Capítulo 4

Trayectorias y causas de la sucesión temprana en un deslizamiento situado en un ecosistema tropical seco

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Resumen

La sucesión ecológica en grandes deslizamientos de ladera situados en áreas altamente humanizadas de clima tropical seco no ha sido estudiada en profundidad. En este estudio se documentó la recuperación de la cubierta vegetal durante los cuatro primeros años de sucesión en un deslizamiento de este tipo (Volcán Casita, Nicaragua), con el objetivo determinar las principales trayectorias y causas del cambio en algunas características de las comunidades como la riqueza específica, la biomasa y la composición de especies, y verificar el papel jugado por la heterogenidad ambiental del deslizamiento en el mismo. Se obtuvieron datos acerca del número, la cobertura y la altura media de las especies leñosas, así como de varios factores abióticos relacionados con la productividad y la estabilidad de los sustratos, en varias parcelas permanentes situadas en sectores previamente definidos. Las trayectorias de sucesión temprana fueron altamente dependientes de la heterogeneidad ambiental, más complejas de lo esperado, y resultaron estar controladas principalmente por el estrés abiótico, los factores limitantes relacionados con la productividad y las perturbaciones humanas. Estos resultados podrían ser la base de un modelo de sucesión temprana para deslizamientos situados en áreas densamente pobladas del trópico seco. Nuestros resultados sugieren que el estudio de la sucesión en deslizamientos del tipo del que tuvo lugar en el Volcán Casita, debe centrarse, más que en la respuesta de los ecosistemas ante una perturbación a gran escala como el deslizamiento, en la respuesta a un régimen de perturbaciones mucho más complejo en el que aquellas que tienen un origen antrópico juegan un papel primordial.

Pathways and causes of early succession on a landslide in a tropical dry ecosystem

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Abstract

Early succession on large landslides in highly humanized areas that have a tropical dry climate is not well studied. This study documented vegetation recovery during the first four years after disturbance at a landslide on Casita Volcano, Nicaragua. We aimed to determine the main pathways and causes of change in community features, such as richness, biomass accumulation, and species composition, and verify the role played by environmental heterogeneity. Data consisting on number, covers and mean height of woody species, and several abiotic factors related to productivity and stability of substrates were obtained from permanent plots in previously defined sectors. Pathways of early succession were highly contingent on abiotic heterogeneity and landscape context, and were mainly controlled by abiotic factors associated with productivity of sites, and human disturbance. Those results might form the basis of a model of early succession on landslides located in densely populated areas within dry tropical ecosystems. Our results suggest that, rather than focusing research on large-scale disturbances, only, the study of succession in landslides of the type that occurred on Casita Volcano, must point towards the response of ecosystems to a much more complex disturbance regime, in which human-induced disturbances play a major role.

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

Introduction

Succession implies changes in plant communities through time (Pickett and McDonnell 1989), and determining the major pathways of these changes leads to a better understanding of the process, which provides a sound basis for directing rehabilitation of degraded lands (Walker and del Moral 2003). Generalizations about successional changes in important community features as biomass, richness and species composition are abundant (Bazzaz 1979, Odum 1969), and they have been thoroughly studied for extended periods in a variety of ecosystems. There is, however, less information about what to expect during early succes-

sion (Del Moral 1999). In highly disturbed sites such as landslides, where the seed bank plays a minor role, the first few years after disturbance are crucial for the establishment and germination of external propagules (Hupp 1983), and the study of early successional pathways might be very important in forecasting future successional patterns (Lundgren 1978).

Some authors affirm that succession is probably more dependent on environmental heterogeneity than on time (Lovett 2000) and landslides present a large abiotic heterogeneity (Walker *et al.* 1996). According to the "emerging paradigm" in ecology, "contingencies" associated with specific site conditions

and histories, spatial context, and the occurrence of episodic events determine ecosystem processes, such as seed dispersal, germination, establishment, and soil formation, and promote the development of multiple dynamics in different patches at different scales (Pickett and Ostfeld 1995, Wu and Loucks 1995). In that way, landslides might be considered as "patch-dynamics systems" (Myster and Walker 1997, Pickett and White 1985).

Firstly, the high abiotic heterogeneity of landslides is a product of the large differences in geomorphological stability and fertility between their upper or "erosional" zones, where soil and vegetation are completely removed and barren substrates are often exposed, and their lower or "depositional" zones, which have a high "biological legacy" that consists of the original soil and heterogeneous mixtures of broken plant parts, seeds, organic matter and rock fragments from the upper zone (Francescato et al. 2001, Guariguata 1990, Myster and Fernández 1995, Walker *et al.* 1996). Some community features as biomass accumulation, which is governed by moisture and nutrient levels (Walker and del Moral 2003), increase fast in the stable and fertile zones of landslides (Aplet and Vitousek 1994, del Moral and Jones 2002, Hull and Scott 1982, Nakamura 1984).

