Capítulo 5

Cambios en las comunidades herbáceas del deslizamiento del Volcán Casita, Nicaragua, durante la sucesión temprana

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

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Resumen

En este estudio se examinaron los principales cambios en las comunidades herbáceas durante los cuatro primeros años de sucesión en un gran deslizamiento situado en el Volcán Casita, Nicaragua, situado en un área densamente poblada y con clima tropical seco. El objetivo principal fué determinar las principales trayectorias de cambio en algunas características de las comunidades como la riqueza específica, la biomasa, la composición de especies y la abundancia de atributos morfo-funcionales, y verificar si estas variaban entre las distintas áreas del deslizamiento en función de la heterogeneidad abiótica y el contexto ecológico externo. Para ello se muestrearon el número de especies, el porcentaje de cobertura, la altura media y la abundancia de atributos morfo-funcionales en la vegetación herbácea, así como varios factores abióticos relacionados con la fertilidad y la estabilidad geomorfológica de los sustratos, en 28 parcelas situadas en siete sectores. La heterogeneidad ambiental influenció fuertemente los cambios desarrollados durante la sucesión temprana durante los cuatro años del periodo de estudio. La biomasa aumentó en las áreas inestables e infértiles y disminuyó en las áreas estables y fértiles del deslizamiento. En la mayor parte de los sectores la riqueza específica disminuyó significativamente debido a la expansión de unas pocas especies dominantes que desarrollaron una gran cobertura y excluyeron a otras. Estas fueron las principales responsables de los cambios en la composición de especies e incluían forbios perennes fijadores de nitrógeno, ej. *Clitoria ternatea*, graminoides con rizomas y estolones, ej. *Hypharrenia rufa*, y forbios anuales, ej. *Calopogonium mucunoides* y *Stizolobium pruriens*. Pueden tener una influencia determinante en las trayectorias sucesionales que se desarrollen a largo plazo en el deslizamiento del Volcán Casita.

Changes in the herbaceous communities on the landslide of the Casita Volcano, Nicaragua, during early succession

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Abstract

This study examined the main changes in the herbaceous communities during the first four years of succession in a large landslide on Casita Volcano, Nicaragua, located in a densely populated area that has a tropical dry climate. Our main objective was to determine the major patterns of change in community features, such as richness, biomass, species composition, and abundances of plant traits and to verify if they varied between the different areas of the landslide based on abiotic heterogeneity and landscape context. Number, percent cover, mean height and traits of herbaceous species, and several abiotic factors related to fertility and geomorphological stability of substrates were sampled in 28 permanent plots located in seven sectors. Environmental heterogeneity strongly influenced early successional changes in the community during the four years of the study. Biomass increased in the unstable and infertile areas and decreased in the stable and fertile areas of the landslide. In most of the sectors, species richness decreased significantly because of the expansion of a few dominant species that developed a large cover and excluded other species. Those dominant species were mainly responsible for changes in species composition and included perennial nitrogen-fixing forbs, e.g., *Clitoria ternatea*, graminoids that have rhizomes or stolons, e.g., *Hypharrenia rufa*, and annual forbs, e.g., *Calopogonium mucunoides* and *Stizolobium pruriens*. They might be important in determining future successional patterns on the Casita Volcano landslide.

Key words: richness, biomass, species composition, plant traits, environmental heterogeneity.

Nomenclature: Flora de Nicaragua (Stevens *et al.* 2001).

Introduction

Herbaceous communities play an important role in a wide range of ecosystem functions, such as energy flow and nutrient cycling (Frelich *et al.* 2003) and, during early succession, experience significant changes in features, such as richness, biomass, species composition, and abundance of plant traits (Roberts and Zhu 2002). Typically, in the first years following a disturbance, herbaceous communities contribute to high species richness (Roberts 2004), which usually persists because of the high rates of species turnover (Walker and Willig 1999), although it can decline rapidly if competition for resources in the soil occurs among the dominant species (Huston 1994, Pausas and Austin 2001). In a newly opened site, herbaceous communities can generate a large biomass in a few years, (Silvertown *et al.* 1994, Grace 1999), and marked differences in species composition can occur within them depending on the abiotic heterogeneity of the area being colonized (Gómez-Sal *et al.* 1986, Inouye *et al.* 1987, Pineda *et al.* 1987).

In addition, herbaceous communities can exhibit a wide variety of plant traits (McIntyre et al. 1995). The environmental conditions at a site influence the abundances of plant traits within communities (Montalvo *et al.* 1991, Rodríguez *et al.* 1997) and these abundances can change considerably even in the years immediately after disturbance (Pywell *et al.* 2003, Bonet and Pausas 2004). That is particularly true of plant traits associated with vegetation type, life history, and the geographic origin of the species (McIntyre *et al.* 1995, Tsuyuzaki y del Moral 1995). On the other hand, the species often use to show some associated traits that are rarely considered individually; rather, they are treated collectively as a "plant strategy" (Leishman and Westoby 1992).

