

Vegetation of a tropical dry forest in a landscape with chronic disturbance: the case of the indigenous community of San Nicolás Zoyatlan (Guerrero, Mexico)

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Abstract

Background: Tropical dry forests (TDF) provide numerous environmental services to its residents; this has led them to be humanized landscapes subjected to chronic disturbance with a high risk of disappearing.

Research question: To establish the relationship of vegetation structure and composition of a chronically disturbed TDF, with some environmental factors and the intensity of agricultural land use.

Study site and period of research: Our study was conducted during six months (July through November) in the TDF of the community of San Nicolas Zoyatlan (Guerrero, Mexico); a territory with a history of over 500 years of agricultural use. This use has led to a complex mosaic of vegetation fragments.

Methods: A selection of 36 fragments was studied to determine vegetation structure and composition as well as environmental factors. Representative plants from sampled areas were collected. Data gathered was explored with regression and multivariate statistical analysis techniques.

Results: A total of 59 families, 178 genera and 279 species were recorded. Species richness varied widely among fragments, in general with a low dominance and high turnover of species. Slope was the only factor that showed a solid relationship with vegetation variables. Three groups of fragments were established and the statistical differences between them were explained by the duration of fallow. The fragments with longer fallow period showed the best conditions in vegetation variables and 66.9 % of the species were found in them.

Conclusions: Composition and structure of the tropical dry forests were related to intensity of agricultural land use. Although there is a process of impoverishment, vegetation dynamics involving species of the Fabaceae, Asteraceae and Burseraceae families show a potential for their use in the environmental restoration of Zoyatlan.

Keywords: Balsas watershed, chronic disturbance, composition and structure, intensity of agricultural use, potential species.

Resumen

Antecedentes: Los bosques tropicales secos (BTS) aportan numerosos servicios ambientales a sus habitantes, esto los ha llevado a ser paisajes humanizados sujetos a disturbio crónico con riesgo de desaparecer.

Pregunta: ¿Cuál es la relación de la composición y estructura de la vegetación de un BTS sujeto a disturbio crónico, con algunos factores del medio físico y la intensidad de uso agrícola del suelo?

Sitio de estudio y fecha: El estudio se realizó en la comunidad de San Nicolás Zoyatlan (Guerrero, México) durante seis meses (junio-noviembre). Este territorio cuenta con más de 500 años de uso agropecuario, lo que ha propiciado un complejo mosaico de fragmentos de vegetación.

Métodos: Se muestrearon 36 fragmentos para determinar la composición y estructura de la vegetación y los factores ambientales. Se recolectó y herborizó el material botánico representativo de las áreas muestreadas. Utilizando análisis de regresión y técnicas multivariadas se establecieron, tanto relaciones entre la vegetación y los factores ambientales como grupos específicos de fragmentos.

Resultados: Se registraron 59 familias, 178 géneros y 279 especies. Entre fragmentos la riqueza específica varío ampliamente presentándose una dominancia baja y un alto recambio de especies. Únicamente la pendiente mostró una relación consistente con las variables de vegetación. Se obtuvieron tres grupos de fragmentos cuyas diferencias estadísticas se explicaron por los periodos de descanso agrícola; las zonas con mayor tiempo de barbecho presentaron 66.9 % de las especies y las mejores condiciones en las variables de vegetación.

Conclusiones: La composición y estructura de la vegetación del BTS estuvo relacionada con la intensidad de uso agrícola del suelo. Aunque se presenta un proceso de empobrecimiento de la vegetación, existe una dinámica en la que participan especies de las familias Fabaceae, Asteraceae y Burseraceae, con potencial para utilizarse en la restauración ambiental de Zoyatlan.

Palabras clave: composición y estructura, cuenca del Balsas, disturbio crónico, especies potenciales, intensidad de uso agrícola.

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ropical dry forests (TDF) are severely reduced in extension by human influence (Murphy & Lugo 1986, Janzen 1988, Gentry 1995). Miles *et al.* (2006) indicate that 97 % of their surface is threatened by the conversion to agricultural croplands; the increase of population density; the blazes caused by misuse of fires in agriculture; habitat fragmentation; and climate change. Likewise, Newton & Tejedor (2011) also consider the accelerated urbanization of these areas as a threat.

TDFs still cover 3,178,000 km2 across the world (Bezaury 2010); almost half is located in developing countries (UNDP 2004) and 8.8 % in Latin America and the Caribbean (Bezaury 2010). In this region, an important part of the inhabitants depends directly on environmental services of the forest. Weather and soil fertility of these areas also offer proper conditions for the development of several types of crops (Murphy & Lugo 1986). In Mexico, the presence of settlements in TDFs is related to the process of domestication of many food and medicinal plant species (Argueta 1994, Casas *et al.* 1994, Challenger 1998, Hernández-X 1998, Soto 2010); for this reason, they play a unique role in the social and economic context. Estimates indicate that people living in this kind of forests use a great number of vegetation species for their benefit (Dorado *et al.* 2002, Guízar-Nolazco *et al.* 2010).

In Mexico, TDFs stand out for their floristic diversity (Lott *et al.* 1987, Gentry 1995); approximately 20 % of Mexican flora is present in this type of vegetation (Rzedowski 1991a). Besides their great number of endemism (Rzedowski 1991b), TDFs are characterized as the richest forests of the world (Bezaury 2010, Rzedowski & Calderón 2013). Unfortunately, deforestation and fragmentation caused by agriculture contribute to their degradation (Rzedowski & Calderón 1987, Trejo & Dirzo 2000, Trejo 2010), as well as other less known social and environmental threats.

Regardless of the importance for the conservation of biodiversity and for the environmental services that sustain a considerable part of Mexico's rural population (Toledo *et al.* 1989, Toledo & Ordoñez 1998, Dorado *et al.* 2002), the knowledge of the floristic, vegetation structure and composition, their current situation and change dynamics, as well as of the forces that promote their degradation is limited (Trejo 1998, 2010, Cervantes *et al.* 2001, Quesada *et al.* 2009). Although this tendency is changing, knowledge is focused only in few places of the country (Noguera *et al.* 2002, Gallardo-Cruz *et al.* 2005, Maass *et al.* 2005, 2010, Álvarez-Yépiz *et al.* 2008, Lebrija-Trejos *et al.* 2008) and reference to the causes of disturbance, when present, is superficial (Quesada *et al.* 2009).

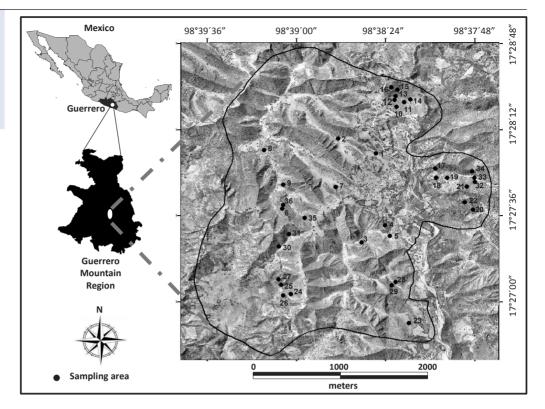
It has been suggested that chronic disturbance in TDFs can have effects of similar magnitude to those of an acute disturbance (Singh 1998); hence, it is indispensable to recognize that these ecosystems are part of a matrix of humanized landscapes that are exposed to chronic disturbance. Thus, it is necessary to research on the causes of disturbance and the use forms of the human populations in the socio-ecological systems; this will help to ascertain the influence of management in the maintenance of the vegetation dynamics and to ponder the opportunities for conservation and restoration of these systems.

This paper approaches the analysis of the composition, structure and diversity of the TDF of the community of San Nicolás Zoyatlan. The investigation integrates: (1) a descriptive analysis of vegetation and the elaboration of a species list; (2) the relationship of the composition and structure of the vegetation with some environmental factors and the intensity of agricultural land use; and (3) the identification of species groups that may allow to ascertain the state and dynamics of the vegetation, as well as the potential for their use in restoration actions.

Materials and methods

Research area. The rural community of San Nicolás Zoyatlan is part of Xalpatlahuac, one of 19 municipalities that shape the region called "La Montaña" in the State of Guerrero (Figure 1); this region is part of the Balsas watershed. The climate is semi-warm, sub-humid and annual average temperature is 27.5 °C with no frosts (García 1998). The rainy season occurs during summer, with average annual precipitation of 781 mm and a P/T ratio of 30.2. November to April is a period of water shortage, while the rainy season is from May to October. Zoyatlan covers an area of 924 hectares with a complex terrain characterized by altitudes ranging from 1,300 to 1,800 m a.s.l., a morphology of hills and summits in 83.62 % of the total surface, as well as

Figure 1. Location of the indigenous community of San Nicolás Zoyatlan, Gro. México. The figure also shows the position of the fragments where vegetation sampling was done.



slopes higher than 10° dominating 70 % of the landscape. Lithology is very diverse with materials of volcanic and sedimentary origin (Cervantes *et al.* 2014). Soils are shallow and rocky and are classified as Anthropic Regosol and Mollic Leptosol (Cervantes *et al.* 2005).

Zoyatlan has a long story of use of natural resources. The population is mostly of Nahua origin and the record of their settlements goes back to 1490 (Vega 1991). It is estimated that the factors that have contributed to the reduction of the vegetation cover in the territory are: transhumant flocks (which began with the Spanish conquest); the conflicts of land invasion at the beginning of the XX century and their negative impact both in the physical and biotic environment of the socio-ecological system, and in the disintegration of agricultural production systems (Cervantes & De Teresa 2004). In 1998 the main activities were subsistence farming, animal husbandry of goats, the collection of forest products and migration. Agriculture has been practiced with different intensities of land use and various agronomic practices (Cervantes *et al.* 2014) that are influenced by soil quality, water availability, landforms and socioeconomic aspects related with the production unit (Cervantes *et al.* 2005). Family ranching has been developed in fallow land and forest areas that belong to the owners of the herds. In 1998 the most important forestry activity carried out by the families in the community was firewood collection (Cervantes *et al.* 2014).

