

## Capítulo 6

### Cambios en los patrones espaciales durante la sucesión temprana en un deslizamiento

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Velázquez, E., de la Cruz, M. and Gómez-Sal, A. *In preparation*. Shifts in spatial patterns during early succession in a landslide. *Journal of Vegetation Science*.

#### Resumen

**Preguntas:** 1. ¿Cambia el patrón espacial general de colonización respecto al tiempo y entre las distintas áreas del deslizamiento? 2. ¿Cambian los patrones espaciales de colonización de las especies pioneras dominantes respecto al tiempo y entre las distintas áreas del deslizamiento? 3. ¿Existen cambios en los patrones espaciales de germinación y mortalidad? 4. ¿Difieren las interacciones intra- e inter-específicas entre las distintas áreas del deslizamiento?

**Localización:** Un deslizamiento de gran tamaño y enormemente heterogéneo (Volcán Casita, Nicaragua).

**Métodos:** Se llevaron a cabo análisis de patrones de puntos mediante el uso de las funciones de densidad univariadas de la  $K(t)$  de Ripley y la  $J(t)$  de Van Lieshout y Baddeley bajo un modelo nulo de tipo CSR ("completa azarosidad espacial" según sus siglas en inglés), y extensiones bivariadas de estas funciones bajo modelos nulos de independencia y etiquetado al azar.

**Resultados:** El patrón espacial general de colonización cambió sustancialmente durante la sucesión temprana, variando de la misma forma en la que lo hicieron los patrones espaciales de las especies pioneras dominantes. La agregación aumentó en las áreas inestables e infértiles del deslizamiento debido a la heterogeneidad abiótica de las mismas, y la regularidad aumentó en las áreas más estables y fértiles debido a la ocurrencia de interacciones negativas según los postulados de la Hipótesis de Mortalidad no-azarosa. Existió competición inter-específica entre los individuos de *Muntingia calabura* y *Trema micrantha*, y competición intra-específica entre los individuos de *T. micrantha*. La naturaleza de las interacciones cambió entre las diferentes áreas del deslizamiento. La presencia agregación estuvo fuertemente influenciada por las perturbaciones humanas, especialmente el fuego.

**Conclusiones:** La estabilidad geomorfológica y la fertilidad de los sustratos, así como la presencia de perturbaciones humanas, determinaron los cambios espacio-temporales en el patrón de colonización, y la naturaleza y la intensidad de las interacciones entre plantas vecinas.



## Shifts in spatial patterns during early succession in a landslide

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### Abstract

**Questions:** 1. Do the general spatial patterns of early colonization change over time and differ among the areas of the landslide? 2. Do the spatial patterns of the dominant pioneer species change over time and differ among the areas of the landslide? 3. Are there changes on the spatial patterns of germination and mortality? 4. Do the intra- and inter-specific interactions differ among the areas of the landslide?

**Location:** A large, highly heterogeneous landslide (Casita Volcano, Nicaragua).

**Methods:** We performed point patterns analyses using univariate Ripley's  $K(t)$  and Van Lieshout and Baddeley's  $J(t)$  density functions under a null model of CSR (Complete Spatial Randomness), and bivariate extensions of these functions under null models of independence and random labelling.

**Results:** The general spatial pattern of colonization changed substantially during early succession, and varied in the same way as the spatial patterns of the dominant pioneer species. Aggregation increased in the unstable and infertile areas of landslide because of abiotic heterogeneity, and regularity increased in the most stable and fertile areas of landslide because of the occurrence of negative interactions, as predicted by the Non-random Mortality Hypothesis. Inter-specific competition existed between *Muntingia calabura* and *Trema micrantha*, and intra-specific competition occurred among individuals of *T. micrantha*. The nature of the interactions shifted among the different areas of the landslide. Presence of aggregation was strongly influenced by human-induced disturbances, especially fire.

**Conclusions:** Geomorphological stability and fertility of substrates, and presence of human disturbances, dictated spatiotemporal changes in colonization pattern, and the nature and intensity of interactions between neighbouring plants.

**Keywords:** Abiotic heterogeneity, competition, disturbances, *Trema*, *Muntingia*, *Wigandia*.

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

### Introduction

Due to the sessile nature of plants, the spatial patterns of plant communities are influenced by many processes, including seed dispersal, intra- and inter-specific competition, facilitation, disturbance, and herbivory (Wiegand and Moloney 2004, de la Cruz 2006). Despite the

difficulties associated with pattern-process inference (Stoyan and Penttinen 2000), increasingly, spatial pattern analyses are used by ecologists to generate testable hypothesis about the mechanisms that determine the structure of vegetation (Skarpe 1991, Levin 1992, Barot *et al.* 1999, Dale 1999, Jeltsch *et al.* 1999, Camarero *et al.* 2000, He and

Duncan 2000). In addition, those analyses may provide significant insights into the main causes and mechanisms of successional change in plant communities (Lookingbill and Zavala 2000).

To date, only a few of the studies of spatial patterns in plant communities have concerned more than a single point in time (Peterson and Squiers 1995, Zhang and Skarpe 1995, Malkinson *et al.* 2003). Some believe that a general shift toward regularity is expected during succession, (Greigh-Smith 1952, Antonovics and Levin 1980), yet spatial patterns often exhibit large variations in space and time during early succession because of differences in seed dispersion, competition and environmental heterogeneity (Stoyan and Penttinen 2000). Often, changes usually are influenced by the fertility (nutrient content and texture of soils) and stability (in the context of geomorphology) of sites, and by the effects of disturbance during succession. In fertile and stable sites, regularity increases, but in highly infertile sites (Wells and Getis 1999, Schenk *et al.* 2003) or sites affected by disturbance (Rebertus *et al.* 1989), aggregated patterns appear early and tend to persist.

