Capítulo 3

Control ambiental de la sucesión temprana en un deslizamiento de ladera de gran tamaño situado en un ecosistema tropical seco (Volcán Casita, Nicaragua)

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

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Resumen

En el presente artículo se describen las comunidades vegetales en un gran deslizamiento situado en un área intensamente humanizada del trópico seco (Volcán Casita, Nicaragua) y en el bosque adyacente, tres años después de la perturbación. En ambos sitios, se determinó la relación existente entre la variación espacial de los factores ambientales y la distribución de las distintas especies y sus características. Posteriormente, se comprobó si la similaridad composicional entre el bosque y el deslizamiento aumentaba en función de la distancia al borde del bosque y la anchura del deslizamiento. Se encontraron grandes diferencias entre las comunidades vegetales de ambos sitios. En el bosque la distribución espacial de las especies y sus características venía determinada por un gradiente altitudinal relacionado con la cobertura de suelo desnudo, mientras que en el deslizamiento, dicha distribución estaba mayormente influenciada por la presencia de suelos residuales agrícolas y forestales, y de perturbaciones humanas. No se encontró incremento alguno en la similaridad composicional entre el bosque y el deslizamiento ni en los bordes ni en las zonas más estrechas de este último. En comparación con otros deslizamientos, el proceso de recuperación de la cubierta vegetal en el deslizamiento del Volcán Casita está fuertemente influenciado por la extrema heterogeneidad ambiental, la estacionalidad climática y los usos humanos presentes en el área. El estudio de la sucesión ecológica en deslizamientos situados en zonas densamente pobladas del trópico seco debe centrarse en la respuesta de los ecosistemas regionales frente a un complejo régimen de perturbaciones en el que aquellas provocadas por el hombre juegan un papel primordial.

Environmental Control of Early Succession on a Large Landslide in a Tropical Dry Ecosystem (Casita Volcano, Nicaragua)

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Abstract

We described the plant communities on a large landslide in a human-dominated area of tropical dry forest landscape (Casita Volcano, Nicaragua) and in the adjacent forest, three years after landslide occurrence. At both of the sites, we determined the relationships between spatial changes in environmental factors and the spatial distribution of species and plant traits. Subsequently, we tested the hypothesis that the compositional similarity between the landslide and the forest increased with a decrease in the distance from the forest edge and the width of the landslide. In the forest, the spatial distribution of species and plant traits was determined mainly by an elevational gradient that was associated with the amount of bare soil, whereas, on the landslide, there was no such gradient but species distributions were influenced mostly by the presence of residual agricultural and forest soils and human disturbance. We did not find an increase in compositional similarity between the landslide and the forest at the edge or in the narrow zones of the landslide. Compared to other landslides, the recovery process was strongly influenced by the extreme abiotic heterogeneity, climate seasonality, and human use in the area. The study of succession in tropical dry landslides located in densely populated zones should focus on understanding the response of regional ecosystems to a complex disturbance regime in which human-induced disturbances play a major role.

Key words: environmental factors; forest recover; human disturbance;plant communities.

Introduction

Landslides are severe disturbances (Guariguata 1990, Francescato *et al.* 2001,) that intensify the role of environmental factors along slope gradients, affect the spatial distribution of species, and shape the specific composition and structure of pioneer plant communities (Garwood 1985, Miles and Swanson 1986, Dalling 1994, Walker *et al.* 1996). The species composition of pioneer plant communities on landslides is usually very different from those of the surrounding habitat. Landslides promote the expansion of species that are not abundant in nearby mature forests but are frequently found locally in disturbed areas (Lundgren 1978, Garwood 1985, Restrepo and Vitousek 2001). Furthermore, plant colonization on landslides is very different from colonization in treefall gaps or in sites opened by other disturbances, such as fire or hurricanes (White 1979, Dalling 1994). Typically, landslides create high abiotic heterogeneity, and there are marked differences in species composition within pioneer plant communities depending on the stability and productivity of substrates (Guariguata 1990, Myster and Fernández 1995, Walker *et al.* 1996, Francescato *et al.* 2001,).

Most landslides begin as rock avalanches that quickly become mud or debris flows ("lahars") when they reach the lower parts of the slope (Gryta and Bartolomew 1989, Kull and

Magilligan 1994). In the upper or "erosional" zones, soil and vegetation are completely removed and often bedrock is exposed, whereas in the lower or "depositional" zones, the agricultural and forest soils that existed before the disturbance remain. Often, depositional zones exhibit a rich biological legacy that consists of heterogeneous mixtures of broken plant parts, seeds, organic matter, and rock fragments from the erosional zone (Walker *et al.* 1996). Consequently, natural recovery occurs faster in the depositional zone than in the erosional zone, and the species composition of plant communities in depositional zones is quite similar to those of adjacent forests (Guariguata 1990). In addition to differences in the species composition of pioneer plant communities, habitat requirements, plant traits, and the biogeographic distribution of pioneer species on landslides are very different from those in adjacent, undisturbed areas (Garwood 1985, Guariguata 1990, Dalling and Tanner 1995, Restrepo and Vitousek 2001). Thus, the traits common to the pioneer species of landslides, particularly in the erosional zone, include light-demanding, short life span, ability to resprout, N^2 fixation, dispersal by wind, no peaks in the timing of flowering and fruiting, and a broad geographic distribution. Yet, adjacent forests can play an important role in the vegetation recovery of landslides through the process of 'seed rain' (Walker and Neris 1993) and through the vegetative expansion of species or "edge colonization" (Francescato *et al.* 2001). Thus, the compositional similarities between landslides and their adjacent forests increase as the distance from forest edge and the width of the landslide decreases.

