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EVALUACIÓN DEL EFECTO DE BORDE SOBRE LA
COMPOSICIÓN DE LA COMUNIDAD DE
HERPETOFAUNA EN ÁREAS CON DIFERENTE USO DEL
SUELO Y ORIENTACIÓN DEL BORDE EN LA RESERVA
LOS TUXTLAS, VERACRUZ.

T E S I S

QUE PARA OBTENER EL GRADO ACADÉMICO DE

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JOSÉ NICOLÁS URBINA CARDONA

DIRECTOR DE TESIS:

DR. VÍCTOR HUGO REYNOSO ROSALES

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Dr. Rodolfo Dirzo

Dr. Gerardo Ceballos

“Cada especie, aun en el sitio en que más abunda, sufre una constante y enorme destrucción en algún período de su existencia, a causa de los enemigos que compiten por la zona y el sustento” ... “la naturaleza puede actuar sobre cada órgano interno, en cada sombra de diferencia constitucional, en la totalidad de la maquinaria completa de la vida... mientras el hombre escoge sin mas miras que su propio bien”.

Charles Darwin (1859)

“La extinción de algunas especies ha sido causada por la destrucción total de los bosques y la consiguiente perdida de comida y abrigo”.

Charles Darwin (1837)

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RESUMEN

La deforestación de los ecosistemas tropicales es una de las mayores amenazas para la diversidad biológica. Genera una gran cantidad de hábitat de borde que limita con ambientes antropogénicos como el potrero, y determina la distribución de las especies en los fragmentos remanentes. Así mismo, en los fragmentos de bosque se alteran las dinámicas microclimáticas y la estructura y composición de la herpetofauna, reduciendo la viabilidad de las poblaciones e incrementando su vulnerabilidad a la extinción. Se sabe que aquellas especies que hacen uso del potrero para la dispersión y reproducción se ven menos afectadas por la fragmentación del hábitat. Pero existe un grupo reducido de especies que habita el interior de los bosques, evitan los bordes y nunca atraviesan el potrero, siendo más vulnerables a la extinción por causa del efecto de borde. En este estudio se determinó el efecto de borde sobre la diversidad de anfibios y reptiles en la región de Los Tuxtlas, y su relación con el microhábitat.

Se ubicaron 18 ecotonos de 250 x 50 m en seis fragmentos de Selva Alta Perennifolia en la región de Los Tuxtlas, Veracruz, México. Cada ecotono fue dividido en tres hábitats: matriz (que comprende la franja externa entre el borde de la selva y 50 m hacia el potrero o el acahual), borde de selva (que va desde el borde interno de la selva hasta 20 m hacia el interior) e interior de selva (que va perpendicular al borde desde 50 hasta 200 m hacia el interior de la selva). En cada hábitat se ubicaron tres transectos lineales de 50 x 2 m, paralelos al borde de la selva y a distancias preestablecidas de éste, para un total de 162 transectos en el estudio. En cada transecto se midieron doce variables incluyendo el microclima, la estructura vegetal, la topografía y la distancia a cuerpos de agua, con el fin de determinar patrones en la composición y diversidad de anfibios y reptiles y su relación con el microhábitat. Cada transecto fue muestreado por dos personas durante el día y la noche invirtiendo el mismo esfuerzo de captura en seis temporadas (de junio de 2003 a abril de 2005) para un esfuerzo total del estudio de 1296 horas hombre.

Al final de las seis salidas al campo se registraron 2835 individuos de 24 especies de anfibios (12 en potrero, 8 en acahual, 19 en borde y 20 en interior) y 1498 individuos de 42 especies de reptiles (12 en potrero, 10 en acahual, 31 en borde y 32 en interior). La composición de especies en el potrero es diferente a la del borde e interior de selva. El potrero estuvo dominado por *Lithobates berlandieri*, *Leptodactylus fragilis*, *Syrrhophus leprus* y *Sceloporus variabilis*, y el borde e interior de selva por *Craugastor rhodopis* y *Anolis uniformis*. Se detectaron dos lagartijas típicas de matriz (*Sceloporus variabilis* y *Ameiva undulata*), que pueden invadir el interior del bosque haciendo uso del microhábitat generado por las aperturas en el dosel. Se determinó que *Pseudoeurycea orchimelas*, *Ollotis valliceus*, *Craugastor vulcani*, *Imantodes cenchoa*, *Scincella cherriei* y *Plestiodon sumichrasti* son especies típicas de interior que reflejan la calidad del hábitat en la selva, y su ausencia podría indicar una degradación en el hábitat o que el fragmento no es lo suficientemente grande como para amortiguar los efectos del borde. Hacia el potrero aumentan las especies de anfibios y reptiles con preferencia por hábitat terrestres y anfibios con modo reproductivo de huevos y larvas acuáticas. Hacia el interior de la selva aumentan las especies de reptiles grandes y arborícolas, y de anfibios pequeños con desarrollo directo y preferencia por hábitat fosoriales y arborícolas.

La estacionalidad y el tipo de hábitat tienen un efecto sobre la abundancia y composición de los reptiles. Para los anfibios se determinó que la estacionalidad y el tipo de hábitat y la orientación del borde tienen un efecto sobre la abundancia y composición. El patrón en la estructura de la herpetofauna fue explicado, durante la época de secas, por la combinación de cobertura de dosel, temperatura y cobertura de hojarasca; mientras que en lluvias fue explicado por la combinación de distancia a cuerpos de agua, temperatura, y cobertura y profundidad de hojarasca.

Determinar la distribución de los anfibios y reptiles en el gradiente potrero-borde-interior y su relación con el microhábitat, nos da herramientas robustas para el desarrollo de estrategias de conservación de herpetofauna en ambientes altamente fragmentados. Este trabajo hace un aporte a la historia natural de la herpetofauna que habita las tierras bajas en la región de Los Tuxtlas, complementa la teoría sobre el efecto de borde en la herpetofauna tropical y propone herramientas concretas para el manejo y conservación local de los anfibios y reptiles. Es necesario desarrollar más investigación acerca de los mecanismos que determinan la distribución de anfibios y reptiles en el interior de las selvas, para entender mejor sus fluctuaciones temporales, su estructura poblacional y su grado de amenaza a la extinción.

ABSTRACT

Deforestation of tropical ecosystems is one of the major threats to biological diversity. It generates great amount of forest edge that limits with anthropogenic habitat, such as pasture, and determines species distribution in the forest remnants. Within the remnants, changes in microclimate and herpetofaunal structure and composition, reduce population viability and increase herps vulnerability to extinction. The species that tolerate and use the pasture to disperse and reproduce are less affected by forest fragmentation. In contrast, some forest interior affine species are the most vulnerable to extinction due to their sensibility to edge effect. I evaluated the edge effect on amphibian and reptile's diversity in a tropical rainforest in Los Tuxtlas region and their relationship with microhabitat dynamics.

Eighteen ecotones of 250 x 50 m were set in six tropical rainforest fragments in Veracruz, Mexico. Each ecotone was divided into three habitats: matrix (delimited within the first 50 m of the pasture), forest edge (delimited within the first 20 m of forest) and forest interior (placed beyond the first 50 m of forest from the edge). 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 18 ecotones containing 162 transects. On each transect I measured 12 environmental variables describing the microclimate, vegetation structure, topography and distance to forest edge and streams to evaluate the main correlation patterns among microhabitat variables and herpetofaunal species composition and diversity. Each transect were sampled six times (form June 2003 to April 2005) by two persons at day and night for a total effort of 1296 man hours.

After six field seasons, 2835 individuals of 24 amphibian species (12 in pasture, 8 in secondary forest, 19 in forest edge and 20 in forest interior) and 1498 individuals of 42 reptile species (12 in pasture, 10 in secondary forest, 31 in forest edge and 32 in forest interior) were captured. I found that amphibian and reptile composition were different in pasture than in forest edge and interior. The surrounding pasture matrix was dominated by *Lithobates berlandieri*, *Leptodactylus fragilis*, *Syrrhophus leprus* and *Sceloporus variabilis*, while forest edge and interior were dominated by *Craugastor rhodopis* and *Anolis uniformis*. I detect two pasture species (*Ameiva undulata* and *S. variabilis*) that could invade the forest interior using the microhabitat created under the canopy gaps. I determined that *Pseudoeurycea orchimelas*, *Ollotis valliceptis*, *Craugastor vulcani*, *Imantodes cenchoa*, *Scincella cherriei* and *Plestiodon sumichrasti* were truly forest interior species 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. Towards the pasture the number of species of amphibians and reptiles with terrestrial habitats increased, as did the amphibians with reproductive mode of eggs and larvae in water. Towards the interior of the forest the number of species of reptiles with larger size and arboreal habitats increased, as did the amphibians with direct embryo development and with fossorial and arboreal habitats.

I found that seasonality and habitat type (pasture, forest edge or forest interior) had a strong effect on reptile's abundance and composition, while seasonality, habitat type and edge orientation had a strong effect on amphibian's abundance and composition. During wet season the combination of canopy cover, temperature and leaf litter cover best explained amphibian and reptile pattern; during dry season the combination of distance to streams, temperature, leaf litter depth and leaf litter cover best explained amphibian and reptile pattern.

Determining the distribution of amphibians and reptiles across the pasture, forest edge and forest interior gradient and their relationship with microhabitat will allow for the creation of robust tools for conservation and management of the herpetofauna in highly fragmented tropical landscapes. This dissertation provides robust data on natural history of Los Tuxtlas lowlands herpetofauna, complements the edge effect theory on tropical environments and propose concrete local management and conservation strategies for the amphibians and reptiles. Future research efforts most focus on the mechanisms that determine amphibian and reptile's distribution in rainforest interiors to better understand their seasonal fluctuations, population ecology and their threats to extinction.

INTRODUCCION GENERAL

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La deforestación de áreas naturales ha generado paisajes altamente fragmentados a lo largo del mundo siendo la principal amenaza para la supervivencia de la biodiversidad actual (Withmore 1997, Dirzo y Raven 2003). El uso del suelo determina la extensión de la deforestación, el grado de transformación y el tiempo de la explotación (Guevara *et al.* 2005a). Las principales causas de la pérdida de hábitat son la explotación forestal, apertura de campos para cultivo y ganadería, y el desarrollo de infraestructura (Geist y Lambin 2002, Dirzo y Raven 2003) que traen como consecuencia la división del hábitat original. La fragmentación del hábitat es un proceso por el cual una gran cantidad de hábitat es transformado a un gran número de pequeños parches que se encuentran aislados entre sí por ambientes antropogénicos de hábitat diferentes al original (pastizal, tierras agrícolas y bosque secundario) (Wilcove *et al.* 1986, Saunders *et al.* 1991, Culotta 1995).

Actualmente se sabe que los efectos de la fragmentación, van más allá de la pérdida de especies en los fragmentos, planteada originalmente por la Teoría de la Biogeografía de Islas (MacArthur y Wilson 1967), en la cual se veía a los fragmentos remanentes como “islas de hábitat” inmersos en un mar de hábitat alterado (Whittaker 1998). Sin embargo, la invasión de especies foráneas en ambientes fragmentados y la posibilidad de dispersión de algunas especies entre fragmentos haciendo uso de la matriz antropogénica son radicalmente diferentes al confinamiento dado por el mar salado (Whittaker 1998). Por ello en los paisajes fragmentados se visualiza un patrón en el cual, el hábitat remanente presenta efectos de borde y de la matriz que determinan la manera como el fragmento evoluciona luego de la perturbación (Gascon y Lovejoy 1998, Gascon *et al.* 1999, Laurance *et al.* 2002). De esta manera, la fragmentación del hábitat es un proceso dinámico en espacio y tiempo (Lovejoy 1999, Schlaepfer y Gavin 2001, Lehtinen *et al.* 2003) que implica diversos efectos sobre los patrones del hábitat (Fahrig 2003, Guevara *et al.* 2005b): disminución de la cantidad de hábitat, aumento en el aislamiento, incremento en el número de parches de bosque, distribución y reducción del área de los fragmentos.

En los fragmentos de hábitat remanente, ocurren cambios que se manifiestan a diferentes niveles. Primero se afecta el ambiente físico, por ejemplo en ambientes tropicales, aumenta la luz y la temperatura (Murcia 1995, Hunter 1996); segundo, se altera la distribución y abundancia de los organismos (Saunders *et al.* 1991, Abensperg-Traun *et al.* 1996, Bender *et al.* 1998); tercero, se alteran las interacciones entre especies (por ejemplo: la predación y el parasitismo) (Murcia 1995, Kattan y Álvarez-López 1996); y cuarto, se genera una gran cantidad de hábitat de borde que separa el bosque de la matriz (Hunter 1996, Murcia 1995). La matriz es definida como un área que presenta gran extensión en el paisaje, rodea los parches de hábitat original y actúa como un filtro selectivo para el movimiento y dispersión de las especies de animales y plantas a lo largo del paisaje (Wilcove *et al.* 1986, Hunter 1996, Gibbs 1998, Gascon *et al.* 1999). El patrón de la fragmentación determina los procesos y flujos ecológicos en el paisaje y regula la biodiversidad local (Guevara *et al.* 2005b).

Desde el punto de vista de la pérdida de hábitat, la fragmentación tiene efectos negativos muy marcados debido a que cada parche no puede sostener por sí solo una población local (Fahrig 2003). De esta manera, las especies que no pueden cruzar la matriz quedan confinadas al hábitat remanente, aumentan su vulnerabilidad, pueden tender a la endogamia y a la extinción local (Burkey 1989, Fahrig y Merriam 1994, Bender *et al.* 1998, Gascon *et al.* 1999, Fahrig 2003). Este patrón se ha documentado para grandes mamíferos (Lovejoy *et al.* 1986), primates (Gilbert y Setz 2001), aves del sotobosque (Stratford y Stouffer 1999) e insectos (Didham 1997) tales como: abejas (Powell y Powell 1987), hormigas (Vasconcelos 1988), escarabajos (Klein 1989), termitas (Souza y Brown 1994) y mariposas (Brown y Hutchings 1997). Se ha determinado que aquellas especies de anfibios y reptiles tropicales que tienen alta capacidad de dispersión y tolerancia a la matriz, tienden a ser menos vulnerables a la fragmentación que aquellas que la evitan (Gibbs 1998, Gascon *et al.* 1999, Laurance 1999, Lehtinen *et al.* 2003). Además debido a la invasión del fragmento por parte de especies asociadas a la matriz, ésta ejerce una fuerte influencia en las dinámicas de la fauna del bosque remanente (Laurance 1994, Brown y Hutchings 1997, Tocher *et al.* 1997, Sartorius *et al.* 1999).