Spatial and temporal shifts in spatial patterns are strongly influenced by the underlying and changing interactions between individuals within plant communities (Malkinson *et al.* 2003). Although negative interactions (intra- and inter-specific competition) occur in many types of habitats (Goldberg *et al.* 1999), they are found most often in high-density stands existing in the favourable conditions of fertile and geomorphologically stable sites. In those environments, resource acquisition is rapid and the mortality of adults and saplings increases in the proximity of neighbours, which

enhances the development of regular patterns (Aldrich *et al.* 2003). This process is predicted by the Non-random or Density-dependent Mortality Hypothesis (Leps and Kindlman 1987, Kenkel 1988, Chapin *et al.* 1989). In contrast, positive interactions (i.e. facilitation) mainly occur between colonizers on highly infertile and unstable sites (Hunter and Aarssen 1988, Bertness and Callaway 1994). In those zones, typically, the mortality of saplings decreases in the proximity of adults because of improvements in micro-climatic conditions, soil texture or nutrient content, and water-holding capacity (Hunter and Aarssen 1988, Callaway and Walker 1997, Brooker and Callaghan 1998), which favours the progressive clumping of individuals and leads to aggregated patterns (Wiegand and Moloney 2004). This process is referred to as the Nurse-plant Syndrome (Callaway 1995).

The relative importance of negative and positive interactions can change over time, and specifically, if the intensity of competition increases during succession, spatial patterns will become increasingly regular (Malkinson *et al.* 2003).

In this article, we examined the spatial patterns of pioneer communities in a landslide on Casita Volcano, Nicaragua, during the first few years after the disturbance. The landslide exhibited high heterogeneity and a wide range of contingencies for vegetation recovery. In general, the upper (erosional) and lower (depositional) areas of landslides differ significantly in fertility and stability (in relation to geomorphology). In the erosional zone, the original soil and vegetation are removed entirely and, often, bedrock is exposed. The depositional zone has a rich "biological legacy" that consists of the original soils and heterogeneous

mixtures of broken plant parts, seeds, organic matter and rock fragments that have come from the upper zone (Guariguata 1990, Walker *et al.* 1996). The Casita Volcano landslide was very large, and had high abiotic heterogeneity, "transitional" areas between the erosional and the depositional zones, and depositional areas at mid-slope (Velazquez and Gómez-Sal *submitted*). In addition to the importance of the conditions within the landslide, the surrounding area was a highly heterogeneous landscape and had a high degree of human-induced disturbances, such as resource extraction, burning, clearcutting, and urban sprawl (Salas-Estrada 1999, Gillespie *et al.* 2000), and the landscape context influence the availability of propagules and is an additional source of contingency for early succession.

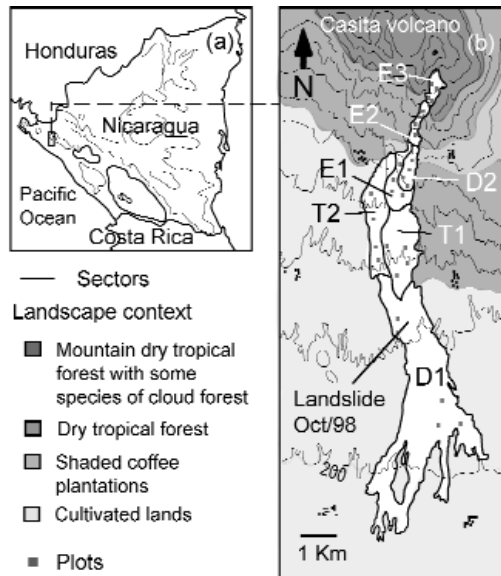
The main objective of this study was to analyze the colonization process and assess the presence of interactions in the pioneer communities at three levels: (1) among individuals irrespective of their taxonomic identity ("species"), (2) within species, and (3) between pairs of the most abundant pioneer species. The study was conducted during three years of early succession and considered not only the evolution of patterns over time, but the variations among the different areas of the landslide. The study also compared the performance of several methods of point pattern analysis. Specifically, we addressed the following questions: 1) Do the general spatial patterns of early colonization change over time and differ among areas of the landslide based on abiotic heterogeneity and landscape context? 2) Do the spatial patterns of the dominant pioneer species change over time and differ among the areas of the landslide? 3) Are there changes in the spatial patterns of germination and mortality? 4) Do the intra- and inter-specific interactions differ among the areas of the landslide?

## Methods

### Study area

This study was conducted on a landslide situated in the Casita Volcano (12,41 N; 85,57 O), which is part of the "Maribios" volcanic range of 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, Kerle *et al.* 2003), moved down 2.000.000 m<sup>3</sup> of highly fractured material which rapidly formed an enormous lahar at mid-slope (Kerle 2002). The lahar devastated the two largest villages at the base of the volcano. More than 2000 people died and 8000 were displaced as a consequence of the event (CEPAL 1999). With an altitude range of 150-1350 m.a.s.l., and an area of 11.21 km<sup>2</sup>, the Casita Volcano landslide is much larger than others studied in Central America and the Caribbean region. In addition, the ecological and socioeconomic characteristics of the surrounding region are rather different than those at other landslides that have been studied (Velázquez 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 and heavy rainfall events that trigger landslides, is lower [long-term average of hurricane strikes per year = 0.2 (Pielke *et al.* 2003)]. In western Nicaragua, the population density [172 Habs/km<sup>2</sup> (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



**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.

relatively well-preserved forests remain in the upper part of Casita Volcano (Salas-Estrada 1999). Those forests have been partially converted into "shaded" coffee plantations at mid-slope and farther down they are interspersed with small-holding lands and scattered huts. Human disturbance are common in this area. These include clearance of forest fragments for firewood extraction and expansion of crops (Salas-Estrada 1999), and fire (Corrales-Rodríguez 1983), which is mainly used by peasants as an agricultural practice to remove stubble (December) or to prepare land for sowing (May and August) (P. Dávila, personal communication). At the base of the volcano, the landscape is dominated by large real estates that grow sugar cane, sorghum or peanuts.

