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Research Article

High resilience of herpetofaunal communities in a human-modified tropical dry forest landscape in western Mexico

Ireri Suazo-Ortuño[1]*, Javier Alvarado-Díaz[1], Eduardo Mendoza[1], Leonel López-Toledo[1], Nancy Lara-Uribe[1], Cesar Márquez-Camargo[1], José Gil Paz-Gutiérrez[1] and Jorge David Rangel-Orozco[1]

[1]Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo. Av. San Juanito Itzícuaro s/n, Col. Nueva Esperanza, Morelia, Michoacán, CP 58330, México.
*Corresponding author: ireri.suazo@gmail.com

Abstract

Secondary forests are replacing mature primary forests in the tropics because of increasing demand for agricultural land to support the growing human population. It is important to determine the potential of these secondary forests to support old-growth forest species, particularly threatened animal groups such as reptiles and amphibians. Moreover, existing studies are biased towards tropical rain forests, even though tropical dry forests (TDF) are comparatively more threatened. Here we examine how different TDF successional stages support old-growth forest species of amphibians and reptiles in the Chamela region, western Mexico. Over the course of two years we conducted seven surveys for amphibians and reptiles in 15 one-ha plots representing four different stages of the succession chronosequence of the TDF, ranging from pasture to old-growth forest. We found that anurans, lizards and snakes did not differ greatly in abundance and species richness among vegetation successional stages. Moreover, dominant species were shared among most of the vegetation stages, indicating low habitat specialization. Herpetofauna species composition did not differ among vegetation stages, and species turnover among stages was relatively low. These results differ greatly from those found in some tropical rainforest sites, where characteristics of herpetofauna communities differ markedly among vegetation successional stages. Our results suggest that secondary TDF in human-dominated landscapes might support substantial reptile and amphibian diversity.

Key words: Herpetofauna; tropical dry forest; successional stages; tropical diversity.

Resumen

Los bosques secundarios están reemplazando aceleradamente a los bosques tropicales maduros debido al sostenido incremento de la demanda de tierras agrícolas por la creciente población humana. Resulta esencial evaluar el potencial de la vegetación secundaria para mantener especies asociadas a los bosques maduros, en especial en el caso de grupos de animales amenazados, como anfibios y reptiles. Actualmente, existe un sesgo en los estudios existentes hacia las selvas tropicales lluviosas, a pesar que son las selvas secas (SS) las que están más amenazadas. En este estudio evaluamos el papel que diferentes estadios sucesionales de la SS juegan para mantener la diversidad de anfibios y reptiles presente en la región de Chamela, en la costa Oeste de México. En el transcurso de dos años realizamos siete muestreos de la herpetofauna presente en 15 parcelas de una hectárea que representaban distintos estadios de la sucesión, desde pastizales para ganado hasta bosque maduro. En general, no encontramos contrastes importantes en la abundancia y riqueza de especies entre estadios sucesionales. Asimismo, las especies dominantes se compartieron entre la mayoría de los estadios sucesionales indicando la existencia de una baja especialización de hábitat entre las especies. Como consecuencia de esto, los distintos estadios sucesionales no fueron distinguibles en términos de su herpetofauna y el reemplazo de especies entre parcelas fue bajo. Estos resultados contrastan fuertemente con lo encontrado en algunas selvas húmedas en donde la herpetofauna difiere marcadamente entre estadios sucesionales y sugieren que los paisajes de selva seca influenciados por la actividad humana pueden ser capaces de mantener una importante diversidad de anfibios y reptiles.

Palabras clave: Herpetofauna; selvas secas; estadios sucesionales; diversidad tropical.

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Introduction

Secondary forests are rapidly replacing mature primary forests in the tropics due to increasing demand for agricultural land to support the growing human population[1, 2]. It is estimated that currently degraded and secondary forests represent as much as five of the 11 million km^2 remaining of tropical forests worldwide [3]. Of great concern is the potential for human-dominated tropical landscapes to support a representative proportion of their original biodiversity, especially that associated with old-growth forest [1, 4-7], and how the different vegetation successional stages can support diversity of highly threatened animals such as amphibians and reptiles [8-11.]. Available evidence suggests that richness of tropical amphibian and reptile species is lower in vegetation successional stages than in old-growth forest [10-14]. However, the scant number of studies addressing this issue, and the use of contrasting sampling designs and response metrics (diversity vs. similarity), weaken generalization [2, 5, 10]. Moreover, current evidence mostly comes from studies conducted in tropical rain forests, despite the fact that tropical dry forests likely face a greater threat due to current land-use and cover change patterns [15].Therefore, there is an urgent need to assess how conversion of old-growth forests to vegetation successional stages will affect amphibian and reptiles diversity in tropical dry forests [7, 10].

In this study we examine the role that vegetation successional stages play in supporting amphibian and reptile species in a dry tropical forest in the western coast of Mexico. This region supports a rich herpetofauna, with a high level of endemism, in one of the most important remnants of dry forest in Mesoamerica [16]. Specifically, we address the following questions: a) Do different vegetation successional stages in tropical dry forest differ in habitat characteristics that can affect amphibian and reptile communities? b) To what extent do richness and diversity of amphibian and reptile communities differ among these different successional stages? c) What is the magnitude of the turnover of species of amphibians and reptiles among the different vegetation successional stages? and d) Are there species whose occurrence is associated primarily with old-growth forest or other vegetation successional stage? We expect to observe more marked differences among vegetation successional stages in amphibian communities than in reptile communities because amphibians are more affected by changes in direct solar radiation, air temperature and environmental humidity [17].

Methods

Study Area

This study was conducted in the Chamela region (La Huerta municipality) and the Chamela-Cuixmala Biosphere Reserve, both located in the western coast of Jalisco, Mexico (19°30′ N, 105′ 03′W) (Fig. 1). Mean annual temperature in the region is 25.1 °C and average annual rainfall is 788 mm (range: 384 – 1,392 mm). The predominant vegetation is tropical dry forest (TDF), with a canopy height ranging from 5 to 10 m. Strips of taller and denser vegetation (semi-deciduous forest) run along rivers crossing the TDF [18]. The rainy season lasts from July to October and provides 80% of the annual precipitation [18]. In the dry season most of the plants (> 95%) drop their leaves. Tree species richness in the Chamela-Cuixmala TDF exceeds 200 species [18]. Our study area is part of the Mexican Pacific lowlands, which are a hot spot of herpetofaunal species richness and endemism, supporting one third of the species of amphibians and reptiles known in Mexico [19].