Una de las principales consecuencias de la fragmentación, es el efecto de borde, entendido como el resultado de la interacción entre distintos tipos de vegetación, hábitat boscosos y no boscosos, o dos ecosistemas adyacentes separados por una transición abrupta conocida como ecotono, interfase o límite (Murcia 1995, Ries *et al.* 2004, Harper *et al.* 2005). Este borde antropogénico (borde inducido de Harper *et al.* 2005) debe diferenciarse de zonas de ecotonos naturales donde se presentan gradientes entre dos tipos de hábitat naturales (Gascon y Lovejoy 1998). Los cambios generados por la influencia de bordes antropogénicos se manifiestan localmente en el ambiente (microclima y régimen de disturbio, entre otros) y en las poblaciones (parásitos, predadores y herbívoros, entre otros) (Murcia 1995, Turton y Freiburger 1997, Williams-Linera *et al.* 1998). Por ello, hacia los límites del fragmento con la matriz, se incrementa la densidad de especies de borde (Leopold 1933, Hunter 1996, Bender *et al.* 1998, Whittaker 1998) que toleran ambientes más secos, con temperaturas más altas y con mayor grado de exposición al viento proveniente de la matriz (Chen *et al.* 1992, Murcia 1995, Urbina-Cardona *et al.* 2006). Estas variables cambian dependiendo de la edad, orientación y aspecto del borde (Kapos *et al.* 1997, Turton y Freiburger 1997) al igual que evolucionan con el tiempo a medida que el borde se cierra por el crecimiento de vegetación secundaria (Camargo y Kapos 1995, Laurance *et al.* 2002).

La intensidad del efecto de borde ha sido medida como la distancia hacia el interior del bosque, en la cual los cambios en la abundancia de las especies desaparecen (Murcia 1995). Otro enfoque más reciente es medir la influencia del borde entendida como el grado en el que un parámetro en el borde difiere al compararlo con el interior del bosque (Harper *et al.* 2005). La magnitud del efecto de borde varía según la sensibilidad del grupo estudiado, las variables medidas y la localidad de estudio (Chen *et al.* 1992, de Maynadier y Hunter 1998, Schlaepfer y Gavin 2001, Toral *et al.* 2002, Harper *et al.* 2005). Para la herpetofauna el efecto de borde se describe como un proceso dinámico en espacio y tiempo (Osorno 1999, Schlaepfer y Gavin 2001, Lehtinen *et al.* 2003) y puede variar entre diferentes usos del suelo (de Maynadier y Hunter 1998, Gascon *et al.* 1999, Toral *et al.* 2002) siendo más fuerte para la herpetofauna neotropical en tierras bajas (Gascon 1993, Pearman 1997, Urbina-Cardona *et al.* 2006) en relación con bosques de montaña (bosque Andino; Marsh y Pearman 1997, Toral *et al.* 2002). Algunos estudios

demuestran la existencia de efectos de borde positivos sobre la distribución y abundancia de ranas como aparente resiliencia al perturbación (Gascon 1993, Pearman 1997, Tocher *et al.* 1997, Gascon *et al.* 1999). Sin embargo existe un grupo reducido de especies que habita el interior de las selvas, evitan los bordes y nunca atraviesan la matriz siendo mas vulnerables a la extinción por causa del efecto de borde y la perdida de habitat (Lehtinen *et al.* 2003, Urbina-Cardona *et al.* 2006).

La región de Los Tuxtlas se encuentra altamente fragmentada por la alta deforestación, por lo que es un sistema de estudio excepcional para analizar los efectos derivados de la pérdida de hábitat, como es el estudio del efecto de borde en ecotonos antropogénicos. El objetivo general de mi tesis fue determinar el efecto de borde sobre los anfibios y reptiles de la selva de Los Tuxtlas, y su relación con el microhábitat, la estacionalidad y la orientación del borde.

En el Capítulo 1 (Urbina-Cardona y Reynoso 2005) se evalúa el efecto de borde sobre los anfibios y reptiles de la selva alta perennifolia de Los Tuxtlas, con el fin de determinar la diversidad local, y de recambio en el gradiente potrero, borde e interior de selva. Debido a que nunca se había estudiado el efecto de borde a la luz de la historia natural de las especies (*sensu* Zimmerman y Bierregard 1986) se encontraron patrones muy interesantes al clasificar las especies por categorías de hábitat, habito, talla y modo reproductivo a lo largo de este gradiente potrero-borde-interior de selva. Este capítulo presenta una exploración de los datos obtenidos a partir de las primeras cuatro salidas al campo.

Durante el transcurso del presente trabajo, la taxonomía mundial de los anfibios tuvo un cambio abrupto a nivel de familia, género y especie a partir de los trabajos de Faivovich *et al.* (2005) y Frost *et al.* (2006a). Durante el Capítulo I (Urbina-Cardona y Reynoso 2005) usé la nomenclatura antigua de las especies y a partir del Capítulo II (Urbina-Cardona *et al.* 2006) uso la nueva nomenclatura oficial para las especies que se distribuyen en la región de Los Tuxtlas. Un error en la taxonomía propuesta por Frost *et al.* (2006a) asignó a uno de los géneros de sapo (anteriormente *Bufo*) el nombre de *Cranopsis* sin percatarse que ese nombre ya había sido asignado previamente a un molusco. Este error se corrigió posteriormente en una nota científica dándole el nombre

de *Ollotis* (Frost et al. 2006b) pero el cambio no alcanzo a ser incluido en el presente trabajo.

En el Capítulo 2 (Urbina-Cardona *et al.* 2006) se presenta un estudio del efecto de borde sobre la composición, riqueza y distribución de los anfibios y reptiles de Los Tuxtlas. Se describe exhaustivamente la relación entre las variables ambientales y su fluctuación en relación a la distancia al borde de la selva. Se clasificó a la herpetofauna en cinco categorías que representan la afinidad de las especies por determinada porción del gradiente y se determinó su relación con el microhábitat. Con base en los resultados se proponen estrategias de manejo local de los bordes de selva para la conservación de las especies en los remanentes.

En el Capítulo 3 se presenta un enfoque teórico de información para la selección de modelos que explican la presencia de algunas especies de ranas y lagartijas a través del criterio de información de Akaike. Esta técnica permite evaluar simultáneamente diversas hipótesis generadas *a priori* con base en el conocimiento de la literatura y la historia natural de las especies. Se pudo valorar cuales son las variables que determinan la presencia de algunas especies en la región de Los Tuxtlas a diferentes escalas espaciales: microhábitat, fragmento, y paisaje. Éste capítulo representa el primer estudio de caso para especies neotropicales evaluando simultáneamente la influencia de diversas variables ambientales a diferentes escalas espaciales.

En el Capítulo 4 se presenta la evaluación del efecto de borde sobre la composición y abundancia de los anfibios y reptiles y su relación con la estacionalidad y la orientación del borde en la selva de Los Tuxtlas. Esta es la primera vez que se demuestra que la orientación del borde puede llegar a tener un efecto considerable en ambientes tropicales, en contraste con lo reportado por las revisiones de literatura más recientes (Ries *et al.* 2004, Harper *et al.* 2005). En conjunto el Capítulo 2 y el Capítulo 4 representan una base sólida en el estudio del efecto de borde en la herpetofauna neotropical que enriquece ampliamente la reducida literatura al respecto.

Los Apéndices I y II presentan estudios complementarios al proyecto de mi tesis doctoral. Ambos estudios abordan el microhábitat de los anfibios y reptiles en la selva alta perennifolia de Los Tuxtlas. En el Apéndice I se determinó el uso del hábitat por parte de la herpetofauna de Los Tuxtlas haciendo uso de modelos nulos que describieron

el grado de anidamiento de la herpetofauna y la sobre posición de nicho espacial. En el Apéndice II se realiza una descripción detallada del microhábitat de las especies más abundantes en la selva alta perennifolia de Los Tuxtlas y se modelan los parámetros que determinan la presencia de estas especies.

En conjunto este trabajo hace un aporte importante en la historia natural y la autoecología de las especies que habitan la selva alta perennifolia de Los Tuxtlas, amplía la teoría sobre el efecto de borde en la herpetofauna tropical y propone herramientas concretas para el manejo y conservación local de los anfibios y reptiles.

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CAPÍTULO 15:

Recambio de anfibios y reptiles en el gradiente potrero-borde-interior en Los Tuxtlas, Veracruz, México

José Nicolás Urbina-Cardona

Colección Nacional de Anfibios y Reptiles
Departamento de Zoología
Instituto de Biología
Universidad Nacional Autónoma de México
México, D.F. 04510 México
nurbina@yahoo.com

Víctor Hugo Reynoso

Colección Nacional de Anfibios y Reptiles
Departamento de Zoología
Instituto de Biología
Universidad Nacional Autónoma de México
México, D.F. 04510 México
vreynoso@biologia.unam.mx

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**RECAMBIO DE ANFIBIOS Y REPTILES EN
EL GRADIENTE POTRERO-BORDE-INTERIOR
EN LOS TUXTLAS, VERACRUZ, MÉXICO**

José Nicolás Urbina-Cardona
& Víctor Hugo Reynoso

Resumen: A partir de 672 horas de muestreo a lo largo de 126 transectos en sitios de potrero, borde e interior de Selva Alta Perennifolia en Los Tuxtlas, se encontraron 21 especies de anfibios y 33 de reptiles. La riqueza de anfibios y reptiles tiende a aumentar en el borde de la selva. Se constató que hacia el interior aumentan las especies de reptiles grandes y arborícolas, y de anfibios pequeños con desarrollo directo y preferencia por hábitats fosoriales y arborícolas. Los sitios de potrero e interior de selva presentaron el mayor grado de recambio de anfibios y reptiles. Para poder entender los patrones de la diversidad es importante tener en cuenta la historia natural de las especies, que nos da información valiosa para la conservación.

Palabras clave: Anfibios, reptiles, diversidad, grupos conceptuales, bordes de selva, Los Tuxtlas, México.

Amphibian and reptile exchange along the pasture-edge-interior gradient at los Tuxtlas, Veracruz, Mexico

Abstract: Based on 672 hours of sampling carried out in 126 transects set up in pasture, forest edge and forest interior at the Los Tuxtlas Selva Alta Perennifolia, a total of 21 amphibian and 33 reptile species were found. Amphibian and reptile richness increased at the forest edge. Towards the interior of the forest the number of species of reptiles with larger size and arboreal habitats increased, as did the amphibians with direct embryo development and with fossorial and arboreal habitats. The greatest species exchange was forest in pastures and forest interior for both amphibians and reptiles. To understand the patterns of species diversity it is important to consider the natural history of the species, which offers useful information for species conservation.

Key words: Amphibians, reptiles, species diversity, conceptual groups, forest edge, Los Tuxtlas, Mexico.

1. Introducción

1.1 HISTORIA DE LA FRAGMENTACIÓN EN LOS TUXTLAS

En la selva de los Tuxtlas, se han registrado actividades antropogénicas a partir del año 31 A. C. (Dirzo, 1991), pero solo a partir de 1940 se generó una gran mezcla entre etnias y se dio una vertiginosa expansión de la ganadería (González-Sierra, 1991; Skerritt, 1992). Esto hace pensar, que el periodo más agresivo de la fragmentación en la región de Los Tuxtlas es reciente. Actualmente los pobladores urbanos se dedican al comercio agrícola, ganadero y al turismo, mientras que los pobladores rurales se dedican a la ganadería extensiva de doble propósito, a la agricultura, la pesca y a la extracción de madera en los remanentes de bosque (Guevara *et al.*, 1997).

Debido al intenso uso de la tierra, en Los Tuxtlas, se ha generado una acelerada transformación que ha traído como consecuencia la alteración de los ecosistemas naturales. Se calcula que para 1986, los remanentes forestales habían perdido el 84% de la cobertura original de bosque húmedo tropical (Dirzo & García, 1992). En la zona se presentan también diversos elementos arbóreos tales como fragmentos de selva, acahuals, corredores de

vegetación ribereña, cercas vivas y árboles aislados inmersos en áreas de potrero, que generan un mosaico en el paisaje (Ibarra-Manríquez *et al.*, 1997). Así, el paisaje ha presentado una pérdida de continuidad en la cual una gran cantidad de hábitat es transformado a un gran número de pequeños parches que se encuentran aislados entre sí por una matriz de hábitats diferentes al original (potrero, tierras agrícolas y bosque en regeneración) (Wilcove *et al.*, 1986; Saunders *et al.*, 1991; Culotta, 1995; Villard *et al.*, 1998). Esta matriz, presenta una gran extensión en el paisaje y puede llegar a convertirse en una barrera para la dispersión de animales y plantas (Hunter, 1996). Sin embargo, la matriz también puede actuar como un filtro selectivo para el movimiento de las especies a lo largo del paisaje (Gibbs, 1998; Gascon *et al.*, 1999).

Se ha determinado que aquellas especies de vertebrados tropicales que toleran o hacen uso de la matriz, tienden a ser menos vulnerables a la fragmentación que aquellas que la evitan (Gascon *et al.*, 1999; Laurance, 1999). Debido a la invasión del fragmento por las especies asociadas a la matriz, ésta ejerce una fuerte influencia en las dinámicas de la fauna del bosque remanente (Laurance, 1994; Brown & Hutchings, 1997; Tocher *et al.*, 1997). Pero los diferentes efectos de la fragmentación sobre los patrones de hábitat, no afectan la biodiversidad de la misma manera (Fahrig, 2003).

