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Herpetofauna diversity and microenvironment correlates across a pasture–edge–interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico

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ABSTRACT

We evaluated the relationship between amphibian and reptile diversity and microhabitat dynamics along pasture–edge–interior ecotones in a tropical rainforest in Veracruz, Mexico. To evaluate the main correlation patterns among microhabitat variables and species composition and richness, 14 ecotones were each divided into three habitats (pasture, forest edge and forest interior) with three transects per habitat, and sampled four times between June 2003 and May 2004 using equal day and night efforts. We measured 12 environmental variables describing the microclimate, vegetation structure, topography and distance to forest edge and streams.

After sampling 126 transects (672 man-hours effort) we recorded 1256 amphibians belonging to 21 species (pasture: 12, edge: 14, and interior: 13 species), and 623 reptiles belonging to 33 species (pasture: 11, edge: 25, and interior: 22 species). There was a difference in species composition between pasture and both forest edge and interior habitats. A high correlation between distance to forest edge and temperature, understorey density, canopy cover, leaf litter cover, and leaf litter depth was found. There was also a strong relationship between the composition of amphibian and reptile ensembles and the measured environmental variables. The most important variables related to amphibian and reptile ensembles were canopy cover, understorey density, leaf litter cover and temperature.

Based on amphibian and reptile affinity for the habitats along the ecotone, species were classified into five ensembles (generalist, pasture, forest, forest edge and forest interior species). We detected six species that could indicate good habitat quality of forest interior and their disappearance may be an indication of habitat degradation within a fragment, or that a fragment is not large enough to exclude edge effects. Different responses to spatial and environmental gradients and different degrees of tolerance to microclimatic changes indicated that each ensemble requires a different conservation strategy. We propose to maintain in the Los Tuxtlas Biosphere Reserve the forest remnants in the lowlands that have gentler slopes and a deep cover of leaf litter, a dense understorey, and high relative humidity and low temperature, to buffer the effects of edge related environmental changes and the invasion of species from the matrix.

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1. Introduction

Extensive deforestation on tropical landscapes has resulted in a mosaic of native vegetation set in a matrix of land under different types of human use, such as pasture and cultivated fields (Saunders et al., 1991). Several factors influence the richness, distribution and abundance of species within native vegetation fragments, including incident light, temperature and relative humidity (Murcia, 1995; Harper et al., 2005). In response to high temperatures and dry climate, amphibians undergo changes in their individual growth rate, home range, activity patterns, habitat use, ability to reproduce and the duration of the reproductive period (Crump, 2003). Deforestation usually modifies environmental factors as well as interspecific interactions (i.e., predation, parasitism and competition), generating an edge effect at the interface between the forest and the surrounding matrix (Murcia, 1995; Harper et al., 2005).

The edge can be defined as the transition between natural habitat and that modified by humans, and results in an ecotone of two structurally different vegetation communities (Murcia, 1995; Harper et al., 2005). The matrix is usually an extensive area that surrounds patches of original habitat which can act as a barrier to gene flow and dispersion of the animals and plants that are confined to forest remnants (Wilcove et al., 1986). In some cases, the matrix is also a selective filter for species throughout the landscape (Gascon et al., 1999).

To understand how the matrix and edges affect the diversity of amphibians and reptiles, it is important to determine the changes in microclimate along the gradient from the edge to the interior of the forest remnants, as well as from the edge into the matrix (Harper et al., 2005). Studies by Lehtinen et al. (2003) on the amphibians and reptiles of Madagascar determined that the species found in the forest interior, which tend to avoid the edges are more susceptible to extinction. Similarly, Gascon et al. (1999) and Laurance (1999) demonstrated that the species of anurans that tolerate induced grasslands in the Amazon tend to be less vulnerable to habitat fragmentation than those that avoid them. The effect of habitat fragmentation on different species depends on their particular autoecology, movement patterns, habitat use and ability to cope with biotic and abiotic microhabitat changes caused by disturbances (Marsh and Pearman, 1997; Pearman, 1997; Green et al., 2001; Urbina and Londoño, 2003; Fischer et al., 2005).

Amphibian and reptile responses to microhabitat perturbation and the degree to which these organisms use the pasture-forest ecotone are virtually unknown, though they are usually embraced by conservation programs. This information is vital to understand the structure of these communities and to design conservation strategies that can maintain rare and vulnerable species inhabiting fragmented landscapes. The number of species in pasture habitats is expected to be less than that of forest habitats because of the extreme microclimatic conditions in their structural simpler vegetation. Edge species richness should be higher than both pasture and interior habitats because of the well documented increase of species richness in such edge habitats (e.g., Leopold, 1933; Ries et al., 2004). Wind disturbance may be higher

on edge habitats, thus increasing amphibian vulnerability to desiccation and reproductive habitat loss (Crump, 2003). Under this scenario, forest interior species would probably avoid edges which are more susceptible to microclimatic changes, and prefer habitats that are moister and cooler in the forest interior.

In this study, we evaluated changes in amphibian and reptile diversity along the pasture–edge–interior ecotone and their relationship to microhabitat dynamics in Los Tuxtlas, a fragmented tropical rainforest in Mexico. The environmental variables measured across the boundary were established under the hypothesis that they co-vary with the pasture–edge–interior ecotone and therefore may alter the diversity of amphibians and reptiles. Species were grouped into ensembles based on their affinities for pasture, forest edge and forest interior habitats. Environmental variables were examined for correlation with the habitat preference of each ensemble. Following Fauth et al. (1996), we use the term “ensemble” to identify a group of species belonging to a particular taxon and exploiting a common resource. We tested specific research questions such as: (1) is there any difference in species composition between (a) ecotones, and (b) habitats?, (2) is there any difference in species richness between habitats?, (3) which are the distribution of the amphibian and reptile species within environmental gradients?, and (4) which are the relationship between environmental variables and ensembles species richness?

2. Methods

2.1. Study area

Fieldwork was carried out in the tropical rainforest and adjacent habitat of the Los Tuxtlas Biosphere Reserve, in the state of Veracruz, Mexico (18°32'N, 95°6'W). The study area was limited to an altitudinal range between 30 and 275 m. Slope at the sites varied between 1% and 44% (Table 1). Mean annual temperature is 27 °C, ranging from 35 °C in May to 13 °C in February. Mean annual precipitation is 4964 mm with a marked dry season from March to May (Soto and Gama, 1997).

The original dominant land cover type was tropical evergreen forest, also known as “selva alta perennifolia”. Los Tuxtlas Biosphere Reserve constitutes the northernmost distribution of tropical rainforest on the American continent (Dirzo and Miranda, 1991). However, because of human activities, the tropical rainforest of Los Tuxtlas has lost 84% of its original cover (Dirzo and García, 1992). It is now a mosaic landscape composed of forest fragments, secondary or regenerating forest, riparian vegetation, living fences and isolated trees, immersed in a larger matrix of pastures (Ibarra-Manríquez et al., 1997). The Los Tuxtlas Biosphere Reserve is partly tropical evergreen rainforest, but there is also pine and oak-pine forest in the highlands.