In the unstable and infertile zones, however, succession is controlled by abiotic conditions and changes are less dramatic (Walker *et al.* 1996). Changes in these zones resemble those reported for primary succession in other hostile environments. In recently deglaciated zones (Rydin and Borgegard 1988) and pumice plains (del Moral 1998), for example, biomass accumulates slowly and richness may even decrease due to mortality of early established species that are unable to survive in

the hostile conditions of these areas. In this case, the species composition of the different pioneer communities tend to converge (del Moral and Jones 2002). In other low fertility ecosystems as mountain moorlands, "autosuccessional" patterns in which succession does not imply a gradual replacement of species, but changes in the abundances of the existing, have been reported (Sarmiento *et al.* 2003). Spatial context is the second source of contingency for vegetation recovery (Pickett *et al.* 2001). In large disturbed areas surrounded by heterogeneous landscapes, availability of propagules varies depending on the type of habitat at the edges and the distance to the adjacent forests (Aide and Cavelier 1994, Myster and Pickett 1992, Pickett *et al.* 2001, Rydin and Borgegard 1991). That is very critical in the tropics, where the seed rain is strongly reduced even over very short distances because of the heavy weight of the seeds of most forest species (Clark *et al.* 2005, Nathan *et al.* 2001).

In this article, early successional patterns are studied in a landslide which presents a high abiotic heterogeneity and is located in the Central American pacific region of Nicaragua. In this area, the climate is characterized by low, seasonal rainfall, and the landscape is highly heterogeneous. Although tropical dry forests predominate (Beard 1953, Murphy and Lugo 1986, Murphy and Lugo 1995), the species and structure of plant communities vary depending on elevation and slope. In this densely populated region, the formerly abundant forests have been reduced dramatically by the effects of human disturbance (e.g., extraction of forest resources, burning and clearing of vegetation, urban sprawl) (Gillespie *et al.* 2000, Janzen 1988).

On the other hand, tropical dry forests are among the most endangered and less known

ecosystems in the world (Gerhardt and Hytteborn 1992, Gillespie *et al.* 2000, Janzen 1988). In the rain and cloud forests of Central America and the Caribbean, vegetation recovery on landslides have been well-studied (Dalling 1994, Garwood 1985, Guariguata 1990, Myster 1993, Restrepo and Álvarez 2006, Walker *et al.* 1996), but those in tropical dry forests have not received similar attention (Lundgren 1978). The unique characteristics, the accelerated rate of degradation and transformation, and a deficit in our understanding of them, makes research a priority in conservation and management of tropical dry forest ecosystems (Bawa *et al.* 2004, Sanchez-Azofeifa *et al.* 2005).

Our principal objective was to determine the major pathways of change in richness, biomass, and species composition in the landslide during the first four years after disturbance. We wanted to verify if they vary between the different areas of the landslide, and to identify their main causes. Specifically, we tested the following predictions.

- Biomass and species richness will increase steadily over the four years of the study. However, pathways of change in species composition will diverge more between the different areas within the landslide.

- In the more stable and fertile zones there will be a significant increase in richness and biomass accumulation, and succession will occur rapidly. Species composition in the areas near to adjacent forests will be increasingly similar to species composition in there.

- In the more unstable and infertile zones, biomass and species richness will increase slowly and there will be convergence in species composition among pioneer communities. Succession will proceed slowly, following an "autosuccessional" pattern, and will

be controlled by abiotic factors.

- Human disturbances might disrupt successional pathways in those areas of the landslide surrounded by cultivated lands.

Methods

Study Area

This study was conducted on a landslide on the Casita Volcano (12º41´ N; 85º57´ O), which is part of the "Maribios" volcanic range in western Nicaragua (**Fig. 1a**). The landslide, which was triggered by an exceptionally heavy rainfall event (500 mm in 24 hours) on 30 October 1998, during Hurricane Mitch (Sheridan 1998), moved 2.000.000 m^3 of highly fractured material that rapidly formed an enormous lahar at mid-slope (Kerle 2002). This lahar devastated the 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 than the others studied in Central America and Caribbean, and the ecological and socioeconomic characteristics of the region are quite different (**Table 1**).

Mean annual rainfall, is considerably lower and the dry season is larger in the dry forests of western Nicaragua than they are in the rain and cloud 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 eastern Central America and on the Caribbean islands (Pielke *et al.* 2003).

Western Nicaragua, which has been occupied by pre-Columbian peoples an European settlers for a long time, also has a high population
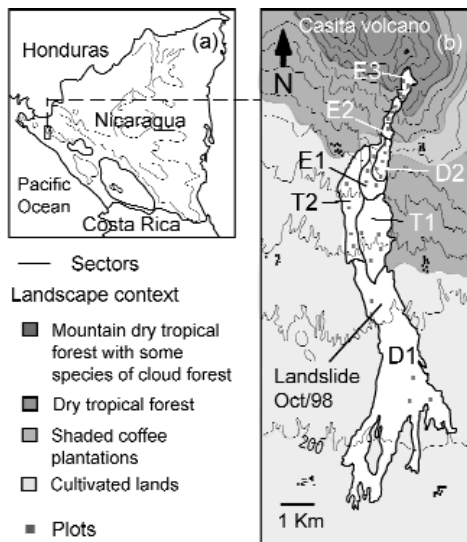
Figure 1. Study area. a) Location in Nicaragua. b) Detailed map of the landslide indicating the different sectors based on abiotic heterogeneity (fertility and geomorphologic stability) and the landscape context; erosional (E1, E2, E3), transitional (T1 and T2), and depositional (D1 and D2). The locations of sampling plots are indicated.

density (Corrales-Rodríguez 1983, Salas-Estrada 1999). Poverty is also high and local ecosystems have experienced a substantial exploitation and reduction accordingly, although large patches of relatively well-preserved forests still remain.