In 1998 Zoyatlan had 681 inhabitants organized in 116 families. That year, human settlements covered 3.17 % of the total area whereas agricultural use 25.9 %. Although 70.8 % of the surface had some type of woody vegetation of *Juniperus* forest, riparian forest, and TDF, their condition and cover was represented in scattered fragments. Considering its extent, TDF is the most represented vegetation type since it occupies 65.1 % of the total area. However, only two fragments with 8.08 ha were found in a moderately preserved condition; the remainder (591.72 ha) was represented by secondary TDF (Cervantes *et al.* 2014).

Vegetation sampling. With the use of the topographic map (1: 50,000; Xalpatlahuac E14D32) and aerial photographs (1: 80,000; 1979) 58 fragments with different vegetation cover (grassland, herbs, shrubs and trees of TDF) were initially identified. This information was verified during four field trips, and 36 fragments were selected with the following criteria: a) that the different vegetation types were distributed across the combinations of relief and lithology type; and b) that fragment size was $\geq 513 \text{ m}^2$ (Figure 1).

Between June and November 1994, 12 plots of 3×3 m (108 m² in total) were sampled and subplots were separated by 5 m between each other. In the higher right corner of each subplot, smaller plots of 1×2 m (24 m² in total) were sampled. In each sampling area, physical environment factors ?altitude, aspect, landform and slope? were recorded.

According to vegetation physiognomy, two layers were distinguished. Top layer (recorded in 3×3 m squares) included trees, shrubs, and succulent plants, with height ≥ 0.60 m. Species composition, percentage of cover per species, number of individuals per species and height were also recorded. Bottom layer included herbaceous plants and seedlings of other life forms: in 1×2 m squares species composition and percentage of cover per species was recorded and average height calculated. All species collected were pressed in the field and for taxonomic identification the specimens were matched in the herbariums of the Faculty of Sciences at UNAM, and MEXU; specialists for each taxonomic group were consulted.

Intensity of agricultural land use. To determine the use intensity of vegetation fragments, it was necessary to identify landowners. To this purpose, information from the genealogic inquiries done by Cervantes & De Teresa (2004) was used. In addition to this, research on the characterization of Zoyatlan production systems (Cervantes *et al.* 2005, 2014) was used to understand better the particularities of agricultural management in the area.

Data analysis. Vegetation data were processed using conventional methods (Mueller-Dombois & Ellenberg 1974, Matteucci & Colma 1982). Frequency and cover (absolute and relative) per fragment and species, as well as their importance value index (IVI = relative frequency specie i + relative cover specie i) were calculated for both layers. To describe physiognomy and the effect of use in stratification, height data in the top layer was separated in two ranges (≤ 2 m; and > 2 m). For the analysis of diversity, species richness (S), diversity index of Shannon-Wiener \log_2 (H') and Simpson index (D) as a measure of dominance ($\lambda = \sum pi^2$), were obtained.

To identify the formation of groups of species composition between the fragments, the method of non-hierarchical K-means clustering (Afifi & Clark 1997) was used. This analysis was based on the average percentage cover values per species —only from those species in the top and bottom layers that were present in four or more fragments—. To confirm the existence of significant differences between the groups, analysis of variance (ANOVA) were applied with the groups as an independent variable, and the Euclidean distances between and within groups (obtained in the analysis of K-means) as the dependent variable.

To explore the relationship between environmental factors of the fragments and vegetation variables, regression analyses (Montgomery 1991) were made relating altitude, lithology, aspect and slope with total cover (TCO) and total richness of species (TSR) and families (TFR). Where a statistically significant relationship was found, variables and factors were selected for a cluster analysis using Ward's hierarchical clustering technique (Everitt & Dunn 1991, Johnson 2000). Subsequently, univariate or multivariate variance analysis (ANOVA or MANOVA) were applied to identify significant differences between the groups formed by the classification analysis. In both cases, groups obtained by the method of Ward were used as independent variables, and the vegetation or environmental factors as dependent variables. To display the formation of the groups that differed statistically, biplots (canonical centroid plot; SAS 1989) were made in a two-dimensional canonical space.

Results

Floristic composition. The floristic list of Zoyatlan includes 316 morphospecies (hereinafter species; Appendix 1) located predominantly in the Magnoliopsida class. Almost all specimens (except 5.06 %) were determined to some taxonomic level: 94.94 % (300) to family; 88.29 % (279) to genus; and 74.68 % (236) to species. Overall, the samples include 59 families, 178 genera and 279 species (Table 1).

From the 59 families, 29 were represented by a single species (Appendix 1); 12 of these families had five or more species and gather 64.61 % of total genera and 74.19 % of all species. The families that are best represented considering the number of genera and species are Asteraceae, Fabaceae and Poaceae. Only in 10 genera, four or more species were found (Table 1).

Although 59 species are shared between the two layers (215 were exclusive to the bottom

Table 1. Floristic composition in the community of San Nicolás Zoyatlan, Guerrero México. Numbers in brackets indicate the number of *taxa* where the species could not be determined. No. FR = number of fragment.

GROUP	FAMILIES	GENERA	SPECIES
 Magnoliophyta			
Magnoliopsida	45	145	202 (+ 34)
Liliopsida	10	27	29 (+ 8)
Pinophyta	1	1	1
Pteridophyta	'	'	'
Lycopodiopsida	1	1	0 (+ 1)
Polypodiopsida	2	4	4
TOTAL	59	178	236 (+ 43)
FAMILIES (5 or more species) Magnoliopsida	Acanthaceae	6	6
iviagrioriopsida	Asteraceae	35	55
	Boraginaceae	6	6 7
	Burseraceae	1 3	8
	Convolvulaceae	3 5	
	Euphorbiaceae	29	14
	Fabaceae		57
	Lamiaceae	2	8
	Malvaceae	6	10
	Rubiaceae	3	6 7
Liliansida	Verbenaceae Poaceae	4 15	23
Liliopsida	Poaceae	10	
GENERA (4 or more species)			
Magnoliopsida	Asteraceae	Eupatorium	5
	Burseraceae	Bursera	7
	Convolvulaceae	Ipomoea	6
	Euphorbiaceae	Euphorbia	8
	Fabaceae	Acacia	4
	Fabaceae	Dalea	4
	Fabaceae	Desmodium	4
	Fabaceae	Marina	6
	Lamiaceae	Salvia	7
	Malvaceae	Sida	4
	PRESENCE OF SPECIE		
No. FR	No. SPE	CIES PR	OPORTION (%)
1	89		29.47
2 a 3	86		28.47
4 a 8	67		22.18
9 a 18	41		13.58
19 a 27	14		4.64
28 a 34	5		1.66

and 26 species to the top layer; Appendix 1), none was found in all 36 sampling sites. More than half of the species were found in one to three fragments (Table 1) and only five species (1.66 %) were found in at least 80 % of the fragments (between 29 and 34 sampling sites): *Bidens aurea* and *Sanvitalia procumbens* (Asteraceae), *Acacia cochliacantha* (Fabaceae), *Loeselia coerulea* (Polemoniaceae) and *Bouteloua curtipendula* var. *caespitosa* (Poaceae) (Appendix 1).

Richness and diversity. The average species richness (\pm 1 SD) of all 36 fragments was 48.28 \pm 18.52 (range: 11-93). For the bottom layer, values were distributed from 11 to 79 and for the top layer from 1 to 28 species (Table 2). Similar trends were established for Shannon diversity index, with values for the bottom layer ranging from 2.60 to 5.64 and for the higher from 0 to 3.99. In both layers there was a strong positive linear relationship between species richness and diversity index (bottom layer: $R^2 = 0.85$, F = 192.24, P < 0.0001; top layer: $R^2 = 0.77$, F = 97.68, P < 0.0001). With regard to Simpson's index, values obtained indicate low dominance, with the exception of five fragments where the values for the top layer were \geq 0.52 (Table 2).

Vegetation structure. The bottom layer was the only one well represented in all 36 fragments since for six of them, the top layer was absent and, in another four it was represented only by individuals ≤ 2 m high (Table 3).

Table 2. Environmental characteristics and species richness, diversity and dominance values for vegetation fragments (VF) studied in the community San Nicolás Zoyatlan, Gro. México. LI = Lithology (QBR – Quartzitic breccia, VBR - Volcanic breccia, AND - Andesite, LAN – Limestone-Andesite, LIM - Limestone, SAC – Sandstones conglomerate, TUF - Tuff); AL = Altitude; SL = Slope; AS = Aspect (S - South, N - North, E - East, W - West); LF = Landform (H - Hillside, Ge - Gentle, St - Steep, VS - Very steep, ES - Extended Summit, Ter – Terrace); Sr= Species richness; H'= Shannon-Wiener Diversity Index log2; D = Simpson Index.