### 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**) (**Table 1**). Based on their abiotic heterogeneity (fertility and geomorphological stability of substrates), the sectors included; i) stable depositional zones in which formerly agricultural or forest soil remained after the landslide (D), ii) unstable 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). In relation to landscape context, 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), and v) had cultivated lands that dominated beyond their western border (T2). A group of remnant trees appeared in the middle of D2. It is important to notice the large standard deviations showed by abiotic factors in the erosional and the depositional sectors that indicate large variations in edaphic conditions within them (**Table 1**)

In 2000, in each of the seven sectors, a long-term permanent 10\*10 m plot was established randomly and, in 2001, an additional three plots were added to each sector. Thus, in 2001 and 2002, the study included 28 plots. In each of the three years, at the end of the rainy season (October to December), within each plot, we mapped to the nearest centimetre the position of all of the woody stems. In 2000, 2001, and 2002, respectively, one, four, and four stem maps were generated for each sector (in

**Table 1.** Characterization of the different areas (sectors) in the landslide according to abiotic factors and presence of disturbances. Mean is at the top of the cells and Standard Deviation, in italics, is below. Asterisks show the statistical significance for each variable in the Kruskal-Wallis test.  $H > \chi^2$  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 <sub>3</sub> ** (ppm)	K** (ppm)	P** (ppm)	Sand* (%)	Silt* (%)	Clay** (%)		
D1	CL	262.5 <sup>a</sup>	6 <sup>a</sup>	5 <sup>a</sup>	4.75 <sup>a</sup>	15.20 <sup>a</sup>	129.91 <sup>ab</sup>	55.9 <sup>a</sup>	72.34 <sup>a</sup>	9.35 <sup>a</sup>	20.52 <sup>a</sup>	Clear.	
		<i>43.37</i>	<i>2.16</i>	<i>2.04</i>	<i>3.57</i>	<i>1.86</i>	<i>13.98</i>	<i>5.09</i>	<i>1.76</i>	<i>1.09</i>	<i>2.80</i>		
D2	DTF, SC	649.5 <sup>b</sup>	5.75 <sup>a</sup>	38.50 <sup>b</sup>	11.18 <sup>ba</sup>	28.50 <sup>d</sup>	139.37 <sup>a</sup>	72.57 <sup>b</sup>	61.73 <sup>b</sup>	7.70 <sup>b</sup>	30.52 <sup>b</sup>	-	
		<i>43.43</i>	<i>1.07</i>	<i>15.80</i>	<i>4.24</i>	<i>8.93</i>	<i>13.32</i>	<i>6.21</i>	<i>5.32</i>	<i>2.7</i>	<i>3.78</i>		
T1	DTF	403.75 <sup>c</sup>	8.5 <sup>ba</sup>	33.75 <sup>b</sup>	10.23 <sup>a</sup>	10.12 <sup>ab</sup>	125.75 <sup>b</sup>	72.52 <sup>b</sup>	71.36 <sup>a</sup>	7.75 <sup>b</sup>	19.56 <sup>a</sup>	Clear.	
		<i>19.65</i>	<i>2.64</i>	<i>24.70</i>	<i>7.29</i>	<i>4.01</i>	<i>11.01</i>	<i>7.01</i>	<i>4.25</i>	<i>1.22</i>	<i>3.72</i>		
T2	CL	459.50 <sup>c</sup>	14.25 <sup>b</sup>	21.87 <sup>b</sup>	29.21 <sup>c</sup>	6.9 <sup>bc</sup>	93.52 <sup>bc</sup>	60.07 <sup>a</sup>	78.48 <sup>a</sup>	4.73 <sup>c</sup>	13.74 <sup>c</sup>	Burn.	
		<i>46.82</i>	<i>2.21</i>	<i>8.00</i>	<i>8.92</i>	<i>2.33</i>	<i>8.73</i>	<i>5.34</i>	<i>3.89</i>	<i>1.56</i>	<i>1.90</i>		
E1	DTF, SC	562.50 <sup>bc</sup>	26.50 <sup>c</sup>	88.75 <sup>c</sup>	27.33 <sup>c</sup>	4.7 <sup>c</sup>	66.37 <sup>d</sup>	5.15 <sup>c</sup>	64.60 <sup>b</sup>	9.53 <sup>a</sup>	26.68 <sup>b</sup>	-	
		<i>12.28</i>	<i>5.32</i>	<i>6.29</i>	<i>4.35</i>	<i>1.34</i>	<i>12.59</i>	<i>1.15</i>	<i>8.27</i>	<i>1.73</i>	<i>6.97</i>		
E2	DTF	849.5 <sup>d</sup>	59 <sup>d</sup>	91.87 <sup>c</sup>	17.14 <sup>b</sup>	5.42 <sup>c</sup>	87.40 <sup>c</sup>	37.42 <sup>c</sup>	76.57 <sup>a</sup>	7.06 <sup>b</sup>	15.62 <sup>c</sup>	-	
		<i>58.35</i>	<i>6.73</i>	<i>5.54</i>	<i>6.88</i>	<i>1.14</i>	<i>8.21</i>	<i>5.57</i>	<i>5.73</i>	<i>2.26</i>	<i>3.10</i>		
E3	DTF - CF	1086.25 <sup>d</sup>	40.75 <sup>d</sup>	97.50 <sup>c</sup>	48.47 <sup>d</sup>	-	-	-	-	-	-	-	
		<i>59.15</i>	<i>17.07</i>	<i>2.04</i>	<i>25.10</i>								

*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 forest, DTF - CF = Mountain dry tropical forest with some species of the cloud forest, SC = Shaded coffee plantations.

total, of 63 stem maps). All of the living stems that survived from one year to the next were considered "established individuals" ("e"), and all of the stems that appeared (seedlings and saplings) were considered "germinated individuals" ("g"). Dead stems were considered "dead individuals" ("d"). During the study, human-induced disturbances occurred in the depositional and transitional sectors (**Table 1**). In 2002, three plots were cleared. In addition, two other plots were cleared in both 2001 and 2002. In the dry season of 2002, peasants in the nearby areas lit fires that spread to the landslide and burned extensively seven of the plots in the transitional sectors.

