decne. & Planch.	Araliaceae	2	2	2
Alchornea latifolia Sw.	Euphorbiaceae	1	1	1
Chionanthus domingensis Lam.	Oleaceae	1	1	1
Citharexylum fruticosum L.	Verbenaceae	1	1	1
Comocladia glabra (Schult.) Spreng	Anacardiaceae	1	1	1
Gonzalagunia spicata (Lam.) M. Gómez	Rubiaceae	1	1	1
Guarea guidonia (L.) Sleumer	Meliaceae	1	1	1
Guettarda valenzuelana A. Rich.	Rubiaceae	1	1	1
Margaritaria nobilis L.f.	Euphorbiaceae	1	1	1
Myrcia coriacea var. *imrayana* Griseb.	Myrtaceae	1	1	1
Nectandra turbacensis (Kunth) Nees	Lauraceae	1	1	1
Phytolacca icosandra L.	Phytolaccaceae	1	1	1
Piper aduncum L.	Piperaceae	1	1	1
Pseudolmedia spuria (Sw.) Griseb.	Moraceae	1	1	1
Rondeletia portoricensis Krug. & Urban	Rubiaceae	1	1	1
Sloanea berteriana Choisy	Elaeaocarpaceae	1	1	1
Urera baccifera (L.) Wedd.	Urticaceae	1	1	1

Table S3. Summary of highly significant ($P \leq 0.001$) standardised path coefficients from the 2006 structural equation model showing multivariate relationships for 18 years after landslide occurrences in Puerto Rico. Bold font indicates the observation that did not follow the hypothesised direction of response.

Response variable	Slope	Easterliness	Distance to Edge	Soil K
Soil development	-0.82	**+0.33**	-0.21	+0.40
Foliar nutrients	-0.88		-0.44	
Canopy openness	+0.61			