VF		ENVIRON	MENTAL FA	CTORS		ВС	TTOM LAY	/ER		TOP LAYER	₹	TOTAL
	LI	AL	SL	AS	LF	Sr	H′	D	Sr	H′	D	Sr
		(msnm)	(%)									
1	QBR	1402	17.6	SE	GeH	23	2.79	0.28	0			23
2	QBR	1520	0 a 4.4		ES	17	3.34	0.12	0			17
3	QBR	1515	33	S	StH	28	4.03	0.07	0			28
4	QBR	1428	65	Ν	VSH	43	4.1	0.11	6	1.43	0.52	44
5	VBR	1453	0 a 10		ES	22	3.16	0.22	0			22
6	QBR	1420	50	Ν	VSH	50	4.42	0.09	14	2.58	0.27	56
7	QBR	1408	55	SE	VSH	48	4.85	0.04	18	3.32	0.12	59
8	QBR	1522	37.5	SE	StH	38	4.22	0.09	8	2.21	0.33	42
9	QBR	1470	45	NE	VSH	33	3.96	0.12	1	0	1	33
10	AND	1348	45	S	VSH	33	4.04	0.1	4	1.88	0.29	34
11	AND	1372	54	SE	VSH	48	4.5	0.07	6	1.23	0.63	49
12	AND	1410	80	SE	VSH	58	4.97	0.05	8	2.97	0.14	63
13	AND	1440	40	S	StH	44	4.39	0.09	11	2.44	0.28	49
14	LAN	1392	34	Ε	StH	61	4.97	0.05	19	3.43	0.13	71
15	AND	1380	55	Ν	VSH	53	4.48	0.07	15	2.9	0.18	63
16	AND	1365	60	Ν	VSH	63	5.23	0.04	16	3.38	0.12	71
17	SAC	1380	65	NW	VSH	59	4.76	0.07	12	2.76	0.22	65
18	LIM	1470	30	W	StH	37	4.52	0.06	14	3.29	0.12	46
19	LIM	1358	0 a 8		ES	22	3.37	0.16	7	2.2	0.26	27
20	LIM	1452	13	NW	Ter	37	4.07	0.11	0			37
21	LIM	1440	51	S	VSH	47	4.59	0.07	19	3.74	0.08	57
22	LIM	1440	35	SW	Ter	11	2.6	0.29	0			11
23	QBR	1475	40	Ε	StH	37	4.33	0.07	1	0	1	37
24	QBR	1442	54	NE	VSH	50	4.77	0.05	10	2.87	0.19	56
25	TUF	1485	45	NE	VSH	40	4.01	0.11	5	2.32	0.2	44
26	QBR	1468	50	SE	VSH	46	4.27	0.11	15	2.8	0.23	50
27	QBR	1460	60	NE	VSH	79	5.48	0.03	27	3.85	0.11	86
28	QBR	1350	0 a 8		ES	25	4.1	0.07	3	1.54	0.35	27
29	QBR	1490	70	NE	VSH	45	4.46	0.06	8	1.76	0.40	49
30	QBR	1460	16	Ν	GeH	52	4.36	0.12	14	2.65	0.29	60
31	QBR	1413	0 a 4		Ter	47	4.51	0.07	10	2.81	0.18	50
32	LIM	1480	40.4	S	StH	45	4.51	0.07	11	2.13	0.35	48
33	LIM	1484	0 a 4		ES	41	3.88	0.17	1	0	1	41
34	LIM	1468	40	NE	StH	79	5.64	0.03	28	3.99	0.08	93
35	QBR	1377	80	NE	VSH	52	4.97	0.04	21	3.73	0.1	60
36	QBR	1450	70	NE	VSH	64	4.88	0.06	17	3.28	0.13	70

Average height (\pm 1 SD) for the bottom layer was 0.174 \pm 0.06 m (range: 0.07 to 0.34 m). For individuals in the top layer with size \leq 2 m, height ranged from 0.53 to 1.90 m, with an average of 1.08 \pm 0.45 m; in the case of those > 2 m this value was three times higher: 3.33 \pm 0.43 m, with heights ranging from 2.23 to 4.21 m (Table 3).

Regarding the number of individuals in the two established height intervals, sharp contrast was found between and within the fragments. For ≤ 2 m, the mean value (± 1 SD) was 65 \pm 70.45; the dispersion of the data with respect to the average value is due to the fact that the number of individuals between fragments ranged from 2 to 316; in the case of the > 2 m interval, this number was significantly lower: 18.04 ± 14.21 , with variations ranging from 1 to 44 individuals (Table 3).

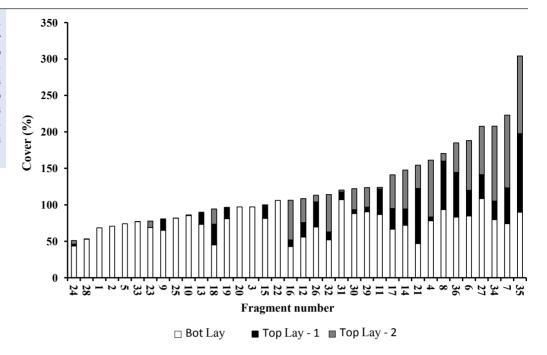
There are also differences in the cover values between fragments and layers (Figure 2). In the bottom layer it ranged from 42.8 to 108.6 %, but only in six fragments cover was > 90 %. In the top layer, the dominant tendency was of low cover values, although they ranged from 0.4 to 107.9 %. For individuals ≤ 2 m in height, cover was > 50 % only in three fragments; as for

Table 3. Average height of vegetation in bottom and top layers, number of individuals and species as well as Importance Value Index (IVI) obtained in the fragments (FR) of San Nicolás Zoyatlan community, Gro. México. Ind = individuals; Sp = species; No. = number. The number in parenthesis besides the IVI corresponds to the name of the species: (1) A. dentata, (2) S. amplexicaulis, (3) E. prostrata, (4) B. curtipendula, (5) B. repens, (6) D. hegewischiana, (7) D. tagetiflora, (8) L. graveolens, (9) T. stans, (10) O. atropes, (11) I. arborescens, (12) B. copallifera, (13) A. pennatula, (14) A. bilimekii, (15) A. cochliacantha, (16) A. farnesiana, (17) J. flaccida.

No.	Botton	n layer				Top laye	er			
Fragment				Size clas				Size clas		
	Height (m)	IVI (%)	Height (m)	Ind. (No.)	Species (No.)	IVI (%)	Height (m)	Ind. (No.)	Species (No.)	IVI (%)
1	0.120	99.20 (1)	0.00	0	0		0.00	0	0	_
2	0.124		0.00	0	0		0.00	0	0	
3	0.161		0.00	0	0		0.00	0	0	
4	0.170	53.69 (2)	0.95	21	5		3.83	38	1	139.89 (14)
5	0.717	89.08 (3)	0.00	0	0		0.00	0	0	
6	0.172		1.17	32	12		4.21	39	3	93.66 (14)
7	0.212		1.35	168	13		3.48	44	11	
8	0.242		0.97	174	8	108.20 (8)	3.64	5	3	
9	0.129	61.74 (4)	1.84	9	1	200.00 (9)	0.00	0	0	
10	0.159	52.51 (4)	0.75	4	3	75.71 (11),	3.50	1	1	
						62.86 (10)				
11	0.190		1.58	26	5	157.10 (11)	3.18	9	4	
12	0.163		0.99	29	7	51.81 (12)	3.34	19	8	
13	0.123	51.66 (5)	0.83	37	11	91.15 (10)	2.66	6	3	
14	0.195		0.99	83	18		3.04	16	6	
15	0.153		0.68	44	14	52.20 (13)	2.60	6	5	
16	0.171		1.10	66	15		3.63	19	7	
17	0.125		1.09	55	12		3.08	18	3	85.55 (17)
18	0.178		1.18	131	12		3.60	10	4	
19	0.800	70.77 (14)	1.24	41	7	58.91 (14)	2.23	4	2	74.26 (13)
20	0.145	53.39 (3)	0.00	0	0		0.00	0	0	
21	0.162		1.22	176	18		3.58	35	8	
22	0.340	103.43 (6)	0.00	0	0		0.00	0	0	
23	0.186		1.90	7	1	200.00 (14)	3.00	1	1	
24	0.152		0.82	15	9		3.50	1	1	75.37 (16)
25	0.149	51.20 (7)	0.53	5	5		0.00	0	0	
26	0.174	62.30 (4)	0.99	96	15	86.34 (8)	3.12	8	3	
27	0.328		1.25	120	24		4.10	20	10	
28	0.121		0.77	3	3	77.78 (14), 77.78 (9)	0.00	0	0	
29	0.201		1.21	24	6	56.07 (9)	3.45	14	3	113.99 (14)
30	0.181	63.79 (4)	0.87	35	12		3.31	12	3	103.98 (14)
31	0.177		0.95	36	9	58.88 (15)	3.25	3	3	
32	0.144		1.20	48	10	` ,	3.38	41	2	111.82 (14)
33	0.111	80.52 (3)	0.55	2	1	200.00 (14)	0.00	0	0	,
34	0.253		1.27	82	25		3.46	35	11	
35	0.321		1.22	316	16		3.20	44	14	
36	0.171		0.92	157	15		3.22	21	6	
Mean	0.174		1.08	65.00	10.24		3.33	18.04	4.85	
± 1D.E.	0.061		0.44	70.45	6.76		0.43	14.64	3.56	
Median	0.010		1.09	37.00	10.00		3.36	15.00	3.00	

those > 2 m, this occurred in nine —for both cases, cover was > 100 % only in fragment 35—. Thus the total cover between all 36 fragments was very dissimilar (ranging from 51 to 304 %), although average total cover (\pm 1 SD) was 122.89 ± 54.39 . Cover values close to 100 % were found in several places that did not had a top layer; in others, it was similar or slightly higher than 100 % even if there was a top layer. Total cover values above 200 % (Figure 2) were found in four fragments only (7, 27, 34 and 35); in these, there was a well-developed top layer in both height intervals; mostly in accordance with the highest values for number of individuals and species (Table 3).

Figure 2. Proportion of vegetation cover of the bottom layer (Bot Lay) and top layer (Top Lay) in the vegetation fragments studied in San Nicolás Zoyatlan, Gro. México. Top Lay-1: includes individuals with heights ≤ 2 m; Top Lay-2: includes individuals with heights > 2 m.