### Data Analysis

Each plot was analysed at three levels. At the individual level, all of the individuals in the plot were considered without regard to species (Question 1) and, at the species level, each species was considered separately (Question 2). At the pairs-of-species level, either different

species, or established, germinated or dead individuals of the same species were considered (Questions 3 and 4). At the species level, only species that had > 10 individuals per map were included in the analyses. At every level of analysis, the spatial patterns of stems were assessed using second-order spatial analyses or "density functions" that include position and inter-point distances in quantifying the characteristics of point patterns (Wiegand and Moloney 2004). These methods are increasingly used in ecological applications (Liebhold and Gurevitch 2002, Perry *et al.* 2002). From among the various techniques available, we chose Ripley's K(t) (Ripley 1981) and Van Lieshout and Baddeley's J(t) (van Lieshout and Baddeley 1996, 1999). K(t) measures stem abundance within a radius t from a focal stem, has been widely used in plant ecology (Wiegand and Moloney 2004), and is a powerful descriptor of spatial patterns because it includes a wide range of scales, not just nearest-neighbour distances (Cressie 1991). To linearize the function and stabilize the variance

(Haase 1995), and to facilitate its interpretation,  $K(t)$  is usually transformed to  $L(t) = [K(t) / 0.5 - t]$ . Although edge effects were considered by including the isotropic correction of Ripley (1976), the importance of these effects in the stem maps led us to use the  $J(t)$  function, which has a high capacity to deal with edge effects and heterogeneous patterns (van Lieshout and Baddeley 1999).  $J(t)$  is defined as  $J(t) = [1 - G(t)] / [1 - F(t)]$ , where  $G(t)$  and  $F(t)$  are the nearest-neighbour distance distribution function and the empty-space function, respectively (Diggle 1983).

To test for departures from the null model of complete spatial randomness (CSR) of spatial patterns at the individual and species levels, univariate  $L(t)$  and  $J(t)$  functions were used. For each pattern, the empirical function was compared to a 95% confidence interval generated using the upper and lower 2.5% function values of 99 simulations of random patterns of the same intensity (Haase 1995). When the observed patterns were similar to those simulated under null model (i.e. when the empirical functions were inside the confidence intervals), the spatial distribution of stems was considered "random". When the number of stems was less than the number expected by chance at a range of distances or spatial scales, the spatial distribution of stems was considered "regular". When the number of stems was greater than the number expected by chance at a range of distances or spatial scales, the spatial distribution of stems was considered "aggregated". (Cressie 1991, Batista and Maguire 1998). Unlike  $J(t)$ , in  $L(t)$ , regular and aggregated patterns imply negative and positive deviations from the null model, respectively. When aggregation was evident at small or medium scales (0 - 2 m), and regularity at large scales (> 2 m), a point pattern was considered "clumped".

When the empirical functions exceeded the limits of the 95% confidence interval, clumped and regular point patterns were considered statistically significant at  $P < 0.05$ .

At the pairs-of-species level, the analyses used bivariate extensions of the functions. The bivariate estimator  $L_{12}(t)$ , which is derived from the bivariate  $K$ -function of Lotwick and Silverman (1982), measures the spatial dependence between two spatial patterns (types 1 and 2). Independent patterns have expected values of  $L_{12}(t) = 0$ , while positive and negative values indicate positive and negative spatial associations, respectively. In the context of the bivariate estimator  $J_{12}(t)$  (van Lieshout and Baddeley 1999), it is defined as  $J_{12}(t) = [1 - G_{12}(t)] / [1 - F_2(t)]$ , where  $G_{12}(t)$  is the distribution function of the distance from a type 1 point to the nearest type 2 point, and  $F_2(t)$  is the distribution function of the distance from a fixed point in space to the nearest point of type 2 in the pattern (Baddeley y Turner 2005). If both types of points are independent,  $J_{12}(t) = 1$ .

Following the recommendations of Dixon (2002), we analyzed the relationships between pairs of patterns under two null models. To evaluate inter-specific competition and facilitation between different species, and intra-specific competition between established and germinated individuals of the same species ("Germination analyses"), the independence or "toroidal shift" model (Lotwick and Silverman 1982) was used. This model assumes that independent processes created the two patterns of a bivariate analysis. Under independence,  $K_{12} = \pi r^2$ ,  $L_{12} = 0$  and  $J_{12} = 1$  regardless of the individual univariate spatial patterns of the two types of events (Dixon 2002, Baddeley and Turner 2005). Thus, the interpretation of the results based on that null model is similar



**Table 2.** Species analyzed; number of stems in each type of sector during the different years of study marked with its last two digits (00, 01 and 02), total number of stem maps in which each species appears (Ns), total number of stem maps in which species account for more than 10 stems (Ns > 10).

Species / year	Sector type									Ns	Ns > 10
	Depositional			Transitional			Erosional				
	00	01	02	00	01	02	00	01	02		
<i>Desmodium incanum</i>	-	-	4	-	-	86	-	2	119	8	4
<i>Desmodium nicaraguense</i>	3	16	15	-	-	285	-	2	21	17	4
<i>Guazuma ulmifolia</i>	-	7	34	-	2	-	-	-	-	9	1
<i>Indigofera guatemalensis</i>	-	-	-	-	-	178	-	-	-	1	1
<i>Melanthera nivea</i>	3	15	12	-	4	4	5	47	37	39	2
<i>Muntingia calabura</i>	3	34	29	2	29	14	-	-	-	25	3
<i>Trema micrantha</i>	45	211	173	6	49	13	25	62	50	44	19
<i>Verbesina Turmacensis</i>	-	-	-	-	-	-	-	19	28	14	2
<i>Wigandia urens</i>	8	26	1	8	27	20	3	237	276	38	13
Unknown 1	-	-	-	-	-	-	-	-	45	5	2

to those of CSR: deviations from randomness evidence either aggregation or repulsion. Inference was based on randomly shifting one pattern over the other (which remains fixed), with the study region treated as a torus (Dixon 2002). In our study, 95 % confidence intervals were generated using the upper and lower 2.5% values of the bivariate functions computed on 99 random toroidal shifts of the original patterns.