The ecology of landslides have been extensively studied in tropical mountains, where they are an important component of the disturbance regime (Garwood *et al.* 1979, Guariguata 1990, Walker *et al.* 1996, Restrepo and Vitousek 2001) and have a significant influence on the specific composition and structure of plant communities (Dalling and Tanner 1995). In Central America and the Caribbean area, most studies of vegetation recovery have been conducted on small landslides, mostly in premontane forests (Holdridge *et al.* 1971), either in lightly populated areas, such as the Blue Mountains in Jamaica (Dalling 1994, Dalling and Tanner 1995), Río Jaqué in Panama (Garwood 1985), and Monteverde in Costa Rica (Myster 1993), or in experimental reserves, such as Luquillo in Puerto Rico (Guariguata 1990, Walker 1994, Myster and Fernández 1995, Walker *et al.* 1996, Myster and Walker 1997). Yet, several authors have emphasized the importance of studying succession on landslides located in highly humanized landscapes due to the little research done in this kind of habitats and its predominance in the tropical areas of the world (Lundgren 1978, Guariguata 1990, Walker *et al.* 1996).

In this study, we examined the influence of environmental factors on species composition, and the characteristics of pioneer communities, on a large landslide and in an adjacent forest three years after the landslide event at Casita Volcano, Nicaragua. The landslide was precipitated by heavy rainfall (500 mm/d) on 30 October 1998 during Hurricane Mitch. The area has a climate that is characterized by low, seasonal rainfall, and is dominated by tropical dry forests (Murphy and Lugo 1986, 1995). As in other parts of the world, these forests have been considerably reduced by the effects of human disturbance (e.g., resource extraction, burning and clearing of vegetation, and urban sprawl) in this densely populated region (Gillespie *et al.* 2000). In addition to being one of the most endangered ecosystems in the world, tropical dry forests are also one of the least well known (Janzen 1988, Gerhardt & Hytteborn 1992), and research is needed to address their conservation and management (Bawa *et al.* 2004, Sanchez-Azofeifa *et al.* 2005).

This study provided the foundation for our research into the patterns, causes, and mechanisms of vegetation recovery on large landslides located in areas with tropical dry climate and exposed to heavy human influence. The overarching goal of the study was to understand the environmental constraints of early succession in the Casita Volcano landslide. Specific objectives included: (1) to describe the environmental factors, species composition, and plant traits that characterize plant communities on the landslide and in the adjacent forest; (2) to determine the relationships between spatial changes in environmental factors and the spatial distribution of species and plant traits at both sites; and (3) to determine whether the compositional similarity between landslide and forest communities increased in the narrow zones of the landslide or in those near to the forest edge.

Methods

Study Area

The study was conducted on a landslide on the Casita Volcano (12°41' N, 85°57' W), which is part of the "Maribios" volcanic range in western Nicaragua (**Fig. 1a**). The landslide, which was triggered by an exceptionally heavy rainfall (500 mm) on 30 October 1998, during Hurricane Mitch (Sheridan 1998), moved 200,000 m^3 of highly fractured material that rapidly formed an enormous lahar at mid-slope (Kerle and Vries 2001). The landslide devastated the two largest villages at the base of the volcano, killed more than 2000 people, and displaced another 8000 (CEPAL 1999). The Casita Volcano landslide is much larger (11.21 km2) than the others studied in Central America and the Caribbean (Garwood 1985, Guariguata 1990, Myster 1993, Dalling and Tanner 1995), and the ecological and socioeconomic characteristics of the region are quite different.

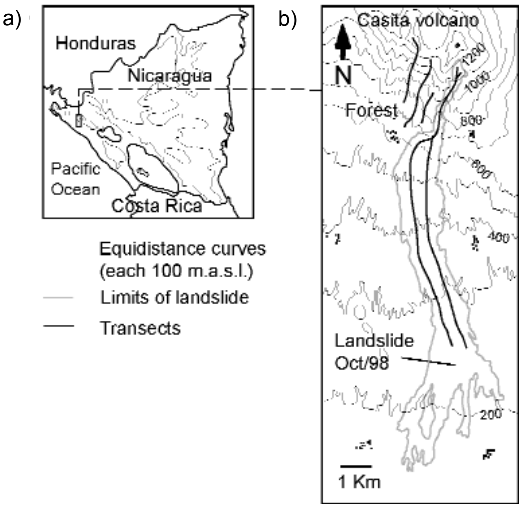

Figure 1. a) Study area and location of the landslide in western Nicaragua. b) Detailed map of southern slope of Casita Volcano showing landslide limits and transects in the landslide and the adjacent forest.

Mean annual rainfall (1250 mm/yr) is considerably lower and the dry season (from November to April) is longer in the dry forests of western Nicaragua than in the moist and wet forests of eastern Central America and on the Caribbean islands. In addition, the frequency of hurricanes and heavy rainfall events that can trigger landslides is lower in western Nicaragua than it is in other regions of Central America (Pielke *et al.* 2003). Locally, forests have experienced substantial exploitation and clearance, although large patches of relatively well-preserved forests still exist.

The plant communities near the crater of the Casita Volcano are fairly similar in structure and composition to those in cloud forests (Salas-Estrada 1999), but the lower area is covered mostly by tropical dry forests that have been partially converted into "shaded" coffee plantations at mid-slope. Farther down the slope, where small patches of forest are interspersed with scattered huts and small land-holdings, human-caused disturbances are common. They include forest clearing for firewood and the expansion of cropland (Salas-Estrada 1999), and fire (Corrales-Rodríguez 1983), which is used mainly by peasants to remove crop stubble (December) or to prepare fields for sowing (May and August) (P. Dávila, pers. comm.). At the base of the volcano, the population density is highest and the landscape is dominated by large real-estate holdings where crops such as sugar cane, sorghum, and peanuts are cultivated intensively.