During our study we sampled tropical rainforest remnants and the surrounding pasture matrix. Study sites were selected by identifying potential forest patches, Landsat-7 image for the year 2000 with six bands and a pixel size of 30 × 30 m (Mendoza et al., 2005). Six fragments between 26 and 472 ha in size were identified as forest and this was verified directly in the field. According to the owners and farmers these frag-

Table 1 – Environmental variables measured along 126 50 m-long transects in the evergreen forest in the Los Tuxtlas Biosphere Reserve, Veracruz, Mexico

Variables per transect	Pasture		Edge		Interior		t-Test	p*
	Mean (range)	SD	Mean (range)	SD	Mean (range)	SD		
Altitude (m asl)	136.5 (30–250)	±67.6	157.3 (40– 275)	±68.5	171.4 (35–270)	±64.2	–0.9	0.33
Slope (%)	18.4 (1.11–44.4)	±10.4	21.8 (12.2–44.4)	±7.4	25.3 (3.3–40)	±10.6	–1.8	0.07
Canopy cover (%)	0.0 (0–0)	±0	40.7 (25.9–67.7)	±9.2	46.7 (23.3–70.9)	±10.1	–2.9	0.004
Understorey density (pole contacts)	0.0 (0–0)	±0	6.0 (3.8–8.6)	±1.1	5.0 (4–6.6)	±0.7	4.6	<0.001
Distance from streams (m)	315.3 (20–1040)	±294.2	311.9 (10–1120)	±317.4	337.0 (10–1270)	±336.5	–0.3	0.72

Mean values were obtained from the 42 transects at every habitat.
 * Student's t test was applied to determine differences between edge and forest interior denoting an edge effect. Note that variables such as altitude, slope, and distance to streams were controlled in this study, and that there is an edge effect for understorey density and canopy cover.

ments have not been altered extensively for more than 15 years. The criteria for fragment selection were: (1) the fragment was completely surrounded by pasture, (2) the size and shape of the fragment would allow us to establish two perpendicular ecotones each extending 200 m into the forest interior, with at least 200 m distance between ecotones (i.e., minimum fragment diameter of 600 m), (3) there was at least one stream crossing the pasture–edge–interior ecotone to equalize biases related to water availability in environmental variables and the richness of water dependant species. All streams were temporal and there were no standing bodies of water near the study habitats.

In each of the six fragments there were two rectangular 50 × 250 m ecotones, both placed perpendicular to the fragment edge, one on the northern edge of the forest fragment and the other on the southern edge. Four ecotones were situated in the largest fragment (Fig. 1). Each ecotone was classified into three habitat types: pasture, forest edge, and forest interior. Following Williams-Linera et al. (1998), the forest edge habitats were delimited within the first 20 m of forest, where major changes in the vegetation structure and density occur. The forest interior habitats were placed beyond the first 50 m of forest from the edge, because the deepest edge effects at Los Tuxtlas were detected further than 40 m into the fragment

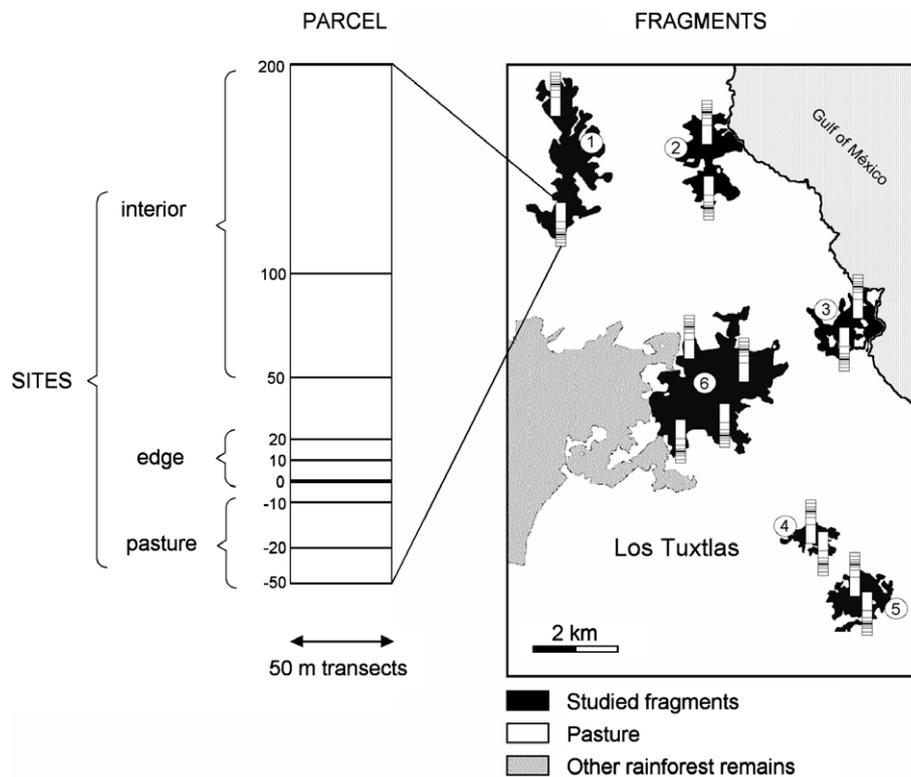


Fig. 1 – Diagram of study site in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Rectangular 50 × 250 m ecotones were situated along the pasture–edge–interior gradient. Lines represent the 50 × 2 m transects parallel to the forest edge and the negative distances are transects within the pasture. Transect lines are not to scale and the dotted area represents another vegetation types over 500 m asl, and adjacent to the larger fragment. Studied forest fragments appears in black colour, other forest in grey, pasture habitat in white and water in white with dark points.

(Williams-Linera et al., 1998). For each habitat we traced a line perpendicular to the forest edge and installed three permanent transects 50 m in length and parallel to the rainforest edge at each habitat. The whole study includes 14 ecotones containing 126 transects. Transects were located at least 10 m from streams to avoid biases resulting from increases in species richness and abundance, which could result in confusion about the true effect of the edge on amphibian and reptile diversity. In pasture habitats, only the grass was sampled. Living fences, isolated standing trees, and water bodies were avoided, to measure the matrix effects of an exclusively grass matrix habitat.

The vegetation composition of tropical rainforest of the pasture–forest ecotone of Los Tuxtlas was described by Williams-Linera et al. (1998). Of the 177 plant species in the pasture–forest ecotone, the most abundant families were Palmae, Moraceae, Rubiaceae, Euphorbiaceae and Leguminosae; and the most abundant species were *Astrocaryum mexicanum*, *Pseudolmedia oxyphyllaria* and *Trophis mexicana*.

2.2. Amphibian and reptile sampling

Data were collected during the wet (June–July and September–October 2003), and dry (February–March and May 2004) seasons. Each ecotone was sampled four times by two persons for six hours (1100–1400 h and 2100–2400 h). The first habitat of the ecotone to be sampled was randomly chosen. Each 50 m transect was sampled by walking for 20 min, and recording all amphibian and reptile encounters within 1 m on both sides of the transect and up to 2 m in height, and restricting sampling to the understorey (Urbina-Cardona and Reynoso, 2005). Marking individuals to avoid overestimation of abundance by recapture was not considered necessary given that no recaptures have been recorded after one month in similar amphibian and reptile studies in Los Tuxtlas (E. Cabrera, unpublished; M. López-Luna personal communication).

To help with species identification in the field, a field guide was produced using live pictures of voucher specimens collected during April 2003 and identified to species level in the lab with specialized taxonomic keys. Specimens for which species was not determined in the field were captured for accurate taxonomic identification. Although most of the individuals were released at the site of their original capture, some were sacrificed and deposited in the Colección Nacional de Anfibios y Reptiles of the Instituto de Biología, Universidad Autónoma de México (UNAM) in Mexico City.

2.3. Microhabitat measurements

Eleven environmental variables were measured. Precipitation was measured for each season. Altitude, slope, distance to streams, canopy cover and understorey density were measured for each transect. Temperature, relative humidity, grass cover, leaf litter cover and leaf litter depth were measured on the site where each of the 1879 individuals were first seen. For data analysis we used all $n = 1879$ observations for each variable because we expected that all variables taken at the seasonal and transect levels would influence the microhabitat at the organism level. Replication along habitats and ecotones controls for the pseudoreplication biases on environmental

variables that might be introduced due to habitat heterogeneity.