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 Volcano 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 forests are interspersed with scattered huts and small-holding lands, human disturbances are common. Those disturbances include the clearcutting of forest for firewood extraction and the expan-

sion of cropland (Salas-Estrada 1999), and fire (Corrales-Rodríguez 1983), which is used mainly by peasants for agricultural practices as removing crop stubble (December) or preparing fields for sowing (May and August) (P. Dávila, personal communication). At the base of the volcano, the population density is the highest and the landscape is dominated by large real estate holdings where crops such as sugar cane, sorghum and peanuts are cultivated intensely.

Fieldwork sampling

In 1999 seven major sectors that will be referred as D1, D2, T1, T2, E1, E2, and E3 on advance, were identified in the landslide following two criteria (**Fig. 1b**). According to abiotic heterogeneity (fertility and geomorphologic stability), they were; i) Depositional zones in which the former agricultural or forest soil remained after the landslide (D), ii) erosional zones in which soil was removed by the landslide (E), and iii) "transitional" zones between the erosional and the depositional zones where the former soil remained in small patches only (T). In relation to landscape context, we distinguished among sectors that; i) had cultivated lands along its edges (D1), ii) were enclosed by mountain tropical dry forests that had some of the plant species typical of cloud forests (E3), iii) had tropical dry forests along its edges (T1 and E2), iv) had shaded coffee plantations along its eastern border (E1 and D2), and v) in which cultivated lands dominated beyond the western border (T2). A group of remnant trees appeared in the middle of D2, a depositional landing zone at mid-slope originated by the existing topography.

To document the early successional changes in each sector, we recorded four data series

Table 1. Landslides studied in the Central American and the Caribbean; Size, climate and socioeconomic characteristics of the surrounding region. Size: Maximum size cited in the study. Mean Annual Rainfall and Seasonality in the region: Data from "AQUASTAT Database", Land & Water development Division, FAO (www.fao.org). Frequency of hurricanes: Long-term average of hurricane strikes per year (Pielke et al. 2003). Ecosystem type: Holdridge Life Zones (Holdridge 1967). Population density refers to province or department (see below). HDI: Human Development Index (UNDP 2005).

Site and country	Study	Size (Ha)	M.A. Rainfall (mm/yr)	Dry period	Frec. hurr.	Ecosystem type	P. dens. (Habs./km2)	HDI (2005)
Casita Volcano (Nicaragua)	Velazquez & Gómez-Sal (*unpublished*)	1120	1250	Nov-Apr	0.2	Tropical dry forest	172[1]	0.690
Río Jaqué (Panamá)	Garwood (1986)	-	2600-5500	Dec-Apr	0.2	Tropical rain forest	3.4[2]	0.804
Blue mountains (Jamaica)	Dalling & Tanner (1995)	0.38	2500-3000	Jun-Aug	1	Tropical moist & wet forest	100.12[3]	0.738
Luquillo (Puerto Rico)	Guariguata (1990)	2.5	3000-4000	Feb-Apr	1	Subtropical wet forest	283[4]	0.872
Monteverde (Costa Rica)	Myster (1993)	< 50	2800	Dec-Apr	0.2	Tropical moist & wet forest	26.1[5]	0.838

Abbreviations; M.A. Rainfall = Mean Annual Rainfall, Frec. Hurr. = Frecuency of hurricanes, P. dens. = Population density, HDI = Human Development Index, [1] Data for Chinandega department according to "Instituto Nacional de Estadísticas y censos", INEC (http://www.inec.gob.ni/); [2] Data for Darién province according to FAO (http://www.pananet.com/gobierno/Info.htm); [3] Data for Portland parish according to Statistical Institute of Jamaica (http://www.statinja.com/); [4] Data for Luq uillo municipality according to Puerto Rican Government (https://serviciosenlinea.gobierno.pr); [5] Data for Puntarenas province according to "Fundación para el Centro Nacional de la Ciencia y la Tecnolog ía", CIENTEC (http://www.cientec.or.cr).

(1999, 2000, 2001 and 2002). In 1999, detailed information on vegetation types and species composition was documented. In 2000, a long-term permanent 10*10 m^2 plot was established randomly, and, in 2001, three more plots were added (each assigned a letter, i.e., a, b, c and d). There were 7 total plots in 2000 and 28 total plots in 2001 and 2002. In each of three years (2000, 2001 and 2002), the vegetation was surveyed in the plots at the end of the rainy season (November to January), when plant cover is at its maximum. 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 of woody species were measured. In 2002 we measured the abiotic factors associated with the stability [Elevation (m.a.s.l.), Slope (%), Stone cover (%) and Mean diameter of stones (cm)] and fertility of substrates [amounts of NO_3, P, and K (ppm), and the proportions of sand, silt and clay]. To determine the content of NO_3, P and K, LaMotte soil test kit (La Motte)

was used. To determine the proportions of sand, silt and clay, 200-gr. weight soil samples were dried and sieved. As we expected, human-induced disturbances occurred during the second (2000-01) and third (2001-02) periods of the study. Human disturbances occurred mostly in the depositional and transitional sectors and involved the widespread and extensive removal of pioneer trees for firewood extraction and the expansion of croplands (D1 and T1), and fires created by peasants nearby, which expanded into the landslide (T1 and T2). In each sampling period, plots were identified as "cleared" or "burned" if there were signs of clearcutting (e.g., presence of tailings) or burning (e.g., scorched individuals and stems), respectively. Species taxonomy and nomenclature follow the "Flora de Nicaragua" (Stevens *et al.* 2001).