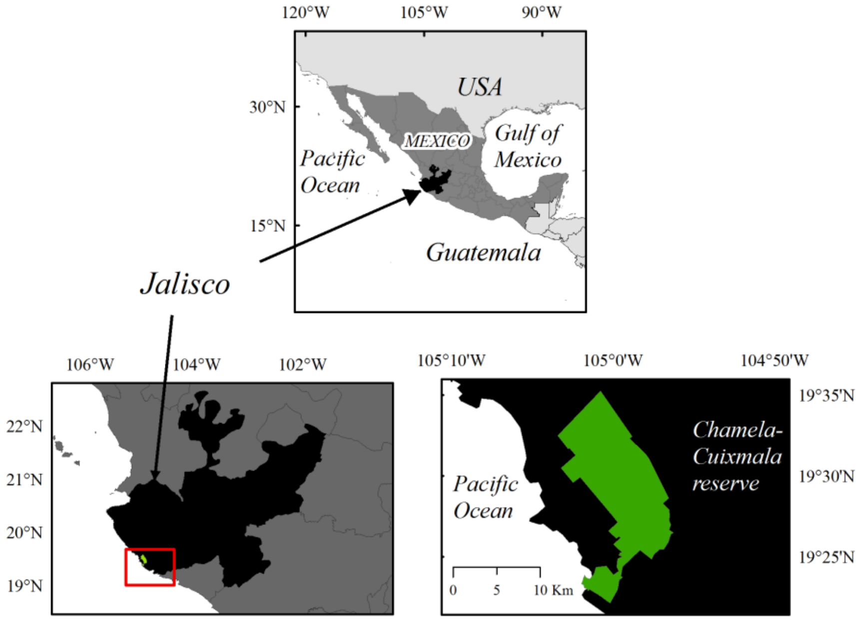

Fig. 1. Location of the study area in the region of Chamela in the coast of Jalisco, Mexico.

Human activities, particularly since the 1960s, have transformed the landscape in the region into a complex mosaic of land cover types and uses. Predominant among these uses are cattle pasture and subsistence crops (corn, squash, and bean) mixed with shrubs and isolated trees [20]. Remaining vegetation consists of a mixture of old forest patches and secondary vegetation in different stages of succession. Early stages of the successional process are usually dominated by herbs and shrubs [21]. Roughly, 25 - 45% of the landscape in the region corresponds to vegetation in different successional stages and 55 - 75% to old-growth forest [22].

Study system

We selected a total of 15 one-ha plots, which were part of a long-term project (MABOTRO) studying succession in tropical dry forest [23]. Plots were selected to represent the following five vegetation stages: pasture, early forest (five to six years of abandonment), young forest (8 - 10 years of abandonment), intermediate forest (15 - 17 years of abandonment), and old-growth forest (OGF, i.e., forest showing no evident signs of human disturbance) (Appendix 1). We had three replicates for each vegetation successional stage. Plots were located a minimum of one km from each other. Time of abandonment was estimated based on interviews with local people. We included only sites where forest succession was not interrupted [21-23].

We surveyed each of the 15 one-ha plots seven times from August 2009 to July 2011. Five of these surveys were made during the rainy season (July-October) and two in the dry season (November-June) in order to incorporate all possible environmental variations. Surveys were made during the day (9:00-16:00) and night (21:00-04:00) by the same team of five people who were familiar with the local herpetofauna. Search for animals was time-constrained (three hours in the morning and three hours at night per site) and was carried out by visually searching vegetation and the ground surface, including lifting cover objects (rocks, logs, and debris). We captured all detected individuals and identified them to species level. To avoid counting the same individual twice during the two-year study period, we clipped toes in frogs and lizards and ventral scales in snakes. All animals were released in the same site where they were captured. We completed a total search effort of 126 person-hours (3 plots x 7 surveys x 5 people x 1.2 hours) in each vegetation successional stage.

To compare habitat characteristics among different vegetation successional stages we measured tree density and canopy and litter cover, following the methods described in Suazo-Ortuño et al. [20]. These habitat variables have been shown to affect amphibian and reptile richness [24]. Differences among habitat attributes were tested using ANOVA and when appropriate, post-hoc Tukey tests.

Sampling completeness of the surveyed herpetofaunal communities

We calculated estimators of species richness for each forest succession stage using two non-parametric methods: ACE and Chao1 [EstimateS, 25]. To assess sampling completeness for each vegetation successional stage, we calculated the percentage that the number of species recorded represented of the corresponding estimated species richness [26].

Comparison of herpetofauna species composition and diversity among different vegetation successional stages

We calculated species abundance, richness and diversity (Shannon-Wiener index) for the different successional stages using the total number of anuran, lizard and snake individuals recorded over the entire study. We conducted comparisons among successional stages using general linear models (GLM's) in R 2.11.1 [27]. For count data (e.g., species richness and abundance) we used poisson errors and logarithmic link function or quasi-poisson errors when evidence of overdispersion was found in the fitted model [27, 28]. Significance of deviance explained by each model was assessed using Chi-square tests [27, 28]. Analyses were made for each group (anurans, lizards and snakes) independently and for all the species pooled (i.e., herpetofauna).We also built rank-abundance curves (log abundance of each species vs. rank within the community) for anurans, lizards, snakes, and for the three groups lumped together. We applied ANCOVA to test for differences in slopes among vegetation successional stages [29, 30].

Species association with vegetation successional stages

We used two complementary approaches to determine the degree of association of amphibian and reptile species with specific vegetation stages. First, we calculated an association index (IA) to conduct paired comparisons to compare the observed abundances of each species between most contrasting vegetation stages (pasture vs. secondary forest, secondary forest vs. OGF and pasture vs. OGF) [19, 31]. We calculated the average abundance of each species over the three secondary forest successional stages (early, young, intermediate) to make it more comparable to abundances recorded in OGF and pasture. We calculated IA using the following equation:

$$IA = (CR1 - CR2)/(CR1 + CR2)$$

where CR1 and CR2 are the corresponding abundances of each of the pairs of successional stages compared. This index ranges from −1 (highest association to CR2) to +1 (highest association to CR1). Species with an IA value equal to zero were considered neutral in their preference for the vegetation successional stages compared. To assess the statistical significance of differences in abundance, we used a 2×2 Chi-square test. We included only species with a total abundance greater than six individuals and applied Yate’s correction when needed [32]. Second, we calculated Dufrêne and Legendre’s [33] IndVal index. This index combines species mean abundances with frequency of occurrence within groups (in this case vegetation successional stages). A high indicator value is obtained by a combination of a large mean abundance within a vegetation successional stage compared to the other vegetation stages (specificity) and presence in most sites of that group (fidelity). For examples of how this index is calculated see [33]. We used R software [34] and package labdsv to calculate IndVal values and followed Borcard et al. [35] to assess their statistical significance (i.e., the probability of obtaining by chance as high an index value as observed) by means of permutation tests. We calculated IndVal index separately for anurans, lizards and snakes.