1.2 EFECTOS DE BORDE Y DE MATRIZ

Las consecuencias de la fragmentación van más allá de la pérdida de especies en los fragmentos según lo sugiere la Teoría de la Biogeografía de Islas (MacArthur & Wilson, 1967). Involucra efectos del borde y de la matriz, que determinan la manera como el fragmento evoluciona luego de la perturbación (Gascon & Lovejoy, 1998). Estos efectos pueden ser atribuidos a cambios en los patrones de hábitat y, de manera independiente, a la pérdida de hábitat, implicando cuatro efectos (Fahrig, 2003): a) disminución de la cantidad de hábitat; b) aumento en el aislamiento; c) incremento en el número de parches de hábitat original; y, d) reducción del área en estos parches.

La creación de un borde incrementa la cantidad de luz incidente que promueve el crecimiento de plantas y cambia la estructura alrededor del bosque (Murcia, 1995; Jules & Ratchcke, 1999). Hacia los límites del fragmento se incrementa la densidad de especies de borde (Hunter, 1996; Bender *et al.*, 1998) que toleran ambientes más secos, con temperaturas más altas y con mayor grado de exposición al viento proveniente de la matriz (Chen *et al.*, 1992; Murcia, 1995). Estas variables cambian dependiendo de la edad, orientación y aspecto del borde (Kapos *et al.*, 1997; Turton & Freiburger, 1997), y evolucionan con el tiempo a medida que el borde se cierra por el crecimiento de vegetación secundaria (Camargo & Kapos, 1995). De esta manera, el proceso de la fragmentación del hábitat presenta una dinámica compleja, en espacio y tiempo para las comunidades (Lovejoy, 1999; Schlaepfer & Gavin, 2001; Lehtinen *et al.*, 2003)

1.3. DIVERSIDAD DE ESPECIES

El objetivo de medir la diversidad de las comunidades es tener un parámetro de comparación de la productividad o estabilidad entre ellas (Pielou, 1975). Nos aporta conocimientos a la luz de la estructuración de las comunidades, sirve de herramienta para tomar decisiones y emitir recomendaciones a favor de la conservación de taxa amenazados, y para monitorear el efecto de las perturbaciones en el ambiente (Moreno, 2001). Algunas de las definiciones del término “diversidad de especies” son: la función de las especies presentes y la equidad con la cual los individuos se distribuyen entre esas especies (Hulbert, 1971); la riqueza y variedad de las comunidades ecológicas (Pielou, 1975); las diferentes razones entre el número de especies y sus valores de importancia (como la biomasa, productividad, abundancia, entre otras; Odum, 1971).

Para poder comprender los cambios en la biodiversidad a lo largo de gradientes espaciales, Whittaker (1972) propone separar los componentes en diversidades alfa, beta y gamma. La diversidad alfa es la riqueza de especies (a nivel local) de una comunidad o ensamble particular a la que se considera homogénea; la diversidad beta es el grado de cambio o reemplazo en la composición de especies entre diferentes componentes en el paisaje; y la diversidad gamma es la riqueza de especies (a nivel regional) del conjunto que integra el paisaje, como resultado de las diversidades alfa y beta (Whittaker, 1972; Murguía & Rojas, 2001; Rodríguez & Vásquez-Domínguez, 2003). De esta manera es posible estructurar la diversidad regional en sus componentes, local y de recambio para generar un análisis detallado de patrones y procesos que, de otra manera, sería imposible comprender (Arita & Rodríguez, 2001).

La diversidad alfa medida como el número de especies de una comunidad (riqueza específica) es la forma más sencilla de evaluar la diversidad puntual y provee información suficiente sobre la expresión de procesos ecológicos e históricos (Halffter *et al.*, 2001) siempre y cuando se definan muy bien el significado biológico de las comparaciones (Ludwig & Reynolds, 1988). Sin embargo, es fácil imaginar como una sola variable de respuesta, como la riqueza, nos puede llevar a conclusiones erróneas acerca de los efectos de la fragmentación del hábitat sobre la biodiversidad (Gascon & Lovejoy, 1998). Por ello, es importante estructurar la diversidad alfa en grupos conceptuales que nos permitan observar a detalle los patrones en la riqueza a lo largo de gradientes ambientales.

1.4. ASPECTOS QUE AFECTAN LA DIVERSIDAD DE ANFIBIOS Y REPTILES

Actualmente, la diversidad de los anfibios y reptiles se ve afectada por factores directos e indirectos, que reducen la viabilidad de las poblaciones y los hacen vulnerables a la extinción (Rueda-Almonacid, 1999; Gibbons *et al.*, 2000; Castaño-Mora, 2002; Semlitsch, 2003; Rueda-Almonacid *et al.*, 2004). La destrucción y deterioro del hábitat presenta una de las mayores amenazas

para la supervivencia de estos organismos (Crump, 2003). La pérdida del hábitat aunado con la cercanía a carreteras o áreas urbanas, potencia la mortalidad de los individuos, y genera una barrera entre los cuerpos de agua y los bosques, impidiendo la colonización o la culminación de su ciclo de vida (Dodd & Smith, 2003).

La acumulación de gases por efecto invernadero reducen la capa de ozono y alteran la precipitación, la temperatura y la radiación ultravioleta (UV-B). Estos factores interactúan entre sí y causan directamente el declive de muchas poblaciones a nivel mundial (Doonelly & Crump, 1998). Como efecto indirecto también se afecta la densidad de invertebrados, causando la alteración en la disponibilidad de alimento y en el tipo de dieta de algunas especies (Crump, 2003).

Los agroquímicos pueden afectar a las poblaciones que habitan incluso el interior de bosques a través de su dispersión por aire (Sparling *et al.*, 2001). Los exponen a altos niveles de contaminantes afectando el éxito reproductivo al impedirse la fertilización de los huevos, causando su mortalidad y generando deformidades en las larvas y juveniles (Beebee *et al.*, 1990). Algunos patógenos como el hongo *Batrachochytridium* spp. y un iridovirus han causado la mortalidad masiva de algunos anfibios que los deshidrata y sofoca, incluso en el bosque (Carey *et al.*, 1999).

La sobreexplotación (extracción de individuos de una población a una tasa mas alta de la que puede sostener la capacidad natural reproductiva, Halffter *et al.*, 2001) genera una amenaza directa para algunas especies a partir de actividades antropogénicas. Entre estas se encuentran: la extracción forestal, la cacería de consumo, el control de plagas o depredadores, y la colecta de organismos para colecciones científicas, tenencia de mascotas, requerimiento de zoológicos o para uso en laboratorio (Rueda-Almonacid *et al.*, 2004).

La introducción de especies en hábitats donde antes no se encontraban, es una de las principales causas de extinción de anfibios y reptiles, ya que se convierten en excelentes competidores y depredadores, y terminan por desplazar a algunas especies nativas (Pilliod & Peterson, 2000). Los casos mas críticos son la introducción de anuros (tales como, *Bufo marinus* y *Rana catesbeiana*), y peces (tilapia, trucha, entre otros) en los sitios de reproducción de anfibios. Además se cree que los peces pueden actuar como vectores de algunas enfermedades en los ambientes invadidos (Blaustein *et al.*, 1994).

Como respuesta a los cambios y su relación sinérgica con otros factores, los anfibios y reptiles experimentan cambios en las tasas de crecimiento de los individuos, en la capacidad reproductiva, fluctuación en la duración de los periodos reproductivos, cambios en el ámbito hogareño, en los patrones de actividad y en el uso del microhábitat (Gibbons *et al.*, 2000; Crump, 2003). Por otra parte, el factor indirecto principal para estos organismos es el estrés; ya que reduce su capacidad inmunológica, los debilita y los vuelve más susceptible a patógenos (Carey *et al.*, 2001). Las especies con mayor especialización de hábitat, son más vulnerables a la extinción y estos cambios tienen repercusiones en la estructuración de las comunidades (Crump, 2003).

Este estudio se enfoca en entender como la diversidad de anfibios y reptiles estructurada en grupos conceptuales basados en la historia natural de las especies, es útil a la hora de evidenciar patrones a lo largo del gradiente potrero-borde-interior en la selva alta perennifolia Los Tuxtlas.

2. Material y métodos

2.1 ÁREA DE ESTUDIO

La Sierra de Los Tuxtlas está situada al sureste del estado de Veracruz muy próxima al litoral del Golfo de México, interrumpiendo la continuidad de la llanura costera. A lo largo de esa cadena se encuentran numerosos conos de rocas basálticas y material fragmentado que constituyen volcanes tales como el de San Martín Tuxtla con 1680 m.s.n.m. y otros de menor altura como el Vigía de Santiago Tuxtla con 860 m.s.n.m. (Soto & Gama, 1997).

Debido a su posición latitudinal es una de las regiones más lluviosas del país. Durante el verano, los vientos alisios húmedos provenientes del Golfo de México presentan una dirección dominante hacia el Norte. En invierno, el sistema se desplaza hacia el sur y los vientos de noreste pierden profundidad e intensidad (Mosiño & García, 1973; Soto & Gama, 1997).

En general el clima es cálido húmedo con abundantes lluvias en verano (Af) y se presenta una precipitación media anual de 4964 mm (DS \pm 862, n= 20 años) (Estrada *et al.*, 1985). Con base en los datos obtenidos de la estación meteorológica de Coyame (tomado de Soto & Gama, 1997), se determinó que la época de mayor precipitación va desde junio hasta febrero, siendo octubre, julio y septiembre los meses donde más llueve. La época de "secas" se presenta entre marzo y mayo. La temperatura media anual es de 27 °C y fluctúa entre 35 °C hacia el mes de mayo, y 13 °C, en febrero.

La región de Los Tuxtlas representa el límite boreal de la selva tropical lluviosa en el continente americano, siendo además, uno de los último relictos en el estado de Veracruz (Dirzo & García, 1992; Torres-Orozco *et al.*, 1997). Según el Diario Oficial de la Federación (1998), fue decretada Área Natural Protegida con el carácter de Reserva de la Biosfera. La flora de la región pertenece al Reino Biogeográfico Neotropical: Región Caribeana y provincia de la costa del golfo de México (Ibarra-Manríquez *et al.*, 1997). En la reserva Los Tuxtlas, se han identificado nueve tipos de vegetación y el más estudiado corresponde a la selva alta perennifolia (Sousa 1968), de las cuales se muestrearon dos variantes:

- Selva alta perennifolia (SAP) sobre suelos profundos: Se localiza en altitudes que oscilan entre los 0-350 m.s.n.m. y se caracteriza por tener un dosel entre 30 y 35 m, alcanzando hasta 40 m de altura en el caso de *Ficus yoponensis*, *F. tecolutensis* y *Ceiba pentandra*. El 50% de la flora pertenece a la familia *Palmae* con especies como *Astrocaryum mexicanum*, *Chamaedorea pinnatifrons* y *C. atterms* (Ibarra-Manríquez *et al.*, 1997).

- Vegetación de zonas perturbadas, potrero: Vegetación compuesta por pastos nativos (*Paspalum conjugatum*, *Axonopus compressus*, *Setaria geniculata*, *Panicum* spp., *Digitaria* spp.) y gramíneas exóticas (*Cynodon dactyliferum*) sembradas para actividades ganaderas. Al igual que algunas especies de árboles aislados provenientes de relictos de selva (Guevara *et al.*, 1992).

El presente estudio fue llevado a cabo entre los 18° 32' - 18° 38' N y los 95° 3' - 95° 6' W dentro del área costera de la reserva de la biosfera que se encuentra fuertemente alterada debido a actividades humanas como agricultura y ganadería (Dirzo & García, 1992).

2.2 MUESTREO DE LOS ANFIBIOS Y REPTILES

2.2.1 Diseño de la investigación

Se ubicaron 14 parcelas de 250 x 50 m en diversos fragmentos de SAP en la región de Los Tuxtlas. Cada parcela fue dividida en tres sitios: a) potrero, que comprende el área entre el borde de la selva y 50 m hacia el potrero (transectos a distancias -50, -20 y -10 m); b) borde de selva, que va desde el borde físico de la selva hasta 20 m hacia el interior (transectos a distancias 0, 10 y 20 m); y, c) interior de selva, que va perpendicular al borde desde 50 hasta 200 m hacia el interior de la selva, (transectos a distancias 50, 100 y 200 m). De esta forma, en cada sitio se ubicaron a distancias preestablecidas tres transectos lineales de 50 x 2 m, y paralelos al borde de la selva, para un total de 126 transectos en el estudio. Todos los transectos se ubicaron fuera de cuerpos de agua, por lo que en el presente estudio no se representa la riqueza de las especies que frecuentan preferencialmente hábitats acuáticos.

2.2.2 Técnica de muestreo

Las capturas se hicieron en cuatro temporadas junio-julio y septiembre-octubre de 2003, febrero-marzo y mayo-junio de 2004, con un total de 4 salidas al campo. Cada salida duró un periodo de 14 días, muestreándose cada día el conjunto de los tres sitios durante 6 horas (3 horas de día y 3 hora de noche). Cada sitio fue muestreado en cuatro temporadas con un total de 224 horas hombre y el esfuerzo total del estudio fue de 672 horas hombre. Al inicio de cada muestreo (tanto diurno como nocturno) se aleatorizó si el muestreo comenzaría en el potrero, el borde o el interior de selva, con el fin de controlar el efecto de la hora del muestreo en los picos de actividad de las especies, evitando visualizar patrones erróneos en el efecto de borde. El registro de los individuos se realizó por búsqueda visual entre dos personas hasta una altura de 2 m y a 1 m a la redonda (Crump & Scott, 1994; Jaeger, 1994; Tocher *et al.*, 1997). Debido a que el método de búsqueda empleado se encuentra influido por la imagen de búsqueda del investigador (Urbina-C & Londoño-M, 2003), los muestreos fueron realizados siempre por las mismas personas. Esta técnica registró el 96% de los individuos y el 69% de las especies entre 0 - 50 cm de altura, y las observaciones se redujeron desde los 60 cm hasta los 200 cm (fig. 1) Por lo cual, es pertinente aclarar que el presente trabajo evalúa la diversidad del ensamble de anfibios y reptiles que habitan el sotobosque de la selva.