Data Analysis

To characterize sectors and determine whether there were significant differences in the

abiotic factors associated with stability and fertility of substrates, Kruskall-Wallis and *posthoc* Mann-Whitney U tests were performed. Pathways of change in community features were interpreted as "vectors" that had a "direction" and a "rate" (Bakker *et al.* 1996). To evaluate the direction of change in richness and biomass, the mean number of species and mean total biovolume [height (m) * cover (m²)] were calculated per sector and year of study, and then represented in diagrams. The use of biovolume as a surrogate for biomass is justified in low stratified communities, which predominate in primary succession (Chiarucci et al. 1999).

To evaluate the direction of change in species composition, a Detrended Correspondence Analyses (DCA) were used (Avis and Lubke 1996). These analyses were performed using all of the species of the inventory and those present in more than a 5%, a 10% and a 20% of the plots. The analysis that had the highest value of inertia explained including the largest number of species was selected. In the evaluation of rates of change, we considered only "incidence rates" (Prach 1993) in richness and species composition because these are highly indicative of changes in species turnover and species abundance (Myster and Pickett 1994). Incidence rates were obtained for each plot between the different year-to-year periods of the study, which are referred to as "st" (first), "nd" (second) and "rd" (third) periods, using subindexes. To calculate rates of change in richness and species composition respectively, Sørensen´s coefficient of dissimilarity (SD) (Kent and Coker 1992), and Euclidean Distances (ED) between coordinates of plots in the DCA space (Wiser *et al.* 1996) were used.

To test for significant effects of sector and number of years following disturbance on the direction of successional changes in richness, biomass and species composition, two-way ANOVA was used. To meet the assumptions of the analyses, where necessary, the data were log- or box-cox transformed. If an ANOVA revealed a significant ($P < 0.05$), we used a multiple comparisons test (Scheffé´s) to determine whether there were differences between pairs of sectors or types of sectors. To determine the main causes of change in each type of sector, Spearman rank correlation coefficients (r) were calculated between the values of richness, biomass and species composition, and those of abiotic factors associated with stability and productivity of substrates. Statistical Analyses were performed using STATISTICA (Statsoft 2001), and CANOCO (Braak and Smilauer 2002).

Results

Characterization of sectors

Depositional, erosional and transitional sectors were well differentiated by elevation, steepness of slope, amount of stone cover, and the nutrient contents of the soil (**Table 2**). In addition, within each type of sector, there were differences among sectors. For instance, T1 was more similar to the depositional sectors than to T2, particularly in terms of nutrient content and texture. D2 differed from D1 based on its greater stone cover (due to the presence of large rocks in the area of D2).

Changes in species richness and biomass

Species richness did not show a clear trend during the study period (**Fig. 2a**), but decreased in the majority of the sectors between 1999 and 2000. Two-way ANOVA results revealed that patterns of change in richness differed more significantly between years ($F_3 = 10.14$, $P < 0.001$) than between sectors ($F_6 = 2.48$, $P < 0.05$). The pattern of change showed by D2 was contrary to the other sectors and T1 experienced a sharp decrease during the third

Table 2. Characterization of the different landslide areas (sectors) in the landslide on Casita Volcano, Nicaragua, based on abiotic factors and presence of disturbances. Means are at the top of the cells and Standard deviations are in italics, below. Asterisks indicate the statistical significance of each variable in the Kruskall-Wallis test. H > chi² with $P < 0.001$ (**) and $P < 0.05$ (*). Values within columns followed by the same superscript letters are not significantly different at $P < 0.05$ in the Mann-Whitney U test.

Sector	Lc.	Stability variables				Productivity variables						Dist.
		Altitude** (m.a.s.l.)	Slope** (%)	Sc.** (%)	Mds.* (cm)	NO_3** (ppm)	K** (ppm)	P** (ppm)	Sand* (%)	Silt* (%)	Clay** (%)	
D1	CL	262.5[a]	6[a]	5[a]	4,75[a]	15,20[a]	129,91[ab]	55,9[a]	72,34[a]	9,35[a]	20,52[a]	Clear.
		43.37	*2,16*	*2,04*	*3,57*	*1,86*	*13,98*	*5,09*	*1,76*	*1,09*	*2,80*	
D2	DTF, SC	649.5[b]	5,75[a]	38,50[b]	11,18[ba]	28,50[d]	139,37[a]	72,57[b]	61,73[b]	7,70[b]	30,52[b]	-
		43.43	*1,07*	*15,80*	*4,24*	*8,93*	*13,32*	*6,21*	*5,32*	*2,7*	*3,78*	
T1	DTF	403.75[c]	8,5[ba]	33,75[b]	10,23[a]	10,12[ab]	125,75[b]	72,52[b]	71,36[b]	7,75[b]	19,56[a]	Clear. Burn.
		19.65	*2,64*	*24,70*	*7,29*	*4,01*	*11,01*	*7,01*	*4,25*	*1,22*	*3,72*	
T2	CL	459.50[c]	14,25[b]	21,87[b]	29,21[c]	6,9[bc]	93,52[bc]	60,07[a]	78,48[a]	4,73[c]	13,74[c]	Burn.
		46.82	*2,21*	*8,00*	*8,92*	*2,33*	*8,73*	*5,34*	*3,89*	*1,56*	*1,90*	
E1	DTF, SC	562.50[bc]	26,50[c]	88,75[c]	27,33[c]	4,7[c]	66,37[d]	5,15[c]	64,60[b]	9,53[a]	26,68[b]	-
		12.28	*5,32*	*6,29*	*4,35*	*1,34*	*12,59*	*1,15*	*8,27*	*1,73*	*6,97*	
E2	DTF	849.5[d]	59[d]	91,87[c]	17,14[b]	5,42[c]	87,40[c]	37,42[c]	76,57[a]	7,06[b]	15,62[c]	-
		58.35	*6,73*	*5,54*	*6,88*	*1,14*	*8,21*	*5,57*	*5,73*	*2,26*	*3,10*	
E3	DTF - CF	1086.25[d]	40,75[d]	97,50[c]	48,47[d]	-	-	-	-	-	-	-
		59.15	*17,07*	*2,04*	*25,10*							