We used non-metric multidimensional scaling (NMDS) to represent, in a reduced dimensional space, the ordering relationships among vegetation successional stages as a function of anuran, lizard and snake species composition and abundance. We also applied NDMS pooling all the species together. We used library Vegan of program R to calculate dissimilarities among communities using the Chao index. The resulting dissimilarity matrix was used together with function metaMDS to conduct the NMDS. Function metaMDS automatically transforms the species abundance data to improve the quality of ordinations and uses random starts to iteratively find the best possible solution (i.e., that with the least stress).To determine whether vegetation successional stages explained a significant amount of variation in the composition of herpetofaunal communities, we applied permutational manova (function Adonis) included in the R library Vegan.

Partitioning of species richness among and within vegetation successional stages

To assess to what extent differences in species composition among and within vegetation successional stages contributed to the overall species richness, we carried out a diversity partition analysis [36]. We used program PARTITION 3.0 [37] to calculate α-diversity (per plot) and species turnover within vegetation successional stages (β_1-diversity) and among vegetation successional stages (β_2-diversity). We carried out individual-based additive partitioning of species richness

independently for anurans, lizards and snakes. To complement this analysis we applied the method proposed by Carvalho et al. [38] to determine the relative roles of changes in species identity and richness among forest successional stages, to generate beta-diversity patterns. We used the following equation to calculate the Jaccard dissimilarity measure: $\beta_{cc}=\frac{b+c}{a+b+c}$
Where a = number of shared species between two sites, and b and c are species exclusive to each site [38]. We used the following equations to calculate the number of substitutions and the absolute difference in species richness between pairs of sites: $\beta_{-3}=2*\frac{\min(b,c)}{a+b+c}$ $\beta_{rich}=\frac{|b-c|}{a+b+c}$. We conducted all the calculations using packages Vegan and MBI for R. For these calculations we pooled all the species together.

Results

Differences in habitat characteristics among vegetation successional stages

There were significant differences in tree density ($F_{4/10}$ = 10.50, P < 0.001) and both canopy ($F_{4/10}$ = 13.23, P < 0.001) and litter ($F_{4/10}$ = 9.63, P < 0.001) cover among vegetation successional stages (Fig. 2). Tukey tests (alpha = 0.05) indicated that pastures had the lowest values for the three variables. There was a trend for canopy cover to increase with successional stages, but differences among more advanced stages were not significant statistically. Similarly, litter cover increased in more advanced successional stages, but differences were not evident among the three more advanced successional stages (YF, IF and OGF). Finally, pastures and early forest showed the lowest tree density, whereas young forest showed medium densities and intermediate and OGF forests showed the highest tree densities (Fig. 2).

Sampling completeness and general characteristics of the surveyed herpetofaunal communities

Overall, we recorded the presence of 1,901 individuals belonging to 50 species and 19 families (Appendix 2, Fig. 3). Hylidae was the most speciose and abundant family of anurans with seven species (50% of all anuran species recorded) and 480 individuals (62.2% of the total abundance of anurans). Phrynosomatidae was the most speciose and abundant family of lizards, with four species (28.5% of the total of lizard species recorded) and 448 individuals (41.3% of the total abundance of lizards). Colubridae was the most speciose and abundant family of snakes with 10 species (45.4% of all snake species) and 37 individuals (45.6% of the total abundance of snakes). Overall, the Largescale Spiny Lizard (*Sceloporus utiformis*) was the most abundant species (325 individuals), followed by the Shovelhead Tree Frog (*Diaglena spatulata*) (254 individuals), the Clouded Anole (*Anolis nebulosus*) (240 individuals) and the Marbled Toad (*Incilius marmoreus*) (196 individuals). The most abundant snake was the Mexican Vine Snake (*Oxybelis aeneus*) (10 individuals) (Appendix 2). Sampling completeness of anurans ranged from 65% (intermediate forest) to 100% (pastures, early and young forest; Table 1). Sampling completeness of lizards varied from 82% (young forest) to 100% (pastures, early forest and OGF; Tab. 1). Sampling completeness of snakes varied from 21% (pastures) to 76% (OGF; Table 1). When considering anurans, lizards and snakes together as a single group, sampling completeness ranged from 46% (intermediate forest) to 97% (pastures; Table 1).

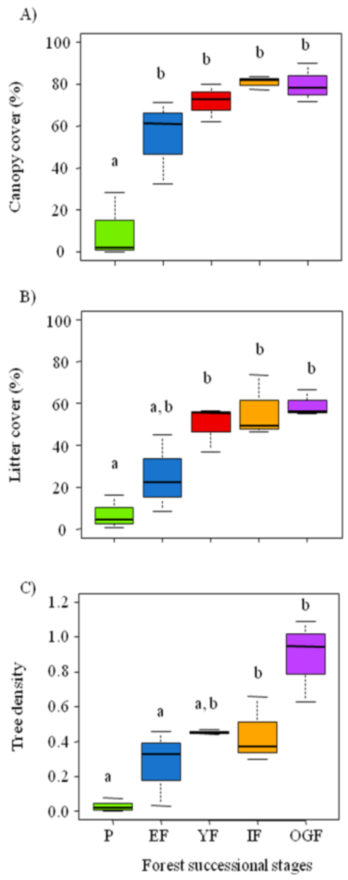

Fig. 2. Differences in habitat attributes among vegetation successional stages of the tropical dry forest in the Chamela region in the coast of Jalisco, Mexico. P= pasture, EF= early forest, YF= young forest, IF= Intermediate forest and OGF= old-growth forest.

Fig. 3. A sample of the species recorded in the different vegetation successional stages surveyed in the Chamela region, coast of Jalisco, Mexico. A) Largescale Spiny Lizard, B) Shovelhead Treefrog, C) Clouded Anole, D) Marbled Toad, E) Philippi's Snail-eating Snake, F) Central American Tree Snake. (Pictures courtesy of Jonatan Torres).

Table 1. Number of species observed, estimated number of species and sampling completeness of herpetofaunal communities in different vegetation successional stages in the tropical dry forest of the Chamela region, Jalisco, México.

Group and successional stages	Number of observed species	ACE	Chao1	Completeness (%)
Anurans				
Pasture	12	12	12	100 - 100
Early forest	9	9.29	9	97 - 100
Young forest	11	11.28	11	97 - 100
Intermediate forest	10	15.4	13	65 - 77
Old-growth forest	8	11.98	11	67 - 73
Overall	15	15.83	15.43	95 - 97
Lizards				
Pasture	10	10	10	100 - 100
Early forest	8	8	8	100 - 100
Young forest	12	14.56	12.75	82 - 94
Intermediate forest	12	13.16	13	91 - 92
Old-growth forest	10	10.75	10	93 - 100
Overall	14	17	14.5	82 - 96
Snakes				
Pasture	11	21.5	35.5	21 - 36
Early forest	7	15.75	10.33	44 - 68
Young forest	11	28.75	25	38 - 44
Intermediate forest	13	34.67	24.25	37 - 54
Old-growth forest	15	22.5	19.67	67 - 76
Overall	25	26.92	25.55	93 - 98
Total				
Pasture	33	37.62	33	85 - 97
Early forest	24	28.77	28	80 - 82
Young forest	34	45.52	51	64 - 73
Intermediate forest	35	67.64	71.5	46 - 50
Old-growth forest	33	42.63	44.58	67 – 70
Overall	54	54.64	52.25	93 – 98

Comparison of structure and diversity of herpetofaunal communities among vegetation successional stages

We did not find differences in species richness and abundance of anurans, lizards and snakes among vegetation successional stages (Table 2). However, we found differences in species diversity among vegetation successional stages in anurans and snakes. These differences were due to the existence of a lower diversity in the early forest stage than in the other successional stages in both groups. The slope of the rank-abundance curves for anurans differed significantly among vegetation successional stages ($F_{4,35}$ = 3.56, P = 0.01). The steeper slope (± SE) corresponded to OGF (b = -0.49 ± 0.13), followed by that of intermediate forest (b = -0.47 ± 0.12), early forest (b = -0.44 ± 0.05), young forest (b = -0.34 ± 0.11) and pasture (b = -0.31 ± 0.11) (Fig.