2.2.3 Determinación de especies

Los organismos fueron determinados en campo hasta especie utilizando una guía fotográfica de las especies reportadas en la SAP de la región de Los Tuxtlas y a partir de los últimos listados de anfibios y reptiles, y de la revisión de los ejemplares de la Colección Nacional de Anfibios y Reptiles (CNAR) del Instituto de Biología de la UNAM. La taxonomía y nomenclatura de las especies se basó en los últimos cambios recopilados por Flores-Villela & Canseco-Márquez (2004). Algunos ejemplares fueron temporalmente recolectados y determinados utilizando claves taxonómicas especializadas (Shannon & Werler, 1955; Savage, 1975; Flores-Villela *et al.*, 1987; Flores-Villela *et al.*, 1995; Lee, 1996; Campbell & Savage, 2000) y los ejemplares (n = 20) que presentaron dificultad para su determinación en campo fueron sacrificados y montados para su posterior revisión con un experto. Estos ejemplares fueron depositados en la CNAR.

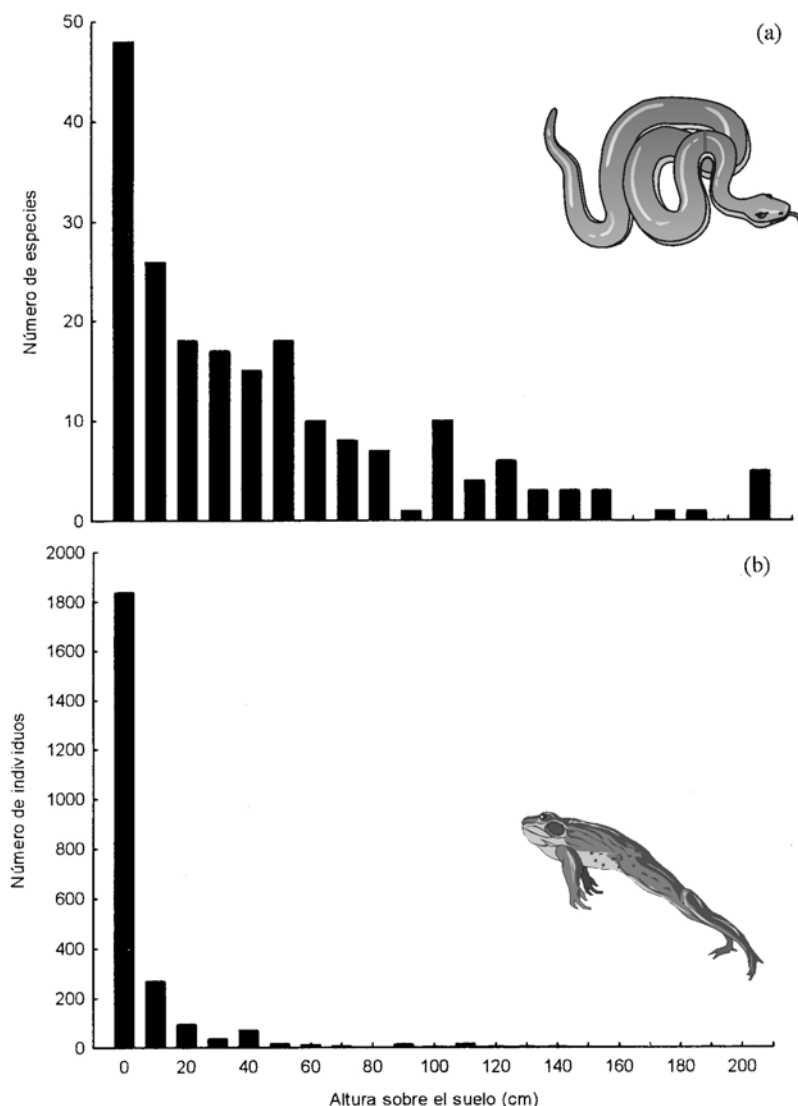
2.3 ANÁLISIS DE DATOS

Se realizaron curvas de acumulación de especies por medio de tres estimadores de riqueza no paramétricos: Bootstrap, ICE y Chao2 en el programa EstimateS (*Version 7*, R. K. Colwell, <http://purl.oclc.org/estimates>); y se graficaron los singletons y los doubletons con el fin de determinar si las especies raras (únicas y duplicadas, respectivamente) se redujeron a medida que el muestreo se intensificó. Con base en los valores máximos de riqueza estimada por los estimadores de riqueza, se determinó el porcentaje de especies observadas que fueron capturadas durante el presente estudio ("completeness" de Soberón & Llorente, 1993).

Se determinó la diversidad alfa de especies como la riqueza específica de cada sitio. Se corroboró la normalidad y se exploró la posible autocorrelación de los datos de riqueza a lo largo del gradiente de distancia. Al cumplir los supuestos, se realizó un ajuste de modelos paramétricos de regresión no-lineal ("forward regression", Zar 1999) en el paquete estadístico STATISTICA 6.0 (StatSoft, 2001), para determinar la forma en la que se relaciona el gradiente de distancia potrero-borde-interior de selva con la diversidad de anfibios y reptiles que habitan el sotobosque de la SAP en Los Tuxtlas.

Con base en los estudios de historia natural de anfibios y reptiles que se distribuyen en la región de Los Tuxtlas (Crump, 1974; Flores-Villela *et al.*, 1987; Flores-Villela *et al.*, 1995; Lee, 1996; Villarreal, 1997; Vogt, 1997a, b), se clasificaron las especies por categorías de hábitat, hábito, talla y modo reproductivo (Apéndice A, Apéndice B). Se subdividió a los anfibios y reptiles en grupos conceptuales, teniendo en cuenta el hábitat preferencial (lugar de actividad más frecuente reportado para la especie; arborícola, terrestre o fosorial), el hábito preferencial (hora de actividad reportada para la especie; diurno o nocturno), la talla corporal (basada en la Longitud Hocico Cloaca, LHC reportada para las especies del estado de Veracruz y la región de Los Tuxtlas, específicamente) y el modo reproductivo de los anfibios (reportado por Crump, 1974; desarrollo directo, huevos y larva en el agua o huevos depositados

Fig. 1. Estratificación vertical de capturas de anfibios y reptiles con la técnica de búsqueda visual a lo largo de transectos paralelos al borde de la selva, a distancias predeterminadas, en la selva alta perennifolia de Los Tuxtlas, Veracruz – México; a) número de especies, b) número de individuos.



fuera del agua) y reptiles (reportado por Zug *et al.*, 2001; ovíparos o vivíparos).

La diversidad beta se definió como el grado de disimilitud en la composición de especies entre pares de biotas. Para su análisis se utilizó la complementariedad, la cuál relaciona el número de especies en un sitio A, con el número de especies en un sitio B y el número de especies en común entre A y B (Colwell & Coddington, 1994; Magurran, 2004).

De esta forma, la riqueza total (S) para ambos sitios combinados es:

$$S_{AB} = a + b - c$$

donde a es el número de especies del sitio A, b es el número de especies del sitio B, y c es el número de especies en común entre los sitios A y B.

El número de especies únicas (U) a cualquiera de los dos sitios es:

$$U_{AB} = a + b - 2c$$

Finalmente, a partir de estos valores se calculó la complementariedad (C) de los sitios A y B como:

$$C_{AB} = U_{AB} / S_{AB}$$

Los valores obtenidos a partir del análisis de complementariedad varían desde cero, cuando ambos sitios son idénticos en composición de especies, hasta uno, cuando las especies de ambos sitios son completamente distintas (Colwell & Coddington, 1994).

3. Resultados

3.1 DIVERSIDAD TOTAL

Al concluir 672 horas de muestreo, las curvas de acumulación de especies de anfibios presentaron una asíntota. Los estimadores ICE y Chao2 llegaron a la asíntota más rápidamente que la riqueza observada y el Bootstrap. Este último, presentó un patrón muy similar al de la riqueza observada (S_{obs}). En general los estimadores reflejaron una mayor riqueza que la observada pero el presente estudio logró representar entre el 88% y 93% de la riqueza. Las especies únicas (singletons) y duplicadas (doubletons) representaron el 33% de los anfibios y se estabilizaron al final del muestreo (fig. 2a; tabla I).

La riqueza de reptiles, nunca llegó a la asíntota. Los estimadores Chao2 y ICE tendieron a sobreestimar la riqueza por más del doble, mientras que el Bootstrap

presentó un patrón muy similar al de la riqueza observada (S obs). Basándose en los dos primeros estimadores se representó entre el 40 y 52% de la riqueza, mientras que basándose en el Bootstrap la riqueza representada es del 84.1%. Las especies únicas tendieron a aumentar a medida que se acumulaba esfuerzo de muestreo, mientras que las especies duplicadas se mantuvieron constantes a lo largo del estudio. En general las especies raras representan el 54% de las especies del

Tabla I. Riqueza, observada y estimada, de anfibios en las catorce parcelas en la selva alta perennifolia de Los Tuxtlas, Veracruz – México.

	Riqueza máxima	Completeness
Sobs	21	
Chao2	22,45	93.5%
ICE	23,8	88.1%
Bootstrap	23,35	89.9%
Singletons	4	
Doubletons	3	

Tabla II. Riqueza, observada y estimada, de reptiles en las catorce parcelas en la selva alta perennifolia de Los Tuxtlas, Veracruz – México.

	Riqueza máxima	Completeness
Sobs	33	
Chao2	84,2	40%
ICE	62,88	52.5%
Bootstrap	39,21	84.1%
Singletons	14	
Doubletons	4	

Tabla III. Complementariedad de anfibios entre sitios de potrero, borde e interior de selva*.

Riqueza de Anfibios	Potrero	Borde	Interior
Potrero	4	8	6
Borde	0.55	2	10
Interior	0.68	0.41	3

*Los valores en la diagonal corresponden al número de especies únicas para cada sitio. Los valores por encima de la diagonal corresponden al número de especies compartidas entre sitios. Los valores por debajo de la diagonal corresponden a la complementariedad (los valores fluctúan entre 0, cuando ambos sitios son idénticos y 1 cuando las especies de ambos sitios son completamente distintos).

Tabla IV. Complementariedad de reptiles entre sitios de potrero, borde e interior de selva*.

Riqueza de Reptiles	Potrero	Borde	Interior
Potrero	1	10	7
Borde	0.61	6	16
Interior	0.73	0.48	6

*Los valores en la diagonal corresponden al número de especies únicas para cada área. Los valores por encima de la diagonal corresponden al número de especies compartidas entre sitios. Los valores por debajo de la diagonal corresponden a la complementariedad (los valores fluctúan entre 0, cuando ambos sitios son idénticos y 1 cuando las especies de ambos sitios son completamente distintos).

ensamble de reptiles (fig. 2b; tabla II) y la mayoría son serpientes.

3.2 DIVERSIDAD ALFA

Durante el estudio se capturaron 21 especies de anfibios, de las cuales 4 fueron exclusivas de potrero, 2 de borde de selva y 3 de interior de selva (tabla III). En total 12 especies fueron encontradas en el potrero, 14 en el borde de selva y 13 en el interior de selva. La riqueza de anfibios fue explicada en un 94.4% por el gradiente de distancia potrero-borde-interior elevado al cuadrado (Apéndice C).

Se capturó un total de 33 especies de reptiles, de las cuales una fue exclusiva de potrero, 6 de borde de selva y 6 de interior de selva (tabla IV). En total 11 especies fueron encontradas en el potrero, 25 en el borde de selva y 22 en el interior de selva. La riqueza de reptiles fue explicada en un 95.1% por el gradiente de distancia potrero-borde-interior elevado al cuadrado (Apéndice D).

3.2.1 Grupos conceptuales por preferencia de hábitat

De las especies de anfibios encontradas en potrero el 58% presentaron una preferencia por el hábitat terrestre, mientras que el 57% de los anfibios de borde y el 61% de los anfibios de interior presentaron una preferencia arborícola (fig. 3a).

De las especies de reptiles encontradas en potrero, el 54% presentaron una preferencia por el hábitat terrestre, similar a la proporción de los reptiles de borde (56%), mientras que el 54% de los reptiles de interior presentaron una preferencia arborícola. La categoría de preferencia por hábitat fosorial, no estuvo representada en el interior de la selva (fig. 4a).

3.2.2 Grupos conceptuales por preferencia de hábitat

En general la mayoría de anfibios encontrados presentaron una preferencia por la actividad nocturna: el 75% de las especies encontradas en potrero, el 85% de los anfibios de borde y el 61% de los anfibios de interior (fig. 3b). Sin embargo, la mayoría de reptiles presentaron una preferencia por la actividad diurna: el 54% de las especies de potrero, el 68% de los reptiles de borde y el 82% de los reptiles de interior de selva (fig. 4b).