Precipitation data were gathered from the meteorological station at the Los Tuxtlas Tropical Biology Station, Instituto de Biología (UNAM). Since precipitation is read daily at noon, data for the sampling day was averaged with that of the previous day ($n = 56$).

Transect variables were measured for each of the 126 transects. Slope and altitude (height above sea level) were measured both with a clinometer and an altimeter by averaging the values obtained from three randomly chosen places on the transects. Canopy cover was obtained by analyzing pictures taken on high luminosity days with a 180° hemispherical lens at a height of 0.5 m with an f11 diaphragm aperture, 1/125 shutter speed, and ASA 100 film. Negatives were scanned, and the percentage of canopy cover was calculated with Winphot 5 software (ter Steege, 1996) as the average from two pictures taken at random on each transect. Relative understorey density was obtained by averaging the number of contacts of the vegetation (branches, stumps and leaves) with a pole 3.5 cm in diameter and 2 m high, placed vertically at five random points located along the transect. Distance from streams was measured by geopositioning the nearest stream to the transect and distance was calculated using Global Positioning System.

Microenvironmental variables recorded on a per organism basis were measured on the site where each individual was first seen. Temperature and relative humidity were recorded with a thermohygrometer after 30 s of exposure. Percentages of grass and leaf litter cover were estimated at every capture site using a 0.5 × 0.5 m wooden quadrat divided into four quadrants with a nylon string. Finally, the leaf litter depth was measured by introducing a graduated ruler into the litter on the soil.

2.4. Data analysis

We generated Bray–Curtis similarity matrices of amphibian and reptile data, using normalized relative abundance of species in each plot. With these similarity matrices, we performed a non-parametric two-way analysis of similarity (ANOSIM subroutine) to test hypotheses regarding spatial differences in amphibian and reptile composition. The ANOSIM procedure is a permutation-based test applied to simple nested designs (e.g. habitats within ecotones) to detect differences between groups of multivariate samples (Clarke and Warwick, 2001). Using PRIMER program (Clarke and Gorley, 2001) we test the null hypotheses that within-ecotone and within-habitat similarity were equal to the between-ecotone and between-habitat similarity.

The percentage of amphibian and reptiles similarity between pasture, forest edge and forest interior habitats, and the taxa responsible for any variability, were determined with similarity percentage analysis (SIMPER subroutine; PRIMER software, Plymouth, UK). To compare abundance patterns and species evenness between habitats, we used rank-abundance curves (Feinsinger, 2001). For each habitat we plotted the relative abundance of each species on a logarithmic scale against the rank order of the species from most to least abundant.

To compare species richness among study habitats with an equal sampling effort, species accumulation curves were generated using the sample-based rarefaction method of the EstimateS 7 program (Colwell, 2004). The number of taxa was plotted as a function of the accumulated number of individuals because datasets may differ systematically in the mean number of individuals per sample (Gotelli and Colwell, 2001). The function of expected richness (S_{obs}) is the accumulation function of species along transects per habitat ($n = 42$). The expected richness function is called *Mao Tau* and allows the confidence intervals to be calculated for the direct statistical comparison of richness between habitats (Colwell et al., 2004).

Pearson correlation coefficients were used to determine correlations among microhabitat variables and to identify non-correlated variables. All measured 12 variables ($n = 1879$ data for each variable) accomplished normality and homoscedasticity of variance. The differences between microhabitat variables measured on the edge and in the interior were studied using independent samples *t* tests (82 df, for each analysis). All data were analyzed with Statistica 6.0 software (StatSoft, 2001).

A canonical correspondence analysis (CCA) was used to detect amphibian and reptile responses to gradients in environmental variables (Pearman, 1997; Hofer et al., 2000; Urbina and Londoño, 2003). Using Canoco 4.0 software (ter Braak and Smilauer, 1998) we examined the relationships between species distribution in pasture, the forest edge and the forest interior habitats, in addition to the distribution of associated microhabitat variables. The analysis combined species abundance \times transect and environmental variables \times transect data matrices. Where colinearity among variables was detected ($R > 0.6$), variables were removed from the analysis until variance inflation factors were at acceptable levels (ter Braak and Smilauer, 1998). In CCA, statistical significance would indicate that the observed associations between species and environmental variables are not random (Kent and Coker, 1992). The statistical significance of the CCA was calculated using the Monte Carlo method. To reduce the influence that the most abundant species might have in the ordination analysis, the abundance of each species was square root transformed, and uncommon species ($n \leq 3$) were excluded from this analysis (Jongman et al., 1995).

To determine which of the environmental variables was most important in structuring amphibians and reptiles pattern during wet and dry season we used BIOENV subroutine (PRIMER software, Plymouth, UK). We applied the Spearman Rank correlation (p_w) to relate the species abundance with the environmental variables similarity matrices (Clarke and Gorley, 2001).

To establish amphibian and reptile species ensembles according to their responses to the pasture–edge–interior ecotone, Non-metric multidimensional scaling (MDS) was used for the most common amphibian and reptile species. This analysis was supported by a distance matrix constructed with amphibian and reptile abundance per habitat (pasture, forest edge and forest interior). This analysis was selected because it is robust and makes no assumptions about data distribution (Legendre and Legendre, 1998). With Statistica 6.0 software (StatSoft, 2001), the ordination space was reduced to a two

dimensional geometric space (stress 0.015 for amphibians and 0.0002 for reptiles). Species with abundances less than three were excluded from the analysis to avoid assigning incorrect ensemble affinity patterns.

Finally, backward stepwise multiple regressions were used to detect the relationship between measured environmental variables as predictors, and species richness as the response variable. The variables with a non significant *F* test result ($p \geq 0.05$) were eliminated from the model. All regression models were significant ($p \leq 0.05$). We tested for normality of regression residuals with the Shapiro–Wilk (*W*) test using Statistica 6.0 software (StatSoft, 2001).

3. Results

3.1. General aspects

After 672 man hours of sampling effort, 1256 individuals of 21 amphibian species and 623 individuals of 33 reptile species were captured. Of the species known to be present at low altitudes in eastern Los Tuxtlas (Pérez-Higareda, unpublished data) we recorded 60% of the amphibian species (100% of the salamanders and 57% of the anurans) and 48% of the reptiles (35% of snakes and 73% of lizards) (Table 2). For the entire area the total amphibians predicted in the inventory was between 88% and 93% and the total reptiles was between 40% and 84% (Urbina-Cardona and Reynoso, 2005).

3.2. Species composition patterns

ANOSIM determined that for amphibian and reptile composition there was no difference between ecotones ($p = 0.499$) demonstrating that the effect of habitat heterogeneity between study ecotones were adequately controlled by the sampling design. There was a difference between the habitats

Table 2 – Distribution of amphibians and reptiles in pasture, edge and interior habitats of the fragmented tropical rainforest at Los Tuxtlas, Veracruz, Mexico

	Habitats			All habitats
	Pasture	Edge	Interior	
<i>Amphibians</i>				
Number of species observed (S_{obs})	12	14	13	21
S_{obs} SD (<i>Mao Tau</i>)	± 0.49	± 2.04	± 1.82	± 1.52
Number of individuals	98	570	588	1256
Adults	80	297	307	684
Juveniles	18	273	281	572
<i>Reptiles</i>				
Number of species observed (S_{obs})	11	25	22	33
S_{obs} SD (<i>Mao Tau</i>)	± 2.75	± 3.34	± 2.67	± 3.79
Number of individuals	157	208	258	623
Adults	113	137	181	431
Juveniles	45	70	77	192
Number of species observed (S_{obs}), expected richness <i>Mao Tau</i> standard deviation, number of individuals, and age (number of adults and juveniles).				

nested within ecotones ($p = 0.001$) and pasture habitat were different from both forest edge and forest interior habitats. There were no difference between forest edge and forest interior.