4a). Therefore, species dominance was greater in OGF, whereas species evenness was greater in pastures. *I.marmoreus* and *D.spatulata* were the most abundant anuran species in the OGF, accounting for approximately 70% of the 59 individuals recorded in this forest stage. *I. marmoreus* was also the most abundant anuran in pastures, followed by the Lowland Burrowing Tree Frog (*Smilisca fodiens*); together these species accounted for approximately 50% of the 196 individuals recorded in this forest stage (Fig. 4a). There were no significant differences in the slope of the rank-abundance curves for lizards among forest successional stages ($F_{4,46}$ = 1.56, P > 0.05; *b* = -0.15), indicating that species dominance was similar (Fig. 4b). The slope of the rank-abundance curves for snakes differed among successional stages ($F_{4,44}$ = 2.9, P = 0.03). It was steeper in pastures (*b* = -0.10 ± 0.06), than in early forest (*b* = -0.07 ± 0.03), young forest (*b* = -0.08 ± 0.06), OGF (*b* = -0.07 ± 0.06) and intermediate forest (*b* = -0.03 ± 0.05) (Fig. 4c). The higher species dominance observed in pastures was due to a high abundance of the Southwestern Cat-eyed Snake (*Leptodeira maculata*) and the Night Snake (*Hypsiglena torquata*), which represented 40% of the total number of individual snakes.

Table 2. Results of generalized linear models applied to compare abundance and species richness and diversity of anurans, lizards and snakes among vegetation successional stages of the tropical dry forest of the Chamela region, Jalisco, México.

	Abundance		Richness		Diversity	
	χ^2	P	χ^2	P	$F_{4,10}$	P
Anurans	3.3	0.49	3.3	0.5	10.9	<0.01*
Lizards	3.4	0.48	2.9	0.58	1.5	0.25
Snakes	5.1	0.27	2.8	0.58	3.3	0.05*

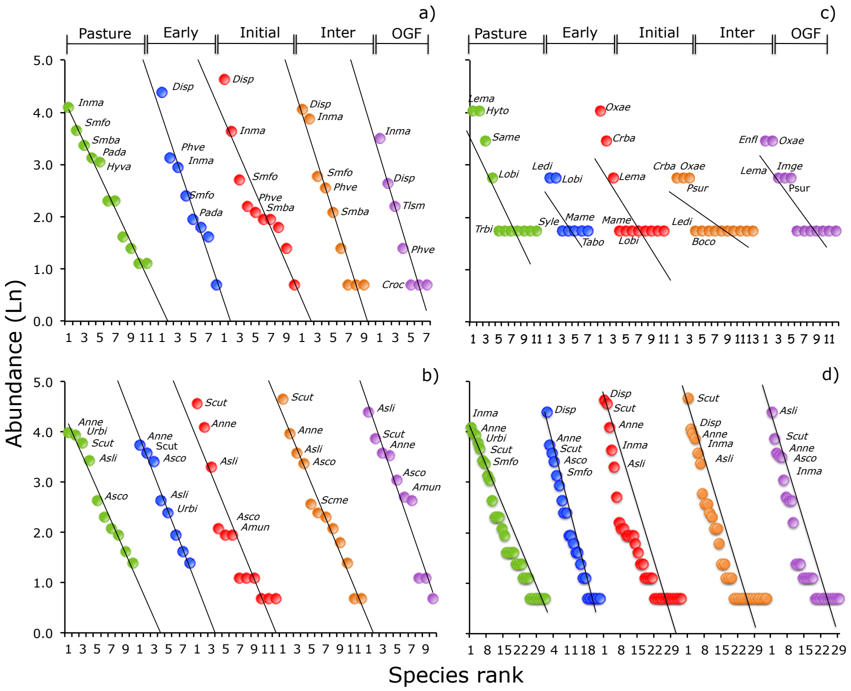

Fig. 4. Rank-abundance curves for herpetofaunal communities among vegetation successional stages of the tropical dry forest in the Chamela region, coast of Jalisco, Mexico. Charts correspond to a) anurans, b) lizards, c) snakes and d) all species.

Comparisons conducted by lumping species from all groups together showed the existence of differences in abundance among successional stages ($F_{4,141}$ = 8.6, P <0.001), but not in species richness and diversity. There were significant differences among the slopes of the rank-abundance curves for the different vegetation successional stages ($F_{4,141}$ = 3.4, P = 0.01; Fig. 4d). The steeper slope (± SE) was found for early forest (*b* = -0.16 ± 0.013), while the old growth forest had the lesser slope (*b* = -0.12 ± 0.02). The lizard *S. utiformis* and the frog *D. spatulata* were the most abundant species, especially at intermediate, initial and early forest, respectively (Fig. 4d).

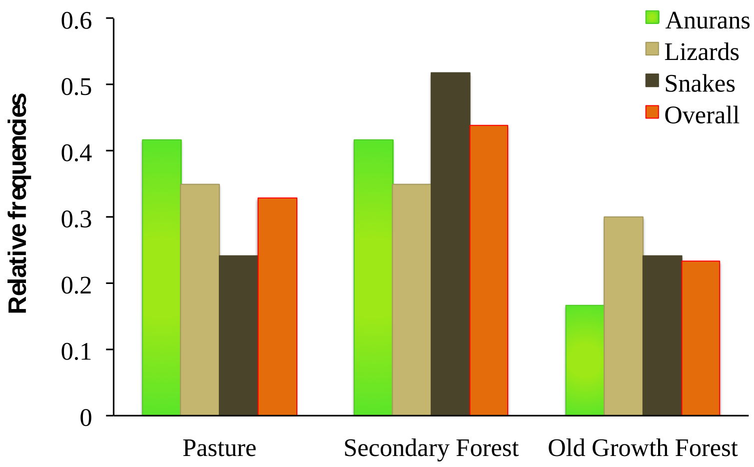

Fig. 5. Relative frequencies of anurans, lizards, snakes and herpetofauna (all three groups lumped together) in pastures, secondary forests and old-growth forest from the Chamela region, coast of Jalisco, Mexico.