Fieldwork sampling

In December 2001, we laid two line-transects on the landslide (Landslide) and three in the adjacent forest to the west (Forest) (**Fig 1b**). It was not possible to sample in the adjacent forest to the east because the land was privately owned. All of transects were laid in the direction of the main slope. The lengths of the transects were much shorter in the Forest (1100, 900, and 500 m) than in the Landslide (3700 and 3300 m) and the range of elevation covered by the Forest site (610-1400 m asl) was smaller and slightly higher than at the Landslide site (170-1150 m asl). To describe the plant communities, two vegetation layers were used: (1) the "woody layer," which included trees, shrubs (height > 20 cm), and lianas, and (2) the "herbaceous layer," which included herbs, grasses, vines, and tree seedlings (height < 20 cm).

Along Landslide transects, 20 m^2 rectangular plots were sampled at selected intervals of 150 m (47 total plots) and, along Forest transects, 100 m^2 plots were sampled at selected intervals of 50 m (52 total plots). The differences between sites in the size of plots and the distance between plots were due to differences in the structure of vegetation and the elevational ranges (Barbour *et al.* 1999). In each plot, the number of individuals of each woody species was recorded, and the height (m) and vertical projection of the crown (m^2) of each individual was measured. These data were used to calculate the proportion (%) of total cover of each species (the sum of vertical projections without overlap), Shannon Index (H), total cover (the total of all vertical projections), and the mean canopy height of each plot. Elevation (m asl) and environmental factors related to stability [Slope (%)] and the productivity of substrates [Bare soil cover (%)] were measured. In the Landslide plots, the presence of remaining agricultural and forest soils and evidence of human disturbances were noted. After the landslide, human disturbances, which occurred mostly in the depositional zone, involved the widespread removal of pioneer trees that grew after the landslide for firewood and the expansion of croplands, and fires created by peasants nearby, which expanded into the landslide. In each sampling period, plots were identified as "cleared" if there were signs of clearance (e.g., presence of tailings) or as "burned" if scorched plants were present.

In each plot, three 1 m^2 quadrants were sampled and the proportion (%) of the cover of each herbaceous layer species was estimated. For each species, we noted the characteristics of the plant, such as the shape, size, and number of fruit, approximate length of the roots, and the presence of N_2-fixation knots. Those data, coupled with the knowledge of locals and botanist expert opinion, were used to categorize plants by their traits, which included reproductive strategy (K or r), depth of root system (surface or deep roots), resprouting ability ("medium" after uprooting or cutting, and "high" after fire), presence of a spreading mechanism (stolons, rhizomes, other), and capacity for N_2 fixation. We used "Flora de Nicaragua" (Stevens *et al.* 2001) to verify for each species the taxonomy, plant traits such as biotype (trees, shrubs, lianas, herbs, perennial and annual grasses), dispersal mode (anemochorial, zoochorial, other), timing of flowering and fruiting (dry season, rainy season, and "no peak"), and origin ("native" if from the local dry tropics or premontane forest, and "exotic") of each species.

Data Analysis

To classify plots and define plant communities, the presence/absence matrices of the woody and herbaceous layers were subjected to TWINSPAN analyses. The maximum number of indicators per division was three and the classification was followed up to the second division, only, because results beyond that level can be erratic (Groenewoud 1992) and groups derived from the analysis contained a sufficient number of plots at that level to describe the plant communities (Vogiatzakis *et al.* 2003). The "characteristic species" of each group were chosen based on "Fidelity" and "Constancy" (Kent and Coker 1992). To define the plant communities of the Landslide and the Forest, plots were grouped based on the characteristic species of each layer. A Kruskal-Wallis test was used to determine differences between plant communities across sites and subsequent pairwise comparisons were performed using Mann Whitney U-test. Classification analyses were performed using the PC-ORD program (MjM 1999) and statistical tests were run using STATISTICA (Statsoft 2001).

To assess the relationships between environmental factors and the spatial distributions of species and plant traits in each of the vegetation layers, Canonical Correspondence Analyses (CCA) (Braak 1986) were used. The CCA axes were evaluated statistically using a Monte Carlo Permutation Test. The analyses of the woody layer and the herbaceous layer were based on matrices of "Importance values" ([Relative Cover + Relative Density]/2) (Kent and Coker 1992) and Relative Cover, respectively. Species that were present in < 15% of the plots were excluded from the analyses and, when necessary, variables were transformed to achieve normality (Sokal and Rohlf 1995). To verify the unimodality of response curves and the presence of important variables that were not taken into account, the results of the CCA were compared with the results from the Detrended Correspondence Analysis of each layer. The CCA and DCA analyses were performed using the CANOCO program (Braak and Smilauer 2002).

To determine whether the compositional similarity between the Landslide and Forest sites was greater in the Landslide plots that were closer to the Forest edge than in the plots that were farther away, we calculated Spearman correlations between "compositional" and "geographical" (real) distances between pairs of Landslide-Forest plots. To determine whether compositional similarity was higher in Landslide plots that were in the narrow zones than in those that were in the wide zones, compositional distances were subjected to an ANOVA. The factor was width of the landslide, and plots were defined as being in either a "narrow" (< 500 m) or "wide" (> 500 m) section of Landslide. To calculate "compositional" and "geographical" distances, we used SPSS (SPSS 1995) and the ANOVA was performed using STATISTICA (Statsoft 2001).