Fig. S1. Conceptual *a priori* models to test hypotheses for positive (+) or negative (-) relationships on Puerto Rican landslides between quantified environmental variables and A) soil development and foliar nutrients; and B) canopy openness. Models were tested using vegetation parameters from 2006 (18 years after disturbance). [ ] indicates concentration, and two-way arrows indicate correlation.
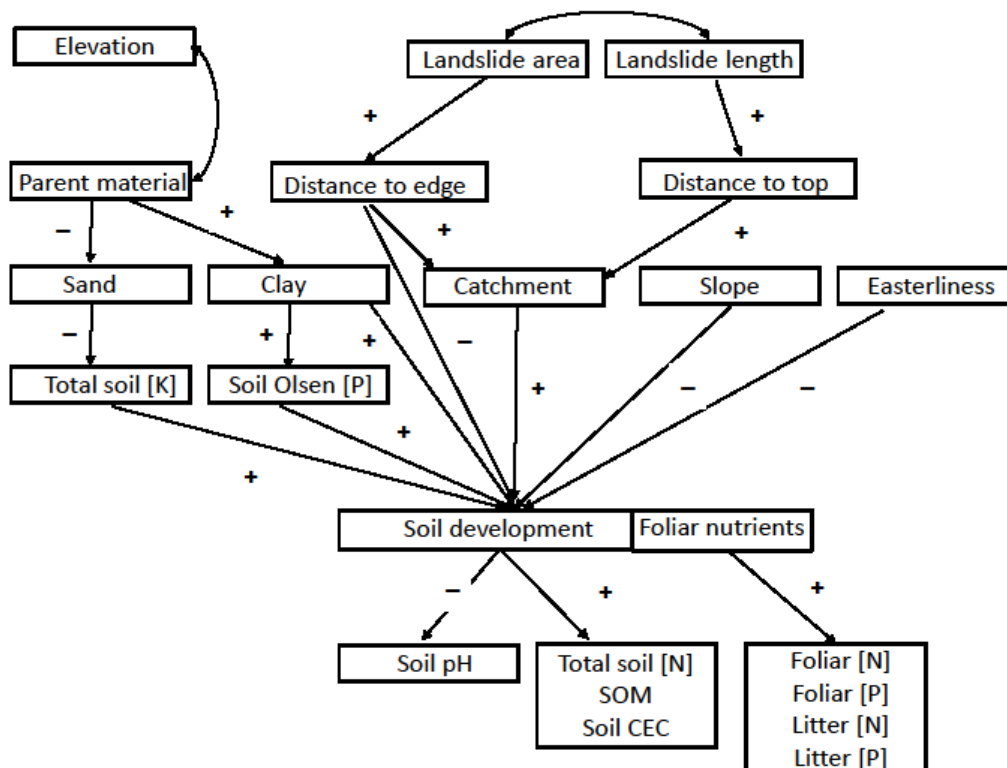
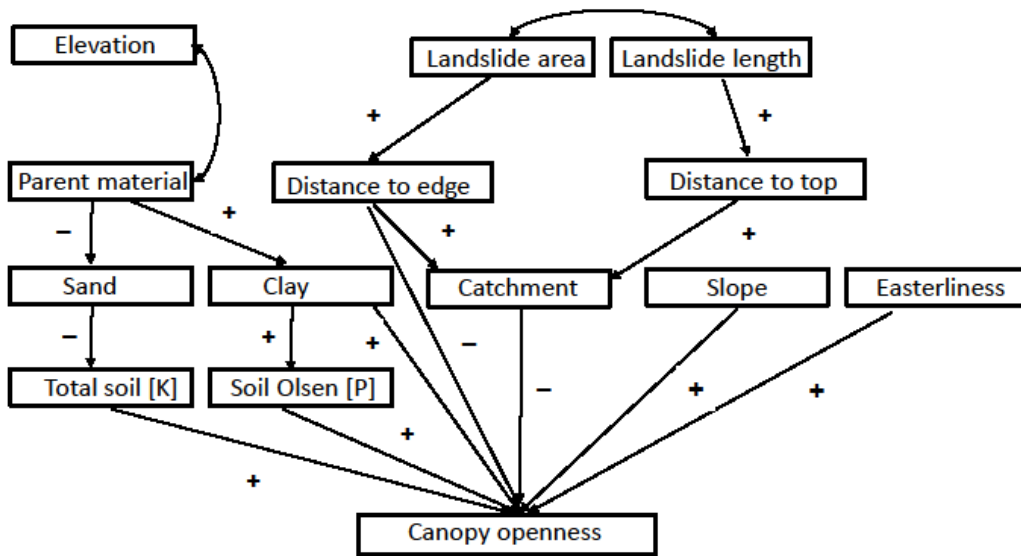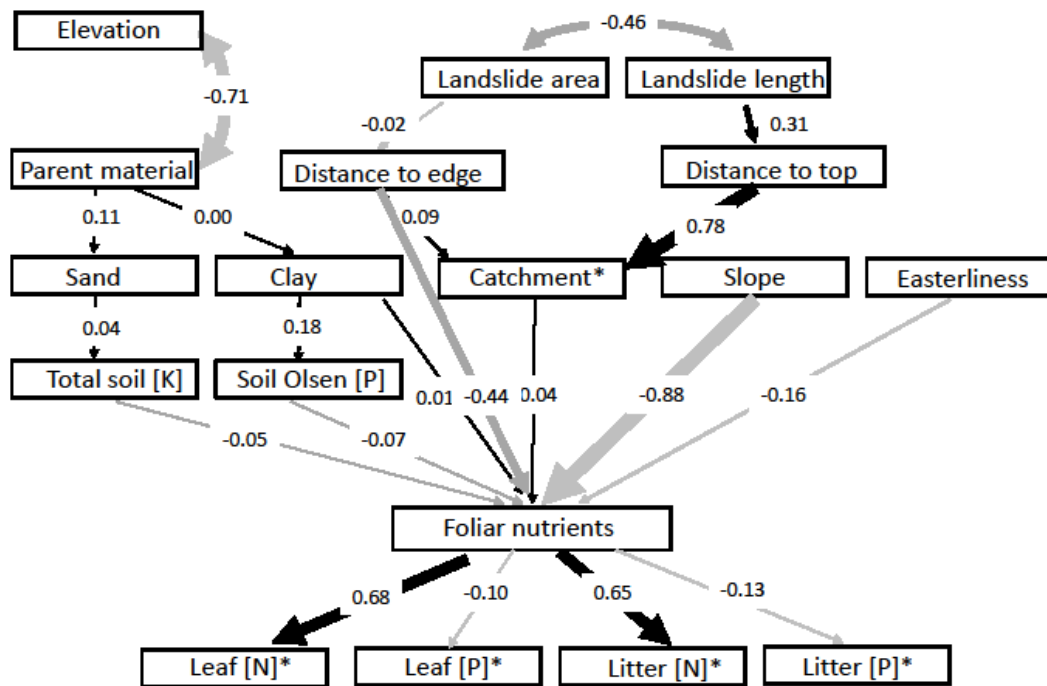Fig. S1A. Soil development and foliar nutrients

Fig. S1B. Canopy openness.