The surrounding pasture matrix was dominated by the rose-belly lizard *Sceloporus variabilis* and the leprus chirping frog *Syrhophus leprus* (SIMPER, percentage of contribution to similarity of 85.7 and 10.8, respectively). The forest edge and forest interior habitat was dominated by the polymorphic robber frog *Craugastor rhodopsis* (SIMPER, percentage of contribution to similarity of 87.4 at the forest edge and 71.3 at the forest interior), and the lesser scaly anole *Anolis uniformis* (SIMPER, percentage of contribution to similarity of 5.8 at the forest edge and 15.2 at the forest interior). Sumichrast's skink (*Plestiodon sumichrasti*) was also an important discriminatory species between the forest interior and the pasture matrix habitats (SIMPER, percentage of contribution to dissimilarity of 6).

The slopes of the rank-abundance curves for amphibians in edge and interior habitats were similar (Fig. 2a). The abundance distribution pattern and hierarchical order of species resembled a log-series model. At pasture habitats the slopes of the rank-abundance curves were not as steep suggesting greater evenness. Dominant species at pasture were not as abundant as those dominant species of edge and interior forest habitats (Table 3, Fig. 2a).

The rank-abundance curves for reptiles (Fig. 2b) on the edge and interior habitats had similar slopes and the same rank-distribution pattern for the three most abundant species including *A. uniformis*, *P. sumichrasti* and Hernandez's helmeted basilisk *Corytophanes hernandezii* (Table 3). In pasture habitats the rank-abundance for reptiles had slopes similar to those of the forest habitats. At the pasture, forest edge, and forest interior habitats the reptile ensemble was distributed according to a log-series model with a small number of abundant species and a large number of rare species.

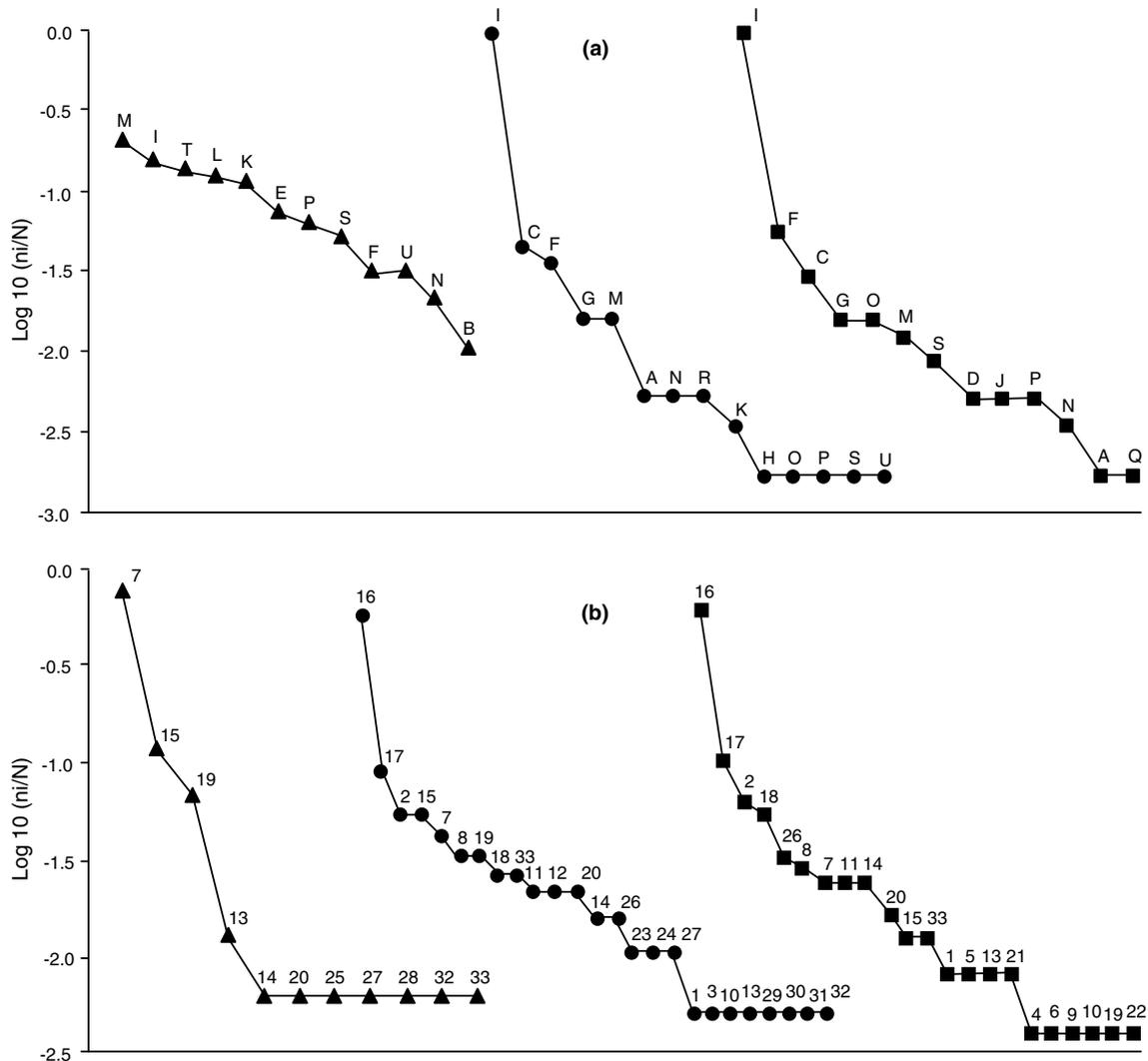


Fig. 2 – Rank-abundance curves for the herpetofauna ensemble at pasture (▲), forest edge (●) and forest interior (■) habitats in the 14 ecotones, Los Tuxtlas, Veracruz, Mexico. (a) Amphibians and (b) reptiles. Species codes are given in Table 3. For each habitat the relative abundance of each species (n_i/N) was plotted on a logarithmic scale against the species rank ordered from most to least abundant.

Table 3 – Total number of individuals of amphibian and reptile species recorded in the 126 transects at the pasture, edge, and interior habitats of the tropical rainforest at Los Tuxtlas, Veracruz, Mexico