The importance value index (IVI) showed very low values; only 17 species (6.09 %) had IVI ≥ 50 (1/4 of the expected value of the IVI = 200). However, only eight did so in at least two fragments (Table 3). In the bottom layer, species that stood out were *Aldama dentata*, *Dyssodia tagetiflora*, *Simsia amplexicaulis* (Asteraceae), *Euphorbia prostrata* (Euphorbiaceae), *Dalea hegewischiana* (Fabaceae), *Bouteloua curtipendula* var. *caespitosa* and *B. repens* (Poaceae). Outstanding species in the top layer were *Acacia bilimekii*, *A. cochliacantha*, *A. farnesiana*, *A. pennatula* (Fabaceae), *Bursera copallifera* (Burseraceae), *Ipomoea arborescens* (Convolvulaceae), *Juniperus flaccida* (Cupressaceae), *Lippia graveolens* (Verbenaceae), *Opuntia atropes* (Cactaceae) and *Tecoma stans* (Bignoniaceae).

Intensity of agricultural land use. From previous research on the history of use of the fragments, we could corroborate that all of them are or were used for agriculture. However, duration of the fallow periods is a distinctive variable that characterizes semi-intensive agricultural systems of Zoyatlan into four distinctive use type. Use1 (U1) - agriculture with fallow periods of 1 to 4 years without residual woody vegetation (fragments 1, 2, 3, 5, 20, 22); Use2 (U2) - agriculture with fallow periods of 1 to 4 years with residual woody vegetation (fragments 9, 10, 11, 15, 19, 23, 24, 25, 28, 31, 33); Use3 (U3) - areas with fallow periods of 8 to 10 years (fragments 4, 6, 12, 13, 14, 16, 18, 26, 30); and Use4 (U4) - areas with fallow periods of more than 10 years (fragments 7, 8, 17, 21, 27, 29, 32, 34, 35, 36).

Floristic composition clusters (FCC). Based on the analysis of K-means applied to species that were present in four or more vegetation fragments, three clusters for the two layers were identified (Table 4). In the bottom layer the count was of 120 species, and 51 (42.5 %) occurred in all three clusters (Appendix 1). Cluster-1 grouped 28 fragments including species that are shared by the three groups and other 69 species; from the latter 10 were unique to this group: Acacia pennatula, Aeschynomene americana, Dalea foliolosa, Indigofera jamaicensis (Fabaceae), Calea hypoleuca, Zinnia violacea (Asteraceae), Euphorbia hirta (Euphorbiaceae), Lantana camara (Verbenaceae) Ruellia hookeriana (Acanthaceae) and Sida angustifolia (Malvaceae). Clusters 2 and 3 grouped few fragments (5 and 3 respectively) and fewer species (91 and 69 respectively). Although species 40 and 18 are different to those that are shared by all three clusters, they are part of Cluster-1 (Appendix 1); perhaps this is why there were no significant differences among these clusters (Table 4).

The top layer had 27 species and, although 21 (77.8 %) were common to all three clusters (Appendix 1); there were significant differences between clusters (Table 4). Cluster-2 differs statistically from Clusters 1 and 3; it stands out because it gathers 21 fragments and incorporates

Table 4. Clusters of the fragments for the K-means analysis in the floristic composition of the bottom and top layers, and for the cluster analysis of the slope and the vegetation variables: total species and family richness and total cover. Also, results are shown of the ANOVA for the K-means analysis (ID = initial distance and MD = maximum distance for the cluster formation) and for the cluster with slope and vegetation variables independently, as well as the MANOVA for the combination of these variables. The asterisk indicates significant differences with p < 0.05; different letters indicate significant differences between groups according to Tukey-Kramer multiple means comparison test. The marks in the number of fragments indicate the land use types: X = agriculture with fallow periods of 1 to 4 years with residual woody vegetation (U-1); X = agriculture with fallow periods of 1 to 4 years with residual woody vegetation (U2); X* = areas with fallow periods of 8 to 10 years (U3); X• = areas with fallow periods of more than 10 years (U4).

GROUP								NL		OF FI	RAGM ns	ENT				F	р
Cluster-1		TTOM 0 = 8.8 2 19	38 3 20	4* 21•	5 22	MI 6* 23	D = 14 8• 24	.682 10 25	11 28	12* 29•	13* 30*	14* 31	15 36•	16*	17•	2.649	0.085
Cluster-2		0 = 8.8 27•		33	34•	MI	O = 15	.930									
Cluster-3	ID 7•	= 10.3 26*	318 35•			MI	D = 16	.693									
Cluster-1	IE	OP LAY 0 = 2.6 8•	19	35•	36•	MI) = 9.°	159								6.566 A	0.004*
Cluster-2	1E 4* 28	0 = 0.0 9 29•	18 10 30*	11 31	12* 32•		D = 8.4 14*		16*	18*	19	23	24	25	26*	В	
Cluster-3		0 = 4.2 21•	64 27•	34•		MI	O = 9.3	342								Α	
									Wa	ard's c	lusteri	ng					
Cluster-1	SIC 1	pe Fac 2	ctor 5	19	20	28	30	31	33							141.041 A	0.0001*
Cluster-2	3 25	6 26	7 32	8 34	9	10	11	13	14	15	18	21	22	23	24	В	
Cluster-3	4	12	16	17	27	29	35	36								С	
Olymban 1			Varial		0	10	10	20	22	22	٥٢	20				47.497	0.0001*
Cluster-1 Cluster-2	1	2 6*	3	5	9	10	19	20 14*	22 15	23	25	28	21.	2.4	2/*	A	
Cluster-2	4* 29•	30*	7 • 31	8• 32•	11 33	12* 36•	13*	14	15	10	17•	18*	21•	24	26*	В	
Cluster-3	27•	34•	35•													С	
Cluster-1	Slop 1	e Fact 2	or and	Vegeta 5	ation \	Variab 10	es 18*	19	20	22	23	28	33			8.205 A	0.0013*
Cluster-2	4*	8•	11	12*	13*	15	24	25	26*	29•	30*	31	32•			AB	
Cluster-3	6*	7•	14*	16*	17•	21•	27•	34•	35•	36•					_	В	

the 27 participant species, including two that only show up at this cluster: *Bunchosia canescens* (Malpighiaceae) and *Cordia curassavica* (Boraginaceae). Clusters 1 and 3 were not statistically different; the first brought together five fragments and the second four. Both clusters had 23 species; 21 common to all three clusters and two more in each case: Cluster-1 *Heliocarpus velutinus* (Malvaceae) and *Tournefortia hirsutissima* (Boraginaceae); Cluster-3 *Lippia dulcis* (Verbenaceae) and *Mimosa polyantha* (Fabaceae) (Appendix 1).

Vegetation and environmental factors. The relationship between lithology and aspect factors with vegetation variables was weak (Table 5). The slope factor showed a reliable relationship with total cover (TCO), total richness of species (TSR) and families (TFR); for altitude this was the case only for the last two variables, but the correlation coefficient was very low. On this basis, slope was chosen as the environmental factor of interest to be analyzed with vegetation. Three clusters of fragments were identified in the classification analysis, for slope as well as for

Table. 5. Results of regression analysis between environmental and vegetation variables of 36 fragments studied in the community of San Nicolás Zoyatlan, Gro. México. STA = statistics, TCO = total cover; TSR = total species richness; TFR = total family richness.

STA	TCO	TSR	TFR
		Altitude	
R^2	0.071	13.497	15.867
F	2.612	5.305	6.412
р	0.115	0.027*	0.016*
		Lithology	
R^2	0.095	0.159	0.109
F	0.509	0.889	0.594
р	0.796	0.516	0.732
		Aspect	
R^2	0.054	0.001	0.001
F	1.929	0.002	0.005
р	0.174	0.961	0.943
		Slope	
R ²	27.676	31.891	30.662
F	13.010	15.920	15.035
р	0.001*	0.000*	0.000*

all vegetation variables (TCO, TSR, TFR); in both cases the ANOVA or MANOVA showed the significant differences between clusters (Table 4).

The differences in the slope clusters are clear: in Cluster-1 (9 fragments), the slope values were the lowest (2 to 17.6 %); in Cluster-3 (8 fragments) slopes were the most pronounced (60 to 80 %); and in Cluster-2 (19 fragments) values were intermediate (30 to 55 %) (Table 4).

Vegetation variables of Cluster-1 (12 fragments) has the lowest values for TCO (53.37 to 106 %), TSR (11 to 44 species) and TFR (6 to 14 families). In Cluster-3 (3 fragments) highest values concurred for TCO (207.7 to 304.4 %), TSR (60 to 93 species) and TFR (28 to 33 families). In Cluster-2 (21 fragments) values for TFR (17 to 26 families) were intermediate compared to the other two clusters (Table 4). Although this trend persisted for TSR and TCO, values similar to those included in the other two clusters occurred in fragments 14, 16 and 33 for the former parameter; and in fragments 7 and 24 for the latter.

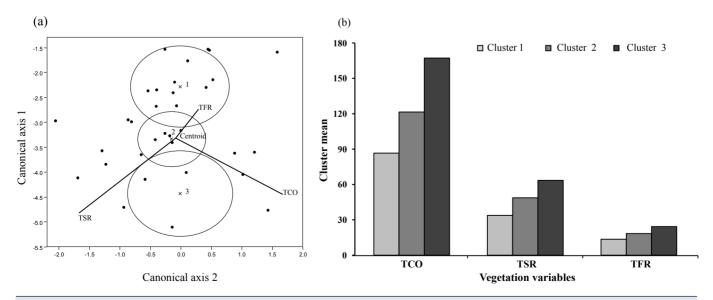


Figure 3. Results of the MANOVA between slope and vegetation variables (TCO = total cover; TSR = total species richness and TFR = total families richness. In (a) clusters formed by the centroid analysis; in (b) cluster means for slope and vegetation variables.