Abbreviations; Lc. = Landscape context, Sc = Stone cover, Mds = Medium diameter of stones, Dist. = Presence of disturbances, Clear. = Clearcutting, Burn. = Burning, CL = Cultivated lands, DTF = Dry tropical fore st, DTF – CF = Mountain dry tropical forest with some species of the cloud forest, SC = Shaded coffee plantations.

period. In contrast to richness, biomass experienced a general accumulation during the study period (**Fig. 2b**). Patterns of change in biomass differed significantly between sectors (F_6 = 15.48, $P < 0.001$) and between years (F_3 = 12.89, $P < 0.001$). The strongest increase in biomass occurred in the depositional sectors during the second period and the sharpest decrease in T1 during the third. Biomass slightly decreased in the erosional sectors (especially in E2), during the first period.

Change in species composition

Although the DCA that used only the species that appeared in more than 5%, 10% and 20% of the plots had the greatest explanatory power (**Table 3**), they excluded many species (e.g., only 22 of 52 species appeared in more than 5% of the plots); therefore, the DCA that included all of the species was finally examined (**Table 3**, **Fig. 3**). The main changes in species composition of plots from one year to the next were reflected mainly along DCA Axis I, which

was associated with time. Plot scores in Axis I showed a gradual increase in dissimilarity, which suggests divergence in species composition among plots during the study period. The plot scores in Axis I differed more significantly between sectors (F_6 = 14.78, $P < 0.001$) than between years (F_3 = 4.32, $P < 0.05$), and the plot scores on Axis II differed significantly between sectors, only (F_6 = 4.5, $P < 0.05$). Pathways of change in species composition seemed to be more strongly influenced by spatial heterogeneity than by the number of years after the landslide, and several trajectories were distinguishable among the sectors.

The plots of D1 and D2 (**Fig. 3**), exhibited convergent trajectories that aimed towards the bottom left of the DCA diagram. Beginning in 2001, the pioneer tree species *Trema micrantha* and *Muntingia calabura* were dominant in most of the plots, although saplings of *Guazuma ulmifolia* and young individuals of some of the species typical of the adjacent forests such as *Maclura tinctorea*, *Heliocarpus*
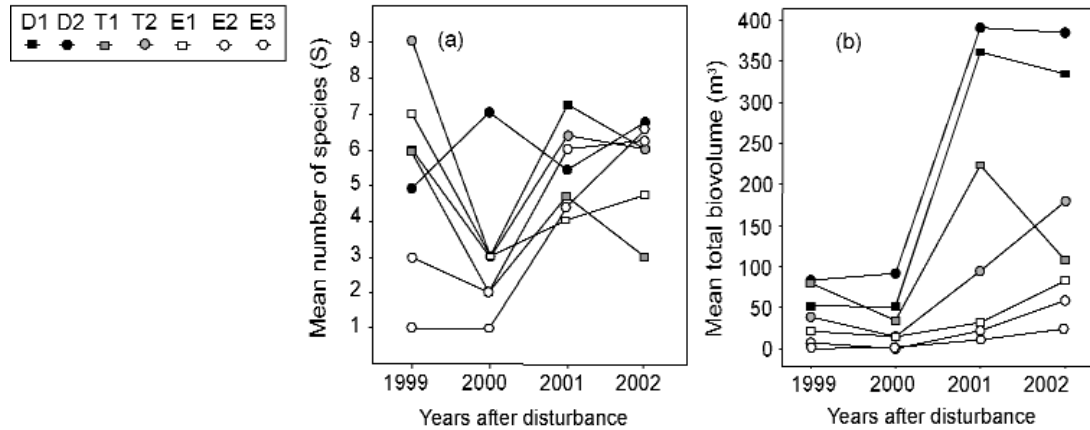
Figure 2. Direction of change in richness and biomass of pioneer plant communities in the landslide on Casita Volcano (Nicaragua), expressed by mean number of species (a) and mean total biovolume (b) per sector, during the four successive years after disturbance.

appendiculatus, and *Enterolobium cyclocarpum*, were common in the understory of D1 and D2, respectively. In contrast, two D1 plots ("b" and "d") showed deflected trajectories towards a high presence of shade-intolerant shrubs such as *Tecoma stans*, *Desmodium nicaraguense*, and *Melanthera nivea*.