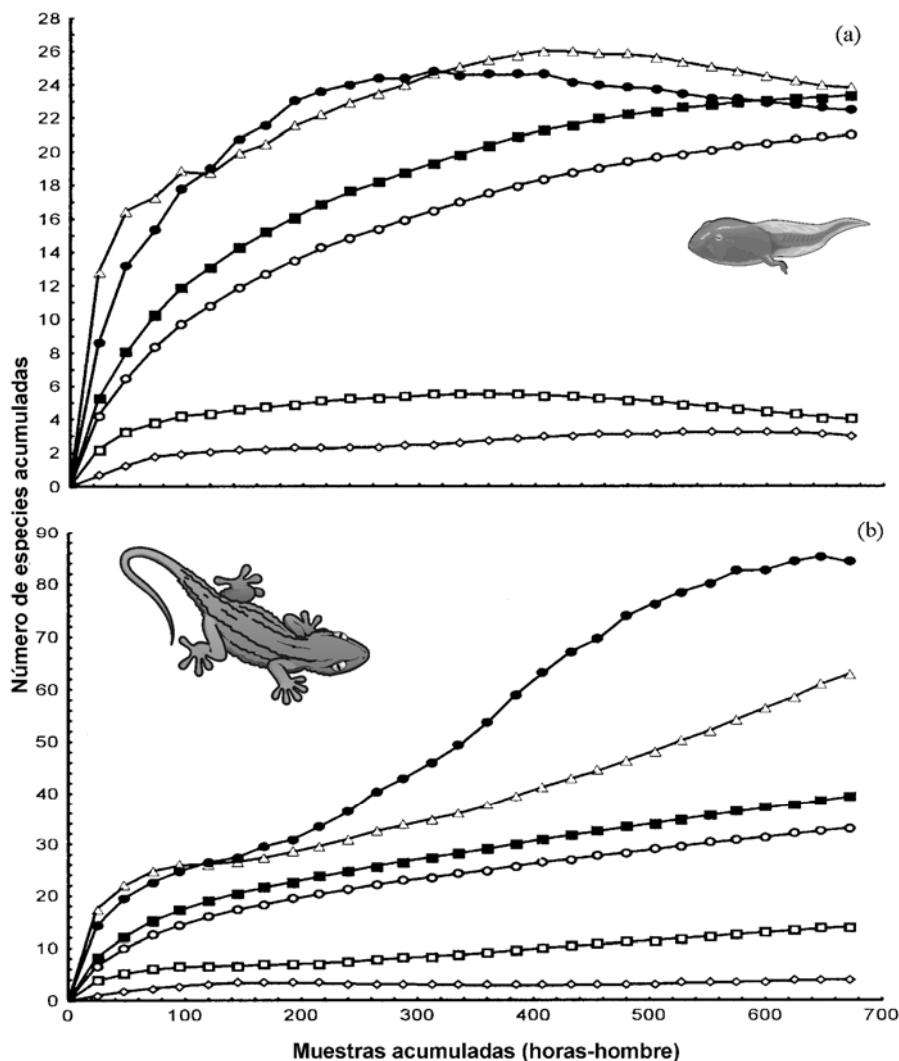
3.2.3 Grupos conceptuales por talla

En el potrero la mayor proporción de anfibios presentó una talla mediana (50%), seguida por especies grandes (33%) y pequeñas (17%). En sitios de borde de selva, el 42% fueron medianos, el 29% grandes y el 29% pequeños. En el interior las proporciones cambian, el 47% de anfibios presentó una talla pequeña, el 38% mediana y el 15% una talla grande (fig. 3c).

De los reptiles encontrados en potrero el 55% presentó una talla mediana, el 27% grande y el 18% pequeña, mientras que entre sitios de selva la proporción fue similar. En el borde el 36% de los reptiles fueron grandes, el 36% medianos y el 28% pequeños; y en el interior el 45% fueron grandes, el 36% medianos y el 19% pequeños (fig. 4c).

Fig. 2. Curvas de acumulación de especies en las catorce parcelas en la selva alta perennifolia de Los Tuxtlas, Veracruz – México; a) anfibios, b) reptiles.

- = S obs,
- △ = Singletons,
- ◻ = Doubletons,
- ◊ = ICE,
- = Chao2,
- = Bootstrap



3.2.4 Grupos conceptuales por modos reproductivos

El 42% de los anfibios de potrero presentaron un modo reproductivo Tipo 1, presentando tanto huevos, como larvas en el agua; y el 33% un modo Tipo 2, presentando huevos depositados fuera del agua y larvas acuáticas. Los anfibios de selva presentaron una tendencia al modo Tipo 2 (35% en borde y 31% en interior) y al modo Tipo 3 presentando un desarrollo directo, sin fase de larva y fuera de cuerpos de agua (29% en borde y 31% en interior) (fig. 3d).

Los reptiles presentaron una mayor tendencia a la reproducción por medio de la oviparidad: el 82% en potrero, el 92% en borde y el 86% en interior (fig. 4d).

3.3 DIVERSIDAD BETA

El mayor grado de recambio de anfibios se presentó entre los sitios opuestos de potrero e interior de selva (68%), mientras que el borde de selva se complementa más con el potrero (55%) que con el interior de selva (41%) (tabla III). La complementariedad promedio entre los tres sitios de potrero, borde e interior es de 54%.

En el caso de los reptiles se presenta la misma tendencia que con los anfibios. La mayor complementa-

riedad se da entre el potrero y el interior de la selva (73%), seguidos por el potrero y el borde de selva (61%), y el borde e interior de selva (48%) (tabla IV). La complementariedad promedio entre los tres sitios de potrero, borde e interior es de 60.6%

Discusión

4.1 DIVERSIDAD Y RAREZA

El muestreo de anfibios por medio de transectos replicados a lo largo del paisaje es un buen método para evaluar la diversidad de especies que habitan el sotobosque. Para el caso de los reptiles se requiere un mayor esfuerzo de captura y aplicar otro tipo de técnica más eficiente que permita aumentar la detección de especies raras y asegurar la representatividad de la mayoría de las especies en el ensamble, sobre todo de serpientes. Se debe tener en cuenta que los valores de riqueza observada y en general de cualquier índice de diversidad, son una función de factores tales como la unidad de muestreo (tipo de técnica utilizada, el tamaño del área de muestreo y el número de replicas y repeticiones realiza-

das), la distribución espacial de las poblaciones objetivo y la heterogeneidad del hábitat (Hayek, 1994; Clarke & Warwick, 2001; Magurran, 2004).

La rareza es un concepto relativo que depende de la escala de la investigación, de la técnica de muestreo y del ensamble de especies (Longino *et al.*, 2002; Magurran, 2004). Para fines prácticos las especies raras son aquellas que se encuentran en el cuarto inferior de la escala de abundancias en el ensamble (Gaston, 1994) y para el presente estudio, son las especies únicas (singletons) y duplicadas (doubletons). La "rareza" de especies de anfibios y reptiles en Los Tuxtlas puede variar a lo largo del tiempo. Muchas veces las especies de anfibios dominantes en el ensamble, son aquellas que se encuentran en época reproductiva (*obs. per.*) y la abundancia o rareza de estos organismos depende de la temporada en que sean muestreados. Debido a esto consideramos que en el ensamble de anfibios las especies raras son escasas y la dominancia va cambiando a lo largo de las estaciones y a lo largo de los años. Por ejemplo, algunas especies pueden estar por más de dos años y volver a aparecer en el ensamble, tiempo después (Zug *et al.*, 2001; Semlitsch, 2003). Algunas especies, como *Gastrophryne elegans* y *Rana berlandieri*, realizan migraciones al comienzo de la época de lluvias y presentan una variación en su abundancia a lo largo del año (*datos no publicados*, Vogt & López-Luna).

Un patrón constante en el ensamble de reptiles de Los Tuxtlas (bajo el sistema de búsqueda empleado, los sitios muestreados y la temporada del estudio) es que la mayoría de las lagartijas son abundantes (exceptuando *Anolis pentaprion*, *A. biporcatus*, *Sceloporus salvini* y *Sphaerodactylus glaucus*) y las serpientes son raras (exceptuando *Bothrops asper* e *Imantodes cenchoa*). Sin embargo, la dominancia y la rareza de algunas especies que habitan Los Tuxtlas han cambiado con el tiempo.

Para la región de Los Tuxtlas, se reportan algunos casos de especies que han variado sus dominancias en el ensamble durante las últimas décadas. Ramírez-Bautista (1977) señaló una baja abundancia de la lagartija *Corythophanes hernandezii* y el presente estudio encontró que en la actualidad esta lagartija es muy abundante, principalmente en los fragmentos de selva. La rana *Agalychnis callidryas* fue reportada por Vogt (1997a) cómo una especie muy abundante en toda la región y en la actualidad esta especie no está presente en la selva y se encuentra restringida a la Laguna el Zacatal. Finalmente, Pérez-Higareda (*com. pers.* 2003) reporta la disminución en la abundancia de las lagartijas *Anolis sericeus* y *Sphaerodactylus glaucus*, las cuáles fueron muy comunes, y un incremento en las poblaciones de *A. uniformis* y la introducción de *Hemidactylus* spp. en la región.

Los resultados mostraron que durante el muestreo, las especies raras aumentaron en el ensamble de reptiles y los estimadores se dispararon, sobrestimando la riqueza. Los estimadores disminuyeron sus valores al aumentar el número de horas de muestreo debido a que algunas especies únicas (singletons) cambiaron a duplicadas (doubletons) sin adicionar más especies nuevas a la muestra (Colwell *com. pers.* 2004). Para el caso de las serpientes, se requiere emplear otro tipo de técnicas y

un esfuerzo mayor de captura para asegurar que las curvas de acumulación lleguen a la asíntota. Con el método de búsqueda activa de organismos a lo largo de transectos fijos y replicados a lo largo del paisaje, la probabilidad de encuentro de estos organismos es muy baja y se hace casi al azar.

Es difícil hacer inferencias sobre las especies raras, ya que la rareza de una especie puede estar dada simplemente por la selección inadecuada de una técnica o método para capturarla en el microhábitat donde es más abundante (Magurran, 2004). Por ello, para poder hablar realmente de la diversidad gamma de anfibios y reptiles, los muestreos se deben complementar con otras técnicas (*e.g.* recorridos libres, trampas de caída con barreras de desvío, registros de vocalizaciones, muestreo en sitios de reproducción, entre otras) y explorar microhábitats poco estudiados como el dosel y los ambientes subterráneos.

4.2 DIVERSIDAD ALFA POR GRUPOS CONCEPTUALES

La diversidad de anfibios y reptiles se ve determinada de una manera no lineal por el gradiente potrero-borde-interior, encontrando los máximos valores en la franja del borde de la selva. Sin embargo, al estructurar la riqueza en grupos conceptuales se encuentran patrones aún más interesantes en este gradiente.

Se debe tener en cuenta que los patrones encontrados en los grupos conceptuales a lo largo del potrero, borde e interior, son reflejo de un muestreo eficiente entre los 0 y 50 cm de altura y podrían variar con el diseño de la investigación, la técnica de muestreo y las épocas climáticas. La clasificación de la riqueza por preferencia de hábitat es una forma de agremiación que aporta información importante para evidenciar la respuesta de los anfibios y reptiles ante el disturbio. Esta clasificación debe hacerse con base en el aporte de estudios específicos del uso del hábitat de las especies. Para algunos anuros, como *Eleutherodactylus* spp., es complicado diferenciar el hábitat preferencial ya que la división del recurso se basa, entre otros aspectos, en la tolerancia de cada especie ante características ambientales puntuales en el microhábitat (Urbina-Cardona & Pérez-Torres, 2002).

Los anfibios y reptiles arborícolas presentan una tendencia a aumentar al interior de la selva y podrían verse más afectados por la cercanía al borde. En contraste, el grupo de los anfibios terrestres y los reptiles fosoriales tienden a aumentar su proporción hacia el potrero y podrían ser menos vulnerables a la fragmentación del hábitat. Crump (2003) ha documentado que las especies que hacen uso de hábitats terrestres presentan mayor tendencia al declive en los trópicos. El patrón que describe Crump de una manera global para los anfibios del Neotrópico es contrastante al encontrado en el presente estudio.

La categoría del modo reproductivo en los anfibios está muy ligado con el microhábitat (Crump, 1974) y justamente los organismos clasificados en estas dos categorías (hábitat y modo reproductivo) presentan una respuesta similar al gradiente de distancia potrero-borde-interior. Los anfibios que presentan huevos y