Clusters obtained from the MANOVA that combined vegetation variables and slope clusters (Table 4) are represented by three centroids (Figure 3a). The first (13 fragments; Table 4) had the cluster mean with lowest values for the slope (range: 2-70 %), TSR, TFR and TCO (Figure 3b), while centroid-3 (10 fragments) has the highest mean values (slope range: 34-80 %). Intermediate mean values are found in the 12 fragments gathered at the centroid-2 (Figure 3b); it stands out that only the fragments included in centroids 1 and 3 differ statistically (Figure 3a, Table 4).

Discussion

Vegetation description. Due to insufficient botanical knowledge of Balsas basin (Fernández-Nava et al. 1998, Jimenez-Ramirez et al. 2003, Pineda-García et al. 2007, Bezaury 2010) and the scarcity of quantitative studies of vegetation structure (Ávila-Sánchez et al. 2010, Guízar-Nolasco et al. 2010) it is difficult to analyze the floristic data originated from the research in Zoyatlan under the light of other studies. However, in a first approximation we can say that the 236 species determined for Zoyatlan represent 6.28 % of the 4,442 known for the basin (Fernández-Nava et al. 1998). Based on studies about the flora of the mid and high Balsas of the state of Guerrero, we find that our records represent 23.43 % of the total of species known for the TDFs of the municipality of E. Neri, which ranks third in diversity for the whole country (Jiménez-Ramírez et al. 2003); for the zone of Papalutla our data represent 49.27 % (Martínez-Gordillo et al. 1997). Considering that this type of vegetation is most common in the Balsas, but also that it stands out for its high species richness and number of endemic species (Rzedowski, 1991b, Bezaury 2010, Rzedowski & Calderón 2013) these ratios give a good idea of the representativeness of the flora of Zoyatlan; both in relation to what is known for the subregions of the Balsas, as to the context of endemic species. According to Jiménez-Ramírez et al. (2003) and Rodríguez-Jiménez et al. (2005) there are seven species endemic to the TDFs of the Balsas of Guerrero: Acacia bilimekii, Colubrina macrocarpa, Hechtia mooreana, Lasianthaea crocea, L. helianthoides, Opuntia atropes and Rhus nelsonii.

The research area has 29 % of all families registered for Balsas basin (Fernández-Nava *et al.* 1998) and between 76 and 44 % of those reported in municipalities of the state of Guerrero that are part of the Balsas center (Jiménez-Ramírez *et al.* 2003, Ávila-Sánchez *et al.* 2010) and high subregions (Martínez-Gordillo *et al.* 1997, Guízar-Nolasco *et al.* 2010). These studies point to Fabaceae, Asteraceae and Poaceae as the richest in species; this is also the case in Zoyatlan. However, while these families gather 48.38 % of the total species, other families represented by ≥ 5 species were, in order of importance: Euphorbiaceae, Malvaceae, Convolvulaceae, Lamiaceae, Burseraceae, Verbenaceae, Acanthaceae, Boraginaceae and Rubiaceae. All these families, except Lamiaceae, are recognized as the most diverse in dry forests around the world (Gentry 1995, Trejo 1998, Pérez-García *et al.* 2001, Jiménez-Ramírez *et al.* 2003, Gallardo-Cruz *et al.* 2005). Also, although in Zoyatlan were listed 71.43 % of the genera that Rzedowski & Calderón (2013) stand out as those with the largest number of species in the TDFs of Mexico, only 10 of these genera presented ≥ 4 species; however, three of them, *Dalea*, *Eupatorium* and *Salvia*, are not included in that study.

The low floristic similarity that occurs between TDFs is a phenomenon described both in terms of different regions of Mexico (Trejo & Dirzo 2002, Rzedowski & Calderon 2013) and between "stands" in a micro-basin (Balvanera *et al.* 2002) or a hill (Gallardo-Cruz *et al.* 2009). Although those investigations took into account only species that make up the tree stratum, according to our results it is likely that the pattern will recur at different scales regardless of the layer considered. For example, in Zoyatlan 71.67 % of the species were recorded only in the bottom layer and 8.7 % exclusively in the top layer. However, species replacement in the 36 fragments was high because no species was found in all of them and very few (*Acacia cochliacantha*, *Bidens aurea*, *Bouteloua curtipendula* var. *caespitsa*, *Loeselia coerulea* and *Sanvitalia procumbens*) were found in more than 75 %. Also, 175 species (57.95 %) occurred only in 1 to 3 fragments, and of these, 64 % were present only in the bottom layer and 23.4 % were common to both layers. Unfortunately, few comparative inferences can be made because there are very few studies in TDFs that analyze the plant component of the bottom layer (Gallardo-Cruz, *et al.* 2005, Quesada *et al.* 2009, Sagar *et al.* 2012).

Despite the recurrent land use in Zoyatlan for more than five centuries, in its flora we can still recognize trends that are common to TDFs of other areas of the Balsas and the rest of the country; however, five species present in over 75 % of the fragments are known to inhabit disturbed areas (Calderón & Rzedowski 2001). Four of these five species are part of the most diverse families; while members of Fabaceae are often associated with primary and secondary vegetation, Asteraceae and Poaceae are always related to secondary vegetation (Guízar-Nolazco *et al.* 2010, López-Sandoval *et al.* 2010, Rzedowski & Calderón 2013). In this way composition, richness and species diversity that was found between fragments and the strata of each fragment in Zoyatlan had a great variability. According to the ideas of Halffter & Moreno (2005) this variability is a typical attribute of secondary vegetation communities.

Vegetation and environmental factors. Despite the variety of environmental conditions of the fragments, only slope showed a positive relation with total richness of species (TSR) and families (TFR) and total cover (TCO). Studies in TDFs from different parts of Mexico, and at different scales, also report a low relationship of species richness and diversity with environmental factors such as altitude, lithology and aspect (Balvanera et al. 2002, Trejo & Dirzo 2002, Durán et al. 2006, Chaparro-Santiago 2016); however, this has not been the pattern in the case of slope. At both national and local level it has been found that these forests are best preserved in areas with shallow soils and steep slopes, usually > 20° (Aranguren-Becerra 1994, Trejo & Dirzo 2000, 2002). This trend also happens in Zoyatlan, since fragments of lesser slope but with most precarious conditions of all vegetation variables (TSR, TFR and TCO) concur in Cluster-1; on the contrary, Cluster-3 showed the best development of vegetation variables but steepest slopes (Figure 3b; Table 4). This phenomenon is not unique to TDFs; several sources report that areas less altered by human activities are those with less favorable soil, climate and access (Hoonay et al. 1999, Prach et al. 2001, Cousins & Eriksson 2002, Graae et al. 2003). In Zoyatlan slope influences the availability of land for the development of any productive activity, as well as the choice of the most promising type of use; for example, the intensity of agricultural land use (Cervantes et al. 2005).

Vegetation and intensity of agricultural land use. Analyses of succession in TDFs using chrono sequences point to inconsistencies between the fallow period and the increased complexity of vegetation, both in richness and diversity of species as in the structure. In this regard, some authors (Burgos & Maass 2004, Hernández-Oria 2007, Lebrija-Trejos et al. 2008, 2010, Álvarez-Yépis et al. 2008) suggest that this is common in places with ≤ 10 years of fallow. However, over time (usually > 20 years) the process is "stabilized" because the effect of agricultural use decreases; this is first revealed in the structure and later in the richness and diversity of species. Others (Van der Wal 1999, Kennard 2002, Cramer et al. 2008, Holz et al. 2009) argue that inconsistencies are influenced by the type of agricultural management prior to the abandonment, and by the characteristics of the physical and biotic environment of the fragments (soil conditions, distance to source of propagules, forms of dispersal of species, etc.).

As was indicated four uses derived from variants of semi-intensive agriculture systems were identified in the fragments. These variants played an essential role in the characteristics of vegetation because they alert about differences in vegetation structure of fragments (Table 3), as well as the way clusters result from the classification analysis (Table 4). For example, in Cluster-1 fragments are from areas with agriculture use (current and in fallow) and show lowest cluster values for slope and vegetation variables (Figure 3b). The six fragments with U-1 lacked the top layer, while in those of U-2 that layer was represented by few individuals and usually with heights ≤ 2 m. Furthermore, these fragments had 8 of the 17 species with IVI ≥ 50 (Table 3). In Cluster-3 all the fragments had at least 10 years without agricultural use (U-3 and U-4; Table 4) and matched with the highest mean cluster values (Figure 3b); in their vertical structure, density was well represented both in the range of ≤ 2 m height, as in the > 2 m range (Table 3).

Perhaps the fragments of Cluster-2, with an intermediate average cluster value not statistically different from the other two (Table 4; Figures 3a and b), represent the inconsistencies regarding time of abandonment of sites and vegetation features, because this cluster includes fragments with three types of uses: from agriculture with residual vegetation (U-2) to nonagricultural use for over 10 years (U-4). Ten species of the top layer with IVI \geq 50 were present in these areas, often with individuals of both height layers; however, as expected in U-2, the

number of individuals was usually lower (Table 3). The condition that Cluster-2 is statistically similar to Cluster-1 and Cluster-3, suggests the evolution of the succession process; it is possible that fragments of Cluster-2 exhibit the extremes of the fallow period. However, the influence of management previous to abandonment should also be taken into account —both in the agricultural process as in residual vegetation—since it's characteristics can help or hinder regeneration (Cramer *et al.* 2008).