Early successional changes in the herbaceous communities have been studied in a wide variety of habitats, including pastures affected by ploughing (Pineda *et al.* 1981, 1987, Gómez-Sal *et al.* 1986, Casado *et al.* 1988, Calvo *et al.* 2002), shrublands and forests affected by fire (Clemente *et al.* 1996, Guo 2001, Kazanis and Arianoutsou 2004), abandoned coppice stands (Gondard and Romane 2005) and old quarries (Khater *et al.* 2003) in the Mediterranean region, old fields (Inouye *et al.* 1987, Kosola and Gross 1999), old-growth (Frelich *et al.* 2003) and harvested forests (Elliott *et al.* 1997, Roberts and Zhu 2002, Howard and Lee 2003), plantations (Brockerhoff *et al.* 2003), abandoned mines (Holl 2002), mine spoils (Jochimsen 2001), and lava flows (del Moral and Wood 1988, Tsuyuzaki and Hase 2005) in temperate zones, and old fields (Aide and Cavelier 1994, Aide *et al.* 1995, Rivera *et al.* 2000), restored forests (de Souza and Batista 2004), areas affected by hurricanes (Chinea 1999), and volcanic eruptions (Whittaker *et al.* 1989, Bush and Whittaker 1995) in the tropics. In many studies of vegetation recovery on disturbed ground, however, herbaceous communities have received limited attention because of the difficulty of assessing successional patterns on them due to their high species turnover (Frelich *et al.* 2003, Small and McCarthy 2003).

Studies of the changes in herbaceous communities during early succession on landslides in the tropics are particularly rare (Lundgren 1978, Walker 1994, Restrepo and Vitousek 2001). Landslides exhibit high abiotic heterogeneity, and successional patterns in the upper or "erosional" zones, which are highly unstable and infertile, are completely different from the patterns in the lower or "depositional" zones, which are stable and fertile (Guariguata 1990, Myster and Fernández 1995, Francescato *et al.* 2001). For that reason, landslides are considered "patch-dynamics systems" (Pickett and White 1985, Myster and Walker 1997) and may be very useful for studying the effect of contingencies associated with geomorphological stability and fertility of substrates, and with landscape context, in the pathways of change of community features.

In this study, we examined the early successional changes in the herbaceous layer of a landslide that had high abiotic heterogeneity and is located in the Pacific region of Central America. The area is densely populated, and the formerly abundant tropical dry forests have been reduced dramatically by the effects of human disturbance (Janzen 1988, Gerhardt and Hytteborn 1992, Gillespie *et al.* 2000), and have became one of the most endangered and least well known ecosystems in the world (Janzen 1988, Gerhardt and Hytteborn 1992, Gillespie *et al.* 2000).

The principal objective of the study was to determine the major pathways of change in species richness, biomass, species composition, and abundance of plant traits in herbaceous communities on the landslide during the first four years following the disturbance. More specifically, we sought to determine whether patterns vary among the different areas of the landslide as defined by abiotic heterogeneity and landscape context, and to identify the factors influencing their main causes.

Specifically, we addressed the following questions: (i) How do richness, biomass, turnover rate, and species composition vary among the early years of succession and among areas of the landslide? (ii) What are the most abundant species? (iii) Within in the landslide, is it possible to differentiate groups of "plant strategies"? (iv) If yes, what are the most important plant traits that distinguish those groups? (v) How does the abundance of plant traits or plant strategies change over time and between areas of the landslide?

Methods

Study Area

The study area was a landslide on the Casita Volcano (12,41 N; 85,57 O), which is part of the "Maribios" volcanic range in western Nicaragua (**Fig. 1a**). The landslide, which was triggered by an exceptional rainfall event (500 mm in 24 h) on 30 October 1998, during Hurricane Mitch (Sheridan 1998), formed an enormous lahar at mid-slope (Kerle *et al.* 2003, Scott *et al.* 2005) that killed more than 2000 persons and displaced another 8000 (CEPAL 1999). With an altitude range of 150-1350 m a.s.l., and an area of 11.21 km^2, the Casita

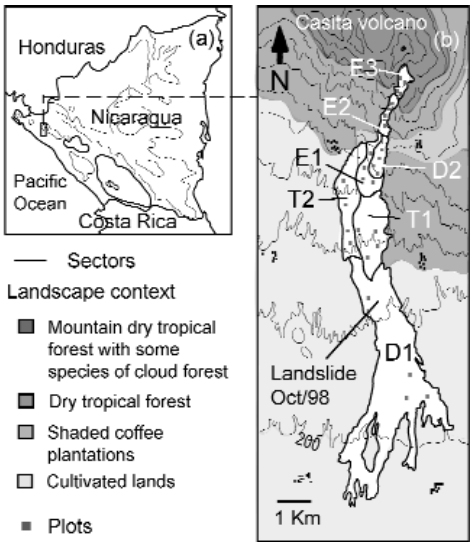

Figure 1. Study area. a) Location in Nicaragua. b) Detailed map of the landslide indicating the different sectors based on abiotic heterogeneity (fertility and geomorphologic stability) and the landscape context; erosional (E1, E2, E3), transitional (T1 and T2), and depositional (D1 and D2). The locations of sampling plots are indicated.

Volcano landslide is much larger than others studied in Central America and Caribbean region. In addition, the ecological and socioeconomic characteristics of the surrounding area are rather different (Velazquez and Gómez-Sal *submitted*). Mean annual rainfall (1250 mm/yr) is considerably lower and the dry season (November to April) is longer 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 [long-term average of hurricane strikes per year = 0.2 (Pielke *et al*. 2003)] and heavy rainfall events that trigger landslides is lower in western Nicaragua than it is in eastern Central America and on the Caribbean islands. In western Nicaragua, the population density [172

Habs/km^2 (INEC 2005)] and poverty levels [0.690 HDI (UNDP 2005)] are high, and local ecosystems have experienced substantial exploitation and reduction (Corrales-Rodríguez 1983), although large patches of relatively well-preserved forests remain. The structure and composition of the plant communities near the crater of the Casita Volcano are fairly similar 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 and are interspersed with scattered huts and small-holding lands at mid-slope. At the base of the volcano, cultivated lands dominate the landscape. Human disturbances, such as the clearcutting of forests and fire are common in the area (Corrales-Rodríguez 1983, Salas-Estrada 1999).