Species association with different vegetation successional stages

Three of a total of 14 anuran species presented a positive association with pastures (Appendix 3, Fig. 5), but the abundance of only two of these species was significantly higher than in secondary forests or OGF (Appendix 3, Fig. 5). On the other hand, abundance of the Dwarf Mexican Tree Frog (*Tlalocohyla smithii*) was significantly higher in OGF than in other successional stages. Moreover, seven anuran species presented a positive association with both pastures and secondary forest stages, but only the abundance of five species was significantly higher than in OGF (Appendix 3, Fig. 5). Three species of anurans presented a positive association with both OGF and secondary forest stages, but abundance only of *D. spatulata* was significantly higher than in pastures. In the case of lizards, three out of a total of 14 species had a positive association with secondary forest, but none of them had abundances significantly higher than in other successional stages. Five species of lizard showed a high association with both secondary forest and pastures, but only two of them were significantly more abundant in these successional stages than in OGF (Appendix 3, Fig. 5). Three lizard species: Giant Whiptail (*Aspidoscelis communis*), Rainbow Ameiva (*Holcosus undulatus*) and *S. utiformis* were highly associated with both OGF and secondary forest successional stages and occurred in significantly higher abundances than in pastures (Appendix 3, Fig. 5). Three lizard species presented a high association with both OGF and pastures, but only two of these species presented abundances significantly higher than in secondary forests (Appendix 3, Fig. 5). In the case of snakes, six of 22 species were associated with secondary forest successional stages, but none presented significantly higher abundances than OGF or pastures (Appendix 3, Fig. 5). Three snake species were positively associated with OGF, but none presented significantly higher abundances than pastures and secondary forest successional stages (Appendix 3, Fig. 5). Two snake species presented an association with pastures, but abundances were not significantly higher (Appendix 3, Fig. 5). When species-habitat relationships were examined to a greater detail, we found that only two lizard species presented a close association with specific successional stages. The Tropical Tree Lizard (*Urosaurus bicarinatus*) was associated with pastures (IndVal = 0.6849, P = 0.012) and Lane's Leaf-toed Gecko (*Phyllodactylus lanei*) with OGF (IndVal = 0.6154, P = 0.033).

NMDS analysis showed that no clear segregation existed among the different vegetation successional stages, both when using abundance data for each group (anurans, lizards and snakes) and when using herpetofauna data (Appendix 4, Fig. 6). These results were in agreement with MANOVA tests in which only anurans and herpetofauna differences among vegetation stages were significant (P = 0.06 and P = 0.08, respectively).

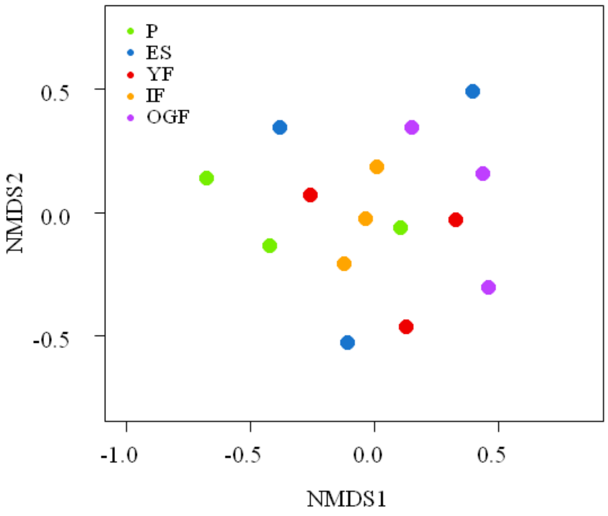

Fig. 6. Non-metric multidimensional scaling (NMDS) of differences in herpetofauna (anurans, lizards and snakes lumped together) among vegetation successional stages of tropical dry forest at Chamela region, coast of Jalisco, Mexico.

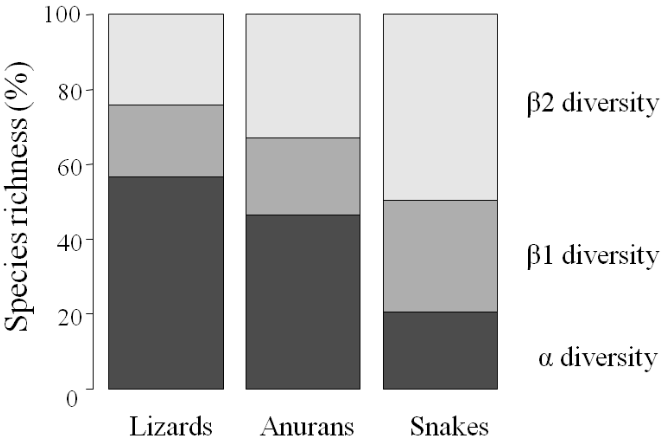

Fig. 7. Diversity (species richness) additive partitioning among sites (β_1) and vegetation successional stages (β_2) for each analyzed group (anurans, lizards and snakes

Partitioning of species richness among and within vegetation successional stages

Combined α-diversity (plot species richness) and β1-diversity (species turnover within forest stages) accounted for the greatest proportion (> 68%) of the observed variation in species richness of lizards and anurans. Therefore, β_2 (species turnover among forest stages) was in both cases relatively small (Fig. 7). In the case of snakes, β_2 was higher and accounted for as much as ca. 50% of overall species richness (Fig. 7). Additional examination of β-diversity, using only species presence data, showed that its magnitude was in general moderate (0.4271 - 0.6587, Tab. 3). Lower β-diversity was observed between pasture and intermediate forest and higher between early forest and old-growth forest (Tab. 3). In general, β-diversity was more related to changes in species identity than to changes in species richness (Tab. 3).

Table 3. Average β-diversity within and among successional stages and the proportion of β-diversity associated with changes in species composition (βcc) and species richness (βrich). Values of βcc and βrich for a given succesional stage do not add to the corresponding total β-diversity because they are averages. P = pasture, EF= early forest, YF = Young forest, IF= Intermediate forest and OG= Old growth forest.

Successional stage	P	EF	YF	IF	OG
A) Total β-diversity					
P	**0.5386**	0.5906	0.5990	0.5329	0.6465
EF		**0.6315**	0.6342	0.6288	0.6587
YF			**0.4522**	0.5563	0.6317
IF				**0.4502**	0.5525
OG					**0.4271**
B) Change in species composition (βcc)					
P	**0.3102**	0.3269	0.5091	0.4534	0.5153
EF		**0.2802**	0.4213	0.3505	0.4648
YF			**0.3754**	0.4739	0.5286
IF				**0.4326**	0.4219
OG					**0.2996**
C) Change in species richness (βrich)					
P	**0.0938**	0.2637	0.0899	0.0795	0.1311
ER		**0.1935**	0.2129	0.2783	0.1939
YF			**0.0768**	0.0824	0.1031
IF				**0.0175**	0.1306
OG					**0.1275**

Discussion

As expected, our vegetation successional stages differed in habitat characteristics. There was a trend for more advanced successional stages to have greater canopy and litter cover and tree density. Pastures and old-growth forest were clearly at the opposite extremes of variation in habitat characteristics, but intermediate successional stages showed a more gradual change. Yet, the studied herpetofauna communities showed an unexpected level of resilience to changes in vegetation structure. This resilience was particularly high for lizards and snakes, which did not show a significant difference in species abundance, richness or diversity among most of the different vegetation successional stages.