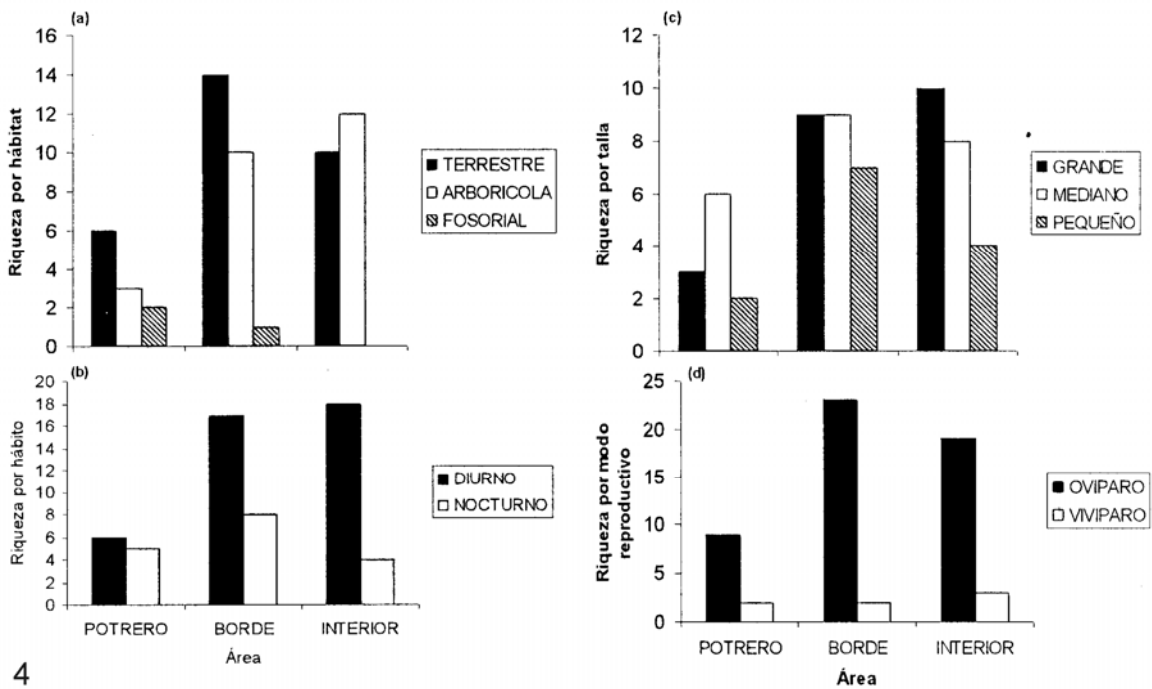
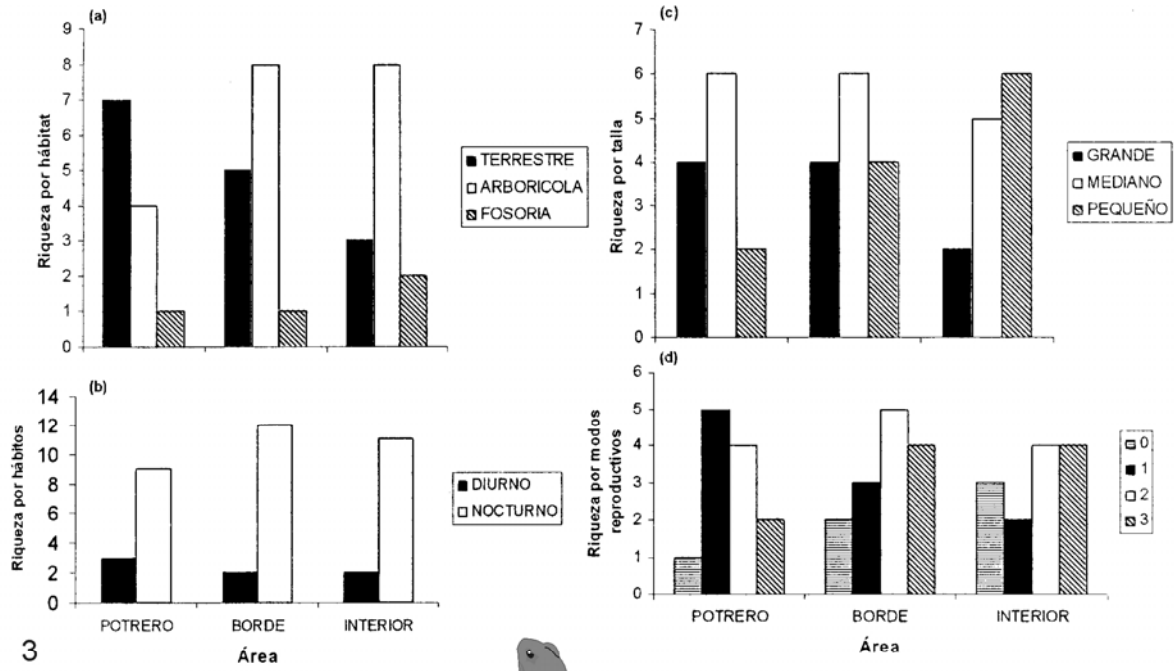


Fig. 3. Riqueza de anfibios por grupos conceptuales en sitios de potrero, borde e interior de selva; a) hábitat preferencial b) hábito preferencial c) tallas corporales y d) modo reproductivo.

Fig. 4. Riqueza de reptiles por grupos conceptuales en sitios de potrero, borde e interior de selva; a) hábitat preferencial b) hábito preferencial c) tallas corporales y d) modo reproductivo.

larvas en el agua (Tipo 1) aumentan hacia el potrero, y los que presentan desarrollo directo fuera de cuerpos de agua (Tipo 3) tienden a aumentar hacia el interior de la selva. De esta manera, la mayoría de anfibios de potrero presentan un modo reproductivo que los liga a cuerpos de agua, mientras que los de selva tienden a independizarse de ambientes acuáticos. Según Crump (2003) 74% de los anfibios neotropicales en declive presentan un patrón de desarrollo larval, siendo el grupo conceptual más propenso. Sin embargo, este estudio muestra que no existe preferencia de estos organismos hacia el interior de selva, aun cuando es un hábitat disponible.

En conclusión, con base en la preferencia de hábitat y modo reproductivo, es incierta la relación entre el efecto de borde y la extinción local en los trópicos en anfibios. Para hacer conclusiones generales sobre los reptiles, es necesario implementar más estudios que relacionen la extinción de grupos conceptuales en el neotrópico pues a la fecha no existe un marco de comparación.

El grupo conceptual de hábito refleja simplemente la preferencia natural de la mayoría de anfibios por la actividad nocturna y la de los reptiles por la diurna, pero no aporta información valiosa para el análisis de la diversidad a lo largo del gradiente de distancia de potrero-borde-interior. Por otra parte, algunas lagartijas (como *Anolis sericeus*, *A. uniformis*, *Corytophanes hernandezii* y *Basiliscus vittatus*) son fácilmente detectables cuando perchan durante la noche pero son netamente diurnos. Por ello es necesario definir muy claramente los parámetros que delimitan la actividad de las especies, así como el tipo de hábito y hábitat preferencial de "actividad", para que los patrones encontrados puedan ser comparados y los estudios replicados.

En cuanto a la talla corporal, los anfibios de talla grande y mediana tienden a permanecer en el potrero y en el borde de la selva, mientras que las especies de talla pequeña prefieren el interior de la selva. El patrón de distribución de las especies, según su talla corporal, a lo largo del gradiente potrero-borde-interior puede estar dado por aspectos ecofisiológicos. Mazerolle (2001) plantea que los organismos de talla grande se encuentran más adaptados al disturbio y son menos sensibles a la desecación. El déficit de las especies de talla grande para realizar el intercambio calórico puede hacer que requieran áreas abiertas para poder termoregular eficientemente. Las de talla pequeña, por su parte, pueden llegar a desecarse más fácilmente en ambientes de potrero y borde, y por ello tienden más al interior de la selva. Este grupo de especies podría verse más afectado por la perturbación ya que son más vulnerables a la desecación corporal y a la pérdida de lugares aptos para reproducirse.

Sin embargo, el estructurar la riqueza por talla corporal pueden presentarse problemas. Si se determina la talla de los organismos por especie, despreciando los patrones corporales que emergen a nivel de Clase, las especies pueden ser clasificadas en categorías ficticias o poco comparables entre sí. Además, al hacer uso del valor máximo de talla por especie se pierde informa-

ción, ya que los juveniles pueden hacer uso de hábitats muy diferentes al de los adultos (López-Luna *com. pers.* 2005).

4.3 DIVERSIDAD BETA

La complementariedad promedio en los anfibios de Los Tuxtlas entre sitios de potrero, borde e interior fue de 54%. Es un valor relativamente bajo, al comparar el recambio promedio de anuros entre el bosque mesófilo de montaña y el potrero subyacente (77.5%) reportado por Pineda & Halfpeter (2004).

En el gradiente de recambio de especies de anfibios y reptiles, la mayor complementariedad se dio entre potrero e interior, y el menor grado de recambio entre el borde y el interior. Este patrón de bajo recambio, es similar al encontrado por Urbina-C & Londoño-M (2003) entre los anfibios y reptiles que habitan bosques primarios y secundarios del chocó biogeográfico de Colombia.

Es necesario preservar los bordes de selva para amortiguar la invasión de especies de potrero hacia el interior de la selva, mantener el gradiente de recambio entre estos tres sitios y permitir que prevalezcan las especies que prefieren el interior, como los anfibios *Eleutherodactylus vulcani*, *Hyla microcephala* y *Lineatriton orchimelas*. Se encontraron 6 reptiles de interior (*Ctenosaura pectinata*, *Iguana iguana*, *Sceloporus salvini*, *Anolis biporcatus*, *Boa constrictor* y *Coniophanes bipunctatus*), pero esta afinidad de sitio no es coherente para algunas de ellas con respecto a lo que se sabe de su historia natural. Es difícil hacer inferencias en especies raras de reptiles, puesto que aparentemente (y según los datos) pueden ser "exclusivas" de algún sitio, pero debido a la falta de muestreo en otro tipo de microhábitats. De esta forma, la diversidad beta de grupos de especies con alta rareza puede ser sobrestimada al no tener un muestreo completo en todos los sitios (*completeness* >90%, Soberon & Llorente, 1993), visualizando patrones equivocados.

5. Conclusiones

La técnica de búsqueda visual a lo largo de transectos lineales a distancias fijas, resulta eficiente para capturar organismos hasta los 50 cm de altura y permite registrar el total de los anfibios de sotobosque; pero es ineficaz para muestrear reptiles, principalmente por la baja capacidad de detección de serpientes.

Se reporta un mayor número de especies de anfibios y reptiles en el borde de selva seguido por el sitio de interior de selva. El mayor recambio de especies de anfibios y reptiles se dio entre potrero e interior de selva, seguido por el potrero y el borde de la selva.

En el sitio de potrero se encontró una alta proporción de anfibios terrestres con modos reproductivos Tipo 1 y 2; y de reptiles terrestres y ovíparos. En el sitio de borde de selva se presentó una mayor proporción de anfibios arborícolas con modos reproductivos Tipo 2 y 3; y de reptiles terrestres ovíparos. En el sitio de interior

de selva se presentó una mayor proporción de anfibios arborícolas con modos reproductivos Tipo 2 y 3; y de reptiles arborícolas y ovíparos.

Apoyando el planeamiento de Zimmerman & Bierregard (1986), en la conservación de las especies es muy importante tener muy claros los aspectos de autoecología de los organismos a conservar para evitar caer en planteamientos confusos que pueden conducir a políticas erróneas. De esta forma, se debe estructurar la riqueza de especies en grupos conceptuales que no caigan en la subjetividad y presenten confusión al momento de ser medidos. Es recomendable hacer análisis de la talla (grande, mediano, pequeño) para hacer inferencias sobre patrones a lo largo de gradientes espaciales, pero por separado para anuros y salamandras, o para lagartijas y serpientes. Por su parte, el análisis a nivel de hábitat preferencial y modo reproductivo (principalmente para los anfibios) es una herramienta que refleja claramente la historia natural de las especies y aporta información importante a la hora de evidenciar patrones de diversidad a lo largo de gradientes de hábitat como el de potrero-borde-interior.

Es muy importante interpretar correctamente los valores estimados de riqueza acumulada y su relación con la riqueza observada para conocer el grado de confiabilidad del muestreo y la representatividad en el ensamble. En ensambles que presentan un alto número de especies raras, como los reptiles, se debe tener especial cuidado al hacer inferencias e interpretar patrones en la naturaleza para generar recomendaciones para su conservación.

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Apéndice A. Clasificación de las especies de anfibios en grupos conceptuales según hábitat y hábito preferencial, talla y modo reproductivo*.

Especies	Hábitat	Hábito	Talla	Modo reproductivo
CAUDATA				
Plethodontidae				
<i>Bolitoglossa alberchi</i> (García-París, Parra-Olea, Brame & Wake, 2002)	A	N	G	0
<i>Bolitoglossa platydactyla</i> (Gray, 1831)	A	N	G	0
<i>Bolitoglossa rufescens</i> (Cope, 1869)	A	N	P	0
<i>Lineatriton orchimelas</i> (Brodie, Mendelson & Campbell, 2002)	F	N	P	0
ANURA				
Bufonidae				
<i>Bufo marinus</i> (Linneaus, 1758)	T	D	G	1
<i>Bufo valliceps</i> (Wiegmann, 1833)	T	D	M	1
Leptodactylidae				
<i>Eleutherodactylus alfredi</i> (Boulenger, 1898)	A	N	M	3
<i>Eleutherodactylus berkenbuschi</i> (Peters, 1870)	T	N	G	3
<i>Eleutherodactylus rhodopis</i> (Cope, 1867)	T	D	M	3
<i>Eleutherodactylus vulcani</i> (Campbell & Savage, 2000)	T	N	M	3
<i>Leptodactylus fragilis</i> (Brocchi, 1877)	T	N	M	2
<i>Leptodactylus melanonotus</i> (Hallowell, 1861)	T	N	M	2
<i>Shyrrhophus leprus</i> (Cope, 1879)	A	N	P	3
Microhylidae				
<i>Gastrophryne elegans</i> (Boulenger, 1882)	F	N	P	1
Hylidae				
<i>Hyla ebraccata</i> (Cope, 1874)	A	N	P	2
<i>Hyla loquax</i> (Gaige & Stuart, 1934)	A	N	M	2
<i>Hyla microcephala</i> (Cope, 1886)	A	N	P	2
<i>Hyla valancifer</i> (Firschein & Smith, 1956)	A	N	M	2
<i>Smilisca baudini</i> (Duméril & Bibron, 1841)	A	N	G	2
Ranidae				
<i>Rana berlandieri</i> (Baird, 1854)	T	N	G	1
<i>Rana vaillanti</i> (Brocchi, 1877)	T	N	G	1

*Para clasificar los anfibios por la categoría de talla se basó en la Longitud Hocico-Cloaca (LHC) reportada por Shannon & Werler 1955, Savage 1975, Flores-Villela *et al.* 1987, Flores-Villela *et al.* 1995 y Lee 1996. Las salamandras pequeñas presentan una LHC < 31 mm, las medianas entre 32-50 mm y las grandes > 50 mm; y los anuros pequeños una LHC < 30 mm, los medianos entre 31-50 mm y los grandes > 51 mm. Las categorías de los grupos conceptuales son las siguientes: Hábitat: A = Arborescente, T = Terrestre, F = Fossorial; Hábito: D = Diurno, N = Nocturno; Talla: G = Grande, M = Mediana, P = Pequeña; Modo Reproductivo: 0 = desarrollo directo (sin larva) en salamandras, 1 = huevos y larvas depositados en el agua, 2 = huevos depositados fuera del agua y larvas acuáticas, 3 = desarrollo directo (sin larva) en anuros.

Apéndice B. Clasificación de las especies de reptiles en grupos conceptuales según hábitat y hábito preferencial, talla y modo reproductivo*.