Fieldwork sampling

In 1999, two criteria were used to define seven major sectors (D1, D2, T1, T2, E1, E2, and E3) in the landslide (**Fig. 1b**). Based on their abiotic heterogeneity (fertility and geomorphological stability of substrates), the sectors included i) depositional zones in which formerly 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 erosional and depositional zones, where the former soil remained in small patches, only (T). Within the context of landscape, we distinguished among sectors that i) had cultivated lands along the edges (D1), ii) were enclosed by mountain tropical dry forests that had some of the plant species that are typical of cloud forests (E3), iii) had tropical dry forests along their edges (T1 and E2), iv) had shaded coffee plantations along their eastern border (E1 and D2), or v) had cultivated lands that dominated beyond their western border (T2). A group of remnant trees was present in the middle of D2, a depositional landing zone at mid-slope.

To document the early successional changes in each sector in the landslide, we collected data in four consecutive years (1999, 2000, 2001, and 2002). In 1999, detailed information on vegetation types and species composition was recorded. In 2000, a long-term permanent 10*10 m plot was established randomly in each of the seven sectors, and in 2001, an additional three plots were added (each designated by a letter, i.e., a, b, c, or d). Thus, in 2001 and 2002, the study included 28 plots (**Fig. 1b**). In each of three years (2000, 2001, and 2002), at the end of the rainy season (November to January), the herbaceous vegetation was surveyed within four quadrants positioned along the diagonal of each of the plots.

We recorded the number of species of herbs, grasses, ferns, and seedlings of woody plants ["low vegetation" (Benitez-Malvido 2006)], and measured the cover (%) and average height (cm) of each species. In addition, species' characteristics, such as shape, size and number of fruit, and the presence of fixation nodules were noted. That information, coupled with local knowledge and expert opinion, allowed us to identify a suite of plant traits or attributes for each species based on the most important categories of plant traits during early succession; vegetation type, life history, and geographic origin (Tsuyuzaki and del Moral 1995). Each trait was coded to "nominal multistate" and "binary" (presence/absence) classes (Leishman and Westoby 1992) (**Table 1**).

Within each plot, we measured the abiotic factors associated with the stability [elevation (m.a.s.l.), slope (%), stone cover (%), and mean

Table 1. Categories of plant traits and their classes, for the species recorded at the Casita Volcano landslide during the study period. Class type and number indicate how each attribute is coded for the analysis. Traits are grouped into three main categories: vegetative, life history, and geographic origin. Class types: B = binary (presence/ absence); NM = nominal multistate.

Categories/ Traits/ Classes	Class type
Vegetative	
Growth form [1]	NM 4
woody [2], graminoid [3], forb [4], fern	
Vegetative spreading mechanisms (rhizomes/stolons)	B
Morphology of the shoots [5]	NM3
Erects, vines, creeping shoots	
Life- history	
Longevity [6]	NM2
perennial, annual	
Nitrogen fixation	B
Resprouting ability [7]	B
Seed biology	
Dispersal mode [8]	
gravity, animal, wind	NM3
Geographic origin [9]	NM2
exotic, native	

[1] Based on the classes of Klinka *et al.* (1989); [2] Seedlings of woody species < 20 cm tall; [3] Grasses and grass-like plants, including sedges and rushes; [4] Non-graminoid herbaceous plants; [5] Based on Orshan´s 1982 "morphological characters"; [6] Based on Tsuyuzaki´s 1989 classes; [7] Based on Leishman & Westoby´s 1992 traits; [8] Based on Tsuyuzaki & del Moral´s 1995 classes; [9] Based on "Flora de Nicaragua" (2001).

diameter of stones (cm)] and fertility of substrates; nutrient content [amounts of NO3, P, and K (ppm)], and texture [proportions of sand, silt, and clay]. The last factors could be measured in 2002, only. To determine the amount of NO_3, P, and K, the 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. The cover (%) of the canopy of the woody layer was also estimated.

In the second (2000-01) and third (2001-02) periods of the study, human-induced disturbances occurred in the depositional and transitional sectors. They involved widespread, extensive removal of pioneer trees for firewood and the expansion of croplands (D1 and T1), and fires created by peasants living nearby that 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 (2001).

Statistical Analysis

To determine the direction of change (Bakker *et al.* 1996) in species richness and in biomass, for each sector and year of study, the mean number of species and mean total biovolume [height (m) * cover (m²)], respectively, were calculated. 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 calculate rates of change in species turnover, we used Sørensen´s Dissimilarity index (S) (Kent and Coker 1992). To assess changes in species composition, frequency distributions of the species present in the landslide were calculated, and ordination Analyses (DCA) were performed on abundance matrices (Avis and Lubke 1996) using all of the species in the inventory and those present in more than a 5%, a 10% and a 20% of the plots. The analysis that explained the highest amount of inertia including the largest number of species was selected, and the species that were included on it were defined as the most abundant in the landslide.