In some of the plots of transitional sectors (e.g., T1a) (**Fig. 3**), vegetation developed rapidly to become a forest dominated by pioneer trees, but in the others, especially in T2, the trajectories were strongly deflected towards a shrubland dominated by *Desmodium nicaraguense*, *Desmodium inca-*

num and *Indigofera guatimalensis*, which was apparent in the third period of the study. Erosional sectors maintained a sparse srhubland dominated by *Melanthera nivea*, *Pluchea carolinensis*, *Lysiloma microphyllum* and *Wigandia urens* during the study period. Although the trajectories of E1 plots run along Axis II, which indicated almost no changes in species composition, a clear convergence occurred among plots in E3, in which species such as *Verbesina turbacensis* and *Iresine angustifolia* dominated from 2001 onward. In E2, the invasion of *Tecoma stans*, *Iresine angustifolia* and *Desmodium nicaraguense* promoted deflected and divergent trajectories.

Table 3. Summary statistics for the Ordination Analyses of plant communities in the landslide on Casita Volcano (Nicaragua), during the first four years following disturbance, using all the species in the inventory (a), those present in more than 5% (b), 10% (c) and 20% (d) of the plots. The low percentages of inertia explained in analyses (a), (b) and (c) depended in the high proportion of low-abundance species in the inventory.

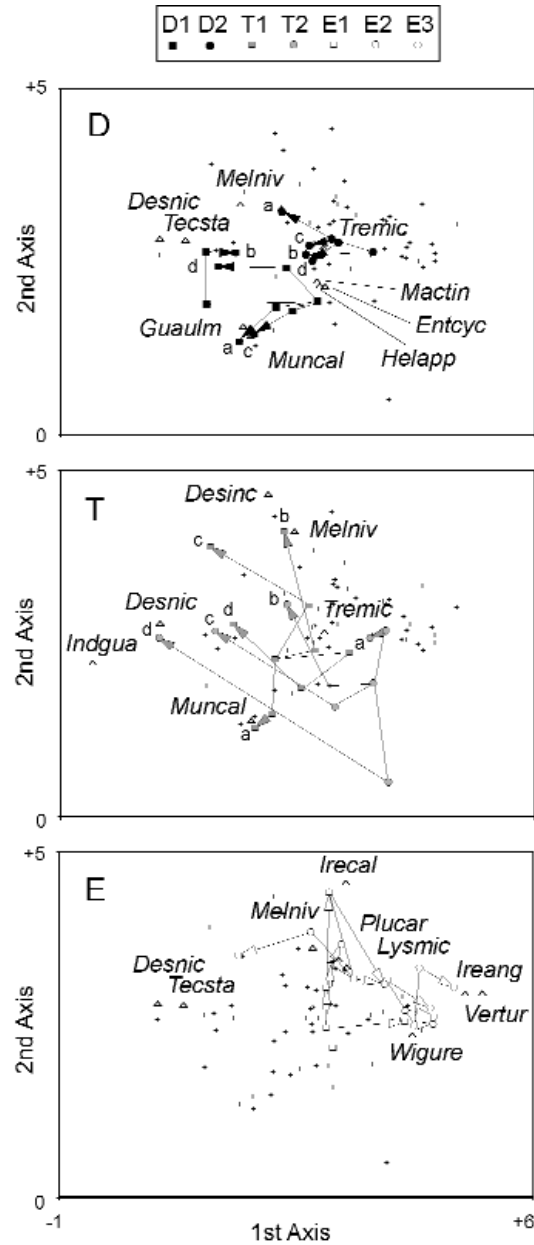|	Eigenvalues (ë)		Gradient lenght		% inertia exp.	
Analyses	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
DCA (a)	0,679	0,490	4,658	4,179	11	7
DCA (b)	0,606	0,479	3,941	3,710	14,2	11,3
DCA (c)	0,598	0,486	3,470	3,702	17,8	14,5
DCA (d)	0,650	0,361	3,008	2,869	29,4	16,4