ORDER	Species	Habitat			Preferred habitat ^a	Species codes
		Pasture	Edge	Interior		
CAUDATA						
Plethodontidae						
	<i>Bolitoglossa alberchi</i>	0	3	1	Edge	A
	<i>Bolitoglossa platydactyla</i>	1	0	0		B
	<i>Nanotriton rufescens</i>	0	25	16	Edge	C
	<i>Pseudoeurycea orchimelas</i>	0	0	3		D
ANURA						
Bufonidae						
	<i>Chaurus marinus</i>	7	0	0	Pasture	E
	<i>Cranopsis valliceps</i>	3	20	31	Interior	F
Brachycephalidae						
	<i>Craugastor alfredi</i>	0	9	9	Forest	G
	<i>Craugastor berkenbuschi</i>	0	1	0		H
	<i>Craugastor rhodopis</i>	15	491	498	Forest	I
	<i>Craugastor vulcani</i>	0	0	3		J
	<i>Syrrhophus leprus</i>	20	9	7	Pasture	M
Leptodactylidae						
	<i>Leptodactylus fragilis</i>	11	2	0	Pasture	K
	<i>Leptodactylus melanonotus</i>	12	0	0	Pasture	L
Microhylidae						
	<i>Gastrophryne elegans</i>	2	3	2	Generalist	N
Hylidae						
	<i>Dendropsophus ebraccatus</i>	0	1	9	Interior	O
	<i>Dendropsophus microcephala</i>	0	0	1		Q
	<i>Ecnomiophyla cf. valancifer</i>	0	3	0		R
	<i>Tlalocohyla loquax</i>	6	1	3	Generalist	P
	<i>Smilisca baudini</i>	5	1	5	Generalist	S
Ranidae						
	<i>Lithobates berlandieri</i>	13	0	0	Pasture	T
	<i>Lithobates vaillanti</i>	3	1	0	Pasture	U
SAURIA						
Corytophanidae						
	<i>Basiliscus vittatus</i>	0	1	2		1
	<i>Corytophanes hernandezi</i>	0	10	15	Forest	2
Gekkonidae						
	<i>Sphaerodactylus glaucus</i>	0	1	0		3
Iguanidae						
	<i>Ctenosaura acanthura</i>	0	0	1		4
	<i>Iguana iguana</i>	0	0	2		5
Phrynosomatidae						
	<i>Sceloporus salvini</i>	0	0	1		6
	<i>Sceloporus variabilis</i>	123	8	6	Pasture	7
Polychrotidae						
	<i>Anolis barkeri</i>	0	6	7	Forest	8
	<i>Anolis biporcatus</i>	0	0	1		9
	<i>Anolis cf. duellmani</i>	0	1	1		10
	<i>Anolis lemurinus</i>	0	4	6	Forest	11
	<i>Anolis pentaprinon</i>	0	4	0	Edge	12
	<i>Anolis petersi</i>	2	1	2	Generalist	13
	<i>Anolis rodriguezi</i>	1	3	6	Interior	14
	<i>Anolis sericeus</i>	19	10	3	Pasture	15
	<i>Anolis unifomis</i>	0	104	148	Forest	16

(continued on next page)

Table 3 – continued

ORDER Family	Species	Habitat			Preferred habitat ^a	Species codes
		Pasture	Edge	Interior		
Scincidae	<i>Plestiodon sumichrasti</i>	0	17	25	Interior	17
	<i>Scincella cherriei</i>	0	5	13	Interior	18
Teiidae	<i>Ameiva undulata</i>	11	6	1	Pasture	19
Xantusiidae	<i>Lepidophyma tuxtlae</i>	1	4	4	Forest	20
SERPENTES						
Boidae	<i>Boa constrictor</i>	0	0	2		21
Colubridae						
	<i>Coniophanes bipunctatus</i>	0	0	1		22
	<i>Coniophanes fissidens</i>	0	2	0		23
	<i>Coniophanes imperialis</i>	0	2	0		24
	<i>Ficimia publia</i>	1	0	0		25
	<i>Imantodes cenchoa</i>	0	3	8	Interior	26
	<i>Leptodeira septentrionalis</i>	1	2	0		27
	<i>Ninia sebae</i>	1	0	0		28
	<i>Oxyrhopus petola</i>	0	1	0		29
	<i>Pseustes poecilonotus</i>	0	1	0		30
	<i>Stenorrhina degenhardti</i>	0	1	0		31
Elapidae	<i>Micrurus diastema</i>	1	1	0		32
Viperidae	<i>Bothrops asper</i>	1	5	3	Forest	33

a Based on MDS analysis habitat affinity by the most common amphibian and reptile species was classified according to the three habitat types (pasture, forest edge, and forest interior).

3.3. Species diversity among habitats

Fifty-seven percent of all amphibian species were captured at pasture habitats, 67% at forest edge habitats and 62% at forest interior habitats. The greatest percentage of amphibian individuals was captured in the interior (47%) and on the edge (45%), while only 8% were captured in the pasture. At the forest edge and forest interior habitats, 52% of the individuals were adults, and 48% were juveniles. In the pasture 81% of the individuals were adults, and 19% were juveniles (Table 2).

For amphibians, rarefaction analysis showed that, with approximately 100 individuals sampled, the pasture was the richest habitat and its species richness was significantly different to that of the edge and forest interior habitats. After the cumulative total of individuals in the sample reached 480, species richness in the forest surpassed that of pasture habitats and was slightly higher for the edge than for the interior, indicating a change in the ensemble (Fig. 3a).

Thirty-three percent of all reptile species were captured in pasture habitats, 76% on the edge and 67% in the interior. The percentage of reptile individuals was greater in the interior (41%) and on the edge (34%), with only 25% captured in the pasture. The age ratio was similar for all three habitat types: 72% adults and 28% juveniles in the pasture, 67% adults and

33% juveniles on the edge, and 70% adults and 30% juveniles in the forest interior (Table 2).

For reptiles, rarefaction analysis showed that, at $n = 158$, the forest edge was the richest habitat, followed by the forest interior and the pasture. During the course of the study, species richness showed a constant pattern with no number of species exchange between habitats. The pasture and the edge did differ in species richness, but there was no difference in species richness between the edge and forest interior habitats (Fig. 2b).

3.4. Correlation among environmental variables

Many of the environmental variables were strongly intercorrelated (Table 4). There was a high, direct correlation between leaf litter cover and leaf litter depth, canopy cover, and understorey density. Similarly, leaf litter depth was directly correlated with understorey density and canopy cover.

The pasture–edge–interior distance gradient was related to canopy cover, understorey density, temperature, and the leaf litter depth and cover (Table 4). Understorey density was greatest on the edge of the forest and the percentage of canopy cover was greatest in the forest interior (Table 1).

Slope, altitude and distance to streams did not correlate significantly with the pasture–edge–interior distance gradient

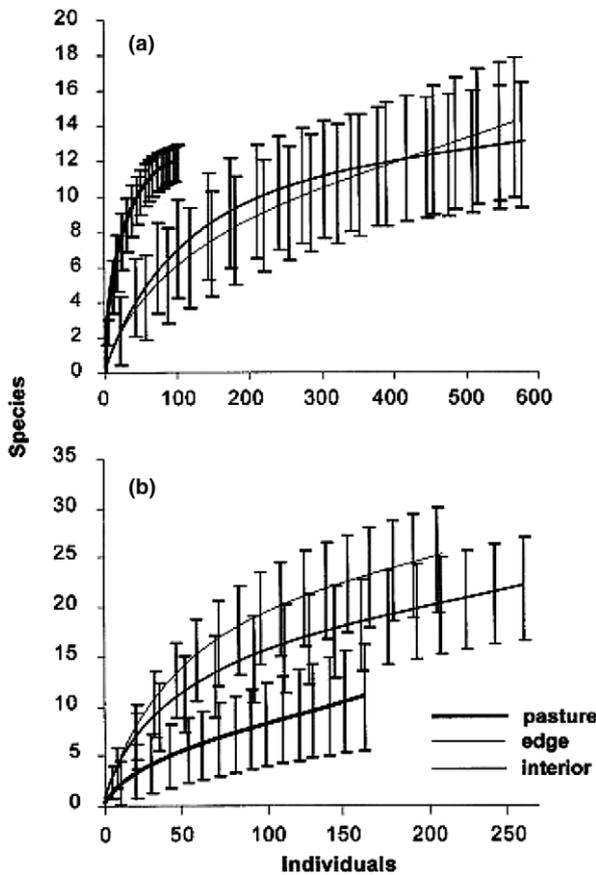


Fig. 3 – Species accumulation curves of sample-based rarefaction (Mao Tau) with confidence intervals for pasture, forest edge and forest interior habitats in 14 ecotones, Los Tuxtlas, Veracruz, Mexico. (a) Amphibians and (b) reptiles.

(Table 4) and there were no significant differences between edge and interior habitats (Table 1), demonstrating that the effect of these variables were adequately controlled for by the sampling design in this study.

3.5. Distribution of the amphibian and reptile ensemble within environmental gradients

Canopy cover and leaf litter depth were excluded from the CCA because of their high correlation with other variables, as seen above (Table 4). In the final test, altitude and slope were also eliminated because they were not significant using Monte Carlo test ($p = 0.124$ and $p = 0.694$, respectively).