To detect groups of species that had suites of traits that could be used to define "plant strategies," the Bray-Curtis hierarchical clustering method was performed (Leishman and Westoby 1992, Tsuyuzaki and del Moral 1995) considering a Dissimilarity index = 0.6 within groups. To test for the effects of sector and year since disturbance on successional changes in community features, two-way ANOVA tests were used. To determine the main causes of change in each sector,

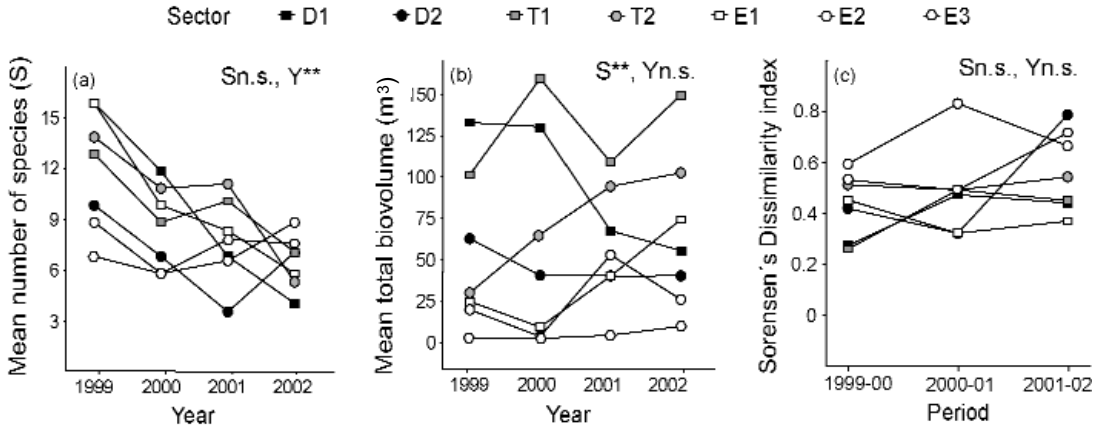

Figure 2. Changes in species richness, biovolume, and species turnover rate in each sector of the Casita Volcano landslide during the first four years after disturbance (landslide). The points indicate the mean number of species, the mean total biovolume, and the Sørensen´s dissimilarity index in each sector and in each year of the study. Asterisks indicate the statistical significance of two-way ANOVA tests for sector (S) and year (Y); * = $P < 0.05$, ** = $P < 0.001$, n.s.= not significant. Degrees of freedom are 3 for year and 6 for sector.

we calculated the Spearman rank correlation coefficients (r) between the mean number of species, the mean total biovolume, the coordinates in the Axis I and II of the ordination space and the abundance of each "plant strategy", and the environmental factors measured in each sector. When it was appropriate, variables were log- or box-cox transformed to achieve normality (Sokal and Rohlf 1995). In all of the multiple tests, the Sequential Rice Correction (Rice 1989) was applied. Clustering, ANOVAS, and Spearman rank correlations were performed using STATISTICA software (Statsoft 2001). Ordination Analyses were performed using CANOCO (ter Braak and Smilauer 2002).

Results

Changes in species richness, biovolume, and turnover rates

Over the life of the study, species richness clearly decreased in the depositional and transitional sectors, and in the E1 sector, but remained unchanged in sectors E2 and E3 (**Fig. 2a**). Although the decline in richness was especially pronounced in D1, it increased slightly in D2 between 2001 and 2002. Changes in richness differed significantly between years ($F_3 = 8.36$, $P < 0.001$) and between sectors ($F_6 = 2.02$, $P < 0.05$). During the four years of the study, changes in biovolume differed significantly between sectors, only ($F_6 = 7.97$, $P < 0.001$). Biovolume decreased in the depositional sectors and increased in the erosional sectors (**Fig. 2b**). The transitional and the erosional sectors had the highest and the smallest biovolumes of the landslide, respectively. Over the course of the 4-yr study, species turnover rates increased slightly and differed significantly neither between sectors nor between years, although they were especially highest in sectors E2 and E3 (**Fig. 2c**).

Changes in species composition

The majority of the plant species were present in < 5% of the plots (**Fig. 3**). The DCA that included all of the species did not reveal clear trends in species composition, and its explanatory power was very low (< 10% of inertia explained in Axis I) (results not shown). The DCA that included only the species that appeared in >20% of the plots was finally selected (**Fig. 4**) because it had reasonably high percentage of inertia explained and, although it excluded a large number of species (71 of 83), these species were not important in determining the overall changes in species composition. The main changes in species composition of plots from one year to the next were not strongly reflected along Axis I. Changes in plot scores in Axis I differed significantly between sectors (F_6 = 11.57, P < 0.001).

Among the erosional sectors, the plots of E2 and E3 exhibited long trajectories between all of the years of the study, and the plots of E1 between the first three years, only. The abundance of *Sporobolus indicus* and *Zornia thymifolia* increased in the plots of E3 and E2, and those of *Clitoria ternatea*, *Hypharrenia rufa*, and *Pityrogramma calomalanos* increased in the plots of E2 and E1. The abundance of *C. ternatea* increased significantly in E1, and covered > 50% of plots E1b and E1c in 2002. In the transitional sectors, at the beginning of the study, *C. mucunoides* was dominant in all of the plots but, over the life of the study, the abundance of *S. pruriens* and *T. rotundifolia* increased significantly. Three of the plots exhibited clear convergent trajectories towards a high abundance of *H. rufa*. In the depositional sectors, species such as *C. mucunoides* and *Galactia striata* became dominant early in the study.