Results

Description and characterization of plant communities

The classification analyses and the grouping of plots based on their characteristic species revealed four plant communities in the Landslide (LC1, LC2, LC3, and LC4) and three in the Forest (FC1, FC2, and FC3), respectively (**Table 1**). Characterization analyses showed that the Landslide was more heterogeneous than the Forest. The plant communities of the Landslide were correlated with different

Table 1. Plant communities identified at landslide (LC1, LC2, LC3, LC4) and forest (FC1, FC2, FC3) sites on Casita Volcano, Nicaragua, derived from the TWINSPAN analysis. General Abbreviations; N = Number of plots in which each community appears, F = "Fidelity" (refers to the degree to which species are confined to a particular group of plots), C = "Constancy" (refers to the number of times each species is present in the plots that belong to a specific community), Biot. = Biotype, Pt/Cf = Other plant traits and community features. Abbreviations of environmental factors; rem. soil = Remaining soil. Abbreviations of Biotypes; T = Tree, S = Shrub, s = seedling, Ph = Perennial herb, Ah = Annual herb, Pg = Perennial grass, Ag= Annual grass. Abbreviations of Plant traits and Community features; H = Shannon Index, Cc= Canopy cover (%), Mxh = Mean canopy height, Vsm = Vegetative spreading mechanisms, Da = Disturbed or degraded areas, Lra = Large resprouting ability.

Community	**N**	**Env. Factors**	**Characteristic species**	**Biot**	**F**	**C**	**Cf/Pt**
LC1 *Trema–Hypharrenia*	18	↑ Elevation ↑ Slope ↑ Bare soil cover	*Trema micrantha*	T/S	4	76.5	↑ H
			Wigandia urens	S	3	83	
			Melanthera nivea	S	4	55	
			Hypharrenia rufa	Pg	3	83	
			Pytirogramma calomalanos	F	4	66.4	
LC2 *Muntingia–Panicum*	10	All rem. soil ↓ Slope ↓ Bare soil cover	*Muntingia calabura*	T	4	99	↓ H
			Trema micrantha	T	4	66.4	Vsm
			Wigandia urens	S	3	69	
			Panicum maximum	Pg	3	63	
LC4 *Desmodium–Thitonia*	8	Some rem. soil	*Desmodium nicaraguensis*	S	3	100	Da
		↓ Slope	*Trema micrantha*	T	4	76.5	Lra.
		↓ Bare soil cover	*Muntingia calabura*	T	4	60	
			Thitonia rotundifolia	Ph	5	66	
			Chamaesyce hyssopifolia	Ah	5	77	
			Euphorbia heterophylla	Ah	4	66	
			Galactia striata	Ah	4	66	
LC3 *Muntingia-Thitonia*	11	Human Use	*Muntingia calabura*	T	4	99	↓ Cc
		Some Or. soil	*Wigandia urens*	S	3	53	
		↓ Elevation	*Thitonia rotundifolia*	Ph	5	66	
		↓ Slope	*Chamaesyce hyssopifolia*	Ah	5	77	
		↓ Bare soil cover	*Euphorbia heterophylla*	Ah	4	66	
			Galactia striata	Ah	4	66	
FC1 *Luehea-Tridax*	32	↓ Slope	*Luehea candida*	T	4	77	↑ Cc
			Malvaviscus arboreus	T	4	72	↑ Mxh
			Tridax procumbens	Ah	5	71	
			Aphelandra scabra	Ag	4	62.4	
			Ardisia revoluta	s	4	55	
			Psychotria tenuifolia	s	3	77	
			Oplismenun burmanii	Ag	3	71	
FC2 *Malvaviscus-Tecoma*	11	↑ Slope	*Malvaviscus arboreus*	T	4	72	
			Luehea candida	T	4	64	
			Heliocarpus appendiculatus	T	3	61	
			Tecoma stans	s	4	72	
			Tephrosia multifolia	s	4	58	
			Ruellia inundata	Ph	4	54	
FC3 *Heliocarpus–Oplismenum*	5	↑ Elevation	*Heliocarpus appendiculatus*	T	3	80.5	↓ H
		↑ Slope	*Oplismenun burmanii*	Ah	3	71.5	↓ Cc

Table 2. Summary statistics for the Ordination analyses performed in the Casita Volcano landslide and in the adjacent forest. DCA^1- woody layer, DCA^2- herbaceous layer, CCA^1- woody layer / species composition, CCA^2- woody layer / plant traits, CCA^3- herbaceous layer / species composition, CCA^4- herbaceous layer / plant traits.

	Eigenvalues		**Gradient length**		**% V. explained (sps.)**		**% V. explained (sps. – env.)**	
	Axis 1	**Axis 2**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
DCA^1	0.992	0.627	4.805	4.485	21.4	13.6	---	---
DCA^2	0.965	0.541	9.789	4.760	13.3	7.4	---	---
CCA^1	0.812	0.355	---	---	17.6	7.6	58.2	25.4
CCA^2	0.108	0.022	---	---	30.6	6.3	78.2	15.9
CCA^3	0.730	0.489	---	---	4.4	3	42.3	28.4
CCA^4	0.081	0.019	---	---	20.1	4.8	69.9	16.7

Abbreviations: V. = Variance, sps. = species, env. = environment

environmental factors and exhibited significant differences in community features, plant traits, and the distributional characteristics of the species (**Table 1**, **Appendix 1**); however, the three plant communities of the Forest site were much more similar and differed only slightly in their species composition and in some of their community features.