Anuran species, such as *D. spatulata* and *I. marmoreus*, showed some variation in abundance but were dominant in most of the vegetation stages. In fact, *I. marmoreus* was equally dominant in the most contrasting stages: pastures and OGF. Likewise, *A. nebulosus* and *S. utiformis* were highly dominant within all lizard communities. All these species are habitat generalists characterized by a combination of one or more morpho-physiological and life-history traits that allow them to thrive in a wide range of environmental conditions. In the case of anurans, both *D. spatulata* and *I. marmoreus* have some adaptations to cope with a drying environment. For example, *D. spatulata* uses tree refuges whose entrance can be sealed using the co-ossified skin of its skull, allowing it to reduce the loss of body fluids. Likewise, *I. marmoreus* has some physiological adaptations that allow this species to cope with high levels of body dehydration [39]. On the other hand, species such as the lizards *A. nebulosus* and *S. utiformis* are disturbance-adapted and therefore are able to occur in a variety of tropical habitats, presenting higher abundances in disturbed areas [20]. Moreover, both species have a broad diet, which includes a variety of arthropods [40]. In contrast, from all the species of anurans and lizards recorded (n = 29) only one anuran, *T. smithii*, and one lizard, *P. lanei,* showed a strong association with or were exclusive to OGF. Both are small, arboreal species endemic to Mexico.

Observed high similarity in species identity and abundance of anuran and lizard species among vegetation stages resulted in β_2 (species turnover among forest succession stages) having a relatively low contribution to each group´s overall species richness. Snake communities showed a slightly greater response to changes in vegetation successional stages. This was evident from pastures showing greater species dominance than more advanced forest succession stages, the early forest successional stage having marginally lower species diversity than intermediate forest, and two arboreal species, the Central American Tree Snake (*Imantodes gemmistratus*) and Philippi’s Snail-eating Snake (*Tropidodipsas philippi*) being restricted to OGF. Overall, our results point toward the existence of a relatively low habitat specialization among the herpetofauna of the tropical dry forest in the Chamela-Cuixmala region.

Regarding the third goal of this study, observed lack of habitat specialization correlated with the existence of relatively low levels of ß diversity among forest successional stages, particularly when compared with ß diversity within stages. Snakes were the group in which $ß_2$ had the greatest contribution to overall species richness. Yet, these results should be taken with some degree of caution because this was also the group with the lowest completeness of the survey. Interestingly, our findings differ greatly from those obtained by Gardner et al. [13] in a tropical rain forest site of the northern Brazilian Amazonia, using a very similar analytical approach. In their study Gardner et al. [13] found that from a total of 23 species of amphibian and 30 species of lizard recorded, about one third, overall, were encountered only in primary forests. Moreover, significantly more amphibian and lizard species were found in primary forest than in secondary forest or *Eucalyptus* plantations. Abundance of either amphibians or lizards was not different among forest stages and plantations, but arboreal lizards were captured more frequently in primary forest than in plantations. Finally, species relative abundance evenness increased from plantations to primary forest as indicated by the slope of rank-abundance curves for both amphibians and lizards. Similar results (decreased species richness and increased species dominance going from primary to secondary forest and presence of primary forest specialist species, 37% and 25%, respectively for anurans and reptiles) were found for herpetofauna communities in a tropical rain forest in Sulawesi [24].

Our results also contrast with greater abundance, species richness and diversity of Phyllostomid bats in advanced forest stages than in pastures in our same study system [41].Our findings thus confirm the idiosyncratic response of animal communities to changes in forest structure associated with ecological succession [5], but also underscore the contrasts in such responses associated with differences in habitat types (i.e. tropical dry vs. tropical rain forests).

Lack of marked contrasts in diversity and composition of herpetofaunal communities among forest stages might be related, at least in part, to the characteristics of the particular matrix configuration in which our surveyed secondary forest plots are immersed. Habitat elements (e.g., live fences and isolated trees) present in the matrix surrounding forest fragments can play a very important role in providing habitat and shelter to herpetofauna species, contributing to relatively high species richness and diversity in transformed habitats [42]. The complex mosaic of patches of cattle pasture, subsistence crops mixed with shrubs and isolated trees, old growth, and secondary forest in different stages of regeneration, might offer in our study area enough variety of habitat types and resources to support the species present in the OGF, perhaps due to the relatively low differentiation in tree density and litter cover among forest successional stages. On the other hand, natural high seasonality in our study area might be favoring a higher abundance of species able to deal with different environmental conditions, which in turn might favor their capacity to use different habitat types. Amphibians and reptiles of the tropical dry forest have morphological, physiological and behavioral adaptations to cope with the prevailing drying conditions. These adaptations may enable these species to endure the environmental features typical of pastures and secondary forests. This is a possibility that warrants further research.

Implications for conservation

Results indicating that OGF herpetofauna species are able to persist in human-dominated tropical dry forest landscapes are of great relevance, given the level of pressure impinging on both tropical dry forests and herpetofauna.Further research is greatly needed to assess the generality of this result. In a wider context, our results highlight the importance of accounting for differences in ecological needs and responses to perturbation among animal groups as well as differences in habitat characteristics, when designing conservation actions and management plans in the tropics. On the other hand, the high resilience of OGF herpetofauna to changes in forest structure and composition presents an opportunity to combine species conservation with productive, income-producing activities for local human communities. There are, however, additional independent causes of herpetofauna mortality (e.g., those related to human aversion to snakes), which need to be addressed in order to secure the integrity of the rich hepetofauna occurring in regions such as Chamela.

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Appendix 1. Age and location of each of the plots representing different vegetation successional stages of the Chamela region, Jalisco, México.