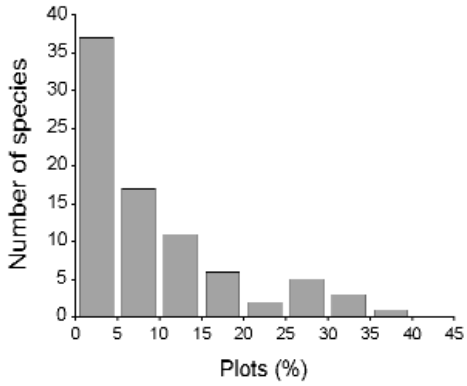

Figure 3. Histogram of the frequency distributions of the species present in the landslide on the Casita Volcano, Nicaragua.

The 12 species that occurred in > 20% of the inventories were considered the most abundant species in the landslide (**Table 2**). Most of those species developed a large cover and were wind-dispersed graminoids and forbs of exotic origin.

Changes in plant strategies

In the herbaceous layer of the landslide, the majority of the species were dispersed by wind and exotic, therefore, "Dispersal mode" and "Geographic origin" were not used in defining groups of plant strategies. The Bray-Curtis cluster analysis revealed six species groups considering a dissimilarity index = 0.6. "Growth form" and "Longevity" were the most important plant traits for distinguishing among the groups. Group 1 included 26 graminoids and 1 fern that have rhizomes or stolons. Although the majority of it species were annuals, the most characteristic species of this group, *H. rufa* and *S. indicus*, were perennial grasses. Furthermore, both species were very abundant in the landslide. Group 2 contained 14 annual

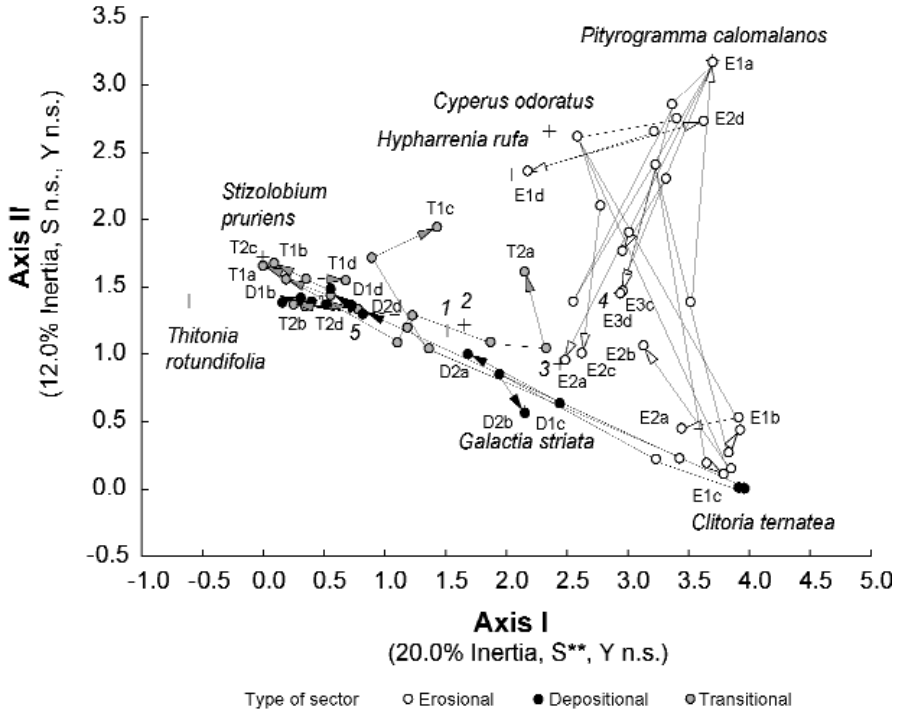

Figure 4. DCA scores of the plots surveyed from 1999 to 2002 on the Casita Volcano landslide, Nicaragua. Species present in >20% of the inventories were used in the analysis. The points represent the species composition of each plot in the four years of the study (1999, 2000, 2001, and 2002). Lines represent changes in the species composition of the plots located within each sector in each year. The lines that correspond to the last year (2001-2002) end with an arrow, and the names of the plots are indicated at the ends of the arrows. Crosses represent the species that were present in more than a 20% of the inventories. The names of that species are indicated, with the exception of some that are indicated by numbers; *Mimosa pudica* (1), *Chamaecrista nictitans* (2), *Zornia thymifolia* (3), *Sporobolus indicus* (4) and *Calopogonium mucunoides* (5).

forbs, including some abundant species of vines, such as *C. mucunoides*, *S. pruriens*, and *G. striata*. Six species of perennial forbs constituted Group 3. Group 4 included most (20) of the seedling species and Group 5 contained six seedling species that are able to fix N_2. Group 6 included four perennial forbs that can fix N_2, such as the abundant species *C. ternatea* and *Z. thymifolia*.

Based on their abundance (mean total cover) in the landslide, the most important plant strategies were, in order of importance, annual forbs (Group 2), graminoids (Group 1), and Perennial N_2-fixing forbs (Group 3) (**Fig. 5**). Abundance of annual forbs differed significantly between sectors (F_6 = 20.82, P << 0.001) and decreased during the period of study. This group was abundant in the transitional sectors. Abundance of graminoids differed significantly between sectors (F_6 = 9.10, P << 0.001) and increased significantly during the period of study. This group predominated in the transitional and erosional sectors.

Table 2. Species present in >20% of the inventories in the Casita Volcano landslide during the first four years after disturbance. Number of plots in which they were recorded, total cover in the landslide (m^2), and their plant traits.