The influence of the intensity of agricultural use was also important in the floristic composition clusters (FCC) derived from K-means analysis. However, it was more evident in the top layer since there were no statistical differences between groups for the bottom layer (table 4). Perhaps the exclusion of species whose presence among fragments was sporadic (1-3 fragments) contributed to this situation because, although this applied to both layers, for the top layer, exclusion of species was only 12.6 % (22) and in the bottom layer it was 64 % (112). Thus, for the top layer Clusters 1 and 3 included almost all fragments (80 %) with more than 10 years without agricultural use and only one with U-3 (Table 4). As in the case of classification analysis, in Cluster-2 three types of use are present: all fragments with U-2, 90 % of those with U-3 and only 20 % with U-4. These proportions and significant differences in Cluster-2 with respect to Clusters 1 and 3, suggest that FCC of the top layer is a good indicator of the periods of fallow and the succession process.

Regarding the types of agricultural use of fragments and their relationship to 175 infrequent species, it stands out that a significant proportion (66.9 % = 117 species) was established in areas with a longer fallow period, U-3 and U-4. The remainder species are distributed almost equally in fragments with shorter fallow periods (16.6 % U-1 and U-2) and those (16.5 %) that inhabit sites with very different periods of fallow (namely with generalist habits). Surely, the high number of species in fragments with a longer fallow period is related to the development of a canopy that provides good vegetation cover. According to Sagar *et al.* (2012) cover in TDFs has an important effect on the species composition and diversity of the bottom layer, since it favors higher water retention, a decrease of water stress and an increase in productivity.

The peculiarities of the floristic composition of the fragments indicate that there is a species flow in the landscape of Zoyatlan. Taking into account the fallow periods and the behavior of species that are common to different layers, it turns out that this phenomenon happens when the parent species are present as well as where they are not part of the top layer; this process was evident also in the six fragments that did not have that layer (Appendix 2). In this dynamic 47 species belonging to 17 families were present, although Fabaceae, Asteraceae and Burseraceae were outstanding in providing the highest number of species. The flow that species showed between fragments suggests that the dynamics occur at different levels. On one hand, there are species steadily arriving to the fragments regardless their use type; in some cases even in spite of being represented as adults in only a few fragments. On the other hand, there are species that scarcely enter the fragments although there are adult individuals of them in at least five fragments (preferably in U-2 and U-3); furthermore, there is a minimum income of certain species exclusively in sites with U-4 (Appendix 2).

Negative impacts of fragmentation and chronic disturbance in population and landscape dynamics are diverse and act at different levels (Saunders *et al.* 1991, Singh 1998, Santos & Telleria 2006, Fisher & Lindenmayer 2007). While it might be expected that they could be evident in Zoyatlan due to fragmentation and chronic disturbance over more than five centuries, this was not conclusive because there are still many features in the vegetation that characterize the TDFs of the Balsas basin. The dynamics of vegetation regeneration, which has its best expression in fragments less suitable for the development of agriculture due to their inaccessibility was also evident; this suggests that agriculture and grazing has not exceed the threshold that would prevent the dynamics and reorganization of the socio-ecological system (Lunt & Spooner 2005, Cramer & Hobbs 2007). According to land use in 1998 (Cervantes *et al.* 2014) and the results of this research, the fragments with U-2, U-3 and U-4 are represented in nearly 600 ha. While this highlights the importance of the process at a landscape scale, the largest area occupied by shrubs and short trees (478 ha), suggests an impoverishment of the structure and composition of vegetation. However, the difference in the movement of species between fragments, points to species whose colonization habits lead the succession process, *e.g.*, species of the genus *Acacia*,

as well as those with specific requirements (U-3 and U-4) to ensure their establishment and development, *e.g.*, species of the genus *Lysiloma* All this is very useful for choosing species with the highest potential for environmental restoration actions; this was, in fact, the basic information for the establishment of plantations and agroforestry systems (Cervantes *et al.* 2001) that currently have successful results in Zoyatlan (Cervantes *et al.* 2014).

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Appendix 1. Plant species list of the agrarian community of San Nicolás Zoyatlan, Gro. México. F1S = Family with only one species; FER = number of fragments in which the species was recorded; ETB = species found in top and bottom layers; ETL = species found only in the top layer; GK = group (s) to which the species belong according to the K-means analysis for the bottom (B) and top (T) layer.

TAXON	F1S	FER	ETB	ETL	GKB	GKT
PTERIDOPHYTA						
LYCOPODIOPSIDA						
SELAGINELLACEAE						
Selaginella P. Beauv. sp.	Χ	12			1,2,3	
POLYPODIOPSIDA						
ANEMIACEAE						
Anemia adiantifolia (L.) Sw.	Χ	2				
PTERIDACEAE						
Cheilanthes skinneri (Hook.) R.M.Tryon & A.F.Tryon		1				
Cheiloplecton rigidum (Sw.) Fée		1				
Pellaea oaxacana Mickel & Beitel		8			1,3	
PINOPHYTA						
PINOPSIDA						
CUPRESSACEAE		10	V		1.0	1 0 0
Juniperus flaccida Schltdl.	Χ	10	Χ		1,2	1,2,3
MAGNOLIOPHYTA						
LILIOPSIDA ARECACEAE						
Brahea dulcis (Kunth) Mart.	Χ	4		Х		1 2 2
ASPARAGACEAE	^	4		^		1,2,3
Agave kirchneriana A. Berger		7		Χ		1,2,3
Agave tequilana F.A.C. Weber		2		X		1,2,3
Smilacina Desf. sp.		1		^		
BROMELIACEAE		,				
Hechtia mooreana L.B. Sm.	Χ	3	Χ			
COMMELINACEAE	~	Ü	,,			
Commelina L. sp.		1				
sp.1		1				
sp.2		1				
sp.3		3				
CYPERACEAE						
Cyperus hermaphroditus Standl.	Χ	1				
DIOSCOREACEAE						
Dioscorea L. sp1.		1				
Dioscorea L. sp2.		6			1,2,3	
IRIDACEAE						
Cipura Aubl. sp.		1				
Sessilanthera citrina Cruden		1				
Tigridia Juss. sp.		1				
LILIACEAE						
sp. 1	Χ	2				
ORCHIDACEAE						
Bletia Ruiz & Pav. sp.		5			1,3	
Malaxis urbana E.W. Greenw.		2				
POACEAE						
Andropogon gerardi Vitman		2				
Andropogon hirtifolius J. Presl		8			1,2	
Aristida gentilis Henrard		8			1,2,3	

TAXON	F1S	FER	ETB	ETL	GKB GKT
Aristida hitchcockiana Henrard		1			
Aristida ternipes Cav.		17			1,2,3
Bouteloua curtipendula var. caespitosa Gould & Kapadia		32			1,2,3
Bouteloua diversispicula Columbus		7			1,2
Bouteloua repens (Kunth) Scribn. & Merr.		18			1,2,3
Cenchrus longispinus (Hack. Ex Kneuch.) Fernald		8			1,3
Chloris virgata Sw.		2			, -
Eragrostis hypnoides (Lam.) Britton, Sterns & Poggenb.		4			1,2
Eriochloa nelsonii Scribn. & J.G. Sm		1			,
Hackelochloa granularis (L.) Kuntze		3			
Ichnanthus P. Beauv.sp.		2			
Lasiacis grisebachii Hitchc.		3			
Melinis repens (Willd.) Zizka		12			1,2
Oplismenus burmannii (Retz.) P. Beauv.		3			,
Paspalum conjugatum P.J. Bergius		1			
Paspalum convexum Flüggé		3			
Setaria geniculata P. Beauv.		5			1,2
Setaria lutescens (Stuntz) F.T. Hubb.		4			1,3
Setaria parviflora (Poir.) Kerguélen		3			.,-
Trachypogon secundus (J. Presl) Scribn.		1			
MAGNOLIOPSIDA					
ACANTHACEAE					
Carlowrightia arizonica A. Gray		2			
Dicliptera thlaspioides Nees		3			
Dyschoriste ovata (Cav.) Kuntze		4			1,3
Elytraria bromoides Oerst.		8			1,2,3
Ruellia hookeriana Hemsl.		5			1
sp. 1		8			1,2
Tetramerium nervosum Nees		9			1,3
AMARANTHACEAE					.,-
Gomphrena globosa L.	Χ	2			
ANACARDIACEAE					
Comocladia mollissima Kunth		1			
Pseudosmodingium Engl. sp.		1			
Rhus galeotti Standl.		4		Χ	
Rhus nelsonii F.A. Barkley		2		Χ	
ANNONACEAE					
Annona L. sp.	Χ	1		Χ	
APIACEAE		•		,,	
sp. 1	Χ	2			
APOCYNACEAE		_			
Gonolobus grandiflorus (Cav.) R. Br. ex Schult.		3			
Haplophyton cinereum Woodson		1			
Marsdenia lanata (Paul G. Wilson) W.D. Stevens		3			
Thevetia thevetioides (Kunth) K. Schum.		3		Χ	
sp. 1		2		. •	
ARISTOLOCHIACEAE		_			
Aristolochia mycteria Pfeifer		1			
Aristolochia orbicularis Duch.		6			1,2
		_			- , —
ASCLEPIADACEAE					