To detect the presence of intra-specific competition by analyzing segregation and the differences in aggregation between dead and alive stems of the same species ("Mortality analyses"), we used the null model of random labelling (Cuzick y Edwards 1990, Dixon 2002, Goreaud y Pelissier 2003). This model assumes the observed positions of the points and tests of the process that assigns labels to them considering a null hypothesis of random assignment (Dixon 2002). In the random labelling model, the expected values of the bivariate functions are identical to the values of the univariate functions of each pattern and the values of the univariate functions of the complete pattern. Labels are ignored because each pattern will be a random thinning of the entire set. To test for departures from random

labelling, the pairwise differences between univariate and bivariate functions were used. To determine whether one is more or less clustered than the other, we used the differences between univariate functions of each type of pattern ( $K_1[t] - K_2[t]$  and  $J_1[t] - J_2[t]$ ) (Diggle and Chetwynd 1991). To evaluate segregation between patterns (whether individuals of each pattern were surrounded by individuals of the same type at a frequency that was more or less than expected), the differences between univariate and bivariate functions ( $K_1[t] - K_{12}[t]$ ,  $K_2[t] - K_{12}[t]$  and the equivalent differences for  $J(t)$  functions) were used.

## Results

### Selection of the species

Only 10 of the 52 species found on the landslide study site had more than 10 individuals on at least one stem map (**Table 2**). *Indigofera guatemalensis* [(Moc., Sessé & Cerv.), Fabaceae] and *Desmodium nicaraguense* [L., Fabaceae] had the highest number of stems per map, with 178 and 285 stems, respectively, in the transitional sectors in 2002. *Trema micrantha* [(L.) Blume, Ulmaceae], *Melanthera nivea* [(L.) Small, Asteraceae], and *Wigandia*

*urens* [(Ruiz & Pav.) Kunth, Hydrophyllaceae] were the most conspicuous pioneer species and were present in the majority of sectors. However, only *T. micrantha* and *W. urens* were included in the analyses of intra-specific competition at the pairs-of-species level because they were the only species that had more than 10 individuals in a large number of stem maps. *T. micrantha* and *M. calabura* [L., Hernandiaceae], the dominant pioneer species in the depositional sectors, were subjected to inter-specific competition analyses. *Verbesina turbacensis* [Kunth, Asteraceae], *W. urens*, and *Unknown 1*, the dominant pioneer species in the erosional sectors, were subjected to inter-specific facilitation analyses.

**Analyses at the individual level**

At the individual level, the results for K(t) and J(t) were similar. The results of J(t) in 2001 and 2002 are shown in **Table 3**. In 2000 only three stem maps could be analyzed, and all indicated random patterns. In 2001, the most of the patterns were random, but uniform patterns occurred in D1 and D2. In 2002, aggregated patterns were apparent in T2, E1 and E3, and a clear tendency towards regularity was evident in D2, but not in D1. Results for plots D1c, T2c, D2c, E2d, E3d, represented these trends properly (**Fig. 2**). The spatial pattern in D2d showed significant positive deviations from the null model (regularity) at spatial scales of > 0.1 and < 0.6 m in 2001 and 2002, although these deviations might be observed clearer in 2002. In D1c, however, the observed values of J(t) for spatial patterns did not differ significantly from the simulated values of the null model, and distributions were random in 2001 and 2002. In the erosional sectors, the point-pattern analyses of E3d indicated significant aggregation (J(t)<1: P < 0.05) at short distan-

**Table 3.** Results of individual level analyses in 2001 and 2002 using J(t) and considering a null model of CSR. Number of stem maps with different point patterns observed within each type of sector, by year. In cases where the spatial pattern was of more than one type within each analysis (i.e. patterns ranged from random to uniform) the dominant pattern at short-scale was assigned.

Year	2001			2002		
	A	R	U	A	R	U
<b>Sector</b>						
Erosional	2	7	3	5	4	3
Transitional	1	5	2	5	2	1
Depositional	1	2	5	2	2	4
Total	4	14	10	12	8	8

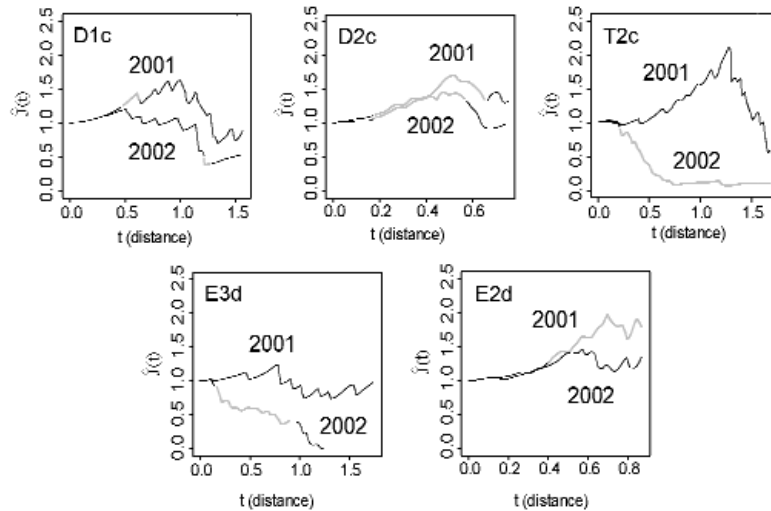
Abbreviations: A = Aggregated, R = random, U = Uniform

**Table 4.** Results of species-level analyses in 2001 and 2002 using J(t) and considering a null model of CSR. Number of stem maps with different point patterns observed within each sector, by year. In cases where the spatial pattern was of more than one type within each analysis (i.e. patterns ranged from random to uniform) the dominant pattern at short scale was assigned.

Species	St.	2001			2002		
		A	R	U	A	R	U
<i>Desmodium incanum</i>	T	-	-	-	2	-	-
<i>Desmodium nicaraguense</i>	E	1	-	-	-	-	-
<i>Guazuma ulmifolia</i>	D	1	-	-	1	-	-
<i>Indigofera guatemalensis</i>	T	-	-	-	1	-	-
<i>Melanthera nivea</i>	E	-	3	-	-	1	-
<i>Muntingia calabura</i>	D	1	-	2	1	1	-
<i>Trema micrantha</i>	T	-	1	-	-	-	-
	E	-	-	-	1	-	-
	D	-	3	2	1	1	2
<i>Verbesina Turbacensis</i>	T	1	3	-	-	-	-
	E	-	5	1	1	2	1
<i>Wigandia urens</i>	E	-	1	-	-	-	-
	D	-	2	-	-	1	-
	T	-	1	-	1	-	-
<i>Unknown 1</i>	E	2	1	-	4	1	-
	E	1	-	-	1	-	-