Species	Nº of plots	Total cover (m^2)	G. form	Veg. spr.	Morph.	Long.	N_2 fix.	Res.	Disp.	Geog.
Calopogonium mucunoides	14	1249.2	forb	no	vine	annual	no	yes	wind	exotic
Chamaecrista nictitans	11	198	"	no	erect	"	"	"	"	"
Clitoria ternatea	13	665.1	"	yes	creep.	per.	yes	"	"	"
Cyperus odoratus	8	26.8	gram.	no	erect	"	no	no	"	"
Galactia striata	13	242.4	forb	no	vine	annual	yes	"	"	"
Hypharrenia rufa	14	365.9	gram.	yes	erect	per.	no	yes	"	"
Mimosa pudica	8	47.3	forb	no	"	annual	yes	no	"	"
Pityrogramma calomalanos	10	131.4	fern	yes	"	per.	no	"	"	native
Sporobolus indicus	11	66.7	gram.	yes	"	"	"	"	"	exotic
Stizolobium pruriens	7	673.8	forb	no	vine	annual	yes	yes	"	"
Thitonia rotundifolia	10	284.4	"	no	erect	"	no	"	"	"
Zornia thymifolia	12	380.2	"	yes	"	per.	yes	"	"	native

Abbreviations: G. form = Growth form, Veg. spr. = Vegetative spreading mechanisms, Morph. = Morphology of the shoots, Long. = Longevity, N_2 fix. = Ability to fix N_2, Res. = Resprouting ability, Disp. = Dispersal mode, Geog. = Geographic origin, gram. = graminoid, creep. = creeping -shoots, per. = perennial.

Abundance of Perennial N_2-fixing forbs (F_6 = 2.61, $P < 0.05$) also differed significantly between sectors. The abundance of this group fluctuated during the four years of the study in the depositional and transitional sectors but, in the erosional sectors increased significantly between 2000 and 2002. Changes in the abundances of seedlings (Group 4) and N_2-fixing seedlings (Group 5) differed significantly between sectors (F_6 = 3.70, $P < 0.05$) and (F_6 = 3.14, $P < 0.05$). These groups were abundant in the erosional and the depositional sectors, respectively. Changes in the abundances of seedlings differed significantly also among years (F_3 = 5.96, $P < 0.001$).

Causes of change

Generally, the correlations between community features and environmental factors were weak. In the depositional sectors, changes in species composition (plot scores in Axis I) were strongly and positively correlated with elevation (r = 0.67, $P < 0.006$), and changes in the abundance of Perennial forbs were strongly and negatively correlated with total woody cover (r = - 0.62, $P < 0.006$). In the erosional sectors, biovolume, and abundances of graminoids and perennial forbs were strongly and positively correlated (r = - 0.65, r = - 0.63, and r = 0.57, respectively, all $P < 0.002$) with elevation. In the transitional sectors, change in richness was strongly and negatively correlated with NO_3 (r = - 0.74, $P < 0.001$), K (r = - 0.75, $P < 0.001$), and P (r = - 0.76, $P < 0.001$) contents.

Discussion

Environmental heterogeneity and general changes in community features

In the first four years after disturbance, changes in species richness, biomass, species composition, and abundances of plant strategies in the herbaceous communities of the Casita Volcano landslide, differed significantly among the areas within the landslide defined by abiotic heterogeneity and landscape context. However, although environmental hetero-

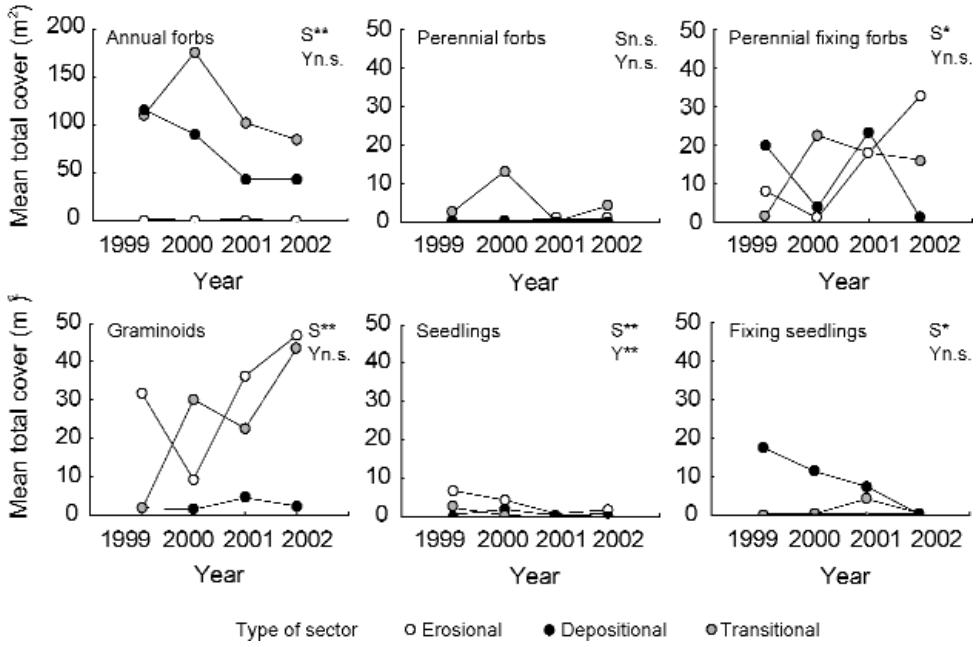

Figure 5. Changes in plant strategies in each type of sector of the Casita Volcano landslide during the first four years after disturbance. The points indicate the mean total cover in each type of sector and in each year. Asterisks indicate the statistical significance of the two-way ANOVA tests for sector (S) and year (Y); * = $P < 0.05$, ** = $P < 0.001$, n.s.= not significant. Degrees of freedom are 3 for year and 6 for sector.

geneity played a major role in the early succession of the herbaceous layer, only species richness and the abundances of some plant strategies differed significantly among the four years of the study. Generally, the correlations between community features and environmental factors were weak. As in other studies, those results highlight the difficulties in identifying distinct patterns and causes of successional changes in herbaceous communities, especially in early years after disturbance (Frelich *et al.* 2003).