Environmental factors, spatial distribution of species, and plant traits

The most meaningful results were from axes 1 and 2 of the CCA referring to the woody layer (**Table 2**, **Fig. 2**). The plot ordinations based on the spatial distribution of species (**Fig. 2a**) and plant traits (**Fig. 2b**) revealed that the Landslide and Forest sites were well-differentiated along axis 1, and the differences in vegetation within each site occurred along axis 2. In both of the ordination analyses (**Fig. 2**), elevation and the presence of remaining soil had the longest arrows, and were the most important factors in explaining the spatial ordination of the plots. Plant traits more clearly differentiated the Landslide and Forest sites. In the Landslide plots, the presence of exotic and anemochorial species, those with an "r" reproductive strategy and high resprouting ability, characterized pioneer communities. By contrast, the communities of the Forest site had a larger total cover, a higher mean canopy height, and were characterized by the presence of lianas and zoochorial species that have a "K" reproductive strategy. Both species composition and plant traits differentiated communities within Forest and Landslide sites.

In the Forest site, plots were linearly distributed along an elevational gradient that was correlated with the proportion of bare soil and, to a lesser extent, with slope (**Fig. 2**) and the tree plant communities appeared in sequence along the gradient. The *Heliocarpus-Oplismenum* (FC3) community, which occurred in areas of high elevation and slope, was characterized by low total canopy cover and low diversity and was the most clearly differentiated community.

By comparison, based on species composition and plant traits, the spatial ordination of the plots on the Landslide site was more complex and did not follow a clear elevational gradient; rather, the distribution of the plots and the differentiation of plant communities in the Landslide site mainly were determined by the presence of remaining soils and human disturbance. On the Landslide site, the *Trema-Hypharrenia* (LC1) community, which occurred in areas of high elevation and slope where predisturbance soils did not remain, was the most

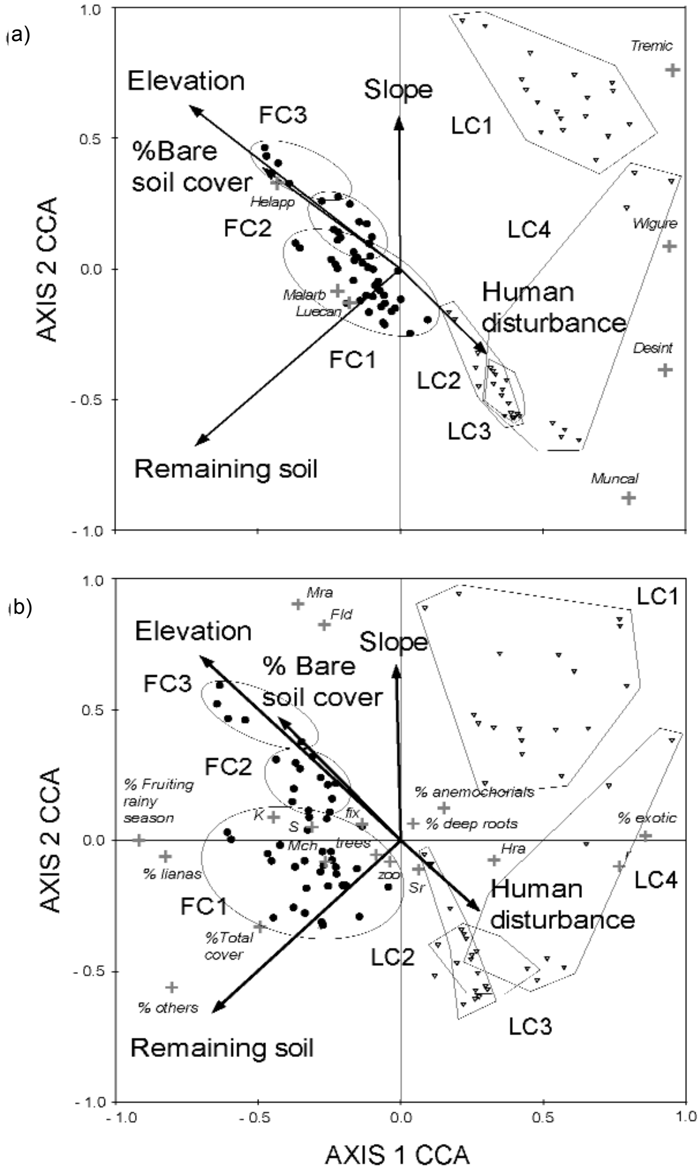

Figure 2. CCA biplot showing the environmental factors that determine change in species composition (a) and plant traits (b) in the woody layer of both, Landslide and Forest. Dots = Forest plots, Triangles = Landslide plots. Envelopes are drawn around Landslide and Forest community types. Abbreviations for species: *Desnic* = *Desmodium nicaraguense*, *Muncal* = *Muntingia calabura*, *Tremic* = *Trema micrantha*, *Wigure* = *Wigandia urens*, *Helapp* = *Heliocarpus appendiculatus*, *Malarb* = *Malvaviscus arboreus*, *Luecan* = *Luehea candida*. Abbreviations for plant traits: Mra = % Medium resprouting ability, Hra = % High resprouting ability, Mch = Mean canopy height, Fld = % Flowering in the dry season, Frr = % Fruiting in the rainy season, TC = % Total cover, fix = % N^2-fixers, zoo = % zoochorials, Sr = % Surface roots.