There was a strong relationship between environmental variables and the amphibian and reptile ensembles. The total ordination of species along environmental variable gradients was significant ($p = 0.008$, Monte Carlo simulations at 499 permutations, CANOCO; ter Braak and Smilauer, 1998). All variables were approximately equal in their explanatory power, and were mostly grouped together, indicating a relatively simple relationship between the ensembles and a group of related variables (Fig. 4a and b).

During wet season the combination of canopy cover, temperature and leaf litter cover best explained amphibian and

Table 4 – Pearson correlation coefficients among 12 environmental variables measured at Los Tuxtlas, Veracruz, Mexico

	Distance to edge	Temperature	Relative humidity	Grass cover	Leaf litter cover	Leaf litter depth	Canopy cover	Understorey density	Slope	Altitude	Distance to streams	Precipitation
Distance to edge	1.00											
Temperature	0.17 ^c	1.00										
Relative humidity	0.16	-0.33 ^c	1.00									
Grass cover	-0.26	0.07 ^c	0.06 ^b	1.00								
Leaf litter cover	0.49 ^c	-0.22	0.13	-0.42	1.00							
Leaf litter depth	0.75 ^c	0.07 ^b	0.19	-0.26	0.65 ^c	1.00						
Canopy cover	0.58 ^c	-0.22	0.16	-0.37	0.81 ^c	0.64 ^c	1.00					
Understorey density	0.74 ^c	0.18	0.10	-0.18	0.55 ^c	0.77 ^c	0.55 ^c	1.00				
Slope	0.14	-0.06 ^b	0.07 ^b	-0.06 ^a	0.13	0.13	0.07 ^b	0.09	1.00			
Altitude	0.11	-0.17	0.17	-0.11	0.23	0.00	0.15	0.07 ^b	-0.07	1.00		
Distance to streams	0.00	-0.05 ^a	0.12	-0.07 ^b	-0.01	0.00	-0.09	-0.03	0.18	0.14	1.00	
Precipitation	0.06 ^b	-0.14	0.31 ^c	0.16	-0.06 ^a	0.06 ^a	0.01	0.02	-0.03	0.13	0.10	1.00

p Values ^a <0.05, ^b <0.01, ^c <0.001.

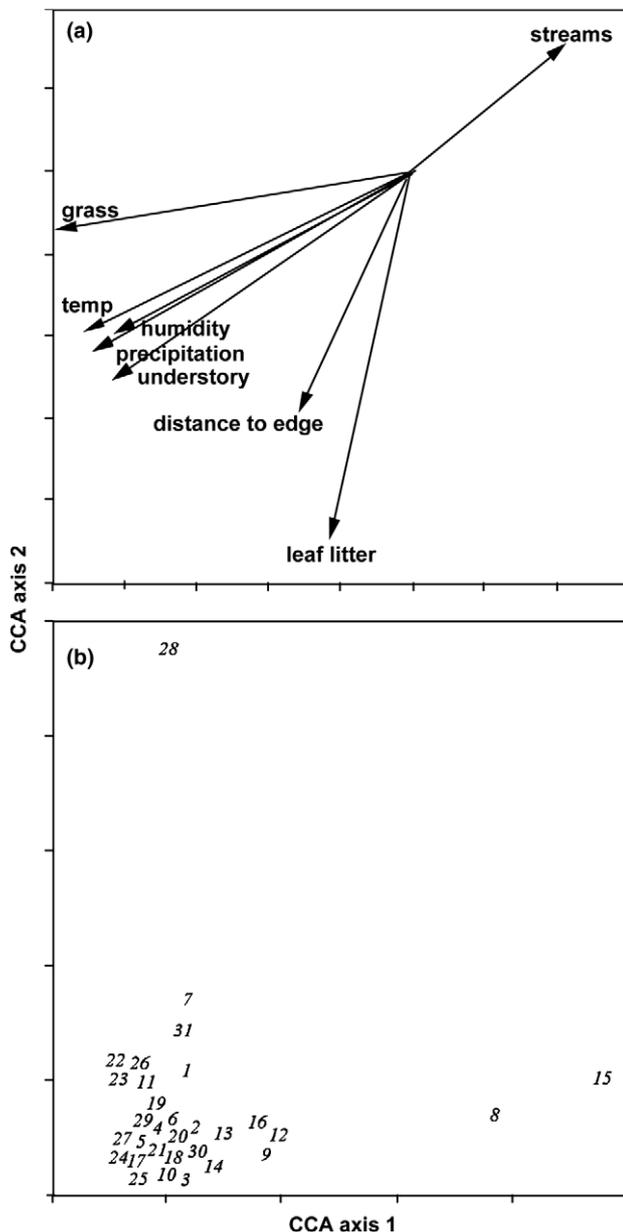


Fig. 4 – Canonical correspondence analysis of the most common amphibians and reptiles. The arrow orientation and length represents the association, direction and strength between the environmental variables and the ordination axis (ter Braak, 1987). (a) The two first axis eigenvalues are 0.582 and 0.215, respectively, and the total eigenvalue for the ordination is 2.18. The distribution of the species represents the top of the unimodal distribution of each species along the two ordination axes. (b) The codes for the reptiles are (1) *A. undulata*, (2) *Anolis barkeri*, (3) *Anolis lemurinus*, (4) *Anolis pentaprion*, (5) *A. petersi*, (6) *A. rodriguezi*, (7) *Anolis sericeus*, (8) *A. uniformis*, (10) *Bothrops asper*, (13) *C. hernandezii*, (16) *P. sumichrasti*, (20) *I. cenchoa*, (21) *L. tuxtlae*, (24) *L. septentrionalis*, (28) *S. variabilis* and (30) *Scincella cherriei*. Amphibian species are (9) *N. rufescens*, (11) *Chaunus marinus*, (12) *Cranopsis valliceps*, (14) *Craugastor alfredi*, (15) *C. rhodopis*, (17) *G. elegans*, (18) *D. ebraccatus*, (19) *T. loquax*, (22) *L. fragilis*, (23) *L. melanonotus*, (25) *P. orchimelas*, (26) *L. berlandieri*, (27) *L. vaillanti*, (29) *S. baudini* and (31) *S. leprus*.

reptile pattern ($p_w = 0.863$); during dry season the combination of distance to streams, temperature, leaf litter depth and leaf litter cover best explained amphibian and reptile pattern ($p_w = 0.868$).

3.6. Relationship of the species ensemble with the pasture–edge–interior microhabitats

With MDS we identified five species ensembles according to their responses to the pasture–edge–interior ecotone: (a) pasture species, (b) generalist species that use both pasture and forest, (c) forest edge species, (d) forest interior species, and (e) forest species using the edge and the interior interchangeably (Table 3). We used a two-dimensional configuration to describe similarities between species because of the small decrease in residual stress values with the addition of further dimensions (Legendre and Legendre, 1998). With two dimensions a relatively high proportion of the variance of the species abundance was explained at the pasture, edge and interior habitats by a fairly low level of residual stress (0.015 for amphibians, and 0.0002 for reptiles).

The total amphibian richness was positively correlated with the distance to forest edge, relative humidity, canopy cover, altitude, and understory density; and negatively correlated with slope. The amphibian richness with an affinity for the pasture was positively correlated with grass cover, and negatively correlated with the distance to forest edge, understory density and leaf litter cover. Amphibian species that showed an affinity for the edges were positively correlated with grass cover and leaf litter depth, and negatively correlated with temperature, while amphibians with an affinity for the forest interior were positively correlated with distance from edge; and negatively correlated with slope. Forest amphibians that indiscriminately use the edge and the interior were positively correlated with distance from forest edge, temperature, leaf litter cover and understory density, and negatively correlated with grass cover. Finally, amphibians were found in both the pasture and the forest interior (generalists) were negatively correlated with understory density (Table 5).