Figure 3. Main directions of change in species composition of pioneer plant communities in the depositional (D), transitional (T) and erosional sectors (E) sectors, in the landslide on Casita Volcano (Nicaragua), expressed by "trajectories" in the DCA ordination diagram. Points represent the species composition of each plot in the four years of the study (1999, 2000, 2001, and 2002). Arrows represent the trajectories of the plots within each sector, marked by capital letters (a, b, c, and d). Triangles represent species whose abundance increased during the whole time frame. The abbreviations of the names of the species are indicated in italics and use the three first letters of genus and species.
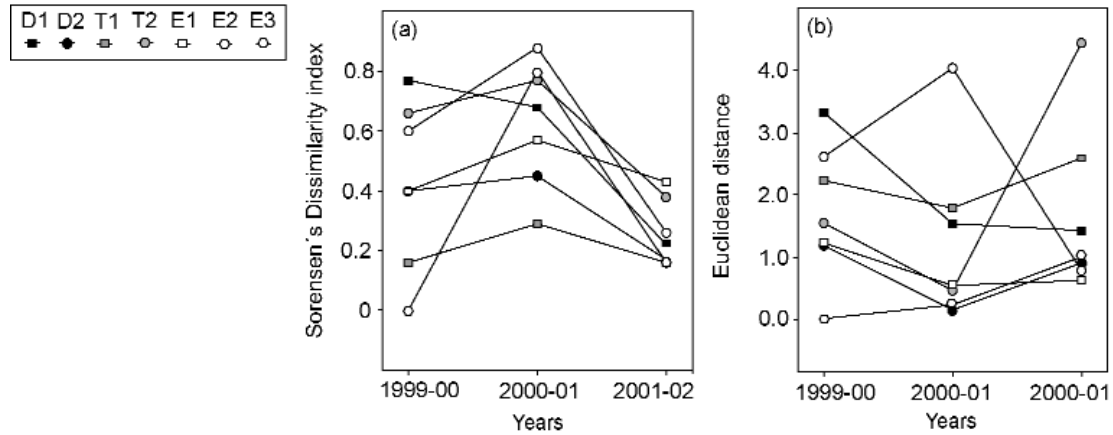
Figure 4. Incident rates of change in richness and species composition of pioneer plant communities in the landslide on Casita Volcano (Nicaragua), expressed by Sørensen's Dissimilarity index (a) and Euclidean distance (b), as a function of years after disturbance.

Rates of change

Rates of change in species turnover (Sørensen´s dissimilarity index) decreased in general terms, but there were especially high during the second period in E2 (MSD_{sd} = 0.88) and E3 (MSD_{sd} = 0.80) (**Fig. 4a**). Rates of change in species abundance (Mean Euclidean Distance) were the highest in E2 (MED_{sd} = 4.01), T1 (MED_{rd} = 2.57), and T2 (MED_{rd} = 4.41), and the lowest in E3 (MED_{st} = 0.01 and MED_{sd} = 0.22) and E1 (MED_{sd} = 0.14) (**Fig. 4b**).

Causes of change

In depositional sectors, elevation (r = 0.79, *P* < 0.01), stone cover (r = 0.75, *P* < 0.01) and mean diameter of stones (r = 0.66, *P* < 0.01) were significantly and positively correlated with change in species composition (plot scores in Axes I and II). Clearcutting and plot scores in Axis I were strongly and negatively correlated (r = - 0.63, *P* = 0.01). In the erosional sectors, factors associated with productivity were signi-

ficantly and positively correlated with richness [NO_3 (r = 0.50, *P* < 0.01)], biomass [P (r = 0.56, *P* < 0.01)], and species composition (plot scores in Axis I) [K (r = - 0.72, *P* < 0.01)]. In the transitional sectors, burning and species composition (plot scores in Axis I), were significantly and negatively correlated (r = - 0.59, *P* < 0.01).

Discussion

As we predicted, biomass and divergence in species composition increased over time. However, species richness decreased in the first period. Although the plants that initially become established usually persist for a long time (Drake 1991), the assembly of pioneer communities is highly stochastic and follows three phases; dispersal, environmental selection and internal dynamics (Belyea and Lancaster 1999). Environmental selection involves the mortality of a large number of seeds that germinate immediately after disturbance but are not adapted to the harsh abiotic conditions of recently exposed substrates. On

the landslide at Casita Volcano between 1999 and 2000, a large number of seedlings might have grown and died immediately, which led to a significant decrease in species richness. Considering that in areas with tropical dry climate, seed germination and seedling establishment are highly dependent on soil moisture and total annual rainfall (Castilleja 1991), the strong decrease in the total annual rainfall reported in the nearest meteorological station (Chinandega 12° 38´ N; 87° 08´ W, 60 m.a.s.l.) between 1999 (2422.5 mm) and 2000 (1668.0 mm) (INETER 2005) also supports this explanation.

Early successional changes differed more strongly between the different areas within the landslide depending on site conditions and landscape context, than among the years of study. Thus, as we predicted, environmental heterogeneity have played a major role in determining the patterns of successional change, although it did so in a much more complex manner than was expected. The landslide created a large number of different areas in which pathways and causes of change were dramatically different.

Early succession proceeded quickly in the more stable and fertile areas (the depositional sectors), which had the highest value of biomass accumulation among the sectors of the landslide. Although D1 and D2 were strongly dominated by the pioneer trees *Trema micrantha* and *Muntingia calabura* during all study period, in D2, the appearance of saplings of forest species in the last period suggests a convergence in species composition with the adjacent habitat. D2 was beside the forest, and the role played by the dispersal of propagules and edge colonization in determining early successional patterns was probably more

important there than it was in D1, which was surrounded by cultivated lands. This is supported by results of recent studies on seed bank in the landslide, which have shown that presence of late-successional species from the adjacent forests (i.e. *Malvaviscus arboreus*) is much larger in D2 than in other sectors (Jirón and Sánchez-Ríos 2003). The group of remnant trees in D2 might have been also a factor for this convergence. Remnant trees are important for promoting vegetation recovery of disturbed areas by mitigation of hostile environments and by acting as perches for fruit-eating birds in temperate (Debussche *et al.* 1996, Neeman and Izhaki 1996, Pickett *et al.* 2001), and tropical old fields (Carrière *et al.* 2002, Da Silva *et al.* 1996, Parrotta *et al.* 1997, Slocum 2001), and in tropical landslides (Shiels and Walker 2003). Although species composition was controlled by presence of clearcutting and large stones, in our study, abiotic factors and human disturbance factors did not emerge as causes of change in species richness and biomass in the stable and fertile areas of the landslide. The main "driving forces" of succession in these areas are expected to be autogenic and develop later.