Especies	Hábitat	Hábito	Talla	Modo reproductivo
SAURIA				
Corytophanidae				
<i>Basiliscus vittatus</i> (Wiegmann, 1828)	A	D	G	O
<i>Corytophanes hernandezi</i> (Wiegmann, 1831)	A	D	M	O
Gekkonidae				
<i>Sphaerodactylus glaucus</i> (Cope, 1865)	T	N	P	O
Iguanidae				
<i>Ctenosaura pectinata</i> (Wiegmann, 1834)	A	D	G	O
<i>Iguana iguana</i> (Linnaeus, 1758)	A	D	G	O
Phrynosomatidae				
<i>Sceloporus salvini</i> (Günther, 1890)	A	D	G	O
<i>Sceloporus variabilis</i> (Wiegmann, 1834)	T	D	M	O
Polychrotidae				
<i>Anolis barkeri</i> (Schmidt, 1939)	A	D	G	O
<i>Anolis biporcatus</i> (Wiegmann, 1834)	A	D	M	O
<i>Anolis</i> sp.	A	D	G	O
<i>Anolis lemurinus</i> (Cope, 1861)	A	D	G	O
<i>Anolis pentaprion</i> (Cope, 1862)	A	D	G	O
<i>Anolis petersi</i> (Bocourt, 1873)	T	D	G	O
<i>Anolis rodriguezii</i> (Bocourt, 1873)	A	D	P	O
<i>Anolis sericeus</i> (Hallowell, 1856)	A	D	M	O
<i>Anolis unifomis</i> (Cope, 1885)	A	D	P	O
Scincidae				
<i>Eumeces sumichrasti</i> (Cope, 1866)	T	D	P	O
<i>Sphenomorphus cherriei</i> (Cope, 1893)	T	D	M	O
Teiidae				
<i>Ameiva undulata</i> (Wiegmann, 1834)	T	D	G	O
Xantusiidae				
<i>Lepidophyma tuxtlae</i> (Werler & Shannon, 1957)	T	N	M	V
SERPENTES				
Boidae				
<i>Boa constrictor</i> (Linnaeus, 1758)	T	N	G	V
Colubridae				
<i>Coniophanes bipunctatus</i> (Günther, 1858)	T	D	P	O
<i>Coniophanes fissidens</i> (Günther, 1858)	T	D	P	O
<i>Coniophanes imperialis</i> (Kennicott, 1859)	T	D	P	O
<i>Ficimia publia</i> (Cope, 1866)	T	N	P	O
<i>Imantodes cenchoa</i> (Linnaeus, 1758)	A	N	G	O
<i>Leptodeira septentrionalis</i> (Kennicott, 1859)	A	N	G	O
<i>Ninia sebae</i> (Duméril, Bibron & Duméril, 1854)	F	D	P	O
<i>Oxyrhopus petola</i> (Linnaeus, 1758)	T	N	M	O
<i>Pseustes poecilonotus</i> (Günther, 1858)	T	D	G	O
<i>Stenorrhina degenhardti</i> (Berthold, 1846)	T	N	P	O
Elapidae				
<i>Micrurus diastema</i> (Duméril, Bibron & Duméril, 1854)	F	N	M	O
Viperidae				
<i>Bothrops asper</i> (Garman, 1883)	T	N	G	V

* Para clasificar los reptiles por la categoría de talla se basó en la Longitud Hocico-Cloaca (LHC) reportada por Flores-Villela *et al.* 1987, Flores-Villela *et al.* 1995, Lee 1996 y Vogt 1997a,b. Las lagartijas pequeñas presentan una LHC < 45 mm, las medianas entre 46-90 mm y grandes >71mm; y las serpientes pequeñas una LHC < 500 mm, las medianas entre 501-1000 mm y las grandes > 1001 mm. Las categorías de los grupos conceptuales son las siguientes: Hábitat: A = Arborícola, T = Terrestre, F = Fosorial; Hábito: D = Diurno, N = Nocturno; Talla: G = Grande, M = Mediana, P = Pequeña; Modo Reproductivo: O = Ovívparo, V = Vivíparo.

Apéndice C. Ajuste de modelo para la riqueza de anfibios en el gradiente de distancia.

Modelo ajustado de regresión no-lineal ($R^2 = 94.43\%$, $F = 50.88$, $p = 0.005$):

$$y = -5488.55 + 0.972 * (a ** 2)$$

Donde a = gradiente de distancia potrero (a -50, -20 y -10 m del borde), borde (a 0, 10 y 20 m perpendicular al borde y hacia interior de la selva) e interior (a 50, 100 y 200 m perpendicular al borde y hacia interior de la selva).

Apéndice D. Ajuste de modelo para la riqueza de reptiles en el gradiente de distancia.

Modelo ajustado de regresión no-lineal ($R^2 = 95.1\%$, $F = 136.36$, $p < 0.001$):

$$y = -18.33 + 0.975 * (a ** 2)$$

Donde a = gradiente de distancia potrero (a -50, -20 y -10 m del borde), borde (a 0, 10 y 20 m perpendicular al borde y hacia interior de la selva) e interior (a 50, 100 y 200 m perpendicular al borde y hacia interior de la selva).

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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

J. Nicolás Urbina-Cardona, Mario Olivares-Pérez, Víctor Hugo Reynoso*

Colección Nacional de Anfibios y Reptiles, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, C.P. 04510 México, DF, 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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* Corresponding author: Tel.: +52 55 5622 8222x47865; fax: +52 55 5550 0164.

E-mail address: vreynoso@ibiologia.unam.mx (V.H. Reynoso).

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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

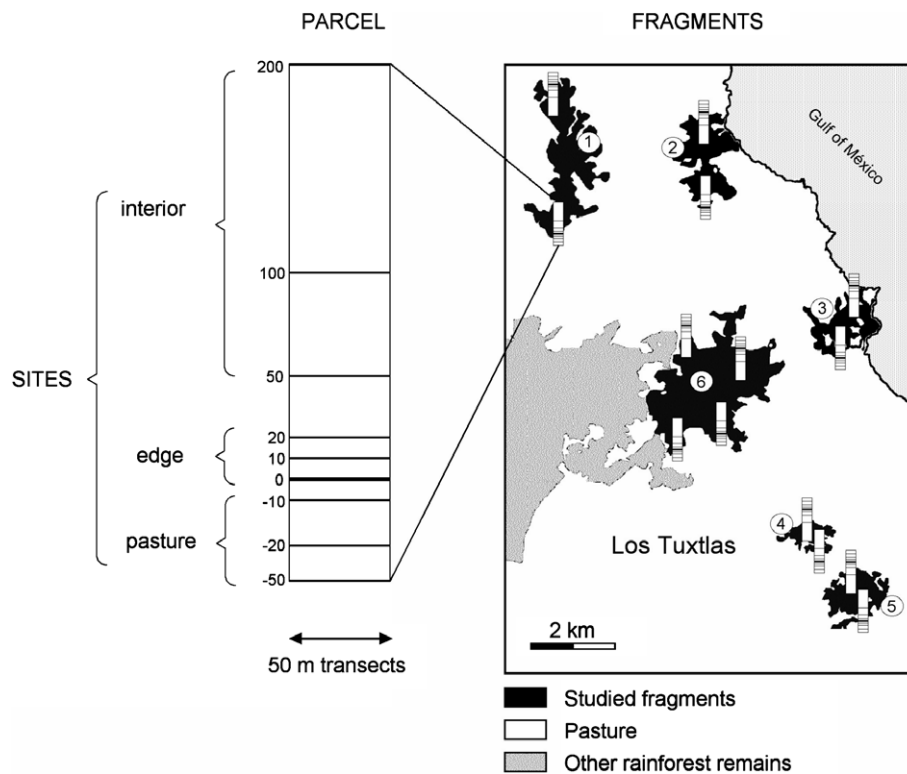


Fig. 1 – Diagram of study site in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Rectangular 50 × 250 m ecotones were situated along the pasture–edge–interior gradient. Lines represent the 50 × 2 m transects parallel to the forest edge and the negative distances are transects within the pasture. 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 were 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.

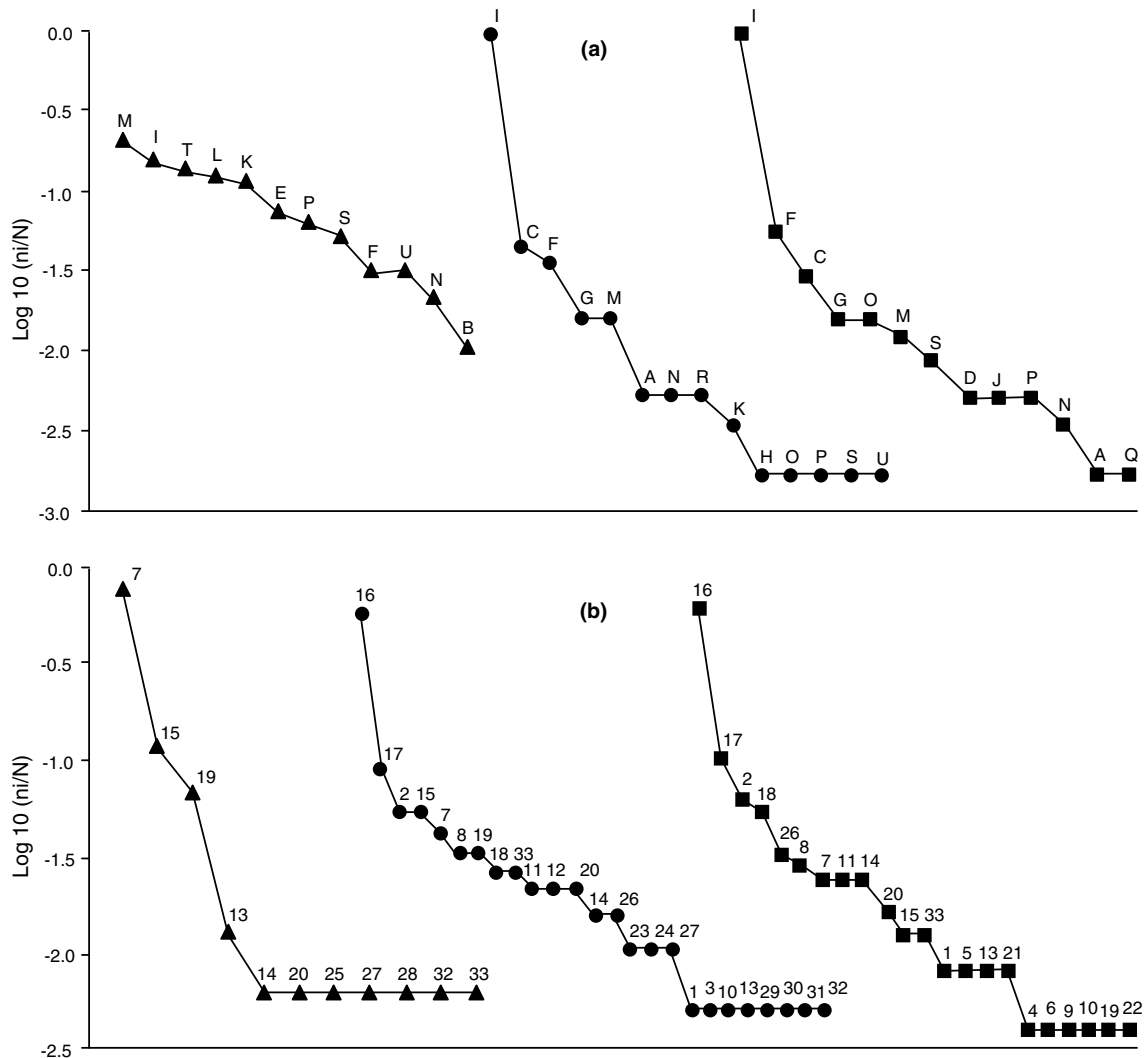


Fig. 2 – Rank-abundance curves for the herpetofauna ensemble at pasture (▲), forest edge (●) and forest interior (■) habitats in the 14 ecotones, Los Tuxtlas, Veracruz, Mexico. (a) Amphibians and (b) reptiles. Species codes are given in Table 3. For each habitat the relative abundance of each species (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>Chaunus 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	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

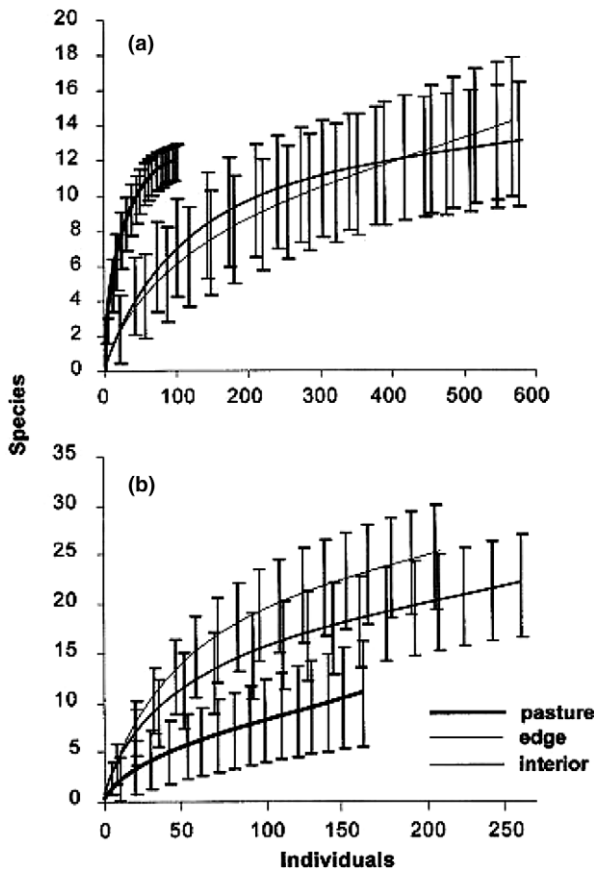


Fig. 3 – Species accumulation curves of sample-based rarefaction (Mao Tau) with confidence intervals for pasture, forest edge and forest interior habitats in 14 ecotones, Los Tuxtlas, Veracruz, Mexico. (a) Amphibians and (b) reptiles.

(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.