Fig. S2. Structural equation models showing multivariate relationships in 2006 on Puerto Rican landslides among quantified environmental variables and A) tree fern foliar nutrients and its components (leaf [N], leaf [P], litter [N], and litter [P]); and B) canopy openness. Two way arrows indicate correlation. Thickness of arrows is proportional to the standardised path coefficients shown on each arrow. Positive relationships are shown in black, negative ones in grey. Asterisks denote values that were log transformed before model fitting. The model was not significantly different from the conceptual *a priori* model after deleting all non-significant paths ($\chi^2 = 3183.97$; d.f. $= 317$; $P < 0.001$; AIC $= 3417.97$). [ ] indicates concentration

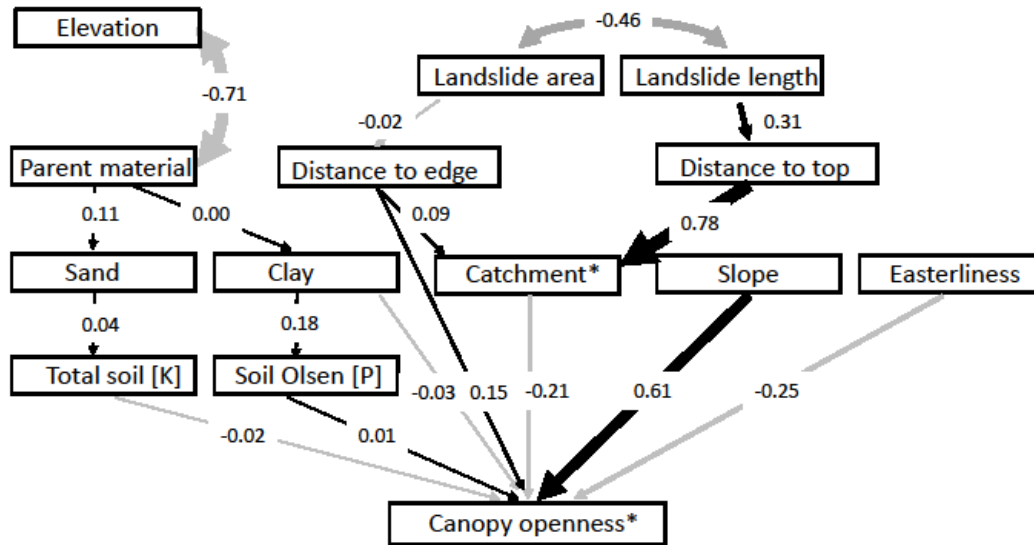Fig. S2A. Foliar nutrients.