Changes in species richness and biomass

In the Casita Volcano landslide, not only did species richness decline in the stable and fertile areas (sectors) of the landslide, it declined in the transitional areas and in one of the unstable and infertile areas examined in our study. The pronounced decline in the richness of the stable and fertile areas might have been caused by the competitive elimination of the opportunistic shade-intolerant species that colonized the areas just after the disturbance in 1998. Most of those species disappeared while others, such as *C. mucunoides*, increased their dominance. At the same time, the late-succession species were not yet well established in the area. Similar patterns are apparent in the herbaceous communities that colonize forest stands after clearcutting (Elliott *et al.* 1997), abandoned groves (Gondard and Romane 2005), and old-fields (Kosola and

Gross 1999, Howard and Lee 2003) of temperate regions.

In the last year of our study, however, species richness increased in sector D2. In that sector, which had higher species richness and a higher percentage of canopy cover than did D1, in the woody layer (Velázquez and Gómez-Sal *submitted*), some of the species commonly found in the understory of the local forests (e.g., *Oplismenum burmanii*) appeared in 2001. Those results suggest that the higher species richness and the greater canopy cover of the woody layer in D2 promoted colonization by species that normally appear in the understory of the local forests, which lead to an increase in richness of the herbaceous communities in the last year of the study. A decline in the abundance of light-demanding pioneer species, and a subsequent increase in the number of shade-tolerant species adapted to forest environments has shown to be higher in the understory of indigenous forests that have high species richness, than in plantations (Brockerhoff *et al.* 2003) and forests that have fewer species (Chinea 1999).

In the transitional sectors of the Casita Volcano landslide, species richness probably decreased over time because of the increase in the abundance of species such as *H. rufa*, *T. rotundifolia*, and *S. pruriens*, which are perennial or can develop a large biomass and, thereby, preclude the germination and establishment of other species. That has occurred in Mediterranean pastures in the first few years after ploughing (Pineda *et al.* 1981, de Pablo *et al.* 1982, Gómez-Sal *et al.* 1986, Casado *et al.* 1988, Calvo *et al.* 2002) and after a fire (Clemente *et al.* 1996). The spatiotemporal changes in the species richness of the transitional sectors were strongly negatively correlated with the nutrient content of the soil, which suggests that the extent of the decline in richness can vary depending on subtle differences in the fertility of plots.

In contrast to the pattern observed in most of the sectors of the Casita Volcano landslide, species richness remained unchanged in the erosional sectors E2 and E3, which exhibited the highest rates of species turnover in the landslide. Forests surrounded E2 and E3, where seed rain was probably high, causing a continuous arrival of herbaceous species. However, those sectors had steep slopes, and erosion probably impeded the germination and establishment of many of the propagules, provoking a steady loss of species and a high rate of species turnover. During early succession in highly unstable, disturbed sites, typically, changes in richness in herbaceous communities do not occur due to high rates of species turnover (Walker y Willig 1999). In the area affected by the eruption of Mount St. Helens (USA), species richness remained unchanged because of the high inhibition of plant germination and establishment caused by erosion and the low availability of resources in substrates (del Moral and Wood 1988). Unlike E2 and E3, in E1, which was not surrounded by forests and the slope was less steep, richness decreased strongly and steadily over time. Earlier, that sector was colonized by perennial species, such as *C. ternatea* and *H. rufa*, which became dominant in 2001 and led to a low turnover and little change during the third period of our study (2001-2002).

Although biomass did not differ significantly among the years of our study, it varied significantly among the sectors of the landslide, and the transitional sectors had the highest values. On the other hand, it highly increased in the

erosional sectors. During early succession in highly unstable and infertile sites, herbaceous communities usually develop a large biomass (Walker 1994, Bush and Whittaker 1995, Holl 2002, Walker and del Moral 2003), but they do not in stable and fertile areas where pioneer trees and shrubs have a large cover (Ovalle *et al.* 2006). Herbaceous biomass can be high in tropical old fields, where the woody layer is sparse (Aide and Cavelier 1994, Aide *et al.* 1995, Rivera *et al.* 2000, de Souza and Batista 2004). This idea suggests that the transitional sectors experienced the highest biomass accumulation in the landslide because of their high fertility relative to the more unstable and infertile sectors, and their lesser development of the woody layer relative to the stable and fertile sectors.