clearly differentiated. This community was characterized by scarce vegetation and was dominated by the perennial grass *Hypharrenia rufa* and the fern *Pytirogramma calomalanos* in the herbaceous layer (CCA results not shown), and the shrubs *Trema micrantha* and *Wigandia urens* in the woody layer. In addition, this community had a relatively high frequency of rare plant species in both layers, and had higher diversity scores than did the other communities at the Landslide site. In the *Muntingia-Panicum community* (LC2), which was found in areas that had a low slope and where pre-landslide soils remained, tall individuals of the pioneer tree species *Muntingia calabura* and *Trema micrantha* were dominant and formed a dense canopy, and grasses that have vegetative growth mechanisms, such as *Panicum maximum* and *Oplismenun burmanii* appeared below the canopy. In both of the vegetative layers, diversity was very low. The LC2 community of the Landslide site was the most similar to the Forest site. The *Muntingia*-*Thitonia* community (LC3) had environmental characteristics similar to those of LC2, but the presence of human disturbance was stronger. In the LC3 community, *Thitonia rotundifolia* formed a dense and continuous "prairie" that was interrupted by scattered tall individuals of *Muntingia calabura* and *Wigandia urens*. For that reason, the canopy cover was lower than it was in the LC2. In contrast to the LC2 and LC3 communities, in the *Desmodium*-*Thitonia* community (LC4), forest and agricultural soils were not present in any of the plots. The vegetation was dominated by a rapidly growthing shrub (*Desmodium nicaraguensis*) and a tall neotropical herb (*Thitonia rotundifolia*), although other species such as *Chamaesyce hissopifolia*, *Euphorbia heterophylla* and *Galactia striata*, were abundant. The eigenvalues of all of the CCA analyses were smaller than those derived from the DCA (**Table 3**), implying that one or more explanatory variables were not included in the analyses.

Compositional similarity, distance from the forest and landslide width

Compositional and geographical distances of Landslide-Forest plots were not significantly correlated (*rho* = 0.017, $P > 0.1$). The species composition of plots in the narrow zone of the landslide was not more similar to the species composition of Forest plots than were plots in the wide zone of the landslide ($F = 0.091$, $P > 0.1$).

Discussion

In our study of the plant communities on and adjacent to a large landslide on Casita Volcano, Nicaragua, the species composition and plant traits at the Landslide and Forest sites differed significantly. Very few of the native species present in the adjacent forest were found on the landslide three years after disturbance, which was dominated by pioneer trees and invasive shrubs, grasses, and herbs that are characterized by high dispersion and resprouting abilities, and were common degraded areas. Those results are similar to the patterns that were observed at landslides in temperate (Mark *et al.* 1964, Hull and Scott 1982, Francescato *et al.* 2001, del Moral and Jones 2002) and tropical regions (Lundgren 1978, Garwood 1985, Myster 1993, Dalling and Tanner 1995).

However, the most important result of this study refers not to these expected differences, but to the role played by environmental factors in determining the spatial distribution of species composition, community features, and plant traits within each site. We propose a model to explain the environmental control of spatial change in vegetation at the Landslide and Forest sites. The Landslide site exhibited greater heterogeneity among its plant communities than did the Forest site, which might be a result of the greater overall length of transects and the slightly wider elevation range covered by the Landslide site compared to Forest site. Yet, our results indicate that elevation is not the most important environmental factor influencing differences in species composition and plant traits among plant communities in the Landslide site; rather, their distribution was most strongly associated with the presence of remaining soil and human disturbance, which did not follow an elevational gradient. At the Forest site, however, communities were clearly distributed along an elevational gradient that correlated strongly with the amount of bare soil and, to a lesser extent, slope. Thus, despite the shorter elevational range of the Forest site, elevation was a much more important factor in determining the stability and productivity of substrates and, consequently, in influencing changes in species composition and plant traits at that site.

With respect to plant communities in the Landslide site, interesting patterns emerge when the large differences between these communities revealed by the characterization and ordination analyses are considered in the light of the biology of the dominant plants. The herbaceous layer of the *Trema-Hypharrenia* community (LC1), which had the highest slope and the barest soil among the communities at the Landslide site, was characterized by species such as *Pytirogramma calomalanos*, which is often observed in mineral and highly weathered substrates throughout the Caribbean region (Herwitz 1981, Garwood 1985, Dalling 1994). In contrast, the herbaceous layer of the *Muntingia-Panicum* community (LC2), which has remaining soils, was dominated by *Oplismenum burmanii*, a very common grass in the understory of the local forests (Ricardo Rueda, pers. comm.).

At the Landslide site, *Muntingia calabura* and *Trema micrantha* were the dominant pioneer tree species. *Trema* was widely distributed but *Muntingia* appeared mainly in the depositional (lower) zone of the landslide (communities LC2 and LC3). Although both are shade-intolerant, fast-growing, and highly fecund species that can rapidly colonize large disturbed areas (Denslow 1980), *Trema* has greater tolerance for more hostile substrates than *Muntingia* and can improve local ecological conditions (Vazquez-Yanes 1998, Rodrigues *et al.* 2004). Moreover, the colonizing ability of *Muntingia* is strongly influenced by the drainage patterns of rainfall runoff, because its fruits are larger than that of *Trema* (Stevens *et al.* 2001) and are more easily transported downslope (Fleming *et al.* 1985). *Muntingia* also appears at lower elevations than *Trema* (Stevens *et al.* 2001). These factors permit *Muntingia* to colonize and establish successfully only in the lowest regions of the landslide.

The herbaceous layers of LC3 and LC4 were dominated by species such as *Thitonia rotundifolia*, *Chamaesyce hissopifolia*, *Euphorbia heterophylla* and *Galactia striata*, which are characteristic of locally degraded areas and agricultural fallows (Laguna 1987). In particular, the germination of *Thitonia rotundifolia* requires intense light and high temperatures (Upfold and Vanstaden 1990) and its expansion might be strongly associated with the occurrence of fire.