Reptile richness was positively correlated with distance from forest edge, grass cover, understory density, and temperature; and negatively correlated with canopy cover, leaf litter cover, and slope. Reptiles that showed affinities for pasture were positively correlated with temperature and distance to streams, but negatively correlated with the distance from forest edge, leaf litter cover and canopy cover. Reptiles that showed affinities for the forest interior were positively correlated with leaf litter cover; and forest reptiles found both at the edge and in the interior were positively correlated with distance from edge and canopy cover (Table 5).

4. Discussion

Amphibians and reptiles inhabiting pastures, forest edges or forest interiors in fragmented tropical environments respond to microhabitat changes in a diverse and complex manner. Results show that different environmental variables influenced the affinities of species at different habitats, reflecting a wide range of ecophysiological tolerances within the ensemble.

Table 5 – Regression models for all amphibian and reptile species and five ensembles (generalist, pasture, edge, interior, and forest species) found in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico

Ensemble		Regression model	Multiple R (%)	F test
Amphibians	All species	$y = 1.53 + 0.858*a + 0.26*h - 0.09*d + 0.28*b + 0.24*e + 0.5*c$	95	1809.20
	Generalist species	$y = 0.058 - 0.14*c$	13	23.81
	Pasture species	$y = 0.72 - 0.181*a - 0.29*j - 0.28*c + 0.107*i$	71	255.10
	Forest species	$y = -0.063 + 0.297*a - 0.18*i + 0.218*j + 0.098*g + 0.146*c$	54	84.41
	Edge species	$y = 0.179 - 0.15*g + 0.155*i + 0.128*k$	23	23.08
	Interior species	$y = 0.255 + 0.117*a - 0.01*d$	14	12.37
Reptiles	All species	$y = -1.161 + 0.789*a + 0.014*i - 0.22*b - 0.4*j + 0.427*c + 0.09*g - 0.05*d$	95	1886.56
	Pasture species	$y = 0.644 - 0.46*a - 0.36*j - 0.17*b + 0.139*g + 0.076*f$	85	273.002
	Forest species	$y = -0.212 + 0.516*a + 0.379*b$	63	137.99
	Interior species	$y = 0.0045 + 0.195*j$	19	24.65

a, distance to forest edge; b, canopy cover; c, understorey density; d, slope; e, altitude; f, distance to streams; g, temperature; h, relative humidity; i, grass cover; j, leaf litter cover; k, leaf litter depth; l, precipitation.

4.1. Species composition patterns

We found that amphibian and reptile ensembles differed in species composition among habitats because of different abundance distribution patterns (e.g., changes in the slope of the rank–abundance curves) and hierarchical position of species (e.g., changes in the species dominance on different habitats). Changes in the amphibian and reptile ensembles between forest edge and interior habitats could be explained by the different patterns of relative abundance and habitat use. As an example, we have observed that some amphibian species, such as white-lipped frog *Leptodactylus fragilis*, Sabinal frog *Leptodactylus melanonotus*, *S. leprus*, common Mexican treefrog *Smilisca baudini* and in general all treefrogs (*Hylidae*) could increased their abundance in a specific habitat during the reproductive season. We found that during wet season, canopy cover was an important variable to the amphibians and reptiles because this variable could protect terrestrial microhabitats during the adverse tropical rainfall. During dry season water deficit is critical so distance to streams, best explained amphibian and reptile pattern. In this regard, the relative importance of habitats could change for a given species through time, resulting in the movement of organisms between habitats caused by changes in resource availability (Van Horne, 1982).

4.2. Habitat quality and changes in microhabitat

Edge effects are a key component to understand how landscape structure influences habitat quality (Ries et al., 2004). Habitat quality is a measure of the importance of habitat type in maintaining a particular species (Van Horne, 1983). In our study, habitat quality along the pasture–edge–interior ecotone was defined as a complex function of the 12 environmental variables we measured and that influenced (sensu Resource mapping, Ries et al., 2004) both amphibian and reptile species richness (as revealed through regression analysis) and abundance (through CCA and BIOENV). We suggest that there is a strong relationship between environmental variables, such as vegetation cover, temperature and relative humidity, and the other factors that modify habitat quality for these organisms such as food and shelter (sensu Fischer et al., 2005).

Species are affected in a major or minor way by their surrounding environment depending on the way they use it. Identifying the variables that affect the presence of amphibian and reptile species in a given habitat is imperative in order to determine the threats that these species might be exposed along the pasture–edge–interior ecotone. This will allow for the creation of robust tools for the conservation and management of species in fragmented tropical forest.

The edge effects for these organisms were an indirect response to a cascade of effects that involved environmental variables of the microhabitat. In Los Tuxtlas, the air and ground temperature in the forest tend to diminish from the fragment edge to the interior, while relative humidity and canopy cover tend to increase (Williams-Linera et al., 1998). According to our results canopy cover, leaf litter cover, understorey density, leaf litter depth, and temperature co-varied with the pasture–edge–interior distance gradient. The first three variables affected the amphibians as a whole, but particularly those with affinities for pastures and forest, co-varying with the edge effect. The first two variables also influenced all the reptiles, but specifically those with an affinity for pastures, also co-varying with the edge effect. Leaf litter depth and temperature influenced those amphibians with an affinity for the edge.

Deforestation in Los Tuxtlas is greater at low elevations where farming is possible, so most of the remaining forest patches are found on mountaintops and steep slopes (Guevara et al., 1998; Laborde, 2004; Mendoza et al., 2005). Steep slopes have been found to be inadequate for the establishment of large trees (Martínez-Ramos et al., 1988) and daily temperature patterns are modified (Pianka, 2000), altering considerably the habitat quality in the forest interior. The difficulty in finding fragments with good habitat quality further restricts the distribution of amphibians exclusive to the interior. This makes the creation of lowland conservation areas even more urgent. If conservation efforts focus on connecting lowland forest fragments with riparian vegetation, secondary forest and living fences, natural restoration could be stimulated in abandoned pastures (Guevara et al., 2004). Our data can assist wildlife managers in the selection of forest fragments appropriate for the preservation of amphibian and reptile species as ensembles. By way of example, maintaining

forest microhabitats with dense canopy cover, a deep leaf litter cover and a dense understorey will prevent the invasion of the forest by amphibian and reptile species from the pasture (see Table 5) and will provide good habitat quality for forest interior species (see Fig. 3a and b).

We found that changes in the total species richness (95% for amphibians and 95% for reptiles) and pasture only species (71% for amphibians and 85.2% for reptiles) were explained by changes in the 12 environmental variables, but this decreased on analyzing more specialized ensembles such as forest species (54% for amphibians and 63% for reptiles), edge species (23% for amphibians), and principally interior species (14% for amphibians and 19% for reptiles). This pattern reflects the high degree of complexity in the species–microhabitat relationships of the forest, and particularly of the interior habitats. The relationship between forest interior species and their microhabitat remains unknown and we feel that future studies should carefully explore the mechanisms that explain the amphibian and reptile ensembles that inhabit the interior of fragmented forest.