			Coordinates	
Plot	Successional stage	Years since abandonment	Lat N	Long W
Ranchitos	Pasture	0	19°36'51.12"	105°01'17.62"
Santa Cruz	Pasture	0	19°35'15.14"	105°02'05.05"
Zapata	Pasture	0	19°22'60.00"	104°56'54.40"
Santa Cruz	Early forest	5	19°35'13.62"	105°02'04.03"
Zapata	Early forest	5	19°23.2'2.8"	104°56'54.42"
San Mateo	Early forest	6	19°34'50.64"	105°03'36.37"
Ranchitos	Young forest	8	19°36'53.92"	105°01'17.45"
Caimán	Young forest	9	19°28'43.61"	104°55'59.69"
Santa Cruz	Young forest	10	19°36'07.33"	105°02'34.54"
Ranchitos	Intermediate forest	15	19°35'31.77"	105°00'32.24"
Santa Cruz	Intermediate forest	15	19°35'58.80"	105°02'54.50"
Caimán	Intermediate forest	17	19°28'01.30"	104°56'12.42"
Gargoyo	Old-growth forest	>50	19°24'16.40"	104°58'59.00"
Tejón 1	Old-growth forest	>50	19°30'05.90"	105°02'36.90"
Tejón 2	Old-growth forest	>50	19°30'34.10"	105°02'23.30"

Appendix 2. Average abundance and standard deviation (SD) of amphibian and reptile species recorded in each of the five vegetation successional stages in the tropical dry forest of Chamela region, Jalisco, Mexico.

	Successional stage										Total
	Pasture		Early stage		Young forest		Intermediate forest		Old-growth forest		
	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	
Anurans											
Bufonidae											
Incilius marmoreus (Marbled toad)	19.7	21.8	6.0	6.2	12.3	8.1	15.7	8.7	11.7	14.4	196
Incilius mazatlanensis (Sinaloan toad)	0.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
Rhinella marina (Cane toad)	0.7	1.2	0.0	0.0	0.3	0.6	0.3	0.6	0.0	0.0	4
Craugastoridae											
Craugastor occidentalis (Taylor’s Barking Frog)	0.0	0.0	0.0	0.0	2.0	3.5	1.0	1.0	0.3	0.6	10
Hylidae											
Agalychnis dacnicolor (Mexican leaf frog)	7.3	10.2	2.0	1.7	2.0	2.0	0.3	0.6	0.0	0.0	35
Dendropsophus sartori (Taylor’s yellow treefrog)	0.0	0.0	0.3	0.6	1.0	1.0	0.0	0.0	0.3	0.6	5
Diaglena spatulata (Shovel head treefrog)	1.0	1.7	26.3	17.6	34.0	9.6	19.0	11.0	4.3	2.1	254
Smilisca baudini (Common Mexican treefrog)	9.3	11.8	1.3	2.3	2.3	2.3	2.3	2.1	0.3	0.6	47
Smilisca fodiens (Lowland burrowing treefrog)	12.7	16.1	3.3	3.5	4.7	4.0	5.0	7.0	0.0	0.0	77

	Successional stage										Total
	Pasture		Early stage		Young forest		Intermediate forest		Old-growth forest		
	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	
Tlalocohyla smithii (Dwarf Mexican treefrog)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	4.6	8
Trachycephalus typhonius (Veined treefrog)	3.0	3.6	7.3	12.7	2.7	3.8	4.0	3.6	1.0	1.0	54
Leptodactylidae											
Leptodactylus melanonotus (Sabinal frog)	3.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9
Microhylidae											
Hypopachus ustus (Two-spaded narrow-mouthed toad)	1.3	1.5	1.7	2.9	0.0	0.0	0.3	0.6	0.0	0.0	10
Hypopachus variolosus (Sheep frog)	6.7	10.7	0.0	0.0	1.7	2.9	0.0	0.0	0.0	0.0	25
Mean Abundance	65.3(60.1)		48.3(43.3)		63.0(5.29)		48.0(25.3)		20.7(22.1)		49.1(34.9)
Lizards											
Dactyloidae											
Anolis nebulosus (Clouded anole)	17.7	9.7	13.7	14.2	19.7	6.5	17.3	8.5	11.7	4.5	240
Eublepharidae											
Coleonyx elegans (Yucatán banded gecko)	1.0	1.7	0.0	0.0	2.0	1.0	1.0	1.0	0.7	1.2	14
Helodermatidae											
Heloderma horridum (Beaded lizard)	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	1

	Successional stage										Total
	Pasture		Early stage		Young forest		Intermediate forest		Old-growth forest		
	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	
Iguanidae											
Ctenosaura pectinata (Mexican spiny tail iguana)	2.0	1.0	2.0	3.5	0.7	1.2	2.3	2.5	0.3	0.6	22
Iguana iguana (Green iguana)	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.6	0.0	0.0	2
Phrynosomatidae											
Sceloporus horridus (Horrible spiny lizard)	3.0	5.2	1.3	2.3	0.0	0.0	0.0	0.0	0.0	0.0	13
Sceloporus melanorhinus (Pastel tree lizard)	2.3	0.6	1.0	1.0	0.7	0.6	4.0	2.6	4.3	3.2	37
Sceloporus utiformis (Largescale spiny lizard)	14.3	10.7	11.7	8.1	31.7	13.3	35.0	9.2	15.7	10.7	325
Urosaurus bicarinatus (Tropical tree lizard)	16.7	8.3	3.3	3.2	0.7	1.2	3.0	2.0	0.7	0.6	73
Phyllodactylidae											
Phyllodactylus lanei (Lane's leaf-toed gecko)	1.3	1.2	0.0	0.0	0.3	0.6	1.7	2.1	5.3	3.2	26
Scincidae											
Plestiodon parvulus (Southern pygmy skink)	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	1
Teiidae											
Aspidoscelis communis (Giant whiptail)	4.3	1.5	9.7	14.2	2.3	4.0	9.3	8.5	11.0	14.9	110

	Successional stage										Total
	Pasture		Early stage		Young forest		Intermediate forest		Old-growth forest		
	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	
Aspidoscelis lineatissima (Many-lined whiptail)	10.0	11.4	4.3	4.0	8.7	8.1	11.7	11.7	26.7	22.2	184
Holcosus undulatus (Rainbow ameiva)	0.0	0.0	0.0	0.0	2.0	2.0	3.3	4.9	6.7	9.0	36
Mean abundance	72.6(25.9)		47.0(12.1)		69.3(30.0)		89.3(28.4)		83.0(52.0)		72.2(31.2)
Boidae											
Boa constrictor (Boa constrictor)	0.3	0.6	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	2
Colubridae											
Drymarchon melanurus (Western indigo snake)	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.6	0.0	0.0	2
Lampropeltis triangulum (Milk snake)	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
Leptophis diplotropis (Pacific Coast parrot snake)	0.3	0.6	0.7	1.2	0.3	0.6	0.3	0.6	0.3	0.6	6
Masticophis mentovarius (Neotropical whipsnake)	0.0	0.0	0.3	0.6	0.3	0.6	0.0	0.0	0.0	0.0	2
Oxybelis aeneus (Mexican vine snake)	0.3	0.6	0.0	0.0	1.3	1.5	0.7	0.6	1.0	1.7	10
Salvadora mexicana (Mexican patchnose snake)	1.0	1.7	0.3	0.6	0.3	0.6	0.3	0.6	0.0	0.0	6
Symphimus leucostomus (Isthmian white-lipped snake)	0.0	0.0	0.3	0.6	0.3	0.6	0.0	0.0	0.0	0.0	2
Tantilla bocourti (Bocourt's blackhead snake)	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	1
Tantilla calamarina (Pacific Coast centipede snake)	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.6	2