At the Landslide site, several exotic and invasive genera, such as *Desmodium* and *Hyparrhenia*, which are common in disturbed areas throughout the tropics, were abundant. Those species were abundant on landslides in eastern Tanzania, which is a region that also has low, highly seasonal rainfall and is highly humanized (Lundgren 1978). *Hyparrhenia* is a perennial African grass that has invaded neotropical savannas (Daubenmire 1972, Pieters and Baruch 1997). Fire promotes seed germination and seedling growth in *Hyparrhenia*, which makes it more abundant (Baruch & Bilbao 1999), but the abundance of this species also promotes the occurrence of fire (Stern *et al.* 2002). In this way, *Hyparrhenia* can activate grass-fire cycles (D´Antonio & Vitousek 1992) and impede the establishment of woody species (Nepstad *et al.* 1996), which contributes to the progressive transformation of forests into impoverished savannas or shrublands. In those Landslide areas in which it is abundant, *Hyparrhenia* might arrest later succession. Furthermore, given that the Landslide site provides a large disturbed area that is suitable for the expansion of that *Hyparrhenia*, it can promote the spread of fires towards the upper slopes of Casita Volcano.

In our study, the LC2, LC3, and LC4 communities formed a mosaic in the lower "depositional" zone, which was associated with spatial variation in human disturbances and the presence of remaining soil. *Muntingia*-*Panicum* (LC2) appeared to be the pioneer plant community that is characteristic of the "depositional" areas; however, that community can be transformed into *Muntingia*-*Thitonia* (LC3) after burning or clearance, and be progressively substituted by *Desmodium*-*Thitonia* in areas that are transitional between the "depositional" and erosional" zones, where the amount of bare soil is greater and soil nutrients and organic matter content is lower. Furthermore, we can consider plant communities on the landslide to be different "stages" of the successional process, which form a chronosequence. The limitations of chronosquences (Pickett 1989) not withstanding, communities similar to LC1 might be considered the first stage of vegetation recovery after disturbance, which progressively transform into communities similar to LC4 and LC2 as conditions improve and long-life span shrubs and trees become more abundant. Disturbances might divert that plausible trajectory toward communities that are dominated by species that have a high capacity to resprout following fire, such as the LC3 community.

Unlike the pattern observed in other studies (Walker *et al.* 1996, Francescato *et al.* 2001), on the landslide of the Casita Volcano, the compositional similarity between the landslide and the forest plots was not correlated with proximity to the forest edge or width of the landslide. In narrow zones, which were characterized by steep slopes and the presence of mineral and heavily weathered substrates, erosion probably impeded the establishment and germination of forest plants. That phenomenon was observed in other tropical (Garwood 1985, Scatena and Lugo 1995) and temperate landslides (Hull and Scott 1982, Hupp 1983, Francescato *et al.* 2001). Furthermore, the structure of the edge between disturbed areas and neighbouring forest patches also influence vegetation recovery (Pickett *et al.* 1999). Apparently, deep gorges in the upper portion of the landslide act as "dispersal barriers" and obstruct "edge colonization" from the forest (Guariguata 1990, Myster 1993, Myster and Fernández 1995, Scatena and Lugo 1995, Walker *et al.* 1996, Francescato *et al.* 2001). At the Landslide site, the plant communities in the plots situated in the depositional zone at mid-slope (600 m asl) were the most similar to those of the forest. In this area, the landslide is narrow enough (300 m) to be colonized easily by propagules from the forest, but unlike the other areas in the narrow zone, the area is almost flat and retains the original forest soil. As a result, erosion is not important and propagules easily establish and germinate. A "vegetation island" composed of a nearby group of remnant trees might have influenced vegetation recovery in that area.

Concluding remarks

Three years after disturbance, the recovery process in the landslide of the Casita Volcano appeared to differ from those observed elsewhere in the Central American and Caribbean Region. Pioneer plant communities are rather different to those of the adjacent forest and support a higher number of species typically growing in local disturbed areas. On the Casita Volcano landslide, the presence of remaining soil and human disturbance are the main environmental factors that influenced the spatial distribution of pioneer communities and, probably, the entire recovery process in the area. The presence of remaining soil determines the availability of potential limiting factors, such as water and nutrients which are extremely important in tropical regions with low or highly seasonal rainfall (Murphy and Lugo 1986, Archibold 1995). Human disturbance is an important factor because the Casita Volcano landslide is in a rural area that has a high population density and acute poverty, where ecosystems are strongly affected by land-use practices, a common feature in most of the landslides currently reported around the world (Martine and Guzman 1999). Moreover, an increase in the frequency and intensity of hurricanes in Central America and the Caribbean (Goldenberg *et al.* 2001, Webster *et al.* 2005) might lead to an increase in the frequency of landslides. This might exacerbate processes such as deforestation (Restrepo and Álvarez 2006) and transformation of tropical dry forests into savannas or shrublands (Dale *et al.* 2000, Quigley and Platt 2003), altering their expression at a landscape scale. Our results suggest that, rather than focusing research only on large-scale disturbances, the study of succession in landslides located in highly humanized tropical dry environments must emphasize the response of ecosystems to a much more complex disturbance regime, in which human-induced disturbances play a major role. Undoubtedly, these findings provide a basis for further research and observation in this type of landslides.

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Appendix 1. Characterization of environmental factors, community features, plant traits, and distribution characteristics (Cf/Pt/Dc) for the plots associated with each community type in the landslide (LC1, LC2, LC3 and LC4), and Forest (FC1, FC2 and FC3) sites on Casita Volcano, Nicaragua. Mean is at the top of the cells and Standard Deviation, in italics, is below. The last two columns show the statistical significance for each variable in the Kruskall-Wallis test at both sites, Landslide and Forest. After Rice´s correction, α'= 0.01 for α = 0.05 in the environmental factors tests, and a´ = 0.002 for a = 0.05 in the plant traits tests.