Changes in species composition and abundance of plant traits

In the Casita Volcano landslide, changes in species composition differed significantly between the different areas of the landslide and were strongly influenced by a few abundant species (*C. ternatea*, *Z. thymifolia*, *H. rufa*, *S. indicus*, *S. pruriens*, *T. rotundifolia*, *C. mucunoides*, and *G. striata*). Similar to other landslides in the tropics (Lundgren 1978, Restrepo and Vitousek 2001), the landslide on Casita Volcano was colonized mainly by "exotic" and "wind-dispersed" species. Furthermore, as in previous studies (McIntyre *et al.* 1995, Guo 2001, Kazanis and Arianoutsou 2004), the most important traits for distinguishing groups of plant strategies were those associated with growth form and longevity. Although annual species dominated in the landslide on Casita Volcano, as has occurred in Mediterranean pastures (Gómez-Sal *et al.* 1986) and in some abandoned mines (Khater *et al.* 2003, Gosling 2005), their abundance decreased, whereas the abundance of perennial species increased during our 4-yr study. That has occurred in the pioneer herbaceous communities of old fields (Casado *et al.* 1988), coppice stands (Gondard and Romane 2005), abandoned mines (Holl 2002), mine spoils (Jochimsen 2001), and lava flows (Tsuyuzaki and del Moral 1995, Tsuyuzaki and Hase 2005) in temperate regions, and in other tropical areas affected by volcanic eruptions (Whittaker *et al.* 1989) and landslides (Walker 1994). In the Casita Volcano landslide, at least, the different sectors of the landslide were dominated by different groups of plant strategies and some of the most abundant species were characteristic of these groups.

In our study, the unstable and infertile areas were dominated by Perennial N_2-fixing forbs and by graminoids, which has been reported in other studies (Weaver 1990, Olander *et al.* 1998, Tsuyuzaki and Hase 2005). The most abundant Perennial N_2-fixing forb, *C. ternatea*, which can propagate vegetatively, formed patches that rapidly enlarged and combined to develop dense ground-level herbaceous thickets (personal observation). That phenomenon has been described for other species during early succession on highly unstable and infertile habitats (Walker 1994, Bush and Whittaker 1995, Tsuyuzaki and del Moral 1995, Zhou *et al.* 2003). Herbaceous thickets can arrest succession by impeding the establishment of woody seedlings (Walker 1994, Zhou *et al.* 2003), but they can be important in soil amelioration and stabilization, thereby promoting germination of later colonists (Walker 1994, Bush and Whittaker 1995, Tsuyuzaki and del Moral 1995). Although *C. ternatea* is probably precluding the colonization by woody plants, it might have a long-term positive effect on succession,

not only by improving the nutrient content of substrates, but by stabilizing them (this species have creeping shoots). Furthermore, in the area of the Casita Volcano, where rainfall and the decomposition of organic matter are low, surface amelioration is particularly important, and the capacity to fix atmospheric nitrogen appears to be an important attribute of these thickets.

In our study, *H. rufa*, an exotic perennial grass that is an aggressive colonizer in Central America (Daubenmire 1972), was the most abundant graminoid, and it dominated the erosional and the transitional sectors of landslide. During the third year of our study, the abundance of *H. rufa* increased, and manmade fires on the cultivated lands nearby spread into the transitional sectors. The presence of invasive grasses affects strongly the pattern in which fire spreads (Mistry and Berardi 2005). In addition to being a highly pyrophytic species, *H. rufa* has a strong post-fire resprouting ability, which promotes grass-fire cycles by which it becomes progressively more abundant (D´Antonio and Vitousek 1992). This suggests the existence of a positive feedback between the presence of *Hypharrenia* and fire in the transitional sectors of the landslide. Moreover, in the landslide, *H. rufa* appeared at higher elevations than it normally occupies in the study area, which suggests that the landslide, like roads (Olander *et al.* 1998), might act as a vector for the dispersal of exotic species onto the upper slopes of the volcano, which indicates that frequency of fires might increase in the upper zones of the landslide and in the upper slopes of the volcano.

In the Casita Volcano landslide, *C. mucunoides* and *S. pruriens* were the most abundant annual forbs in the transitional sectors. Those species are vines, and they developed a large cover. Vines are important in succession and, as in other systems (Bush and Whittaker 1995), in the landslide of the Casita Volcano, they might play an important role in the accumulation of soil organic matter.

In the entire Casita Volcano landslide, the decrease in the abundance of woody seedlings suggests low recruitment by pioneer trees and shrub, however, that normally occurs when the nearest sources of propagules are distant (de Souza y Batista 2004), which was not the case on Casita Volcano. The significant decline in the abundance of woody seedlings might have been caused by the rapid growth of the seedlings of light-demanding pioneer species that arrived just after the landslide. Those plants reached a large height in a few years (personal observation), and became part of the woody layer when seedlings of the trees typical of the adjacent forests were not well established in the landslide.

Concluding remarks

The significant influence of environmental heterogeneity on the early successional changes of the herbaceous communities on the landslide of Casita Volcano, Nicaragua, was undeniable. However, distinct patterns of change over time only occurred in species richness, which decreased in the majority of the sectors because of the expansion of a few dominant species that were able to develop a large cover and exclude other species. In addition, those species caused the main changes in species composition and were characteristic of the different groups of plant strategies identified in the study. Most of them became dominant early in the different areas of the landslide. Our results suggest that Perennial N_2-

fixing forbs, e.g., *C. ternatea*, graminoids that have rhizomes or stolons, e.g., *H. rufa*, and annual forbs, e.g., *C. mucunoides*, are very important in the early succession of herbaceous communities on large landslides in highly humanized areas that have a tropical dry climate. Those species might arrest succession, contribute to the stabilization and amelioration of substrates, or increase the frequency of human-induced disturbances by promoting grass-fire cycles. The results of this study permit predictions for the long-term successional trends in the landslide, and they are useful in developing future research on the mechanisms and interactions during early succession. In addition, they might aid in the development of ecosystem restoration and rehabilitation programs for the poorly understood and endangered tropical dry forests of Central America.

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