	Successional stage										Total
	Pasture		Early stage		Young forest		Intermediate forest		Old-growth forest		
	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	
Trimorphodon biscutatus (Lyre snake)	0.3	0.6	0.3	0.6	0.3	0.6	0.3	0.6	0.3	0.6	5
Dipsadidae											
Dipsas gaigeae (Gaige's thirst snake)	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.3	0.6	2
Enulius flavitorques (Pacific longtail snake)	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	1.0	1.0	4
Hypsiglena torquata (Night snake)	1.3	1.5	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	5
Imantodes gemmistratus (Central American tree snake)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.2	2
Leptodeira maculata (Southwestern cat-eyed snake)	1.3	2.3	0.0	0.0	0.7	1.2	0.3	0.6	0.0	0.0	7
Leptodeira uribei (Uribe's false cat-eyed snake)	0.3	0.6	0.0	0.0	0.0	0.0	0.7	1.2	0.7	0.6	5
Tropidodipsas philippi (Philippi's snail-eating snake)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.6	2
Elapidae											
Micrurus distans (West Mexican coral snake)	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.6	2
Loxocemidae											
Loxocemus bicolor (Mexican burrowing python)	0.7	1.2	0.7	0.6	0.0	0.0	0.0	0.0	0.3	0.6	5
Viperidae											

	Successional stage										Total
	Pasture		Early stage		Young forest		Intermediate forest		Old-growth forest		
	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	
Agkistrodon bilineatus (Cantil)	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	1
Crotalus basiliscus (Mexican west coast rattlesnake)	0.3	0.6	0.0	0.0	1.0	1.0	0.7	0.6	0.3	0.6	7
Mean abundance	6.6(2.5)		3.0(1.7)		5.6(1.1)		5.3(1.5)		6.3(1.6)		5.4(1.5)
Overall total number of individuals											1901

Appendix 3. Association index (IA) for paired comparison of abundances of each species among pastures (P), secondary forest (SF) and old-growth forest (OGF) in the Chamela region, Jalisco, México. N indicates no association to any successional stage. Chi-square statistics and significance values (*P<0.01, **P<0.001) are shown for species with a total abundance higher than six individuals.

	Abundance			IA			Association	X^2
	P	SF	OGF	P-OGF	P-SF	SF-OGF		
Anurans								
Tlalocohyla smithii	0	0	8	1		1	OGF	16.3***
Craugastor occidentalis	0	3	1	1	1	-0.5	OGF/SF	-
Dendropsophus sartori	0	1	1	1	1	0	OGF/SF	-
Diaglena spatulata	3	79	13	0.6	0.9	-0.7	OGF/SF	107.7***
Incilius marmoreus	59	34	35	-0.3	-0.3	0	P	9.4**
Incilius mazatlanensis	2	0	0	-1	-1		P	-
Leptodactylus melanonotus	9	0	0	-1	-1		P	18.3***
Rhinella marina	2	1	0	-1	-0.3	-1	P/SF	-
Agalychnis dacnicolor	22	4	0	-1	-0.7	-1	P/SF	31.8***
Smilisca baudini	28	6	1	-0.9	-0.6	-0.7	P/SF	35.4***
Smilisca fodiens	38	13	0	-1	-0.5	-1	P/SF	43.9***
Trachycephalus typhonius	9	14	3	-0.5	0.2	-0.6	P/SF	7.1*
Hypopachus ustus	4	2	0	-1	-0.3	-1	P/SF	4.4
Hypopachus variolosus	20	2	0	-1	-0.8	-1	P/SF	33.2***
Lizards								
Sceloporus melanorhinus	7	6	13	0.3	-0.1	0.4	OGF/P	3.4
Aspidoscelis lineatissima	30	25	80	0.5	-0.1	0.5	OGF/P	41.1***
Phyllodactylus lanei	4	2	16	0.6	-0.3	0.8	OGF/P	15.7***
Sceloporus utiformis	43	78	47	0	0.3	-0.2	OGF/SF	13.1**
Aspidoscelis communis	13	21	33	0.4	0.2	0.2	OGF/SF	9.1*

Holcosus undulatus	0	5	20	1	1	0.6	OGF/SF	26.1***
Anolis nebulosus	53	51	35	-0.2	0	-0.2	P/SF	4.2
Coleonyx elegans	3	3	2	-0.2	0	-0.2	P/SF	0.5
Ctenosaura pectinata	6	5	1	-0.7	-0.1	-0.7	P/SF	3.7
Sceloporus horridus	9	1	0	-1	-0.8	-1	P/SF	14.8***
Urosaurus bicarinatus	50	7	2	-0.9	-0.8	-0.6	P/SF	70.9***
Heloderma horridum	0	1	0	0	1	-1	SF	-
Iguana iguana	0	1	0		1	-1	SF	-
Plestiodon parvulus	0	1	0		1	-1	SF	-
Snakes								
Leptophis diplotropis	1	1	1	0	0	0	N	-
Trimorphodon biscutatus	1	1	1	0	0	0	N	-
Leptodeira uribei	1	1	2	0.3	0	0.3	OGF	-
Tropidodipsas philippi	0	0	2	1		1	OGF	-
Imantodes gemmistratus	0	0	2	1		1	OGF	-
Oxybelis aeneus	1	2	3	0.5	0.3	0.2	OGF/SF	1.4
Dipsas gaigeae	0	1	1	1	1	0	OGF/SF	-
Enulius flavitorques	0	1	3	1	1	0.5	OGF/SF	-
Micrurus distans	0	1	1	1	1	0	OGF/SF	-
Tantilla calamarina	0	1	1	1	1	0	P	-
Loxocemus bicolor	2	1	1	-0.3	-0.3	0	P	-
Boa constrictor	1	1	0	-1	0	-1	P/SF	-
Lampropeltis triangulum	1	0	0	-1	-1		P/SF	-
Salvadora mexicana	3	1	0	-1	-0.5	-1	P/SF	-
Hypsiglena torquata	4	1	0	-1	-0.6	-1	P/SF	-
Leptodeira maculata	4	1	0	-1	-0.6	-1	P/SF	-
Drymarchon melanurus	0	1	0		1	-1	SF	-

Masticophis mentovarius	0	1	0		1	-1	SF	-
Symphimus leucostomus	0	1	0		1	-1	SF	-
Tantilla bocourti	0	1	0		1	-1	SF	-
Agkistrodon bilineatus	0	1	0		1	-1	SF	-
Crotalus basiliscus	1	2	1	0	0.3	-0.3	SF	-

Appendix 4.- Non-metric multidimensional scaling (NMDS) of differences in herpetofaunal communities among vegetation successional stages of tropical dry forest at the Chamela region, Jalisco, Mexico.