4.3. Amphibians and reptiles in pasture, edge and interior habitats

Pasture has been considered as a high quality habitat for anuran reproduction because of the presence of artificial water bodies. The reproductive success of frogs that reproduce in ponds may be greater in pastures than in the forest (Gascon, 1993; de Lima and Gascon, 1999). However, our results demonstrated that the pasture matrix *sensu stricto* was not necessarily an ideal habitat for the reproduction and maintenance of amphibians. These habitats had the lowest richness, the lowest number of individuals, and the smallest proportion of juveniles compared to the forest edge and interior habitats. The lowest diversity of amphibians and reptiles found in Los Tuxtlas pastures was a consequence of the deliberate decision to sample exclusively on pasture habitats, away from other landscape components such as water bodies, riparian vegetation corridors, isolated forest and trees, orchards (with *Citrus* spp., *Psidium guajava* and *Byrsonima crassifolia*), and living fences of *Bursera simaruba*, *Gliricidia sepium* and *Erythrina folkersii* (Guevara et al., 1994). We expect that if the sampling effort was extended to include all these elements within the pasture areas, the richness of the species of amphibians and reptiles in the pasture would increase significantly, as reported by Gascon (1993) and de Lima and Gascon (1999). We have observed several frog species in pasture areas away from the pasture habitats *sensu stricto*. These include *S. baudini*, Mahogany treefrog *Tlalocohyla loquax*, painted tree frog *Tlalocohyla picta*, Rio grande leopard frog *Lithobates berlandieri* and *S. leprus*, species that actively vocalize in the living fences and small bushes of the pasture throughout the year. However, we have to keep in mind that all these landscape components act as forest edges (de Lima and Gascon, 1999) and cannot be used by interior species to reproduce, disperse, forage or as refuge.

At the forest edge there is a highly dynamic pattern of species flux, from the pasture matrix to the edge that extends into the forest. At the forest edge there are changes in microclimate and an increase in tree mortality caused by wind turbulence (Laurance et al., 2002). The constant canopy openings

caused by tree mortality promote the movement of pasture lizard species into the forest interior (Sartorius et al., 1999). Surprisingly, in Los Tuxtlas we have found the pasture species the rainbow lizard *Ameiva undulata* and *S. variabilis* in forest interior gaps at 200 m from the edge. This supports the findings of Sartorius et al. (1999) for the Brazilian Amazon. We concluded that the intrusion of alien species into the forest interior can modify amphibian and reptile interactions (e.g., competition and predation) as an indirect effect of the creation of gaps in the canopy.

4.4. Species affinities for habitats

Ries et al. (2004) identify three classes of ecological responses with respect to distance from the closest habitat edge, but do not include direct responses to matrix habitats. Using MDS techniques we grouped species into ensembles based on their habitat affinities. Our results suggested that amphibian and reptile ensembles responded in different ways to the pasture–edge–interior ecotone leading to five ensemble categories: (1) Pasture species that preferentially used the pasture matrix habitat and were less affected by human disturbances; (2) generalist species that used both the pasture and the forest habitat and tolerated all the environmental gradients that occurred between the pasture and the forest interior; (3) forest species that used the edge and interior habitats indiscriminately but avoided the pasture, and so were affected by habitat loss; (4) forest edge species that preferentially used the ecotone but tended to avoid the pasture, and so were affected by habitat loss; and, (5) forest interior species that tended to avoid the microclimatic habitat fluctuations characteristic of the edge, and were strongly affected by the edge effect, the loss of habitat and the breaking apart of habitat. These ensembles have to be visualized as different conservation targets since they have different responses to spatial and environmental gradients, different degrees of tolerance to microclimatic changes, and are affected in different ways by edge effects and habitat loss. Different conservation and management strategies are required to ensure the survival of these amphibians and reptiles in fragmented landscapes.

Special care must be taken when attributing affinity patterns to rare species. Some species rare to forest habitats (edge and interior) were the Mexican mushroom tongue salamander *Bolitoglossa alberchi*, worm salamander *Pseudoeurycea orchimelas*, Berkenbusch's stream frog *Craugastor berkenbuschi*, the Central American rain frog *Craugastor vulcani*, elegant narrow-mouth toad *Gastrophryne elegans*, hourglass tree frog *Dendropsophus ebraccatus*, *T. loquax*, yellow tree frog *Dendropsophus microcephalus*, *S. baudini*, Vaillant's frog *Lithobates vaillanti*, *Anolis* cf. *duellmani*, the brown basilisk *Basiliscus vittatus*, and Peter's anole *Anolis petersi*. Finding a small sample of a given species in a particular habitat does not necessarily mean the species prefers that habitat. Such a finding could occur for a species that is abundant in other habitats that were not surveyed (Magurran, 2004). *D. ebraccatus*, *T. loquax*, *D. microcephalus*, *S. baudini*, *L. vaillanti*, *B. vittatus* and the green iguana *Iguana iguana* were found to be associated with pastures, the forest edge or forest interior habitats, but are known to be related to water bodies. Results in similar studies need to be assessed in the light of the natural history and autoecology of each species.

The amphibians *P. orchimelas*, the Gulf coast frog *Cranopsis valliceps*, and *C. vulcani*, and the reptiles the brown forest skink *Scincella cherriei*, *P. sumichrasti* and the blunthead tree snake *Imantodes cenchoa* were truly forest interior species. These species tend to undergo local extinction in Los Tuxtlas because they require forest fragments with high habitat quality (e.g., high leaf litter cover, understorey density and relative humidity, and low temperatures) in order to reproduce and survive. In the Los Tuxtlas Biosphere Reserve, fragments suitable for the preservation of amphibians and reptiles are scarce. Forty percent of the remaining fragments do not have an area free of the edge effect on microclimate, and larger fragments deviate markedly from the ideal circular shapes (Mendoza et al., 2005).

The results of our study showed those species to which special attention should be paid. These species reflect the habitat quality of the forest interior and their disappearance may be an indication of habitat degradation within a fragment, or that a fragment is not large enough to exclude edge effects (*sensu* Saetersdal et al., 2005). These species should be monitored more closely, since they are highly sensitive to perturbation and are often the most vulnerable to fragmentation. They easily disappear from fragments after isolation (Laurance, 1999; Tocher et al., 2001) and can even suffer local extinction (Lehtinen et al., 2003).

5. Conclusions

Pasture habitat is different from both forest edge and forest interior habitats, having the lowest richness, the lowest number of individuals, and the smallest proportion of juveniles. Changes in amphibian and reptile richness across the pasture–forest ecotone were well explained by some microenvironmental variables. We found a high correlation between the distance from the forest edge with temperature, understorey density, canopy cover, leaf litter cover, and leaf litter depth. The distribution of the amphibians and reptiles was strongly affected by canopy cover, leaf litter cover, understorey density and temperature. This is strong evidence of the cascade effects related to the forest edge. To understand the effects of edges on the diversity of herpetofauna, it is important to first understand their relationship with the microhabitat variables that could determine habitat quality along the pasture–edge–interior ecotones.

In addition to regional management initiatives, the survival of amphibian and reptile species should be promoted through local management. Living fences, isolated trees, riparian vegetation and secondary forest all increase shade in the pasture and generate a good substrate (via leaf litter) for the movement of some of the forest and edge species between forest fragments. Although data are needed from additional groups, the results of our study suggest that in order to offer herpetofauna good habitat quality in remnant fragments, it is necessary to maintain the forest remnants in the lowlands that have gentler slopes and a deep cover of leaf litter, a dense understorey, and high relative humidity and low temperature. Understanding the relationships between different ensembles and their microhabitats can improve our knowledge of habitat quality along pasture–edge–interior ecotones and allow for the development of robust conserva-

tion tools for tropical amphibian and reptile species as a whole along habitat gradients. The management of forest edges should be included in habitat conservation programs to preserve tropical rainforest fragments and provide a better habitat for interior species.

Although the protection of forest interior species has been a major issue in conservation biology, any strategies proposed will be incomplete and unsustainable if they do not take amphibians and reptiles, their habitat gradient and their natural history into account. In a modern world, with the preservation of all these environments we can mitigate the massive decline in tropical amphibian and reptile species by maintaining the largest number of processes and biological interactions within and outside the fragments.

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