Abbreviations: St. = Sector type, D = Depositional, E = Erosional, T = Transitional, A = Aggregated, R = random, U = Uniform

ces (0.1-0.5 m) in 2002. In contrast, at distances > 0.4 m in 2001, and between 0.5 and 0.7 in 2002, the spatial patterns of E2d were regular. During the study, the most pronounced changes in the general colonization pattern occurred in the transitional sectors. In 2001, the distribution in T2c was random or even



**Figure 2.** Characteristic functions of results at the individual level using  $J(t)$ , for selected plots representing the main trends in each type of sector. Black lines show the  $J(t)$  functions and the grey ones the parts of the functions showing significant deviations from the null model of CSR. Positive ( $J(t) > 1.0$  with  $P < 0.05$ ) and negative ( $J(t) < 1.0$  with  $P < 0.05$ ) significant deviations indicate uniformity and aggregation, respectively.

positive deviations from null model (non-significant regularity) but, in 2002, at spatial scales between 0.2 and 1.0 m, the pattern was highly and significantly aggregated.

#### **Analyses at the species level**

Based on  $K(t)$  and  $J(t)$ , temporal changes in the spatial patterns of the dominant pioneer species mirrored the changes in the general spatial pattern in the different areas of the landslide (**Table 4**). Depending on sector, individuals of the two most abundant and conspicuous species, *T. micrantha* and *W. urens*, exhibited different spatial patterns. In 2001, individuals of *T. micrantha* were distributed randomly in the erosional and the transitional sectors and they exhibited a more uniform distribution in the depositional sectors. In 2001, *W. urens* were aggregated in the erosional sectors from distances of 1m, and randomly

distributed in the depositional sectors. In 2002, those patterns were more pronounced. In 2001 and 2002, stems of *D. nicaraguense* were strongly aggregated in the depositional and the transitional sectors, although the spatial scale of significant aggregation differed between the two types of sectors (0.2 - 1.5 m for erosional and 0.3-1.1 m for transitional sectors). *D. incanum* was significantly aggregated in the erosional and the transitional sectors. All of the other species appeared in only one type of sector or in one year and did not show any strong tendencies for further discussion.

#### **Analyses at the pairs-of-species level (Intra-specific competition)**

The mortality and germination tests using both,  $K(t)$  and  $J(t)$ , showed significant differences between the patterns of established, germinated and dead individuals of *T. micrantha* and

**Table 5.** Results of pair-of-species level analyses using K(t) and J(t) under nulls models of random labelling (mortality) and independence (germination). Results of univariate analyses of point patterns of established, dead and germinated individuals using K(t) and J(t) under null model and CSR, and number of stems of each type of points. Analyses;  $K_e-K_d$  and  $J_e-J_d$  = Aggregation,  $J_{ed}$  and  $J_{de}$  = Inhibition,  $K_e-K_{ed}$  and  $K_d-K_{ed}$  = Segregation. In cases where the spatial pattern was of more than one type within each analysis the dominant pattern at short scale was assigned.

Species	Plot	Period	Mortality			Gm.	Univariate			N. of stems		
			$K_e-K_d$ $J_e-J_d$	$K_e-K_{ed}$ $J_{ed}$	$K_d-K_{ed}$ $J_{de}$		$K(t)_e$ $J(t)_e$	$K(t)_d$ $J(t)_d$	$K(t)_g$ $J(t)_g$	e	d	g
<i>Trema micrantha</i>	E1c	00-01	ns	ns	>0	ind	R	R	U	11	14	8
	D2c	01-02	<0	<0	ns	-	R	R	-	80	10	-
<i>Wigandia urens</i>	E1d	01-02	ns	>0	>0	ind	A	A	A	76	12	28
	E2c	01-02	>0	>0	>0	-	A	A	-	20	17	-
	E2d	01-02	ns	>0	>0	-	R	A	-	33	24	-
	E3d	01-02	-	-	-	ind	R	-	A	15	-	53
				-	-	-	-	-	-	-	-	-

Abbreviations: Gm. = Germination, N. of stems = Number of stems, e = established, d = dead, g = germinated, A = Aggregated, R = Random, U = Uniform, ns = non significant interaction, ind = independent.

*W. urens* (Table 5). Only two plots (E1c and D2c) had a sufficient number of stems to perform the mortality analyses on *T. micrantha*. Aggregation tests using J(t) ( $J_e-J_d$ ) and inhibition tests ( $J_{ed}$  and  $J_{de}$ ) revealed that, in E1c and D2c, established and dead individuals had a similar distribution and the interaction between them was non-significant. However, aggregation tests using K(t) ( $K_e-K_d$ ) revealed that established individuals were less aggregated than were dead individuals. Segregation tests showed that dead individuals in plot E1c were more surrounded by other dead individuals than randomly expected, and established individuals in D2c were less likely to be surrounded by other established individuals than randomly expected. In plot E1c, the patterns of established and germinated individuals were independent. In E1d and E2d, mortality tests of aggregation using K(t) and J(t) on *W. urens*, were non-significant, which indicates that the spatial patterns of established and dead individuals did not differ significantly. Both, segregation and inhibition tests indicated that there were more established and more

dead individuals than expected by chance ( $K(t) > 0$  and  $J(t) > 1$ ;  $P < 0.05$ ) in the neighbourhood of established and dead individuals, respectively. In E2c, aggregation tests showed that established individuals were more clumped than were dead individuals. Due to the scarce number of germinated individuals in the plots E1c, D2c, E2c and E2d, germination test could be run only in E1d and E3d, where the patterns of established and germinated individuals were independent. Univariate analyses of established, dead and germinated individuals using K(t) and J(t) revealed a predominance of random and uniform patterns for *T. micrantha*, and a predominance of aggregated patterns for *W. urens*, especially in E1d and E2c for dead and germinated individuals.

**Analyses at the pairs-of-species level (Inter-specific competition and facilitation)**

Based on the tests using J(t), most of the patterns of association between the dominant species in the depositional sectors were independent. However, the K(t) test indicated a sig-

nificant ( $K(t) < 1$ ,  $P < 0.05$ ) negative association (repulsion) between *T. micrantha* and *M. calabura* at spatial scales between 2 and 2.5 m in most of the sectors in which they coexisted (Table 6). It is also important to point out that there were very few dead individuals of *T. micrantha*, and where they occurred (E2c), they were not under the canopy of *M. calabura* (personal observation). The patterns of association between the dominant species in the erosional sectors of the landslide (*V. turbacensis*, *W. urens* and *Unknown 1*) were independent (results not shown).