Appendix 1. Continuation.						
TAXON	F1S	FER	ETB	ETL	GKB	GKT
ASTERACEAE						
Acourtia dugesii (A. Gray) Reveal & R.M. King		2				
Ageratina tomentella (Scharad) R.M. King & H. Rob		8	Χ		1,2	1,2,3
Ageratum corymbosum Zuccagni		1				
Aldama dentata La Llave.		11			1,2	
Baccharis multiflora Kunth		1	Χ			
Barroetea subuligera (S.Schauer) A. Gray		11			1,2,3	
Bidens aurea (Aiton) Sherff		29			1,2,3	
Bidens Iemmonii A. Gray		2				
Brickellia cardiophylla B.L. Rob.		1				
Brickellia tomentella A. Gray		1				
Brickellia veronicifolia (Kunth) A. Gray		2				
Calea hypoleuca B.L. Rob. & Greenm.		6	Χ		1	
Cosmos sulphureus Cav.		14			1,2,3	
Dyssodia porophyllum (Cav.) Cav. var. cancellata		7			1,2	
(Cass.) Strother						
Dyssodia tagetiflora Lag.		26			1,2,3	
Eupatorium calophyllum (Greene) B.L. Rob.		1	X			
Eupatorium odoratum L.		1	Χ			
Eupatorium ovaliflorum Hook. & Arn.		1	.,	Χ		
Eupatorium L. sp1		2	Χ			
Eupatorium L. sp2		2		Χ		
Hieracium L. sp.		3			100	
Lasianthaea crocea (A. Gray) K.M. Becker		7	Χ		1,2,3	
Lasianthaea helianthoides DC.		1				
Melampodium americanum L.		1			1 2 2	
Melampodium divaricatum DC.		12			1,2,3	
Melampodium paniculatum Gardner		17			1,2	
Milleria quinqueflora L.		1 3	Χ			
Otopappus imbricatus S.F. Blake Pectis prostrata Cav.		ა 1	^			
Perymenium mendezii D.C. var. verbesinoides		2			Χ	
(D.C.) J.J. Fay		2			^	
Pinaropappus roseus Less.		1				
Porophyllum lindenii Sch. Bip.		2	Χ			
Porophyllum punctatum S.F. Blake		2	^			
Porophyllum tagetoides DC.		2				
Sanvitalia procumbens Lam.		34			1,2,3	
Senecio hederaefolius Hemsl.		3	Χ		1,2,5	
Senecio L.sp.		2	^			
Simsia amplexicaulis Pers.		24			1,2,3	
Simsia foetida S.F.Blake		6			1,2	
Stevia micrantha Lag.		3	Χ		.,_	
Stevia ovata Willd		6	Х		1,2	
Stevia subpubescens Lag.		1	. •		- /-	
Tagetes Iunulata Ortega		6			1,2,3	
Taraxacum officinale F.H. Wigg.		3			1,2	
Tridax mexicana A.M. Powell		11			1,2	
Trixis mexicana Lex var. mexicana		1				
Verbesina serrata Cav.		1				
Vernonia liatroides DC.		1	Χ			

Appendix 1. Continuation.					
TAXON	F1S	FER	ETB	ETL	GKB GKT
Vernonia salicifolia Less.		4	Χ		1,2,3
Viguiera dentata (Cav.) Spreng.		7	Χ		1,2,3
Viguiera oaxacana S.F. Blake		2	Χ		
Wedelia acapulcensis Kunth		2			
Zaluzania pringlei Greenm.		3		Χ	
Zinnia peruviana L.		7			1,3
Zinnia violacea Cav.		6			1
sp. 1		1			
BIGNONIACEAE					
Tecoma stans (L.) Kunth	Χ	22	Χ		1,2,3 1,2,3
BORAGINACEAE					
Bourreria ovata Miers		6	Χ		1,2,3
Cordia curassavica (Jacq.) Roem. & Schult.		7	Χ		1,3 2
Lennoa Lex. sp.		1			
Lithospermum L.sp.		1			
Nama L. sp.		2			
sp. 1		1	X		
Tournefortia hirsutissima L.		21	Χ		1,2,3 1,2
BURSERACEAE				.,	
Bursera ariensis (Kunth) McVaugh & Rzed.		2		Χ	10 100
Bursera bipinnata Engl.		11	X		1,3 1,2,3
Bursera copallifera (Sessé & Moc.) Bullock		25	X		1,2,3 1,2,3
Bursera glabrifolia Engl.		4	Χ		1,2,3
Bursera longipes Standl.		1		X	
Bursera mirandae C.A.Toledo		4		Χ	
Bursera morelensis Ramirez		2			
CACTACEAE Mammillaria Hayy an		3			
Mammillaria Haw. sp.			V		12 122
Opuntia atropes Rose Opuntia pumila Rose		13 12	Χ		1,3 1,2,3
CANNABACEAE		12			1,2,3
Celtis iguanaea (Jacq.) Sarg.	Χ	1		Χ	
CAPRIFOLIACEAE	^	'		^	
Valeriana L. sp.	Χ	1			
CARYOPHYLLACEAE	^	'			
Drymaria tenuis S. Watson	Χ	6			1,2
CONVOLVULACEAE	^	U			1,2
Ipomoea hederifolia L.		2			
Quamoclit coccinea Moench		1			
Evolvulus alsinoides L.		7			1,2
Ipomoea arborescens (Humb. & Bonpl. ex		24	Χ		1,2,3 1,2,3
Willd.) G. Don		- '	,,		1,2,0 1,2,0
Ipomoea capillacea G. Don		17			1,2,3
Ipomoea murucoides Roem. & Schult.		1			. 1-10
Ipomoea L. sp.1		2			
Ipomoea L. sp.2		1	Χ		
sp. 1		1	. •		
sp. 2		1			
CUCURBITACEAE		•			
sp. 1	Χ	2			
•					

TAXON	F1S	FER	ETB	ETL	GKB	GKT
ERYTHROXILACEAE						
Erythroxylum rotundifolium Lunan	Χ	1				
EUPHORBIACEAE						
Acalypha indica L.		10			1,2,3	
Acalypha L.sp.		1				
Acalypha subviscida S. Watson		2				
Croton ciliatoglandulifer Ortega		19	Χ		1,2,3	
Ditaxis Vahl ex A.Juss. sp.		3				
Euphorbia cumbrae Boiss		15			1,3	
Euphorbia cyathophora Murray		15			1,2,3	
Euphorbia dioscoreoides Boiss		2				
Euphorbia heterophylla L.		15			1,2,3	
Euphorbia hirta L.		8			1	
Euphorbia ocymoidea L.		12			1,2,3	
Euphorbia prostrata Aiton		24			1,2,3	
Euphorbia L. sp.		4			1,2	
Tragia nepetifolia Cav.		10			1,2	
FABACEAE					,	
Acacia bilimekii J.F. Macbr.		22	Χ		1,2,3	1.2.3
Acacia cochliacantha Humb. & Bonpl. ex Willd.		29	Χ		1,2,3	
Acacia farnesiana (L.) Willd.		12	Χ		1,2	- / - / -
Acacia pennatula (Schltdl. & Cham.) Benth.		17	Χ		1	1,2,3
Aeschynomene americana L.		4			1	- / - / -
Brongniartia podalyrioides Kunth		2			•	
Brongniartia Kunth sp.		1	Χ			
Calliandra houstoniana (Mill.) Standl.		6	Χ		1,2	1.2.3
Calopogonium mucunoides Desv.		1			- , _	- / - / -
Calopogonium Desv. sp		1				
Chamaecrista absus (L.) H.S. Irwin & Barneby		1				
Chamaecrista nictitans Moench		8			1,2,3	
Coursetia caribaea (Jacq.) Lavin		3		Χ	. 1210	
Crotalaria filifolia Rose		13		,,	1,2,3	
Crotalaria pumila Ortega		5			1,2	
Crotalaria sagittalis L.		3			.,_	
Dalea foliolosa (Aiton) Barneby var. citrina		6			1	
(Rydb.) Barneby		· ·			•	
Dalea hegewischiana Steud.		6			1,2	
Dalea humilis G. Don		5			1,2	
Dalea tomentosa var. psoraleoides (Moric.) Barneby		8	Χ		1,2	
Desmodium procumbens var. transversum		21	,		1,2	
(B.L. Rob. & reenm.) B.G. Schub.		21			1,2	
Desmodium sericophyllum Schltdl.		1		Χ		
Desmodium Desv. sp.		1		^		
Desmodium tortuosum (Sw.) DC.		11			1,2	
Eysenhardtia polystachya (Ortega) Sarg.		6	Χ		1,4	1,2,3
Galactia discolor Donn. Sm.		13	Λ.		1,2	1,2,0
Galactia discolor Bonn. 3111. Galactia P.Browne sp.		1			1,4	
Galactia F.Blowne sp. Galactia viridiflora Standl.		2				
Havardia acatlensis (Benth.) Britton & Rose		2	Χ			
		6	X		1	
Indigofera jamaicensis Spreng. Indigofera platycarpa Rose		2	X		1	

TAXON	F1S	FER	ETB	ETL	GKB	GKT
Indigofera L. sp.		1				
Lonchocarpus Kunth sp.		2		Χ		
Lupinus mexicanus Cerv.		1				
Lysiloma acapulcense (Kunth) Benth.		14	Χ		1,2,3	1,2,3
Lysiloma divaricatum (Jacq.) Benth		14	Χ			1,2,3
Macroptilium atropurpureum (L.) Urb.		7			1,3	
Macroptilium gibbosifolium (Ortega) A. Delgado		3				
Marina greenmaniana (Rose) Barneby var.		2				
muelleri Barneby						
Marina minutiflora (Rose) Barneby		2				
Marina scopa Barneby		3			1,3	
Marina spiciformis (Rose) Barneby		12			1,2	
Marina stilligera Barneby		3			•	
Marina unifoliata (B.L. Rob. & Greenm.) Barneby		4			1,3	
Mimosa affinis B.L.Rob.		21			1,2,3	
Mimosa albida Humb. & Bonpl. ex Willd.		1			-1-1-	
Mimosa polyantha Benth.		8	Χ		1,2	2,3
Nissolia Jacq. sp.		1			- , _	_/-
Pachyrhizus erosus (L.) Urb.		7			1,2,3	
Phaseolus Iunatus L.		3			-1-1-	
Piscidia grandifolia I.M.Johnst. var. glabrescens Sandwith	1	2		Χ		
Pterocarpus Kuntze sp.		1	Χ			
Rhynchosia minima (L.) DC.		22	,,		1,2,3	
Senna argentea (Kunth) H.S. Irwin & Barneby		4	Χ		1,2,3	
Senna racemosa (Mill) H.S. Irwin & Barneby		2	Χ		-1-1-	
Tephrosia vicioides Schltdl.		3				
Zornia gemella Vogel		3				
sp.1		1				
sp.2		1				
sp.3		1				
sp.4		1	Χ			
KRAMERIACEAE						
Krameria cistoidea Hook. & Arn.	Χ	1				
LAMIACEAE						
Asterohyptis mociniana Epling		6	Χ		1,2	
Salvia misella Kunth		14			1,2,3	
Salvia sessei Benth.		1				
Salvia L. sp.1		1				
Salvia L. sp.2		1	Χ			
Salvia L. sp.3		8			1,3	
Salvia L. sp.4		3			, -	
Salvia L. sp.5		2		Χ		
LOASACEAE						
Mentzelia hispida Willd.	Χ	4			1,2	
LYTHRACEAE						
Cuphea wrightii A. Gray	Χ	8			1,3	
MALPIGHIACEAE					.,-	
Bunchosia canescens (Aiton) DC.		7	Χ			2
Galphimia glauca Cav.		1		Χ		_
Gaudichaudia albida Schltdl. & Cham.		3				