As we predicted, the more unstable and infertile areas in landslide (the erosional sectors) exhibited an small amount of biomass accumulation and succession proceeded at an slow rate. Our prediction of an "autosuccessional" pattern of low rate of change in species turnover and high rate of change in species abundance was not observed, and convergence in species composition among pioneer communities occurred in E3 only. Nutrient contents were the main cause of change in species composition. The differences in landscape context, and stability and fertility of substrates between E1, E2 and E3, may explain the diffe-

rent pathways that emerged between these sectors. Colonization is more stochastic and dependent on seed rain in the erosional than on the depositional parts of landslides (Myster 1993). Forests surrounded E2 and E3 and seed rain was probably high, which might have promoted a high rate of species turnover at both sectors. On the other hand, some species typical of the adjacent forest not detected in the aboveground vegetation of E2 plots (e.g., *Malvaviscus arboreus*), have been reported as highly abundant in their seed bank (Jirón and Sánchez-Ríos 2003), that points at edaphic constraints to germination in this sector. However, E2 has steeper slopes and is more unstable than E3, and in highly unstable soils propagules either fail to colonize or repeatedly colonize but are removed through erosion (Bochet and García-Fayos 2004, García-Fayos *et al.* 1995). Thus, in E2, instability of substrates might have been important in determining the strong changes in turnover rates between the different years and the divergent trajectories in species composition.

Convergence in species composition among pioneer communities is fairly common where there are "barriers to invasion" and stressful environmental conditions that limit potential colonizing species (Walker and del Moral 2003). In this way, the extremely low productive substrates of E3 might have caused the clear pattern of compositional convergence that emerged between their plots. In our study, however, soil nutrient content appeared to be the main cause of early successional change within the erosional sectors. In those highly infertile and unstable areas, differences in species composition among plots and sectors may have been caused by subtle differences in availability of limiting factors such as nutrients and water which vary with the topography.

In the transitional sectors of the landslide on Casita Volcano, species richness decreased sharply and the successional trajectories of species composition exhibited a striking deflection compared to the other sectors. In the transitional sectors, stability and fertility factors were important, but the role played by fire in influencing the pathways of change was undeniable. Subsequent disturbances are known to cause deflections in the recovery patterns of previously disturbed areas (Whittaker *et al.* 1989) by creating new environmental conditions or altering the competitive interactions among pioneer species (Law and Morton 1993).

In our study, the abundance of *Desmodium* and *Indigofera* increased after fire, and it is common for burning to lead to a dramatic expansion by a few opportunist shrub species that can form dense thickets (Cochrane and Schulze 1998, Hooper *et al.* 2004) and cause a strong decrease in richness (Nepstad *et al.* 1996, Uhl 1998). Moreover, as observed in Panama (Hooper *et al.* 2004) and Borneo (Cleary and Priadjati 2005), thickets could cause a cessation in species turnover and impede recovery for a long period of time. It is important also to point out at the strong decrease in biomass in T1 during the last period. That was because in T1 there were large *Trema micrantha* trees that were cleared in the period 2001-2002 and their biomass was not recovered.

Concluding remarks

In the landslide of Casita Volcano, Nicaragua, early successional changes differed more significantly between the different areas within the landslide based on abiotic heterogeneity and landscape context than between the different years of study. As a general trend, biomass accumulated at different rates and species

composition diverged between the different areas of landslide, but species richness did not increased at any of the areas during the period of study. In the more stable and fertile areas biomass increased strongly, although clearcutting disrupted this pattern in zones surrounded by cultivated lands. In those zones near to the forest edge, an increase in compositional similarity to adjacent vegetation was detected. In the more unstable and infertile areas biomass increased slightly, and direction and rates of change in species composition were highly variable depending on the nutrient contents of the soil. In the "transitional" areas richness decreased strongly and trajectories of change in species composition were strongly controlled by burning and other human-induced disturbances. Our study suggests that in large landslides located in highly humanized areas with tropical dry climate, pathways of early succession are strongly influenced by abiotic heterogeneity and landscape context, and are mainly controlled by abiotic factors associated with fertility of sites and the incidence of human disturbances.

If considering that in Central America and the Caribbean, climatic change and population growth have spawned, respectively, an increase in the frequency and intensity of hurricanes and heavy rainfall events that trigger landslides (Goldenberg *et al.* 2001, Webster *et al.* 2005), and in the frequency and intensity of human disturbances (Hooper *et al.* 2004). Thus, coexistence and relationships between landslides and human disturbances in the Pacific region of Central America might have severe effects on landscape patch-dynamics by promoting large-scale processes as deforestation (Restrepo and Álvarez 2006), and the transformation of tropical dry forests into impoverished savannas or shrublands (Dale *et al.* 2000, Quigley and Platt 2003). Our findings provide a basis for further research applied to vegetation dynamics and restoration of disturbed areas located in highly humanized ecosystems with seasonally dry tropical climate.

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