## Discussion

### General and specific colonization patterns

In the first four years following disturbance, the general colonization pattern varied among the areas of the landslide on Casita Volcano, Nicaragua. In general, in the depositional sectors, the pattern shifted markedly from random to regular, while in the erosional and the transitional sectors, aggregation increased over time. In some of the plots of the D1 sector, however, the tendency was toward aggregation, which might have been due to presence of variable sized clumps of *Guazuma ulmifolia* saplings in the understory of the forests formed by pioneer trees that were dominant in this area, and to effects of clearcutting (if neighbouring trees were cut, this human-induced disturbance might have even increased aggregation). In the plots of the sector E2, random patterns persisted throughout the study, which might have been caused by the continuous removal of recently colonizing plants by erosion in this steep sector (Velázquez and Gómez-Sal *submitted*).

In the transitional sectors, shifts towards aggregation were the most striking. Abiotic heterogeneity was especially high in those areas of landslide, where manmade fires in the nearby areas spread in 2001 and 2002. Fire has been pointed as an important cause for dramatic changes in composition of vegetation by creating a more heterogeneous allocation of resources (Hooper *et al.* 2004). Fire promotes the activation of seed banks, the resprouting of existing stems, and the appearance of new colonizing species, which lead to aggregated spatial patterns (Rebertus *et al.* 1989, Menaut *et al.* 1990, Skarpe 1991, Bond y van Wilgen 1996). In

**Table 6.** Results of pair-of-species level analyses between *Muntingia calabura* and *Trema micrantha* using functions  $K(t)$  and  $J(t)$  under a null model of independence. Distances (in metres) at which deviations from null model are significant ( $P < 0.05$ ), are shown.

Plot	Year	Function		N. of stems	
		J(t)	K(t)	Mc	Tm
D1a	2001	Ng: 1.7-3.1	Ng: 2-2.5	10	4
D1c	2001	Indep.	Indep.	8	7
D1d	2001	"	Ng: 2.2-2.5	2	16
T1a	2001	"	Ng: 2	14	2
T1b	2001	"	Indep.	3	11
T1d	2000	"	Ng: 1.2-1.4	2	5
"	2001	"	Ng: 2-2.2	9	3
D2b	2001	"	Ng: 1-1.1	4	44
P5C	2002	"	Ng: 1-1.2	7	80

Abbreviations: N. of stems = Number of stems, Mc = *Muntingia calabura*, Tm = *Trema micrantha*. Ng = negative association, Indep. = Independence

our study, the significant shift towards aggregation in the transitional sectors was probably due to an overlapping of the abiotic heterogeneity characteristic of these areas, with fire-induced heterogeneity created at different scales, which caused an especially uneven distribution of soil resources. Those results suggests that a "patch-dynamics system" (Busing 1998) was operating. As it occurs in the study of Malkinson *et al.* (2003), the general pattern varied in the same way

as did the patterns of the most dominant pioneer species in the sectors.

### ***Intra-specific competition***

The spatial patterns of germination and mortality differed among the sectors of the landslide. According to results of bivariate analyses using  $K(t)$ , established individuals of *T. micrantha* were more highly segregated than were dead individuals and, in the neighbourhood of the first, there were fewer established individuals than expected by chance, which reflects negative intra-specific interactions between individuals of this species. That occurred in D2c, but not in E1c, which suggests that a productive substrate is a prerequisite for the development of intra-specific competition between individuals of *T. micrantha*. Furthermore, it suggests that the balance between positive and negative interactions depends on the degree of physical stress (Brooker y Callaghan 1998), as demonstrated in other plant point pattern analyses (Schenk *et al.* 2003). In our study, the results of aggregation tests using  $J(t)$  differed from those based on  $K(t)$ , but too few plots could be subjected to mortality analyses and, therefore, it is unwise to draw a firm conclusion about the significance of that apparent difference.

*W. urens* colonized the entire landslide immediately after the disturbance (personal observation); however, during our study, this species was abundant in the erosional sectors, only. The univariate patterns of *W. urens* (Table 4) and of the established, germinated and dead individuals of this species (Table 5) were strongly aggregated, especially in E2 and E1 sectors. However, while in E3 there were no dead individuals, in E1 and E2 germinated individuals were scarce or inexistent (Table 5).

Furthermore, in E1 and E2, established individuals were more surrounded by established individuals and dead individuals were more surrounded by dead individuals than expected by chance (Table 5). Those results suggest that populations of *W. urens* have different dynamics in E3 than in E1 and E2.

Clumps of plants can originate through vegetative regeneration, short-distance dispersion, facilitation, and the presence of safe-sites for germination and establishment (Harper 1977, Augspurger 1984, Beatty 1984, Leemans 1991, Skarpe 1991). Vegetative reproduction and short-distance dispersion (Peterson and Squiers 1995, Busing 1998) are unlikely to apply to *W. urens* because this species has long-distance dispersal by anemochory and is not a strong resprouter. Facilitation caused by the creation of "fertility islands" around established individuals (Malkinson *et al.* 2003) did not occur because the patterns of germinated and established individuals were independent. Thus, the presence of safe-sites appears to be the best explanation for those results. In a variety of other environments, the spatial heterogeneity of soil resources dictates the germination and establishment of plants (Couteron y Kokou 1997, Maestre *et al.* 2003, Tirado and Pugnaire 2005), which occurs first in the sites where nutrients and water are available, i.e., "microsites" (*sensu* Titus and del Moral (1998).

E3 was much less productive than E1 and E2 and was later colonized by *W. urens*. Therefore, the results of the analyses of mortality and germination in E1-E2 and in E3 can be interpreted as a chronosequence. If the pattern in E3 is considered the first stage of colonization by *W. urens*, the non-clumped patterns suggest that seeds arrived and germinated randomly. Populations of this species mainly

consist of saplings and a few established individuals. In the second stage (illustrated by the spatial patterns of E1 and E2) dead individuals are present and, like the established individuals, occur in dense clumps. Germination is scarce.