Fig. S2B. Canopy openness

Fig. S3. Structural equation model showing multivariate relationships in 2006 on Puerto Rican landslides among quantified environmental variables and soil development and its components (total N, SOM, pH and CEC). Two way arrows indicate correlation. Thickness of arrows is proportional to the standardised path coefficients shown on each arrow. Positive relationships are shown in black, negative relationships in grey. Asterisks denote values that were log transformed before model fitting. The model was not significantly different from the conceptual *a priori* model after deleting all non-significant paths ($\chi^2 = 3183.97$; d.f. = 317; $P < 0.001$; AIC = 3417.97). [ ] indicates concentration
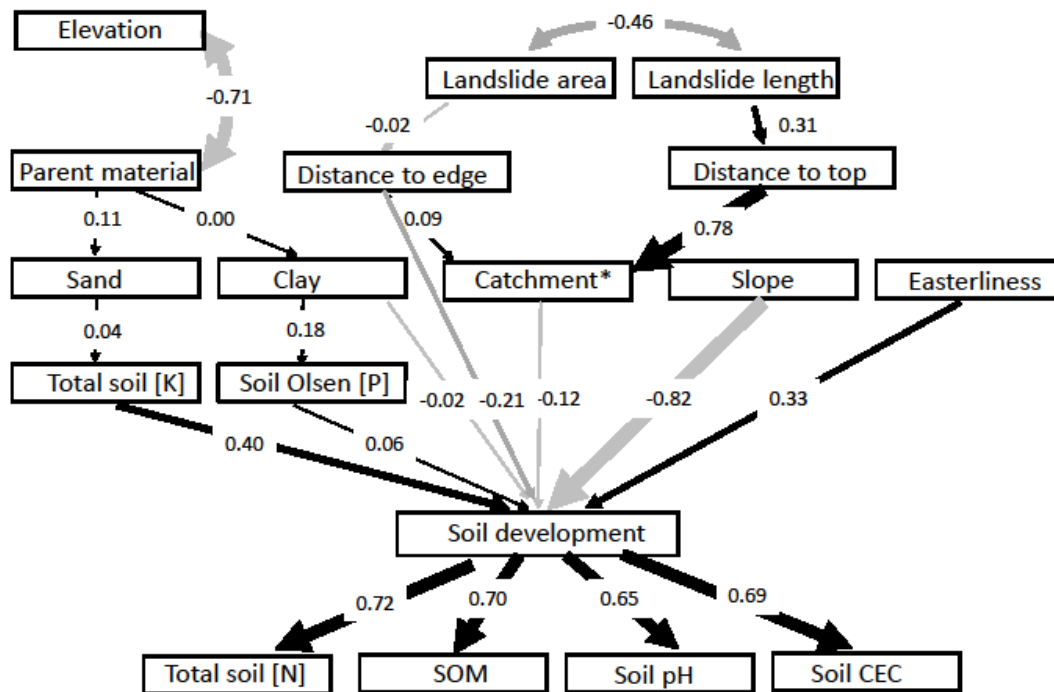
Fig. S4. Structural equation model showing multivariate relationships among quantified environmental variables and 1995 seed plant and tree fern variables on the differences in seed plants (and component variables density, evenness, richness and Shannon index of diversity [H']) between 1995 and 2006 on Puerto Rican landslides. Two way arrows indicate correlation. Thickness of arrows is proportional to the standardised path coefficients shown on each arrow. Positive relationships are shown in black, negative ones in grey. Asterisks denote values that were log transformed before model fitting. The model was not significantly different from the conceptual *a priori* model after deleting all non-significant paths ($\chi^2 = 2442$; d.f. = 232; $P < 0.001$; AIC = 2678).
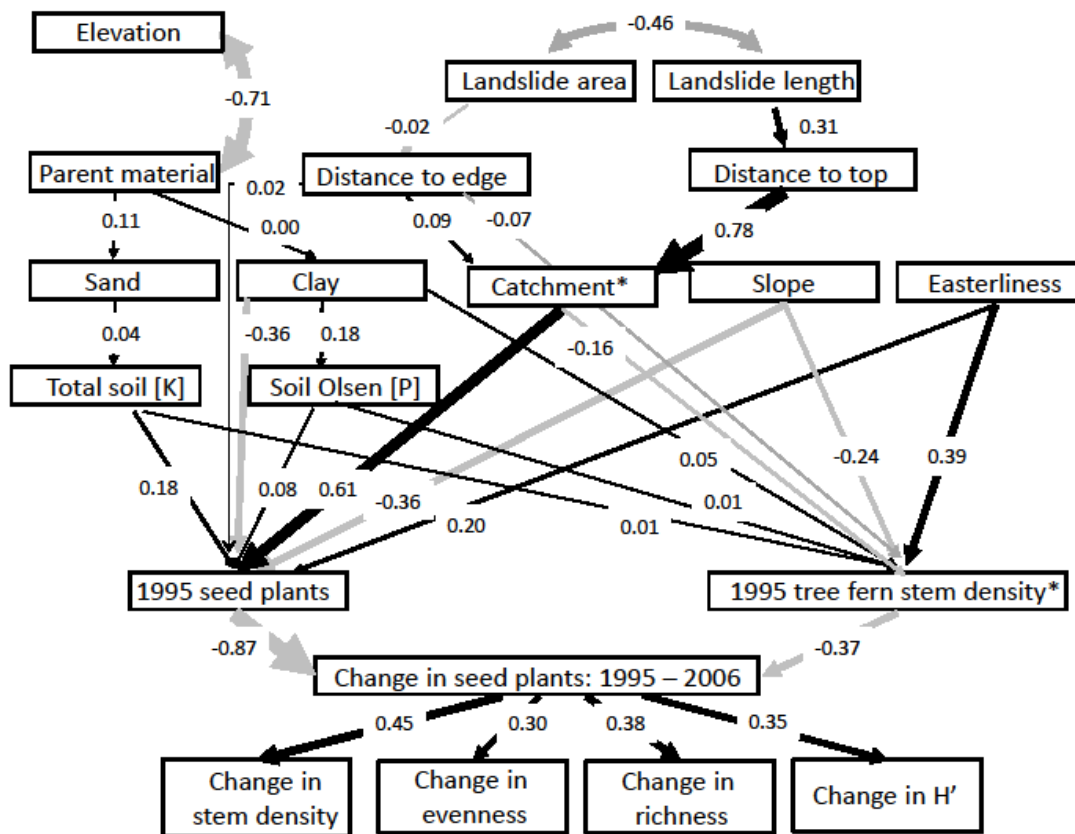
Fig. S5. *Cyathea arborea* tree fern density (stems m^{-2}) on landslide ES1 during 18 years of succession. Dashed lines represent dates of hurricanes that affected the study site from left to right: 18 September 1989 (Hugo), 22 September 1996 (Hortense) and 21 September 1998 (Georges).