TAXON	F1S	FER	ETB	ETL	GKB GKT
sp.2		1		X	
MALVACEAE		'		Λ.	
Anoda cristata (L.) Schltdl.		3			
Ayenia berlandieri S.Watson		2		Χ	
Heliocarpus velutinus Rose		6	Χ		1,2
Sida abutilifolia Mill.		18			1,2,3
Sida angustifolia Lam.		10			1
Sida anodifolia Fryxell		2			
Sida michoacana Fryxell		9			1,2
Triumfetta semitriloba Jacq.		1			
Waltheria americana L.		23			1,2
Waltheria conzattii Standl.		8	Χ		1,3
MYRTACEAE					
Psidium guajava L.	Χ	1	Χ		
NYCTAGINACEAE					
Commicarpus scandens (L.) Standl.		2			
sp.1		6			1,2
OLEACEAE					
Fraxinus purpusii Brandegee	Χ	9	Χ		1,2,3 1,2,3
ONAGRACEAE					
Hauya rusbyi Donn. Sm. & Rose	Χ	1			
OROBANCHACEAE					
Buchnera elongata Sw.		4			1,3
Castilleja arvensis Cham. & Schltdl.		3			
Castilleja tenuiflora Benth.		4			1,2
Lamourouxia rhinanthifolia Kunth		10			1,2,3
PASSIFLORACEAE					
Passiflora suberosa L.		3			
Turnera L. sp.		4			1,2,3
PHYLLANTHACEAE					
Phyllanthus L. sp.	Χ	1			
POLEMONIACEAE					
Loeselia coerulea G. Don	Χ	31			1,2,3
POLYGALACEAE					
Polygala albowiana Chodat		15			1,2,3
Polygala compacta Rose		5			1,2
Polygala serpens S.F. Blake		1			
RANUNCULACEAE					
Clematis L. aff. drummondii		2			
Clematis dioica L.		1			
Thalictrum steyermarkii Standl.		1			
RHAMNACEAE					
Colubrina macrocarpa G. Don		1		Χ	
Karwinskia humboldtiana (Schult.) Zucc.		1			
RUBIACEAE					
Crusea calocephala DC.		24			1,2,3
Crusea longiflora (Willd. ex Roem. & Schult.)		1			
W.R. Anderson					
Crusea setosa (M. Martens & Galeotti) Standl.		1			
& Steyerm					
Galium uncinulatum DC.		2			

Appendix 1. Continuation.					
TAXON	F1S	FER	ETB	ETL	GKB GKT
Gallium Mill. sp.		3			
Richardia tricocca Standl.		2			
RUTACEAE					
Ptelea trifoliata L.	Χ	1		Χ	
SAPINDACEAE					
Cardiospermum halicacabum L.	Χ	10			1,2,3
SAPOTACEAE					
Sideroxylon capiri (A. DC.) Pittier	Χ	1		Χ	
SOLANACEAE					
Datura stramonium L.		1			
Physalis L. sp.		1			
Solanum L. sp.		8	Χ		1,2
VERBENACEAE					
Lantana achyranthifolia Desf.		10			1,2,3
Lantana camara L.		3			1
Lippia alba (Mill.) N.E. Br. ex Britton & P. Wilson		1			
Lippia dulcis Trevir.		17	Χ		1,2,3 2,3
Lippia graveolens Kunth		16	Χ		1,2,3 1,2,3
Priva aspera Kunth		2			
Verbena elegans Kunth		2			
VITACEAE					
sp.1	Χ	1			

Appendix 2. Species from the top layer recognized as new arrivals in some sampling sites. PFR = presence of the species in the fragments: 1 = 1 to 3; 2 = 4 to 8; 3 = 9 to 18; 4 = 19 to 27; 5 = 28 to 34. Use type: U-1 = agriculture without residual vegetation; U-2 = agriculture with residual vegetation; U-3 = agriculture vegetation U-3 = ag

PFR	FAMILY/SPECIE	FRAGMENT NUMBER																												
		1		3 U-1		20 2	2 9	10	11		19 23 J-2	24	25	28	31 3	33	4	6 12	2 13 U- 3		16	1826	30	7 8	17 2	21 27 U-		32 3	34 3	5 36
	Anacardiaceae																													
2	R. galeotti																						Χ							Χ
	Asteraceae																													
2	C. hypoleuca														Χ							Χ	Χ		Χ					
2	L. crocea									Χ											Χ					Χ			Χ	
2	V. dentata							Χ				Χ	Χ		Χ							Χ	Χ			Χ	Χ			
1	Eupatorium sp2														Χ															
1	O. imbricatus																						Χ							
1	P. mendezii var. verbesinoides																												Χ	
1	S. hederaefolius																				Χ									
1	S. micrantha																													Χ
	Bignoneaceae																													
4	T. stans			Χ								Χ																		
	Boraginaceae																													
4	T. hirsutissima				Χ	X	(Χ		Χ	Χ	Χ	Χ	Χ	Χ	Χ	Χ					Χ				Χ	Χ	Χ	Χ	
2	B. ovata																								Χ					
2	C. curassavica									Χ										Χ							Χ			
	Bromeliaceae																													
1	H. mooreana																					Χ								
	Burceraceae																													
4	B. copallifera						Χ				Χ					Χ	Χ	Χ									Χ			
3	B. bipinnata									Χ															Χ					
2	B. mirandae																						Χ				Χ			
1	B. morelensis																												Χ	(X
	Cactaceae																													
3	O. atropes							Χ									Χ													
-	Convolvulaceae																													
4	I. arborescens			Χ		Χ				Χ						Χ						Χ			Χ					
•	Cupresaceae			,,		,,				,,						, ,						,			,,					
3	J. flaccida															Χ														
Ū	Euphorbiaceae															, ,														
4	C. ciliatoglanduliferus					Χ	Χ	Χ	Χ	Χ							Χ	Χ	Χ		Χ		Χ	Χ				Χ	χ	(X
7	Fabaceae					^	/	/	/	/							^	^	^		/		/	/				^	,	. ,
5	A. cochliacantha		Υ	Χ	Υ	Υ	Χ							Χ		Χ		Χ				Χ		Χ			Χ			Χ
4	A.bilimekii		^	^	X	/	٨					Υ	Χ	^		^		^				^		^			/			Λ
3	A. farnesiana	Υ	Χ	Υ	٨		Υ	Υ	Χ	Υ	Χ		^			Χ													Χ	
3	A. pennatula	X		٨			٨	^	X	٨	Λ					^													^	
	L. acapulcense	٨							^														Χ	Χ		Υ				
3	L. divaricata											Χ									Χ		X	X		X X		Χ		
												^									^		X	^		^		^		
2	C. houstoniana			V												V						V		V						
2	D. tomentosa var. Psoraleoides			Χ												Χ					Χ	Χ	Χ	Χ						
2	E. polystachya																													
2	I. jamaicensis	V								Χ								Χ			Χ			V	Χ					\/
2	M. polyantha	Χ											\/							Χ				Χ					V	Χ
1	C. caribaea												Χ										\/						Χ	
1	H. acatlensis									.,													Χ							
1	Lonchocarpus sp.									Χ																				
1	P. grandifolia												Χ																	
1	S. racemosa																										Χ			
	Lamiaceae																													
2	A. mociniana													Χ								Χ	Χ				Χ		X	
1	S. sessei																												Χ	
1	Salvia sp1																									Χ				

Appendix 2. Continuation.

PFR	FAMILY/SPECIE	FRAGMENT NUMBER																						
		1	2 U	3 5 I-1	20 2	22 9	10 11		19 23 U-2	24	25 28	31	33 4	6 1	2 13 U-3		6 18 26	30 7	8 1		27 29 J-4	32	34 3	536
	Malpighiaceae																							
2	B. canescens																				Χ			
	Malvaceae																							
2	W. conzattii										Χ			Χ				Χ	Χ	Χ				Χ
2	H. velutinus																						Χ	
1	A. berlandieri																				Χ			
	Solanaceae																							
2	Solanum sp.						Χ	Χ						Χ							Χ			
	Verbenaceae																							
3	L. dulcis				Χ	Χ			Χ	Χ	Χ	Χ	Χ				Χ	Χ	X	(Χ	Χ)	ХХ
	Undetermined																							
2	Indeterminada 1									Χ			>	X		>	(X	(
2	Indeterminada 9												Χ										Χ	Χ
1	Indeterminada 3													Χ		>	<							