These results suggest that the survival of *W. urens* saplings could be controlled by the soil conditions of the different areas within the plot in which they germinate (microsites). When saplings start to grow, they develop root systems and their nutrient and water requirements increase. "Resource-depletion zones" extend into the rooting zones of neighbouring individuals and competition becomes important (Putz and Canham 1992, Huston and DeAngelis 1994, Wilson 1999). This is critical in the least fertile zones within the plot, where saplings die, but not in the most fertile zones, where saplings survive and become established individuals. As such, our results indicate that in the erosional sectors of the Casita Volcano landslide, subtle differences in nutrient contents, texture and moisture of the soil within plots could be controlling the establishment of *W. urens* after germination, which could lead to the development of clumps of established and dead individuals. The increase in aggregation indicated by the univariate analyses performed at the individual and species levels supports that interpretation.

### ***Inter-specific competition***

The clear pattern of repulsion between *M. calabura* and *T. micrantha*, the dominant pioneer species in the stable and productive zones, indicates competitive interactions between those species. *Trema* was dominant mainly in the D2 plots while *Muntingia* was more abundant in the D1 and T2 plots. Both of

the species are shade-intolerant, fast-growing, and high-fecund trees that can rapidly colonize large disturbed areas (Denslow 1980), but colonization success by *Muntingia* is strongly influenced by the drainage patterns of rainfall runoff. The fruits of *Muntingia* are larger than those of *Trema* (Stevens *et al.* 2001), and are easily transported downslope from points of initial deposition to areas of concentration (Fleming *et al.* 1985). That, together with the low altitudinal range of *Muntingia* relative to that of *Trema* (Stevens *et al.* 2001), suggests that dominance between these species might depend on the species' initial presence in the plots in which they coexist. On the other hand, coincidence of spatial scales at which significant regularity occurs (2-2.5 m), and the mean radius of the crowns of *Muntingia* and *Trema* indicates one-sided competition for light (Grime 1979, Aerts 1999). If competition for nutrients (Tilman 1987, 1988) had occurred, dead saplings or juveniles would have been present in the understory, but they were not. Moreover, our results showed that repulsion occurred at smaller scales (< 1.5 m) in 2000 (T1d) and in D2, which probably was due to the relatively smaller size of the crowns of *Muntingia* and *Trema* in the first year of our study and in D2, where the density of stems is higher.

Haase *et al.* (1997), found significant repulsion between the two main species of dominant shrubs in abandoned Mediterranean semi-arid lands and that was interpreted to be a consequence of competition. However, only a few studies (all in temperate forests) have sought evidence of inter-specific competition among tree species. Peterson and Squiers (1995) found significant repulsion between two tree species caused by the clonal reproduction of one of them, whereas He and Duncan (2000)

observed that the survival of the outcompeted species was influenced by variation in some environmental factors as altitude. In our study, both of those situations are unlikely because neither *Muntingia* nor *Trema* are able to reproduce vegetatively, and the plots in which these species coexisted had similar environmental characteristics.

### **Facilitation**

The results of the bivariate analyses of the main pioneer species that colonized the erosional sectors of the Casita Volcano landslide showed independent spatial patterns, and facilitation was not detected. In the woody layer, facilitation usually occurs between pioneer and "late successional" plants that are unable to colonize a recently opened site (Walker y del Moral 2003), but our study of the Casita Volcano landslide did not cover a rather long period to observe that. In the herbaceous layer, during the first four years after disturbance, facilitation might have proceeded by improving soil fertility caused by expansion of  $N_2$ -fixing herbs (Velazquez and Gómez-Sal *submitted*).

### **Performance of the $J(t)$ and $K(t)$ tests**

Our results suggest that the  $J(t)$  function provides good results for spatial patterns in which distances  $< 1$  m dominate, but it appeared to be inadequate for maps that were composed primarily of widely separated stems. That was apparent in the bivariate analyses of *T. micrantha* and *M. calabura* (Table 6). In that case,  $K(t)$ , but not  $J(t)$ , detected significant regularity between the species because the mean crown size of those pioneer trees frequently is  $>2$  m. On the other hand, mortality analyses detected significant interactions between established

and dead individuals of *T. micrantha* when  $K(t)$ , but not  $J(t)$ , was used (Table 5). In our study,  $K(t)$  was more appropriate than  $J(t)$  for analyzing the large-scale spatial patterns of the depositional sectors, dominated by large shrubs or trees, whereas  $J(t)$  was more appropriate for analyzing the spatial patterns at small and medium scales as in the erosional and transitional sectors in which shrubs and saplings were dominant. This suggests that  $J(t)$  is a very suitable function for point pattern analyses on recently colonized substrates where small pioneer species are abundant.

### **Concluding remarks**

Our study confirmed that the general spatial pattern of colonization at the Casita Volcano landslide changed significantly during early succession, and was determined primarily by changes in the spatial patterns of the dominant pioneer species. Furthermore, the study demonstrated that the development of spatial patterns in areas of the landslide that differed in their abiotic heterogeneity and landscape context, followed different trends and were influenced by different processes. Experiments are required to confirm the suggested underlying mechanisms. Our study compliments recent studies of the development of spatial patterns that involve more than a single point over time (Peterson and Squiers 1995, Zhang and Skarpe 1995, Malkinson *et al.* 2003), and those about changes in space depending on soil conditions (Schenk *et al.* 2003).

### **Acknowledgements**

This research is part of the collaborative program between the "Universidad de Alcalá" (Madrid, Spain) and the "Universidad Nacional Autónoma de Nicaragua-León", and supported



by a grant from the "3rd Scientific Research and Technological Innovation Program" of the Regional Authority of Madrid. In the "Universidad Nacional Autónoma de Nicaragua-León", Pedrarias Dávila and Aníbal Rodríguez were extremely helpful with the planning and the carrying out of the fieldwork, respectively. Ricardo Rueda and Dania Paguaga helped us to identify plant species. We are very grateful to Sevilla family in the community of "Pikin Guerrero" who provided accommodations and supported our fieldwork.

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