Variable	LC1	LC2	LC3	LC4	FC1	FC2	FC3	Landslide	Forest
Environmental factors									
Elevation	665.83 *187.05*	339.5 *226.97*	273.63 *95.94*	290.62 *60.50*	765.46 *131.10*	981.36 *91.76*	1,292 *95.23*	*P* = 0.00001	*P* = 0.00001
Slope	17.22 *7.51*	5 *8.16*	5 *5*	5.62 *6.23*	6.09 *6.80*	20.27 *11.12*	21 *7.41*	*P* = 0.002	*P* = 0.0001
P. remaining soil	0.05 *0.23*	0.9 *0.32*	0.9 *0.3*	0.75 *0.46*	--- ---	--- ---	--- ---	*P* = 0.00001	---
Bare soil cover	32.31 *19.10*	0.7 *2.21*	0.14 *0.48*	1.87 *5.30*	3.2 *4.86*	29.75 *19.15*	35.90 *23.11*	*P* = 0.00001	*P* = 0.002
Cf/Pt/Dc (woody layer)									
H	0.90 *0.46*	0.48 *0.45*	0.54 *0.50*	0.65 *0.29*	1.99 *0.34*	1.54 *0.53*	1.14 *0.12*	*P* = 0.05	*P* = 0.002
Total c. cover	2.77 *11.78*	69.4 *38.24*	44.45 *37.37*	17.87 *34.25*	84.6 *17.49*	80.45 *17.49*	58.85 *11.57*	*P* = 0.001	*P* = 0.08
Mean c. height	1.26 *0.62*	4.11 *2.07*	3.48 *1.20*	1.91 *0.50*	--- ---	--- ---	--- ---	*P* = 0.00001	---
% N^2 fixers	16.01 *19.66*	6.52 *14.31*	12.70 *18.63*	55.57 *22.45*	12.76 *8.35*	31.78 *11.74*	36.33 *7.46*	*P* = 0.0003	*P* = 0.00001
% M. resp. ability	12.42 *14.27*	0 *0*	0 *0*	0 *0*	4.94 *5.69*	8.52 *5.34*	20.72 *10.48*	*P* = 0.0006	*P* = 0.001
% No peak (frt.)	--- ---	--- ---	--- ---	--- ---	78.40 *7.71*	61.49 *9.62*	58.53 *9.51*	---	*P* = 0.00001
% Wet s. (frt.)	0 *0*	0 *0*	0 *0*	6.28 *17.77*	--- ---	--- ---	--- ---	*P* = 0.18	---
% exotic species	87.84 *16.88*	93.72 *13.47*	88.79 *19.40*	89.92 *19.40*	2.47 *4.14*	14.12 *9.02*	27.14 *8.15*	*P* = 0.76	*P* = 0.00001
% T. dry forest	--- ---	--- ---	--- ---	--- ---	79.52 *9.08*	73.49 *9.88*	57.65 *9.32*	---	*P* = 0.0015
Cf/Pt/Dc (herb. layer)									
% k-strategists	57.98 *14.25*	48.31 *6.46*	34.51 *18.19*	35.60 *18.00*	90.55 *18.49*	91.25 *18.49*	35.47 *18.39*	*P* = 0.002	*P* = 0.0006
% stolons/rhiz.	28.21 *10.54*	52.08 *34.44*	8.08 *8.22*	9.94 *3.56*	--- ---	--- ---	--- ---	*P* = 0.00001	---
% others (vg.)	8.38 *7.43*	1.94 *6.13*	1.34 *3.32*	0 *0*	3.28 *8.89*	9.85 *14.31*	18.62 *11.39*	*P* = 0.0005	*P* = 0.004
% M. resp. ability	--- ---	--- ---	--- ---	--- ---	13.36 *12.96*	1.11 *3.69*	0 *0*		*P* = 0.0003
% Annual herbs	33.55 *13.82*	45.66 *11.04*	72.62 *13.75*	71.99 *19.07*	22.7 *18.52*	21.76 *16.91*	44.21 *7.42*	*P* = 0.00001	*P* = 0.02
% No peak (flt.)	70.80 *15.19*	54.23 *19.83*	93.62 *6.75*	84.66 *10.35*	45.30 *21.12*	49.96 *13.49*	23.73 *18.37*	*P* = 0.00001	*P* = 0.02
% No peak (frt.)	74.39 *7.70*	87.27 *13.88*	83.08 *10.33*	74.61 *10.25*	79.73 *17.67*	53.00 *17.23*	89.95 *7.82*	*P* = 0.02	*P* = 0.0004
% T. dry forest	20.48 *11.00*	36.66 *9.99*	6.8 *8.16*	18.69 *12.33*	52.54 *23.83*	46.58 *17.52*	27.18 *16.21*	*P* = 0.0001	*P* = 0.042
% exotic species	79.51 *11.00*	63.33 *9.99*	93.19 *8.16*	81.30 *12.33*	24.14 *23*	36.76 *16.93*	72.81 *16.21*	*P* = 0.0001	*P* = 0.001

Abbreviations: P. rem. soil = Presence of remaining soil, Total c. cover = Total canopy cover, Mean C. height = Mean canopy height, M. resp. ability = Medium resprouting ability, Wet s. = Wet season, T. dry forest = Tropical dry forest, stolons/rhiz = stolons/ rhizomes, others (vg.) = other mechanisms of vegetative spreading, frt = fruiting time, flt = flowering time.