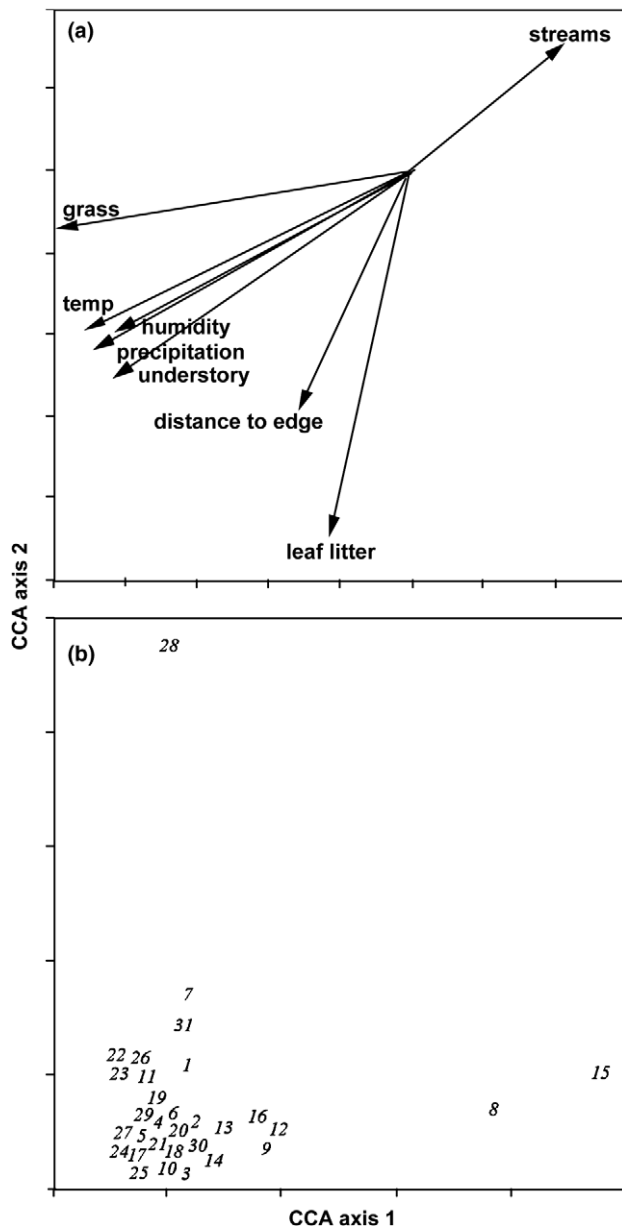


Fig. 4 – Canonical correspondence analysis of the most common amphibians and reptiles. The arrow orientation and length represents the association, direction and strength between the environmental variables and the ordination axis (ter Braak, 1987). (a) The two first axis eigenvalues are 0.582 and 0.215, 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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EDGE EFFECT ON TROPICAL HERPETOFAUNA: TEMPORAL-SPATIAL PATTERNS

José Nicolás Urbina-Cardona¹, Rodolfo Dirzo², and Víctor Hugo Reynoso*¹

¹Colección Nacional de Anfibios y Reptiles, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México. Apartado Postal 70-153, C.P. 04510 México, DF, Mexico

² Biological Sciences, Gilbert Building, 371 Serra Mall, Stanford University, 94305-5020. Stanford, CA, USA.

* Corresponding author. Telephone +52 (55) 5622 8222- Ext. 47865. Fax: +52 (55) 5550 0164. *E-mail address*: vrey noso@ibiologia.unam.mx (V.H. Reynoso)

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Abstract: Edge effect on tropical herpetofauna have been never contrasted along different seasons and edge orientations. We evaluated seasonal (wet v.s. dry, and cold v.s. hot season) and edge-orientation (north v.s. south) effects on amphibian and reptile species abundance and composition across a pasture-edge-interior ecotone in a highly fragmented tropical rainforest at Los Tuxtlas, Veracruz – Mexico. We sampled six tropical rainforest remnants and the surrounding pasture matrix by setting up 14 ecotones, each divided into three habitats (pasture, forest edge and forest interior). Three permanent transects per habitat were sampled during six times between June 2003 and April 2005 recording all visual encounters of amphibians and reptiles using equal day and night efforts. We registered 1111 individuals of 41 reptile species and 2265 individuals of 23 amphibian species. In general reptile's abundance and composition exhibited simpler habitat-seasonality relationships than amphibians do. For the reptiles' abundance and composition a strong edge effect was detected and it changed among seasons. We couldn't detect a direct and strong edge effect on amphibians' abundance and composition, and seasonality and orientation effects were the most important to define edge and interior habitat patterns, with almost the double number of individuals and species in north-faced than in south-faced ecotones. Edge effect on amphibians and reptiles at Los Tuxtlas did differ from highland and Equatorial sites because high number of species inhabiting and using matrix habitat, and a strong effect of seasonality and orientation. We propose to maintain high connectivity to improve matrix and edge affine species dispersal between forest patches, and to managing edges ensuring high habitat quality for forest interior species to reproduce and survive.

1. Introduction

Deforestation and forest fragmentation are the initial phases of a human dominated seminatural landscape, including habitat loss, breaking apart of habitat, matrix effects and edge effects (Laurance et al. 2002, Fahrig 2003, Tabarelli and Gascon 2005). The edge effect is the result of the interaction between distinct vegetation types, forested and non-forested adjacent ecosystems, or land-use classes, that generate an abrupt transition also known as ecotone, interface or boundary (Murcia 1995, Ries et al 2004, Harper et al 2005). Recently the study of edge influence (the effect of processes at the edge that result in a detectable difference in the measured variable) has become a key component to understanding how landscape structure influences habitat quality (Ries et al 2004, Harper et al. 2005).

Edge effect has been evaluated for a great amount of biotic and abiotic variables across different landscapes (*for a review see* Murcia 1995, Laurance et al. 2002, Ries et al. 2004, and Harper et al. 2005). Unfortunately amphibian and reptile group have not been included on those literature reviews because too few studies are available (Ries et al 2004) although habitat degradation and loss are one of the most important factors causing herpetofauna declines (Gibbons et al. 2000, Semlisch 2003). Amphibian and reptile groups are ideal organisms for tracking temporal and spatial edge effects because of their low vagility, and ecological constraints, such as ectothermal associated behavior (Schlaepfer and Gavin 2001). At our knowledge, edge effect (at anthropogenic edges) on amphibians and reptiles has been explicitly evaluated in 16 papers (Gambold and Woinarski 1993, Gascon 1993, Marsh and Pearman 1997, Pearman 1997, deMaynadier and Hunter 1998, Osorno 1999, Schlaepfer and Gavin 2001, Anderson and Burgin 2002, Toral et al. 2002, Lehtinen et al. 2003, Mazerolle 2003, Menke 2003, Bragg et al. 2005, Urbina-Cardona & Reynoso 2005, Lehtinen and Ramanamanjato 2006, Urbina-Cardona et al. 2006). Studies investigating the edge effect of amphibian and reptile's abundance, species richness and composition have revealed inconsistent results for different species and habitats, probably because of differences in topography, elevation, slope, aspect, history of the site (Schlaepfer & Gavin 2001), disturbance regimes, management plans (Toral et al. 2002), forest types, edge

contrast, surrounding matrix, and research design (Murcia 1995, Harper et al. 2005). This approaches could lead to an oversimplification (*sensu* edge effect as a monotonic variation only related with distance from edge, Murcia 1995) ignoring some variables that could confound true edge effects on amphibians and reptiles, such as variation on between-ecotone species composition, slope, elevation, distance to streams, and cascade effects (Schlaepfer & Gavin 2001, Urbina-Cardona et al. 2006), or the relation between seasonal and orientation effects. At now it is known that edge effects on neotropical amphibian and reptile species could be much stronger for lowland (Gascon 1993, Pearman 1997, Urbina-Cardona et al. 2006; *but see* Jellinek et al. 2004) than highland species (Marsh and Pearman 1997, Osorno 1999, Toral et al. 2002), and is highly dynamic in space and time (Osorno 1999, Schlaepfer & Gavin 2001) but the synergistic effects between season, habitat types and orientation have not been explored yet.

Seasonal effects on edge influence may alter resource use or distribution even changing the direction of edge response when comparing different seasons (Ries et al. 2004). Due to temperature and relative humidity are highly correlated with distance from the forest edge (Williams-Linera et al. 1998, Urbina-Cardona et al. 2006), and are important variables in structuring amphibian and reptile pattern and their habitat quality (Urbina-Cardona et al. 2006), we expect that those groups respond to seasonal changes in temperature and rainfall at Los Tuxtlas. Edge effect on tropical herpetofauna at Los Tuxtlas will be strong during dry season due to high differences between edge and interior microclimate (e.g. absence of water influencing amphibian and reptile structure; Urbina-Cardona et al. 2006), and will change depending on the study group. We expected that reptiles' abundance will be higher during dry and principally hot seasons because of the ideal climate for thermoregulate, while amphibian's abundance will be higher during cold and principally wet seasons because of the optimal moist weather needed for this group. And those patterns will change depending on the evaluated habitat (e.g. pasture, forest edge, and forest interior).

Recent revisions have identified that edge effect dynamics vary depending on seasonal effects and edge orientation (Murcia 1995, Ries et al 2004, Harper et al. 2005). Some authors consider a lack of trend in tropical edge effects related to orientation (Harper et al. 2005), little difference between north faced borders and south faced borders (Ries et al.

2004) or no orientation effects (Saunders et al. 1991). In general we expected that at Los Tuxtlas region south-faced edges will have more sun exposition and dryness. North-south edge orientation will have an effect on tropical amphibian and reptile's abundance when comparing different seasons and habitats. This temporal-spatial effects at Los Tuxtlas region, will be caused by dry and cold winds from the north during final part of the year, and dry and hot winds from the south during first part of the year.

In this study we evaluated edge effects dynamics in amphibian and reptile abundance along seasons, habitat types and orientations at Los Tuxtlas, a fragmented tropical rainforest in Mexico. Our objectives were to 1) test if is there any difference in edge effect on amphibian and reptile's abundance and composition between (a) hot and cold seasons, and (b) wet and dry seasons; and 2) test if does edge effect on amphibian and reptile's abundance and composition change between north and south edge orientation along different seasons. Although with this approach we wouldn't be able to detect by-species edge effects, we could include rare species such as snakes in our models and gain robustness when comparing edge effects on amphibian and reptile abundance and composition as a group. We fit models to test the effects of seasonality, habitat type, orientation, and their possible combinations, on total abundance to evaluate edge effects on amphibians and reptiles as a group. A test of these questions is relevant for a tropical fragmented forest in which the combination of several factors such as seasonality and hard elevation gradients (Geissert 2004) could confound true edge response on amphibian and reptile abundance patterns. Our approach allowed us to propose conservation actions that may help local persistence of the herpetofauna at Los Tuxtlas and generate new insights to be included (e.g. covariation between habitat type – season – orientation effects) in other “edge effect” studies on tropical herpetofauna.

2. Study area

Los Tuxtlas Biosphere Reserve is located in southern Veracruz, Mexico, along the Mexican Golf coastal plain (Geissert 2004). Altitude at Los Tuxtlas ranges from sea level to 900 m (Geissert 2004, Laborde 2004). The original dominant land cover type was tropical evergreen forest, also known as “selva alta perennifolia”. The region has been

occupied by humans since 1400 B.C., through this time human population density fluctuations have generated different deforestation extensions and intensities (Laborde 2004). With Spanish colonization, since year 1522, land use changed to different activities such as sugar, and cotton agriculture, wood extraction and cattle (Laborde 2004). And from 1970 extensive cattle exploitation replace in a great extent other land use activities (Guevara et al. 2004a). Those land-use activities were transformed by the year 1986, 84% of the original tropical rainforest into pasture (Dirzo and García 1992), the current dominant land use type (Williams-Linera et al. 1998, Guevara et al 2004b, Laborde 2004). Actually, Los Tuxtlas is the northernmost limit of the distribution of the tropical rainforest in the entire continent (Dirzo and Miranda 1991, Vázquez et al. 2004). The actual landscape is a mosaic of different elements: Primary forest fragments dominated by floral families such as Moraceae, Rubiaceae, Euphorbiaceae, Leguminosae and Palmae (with the most abundant species *Astrocaryum mexicanum*, *Chamaedorea pinnatifrons* y *Chamaedorea atterms*; Ibarra-Manríquez et al., 1997); those patches are interspersed with several habitat types which include secondary forest, riparian vegetation along rivers, lakes and streams, cultivated tree areas (with *Citrus* spp., *Psidium guajava* and *Byrsonima crassifolia*), live fences (*Bursera simaruba*, *Gliricidia sepium* and *Erythrina folkersii*), isolated trees immersed in a larger pasture matrix with native (*Paspalum conjugatum*, *Axonopus compressus*, *Setaria geniculata*, *Panicum* spp. and *Digitaria* spp.) and cultivated (*Cynodon plectostachyus* and *Panicum maximum*) grasses, and dissected by additional anthropogenic elements that include roads, farms, and villages (Ibarra-Manríquez et al., 1997, Guevara et al. 2004b).

We carried out fieldwork at the Los Tuxtlas tropical rainforest and adjacent habitat (18°32'N, 95°6'W). Mean annual temperature is ≥ 25 °C (n = 24 years) and is highly seasonal with low temperatures between October to March and high temperatures between April to September (Fig. 1). Annual precipitation fluctuates from ≤ 60 mm to 4959 mm (Soto 2004), with marked wet and dry seasons (wet from August to December, and dry from January to July, Fig. 2). This unimodal seasonal dynamics in temperature and rainfall lead us to contrast edge effects not just during dry and wet seasons, but hot and cold seasons too.

3. Methods

Forest fragment selection

During our study we sampled tropical rainforest remnants and the surrounding pasture matrix identified previously on a Landsat-7 image for the year 2000, followed by field verification. We selected six fragments between 26 ha and 472 ha in size, completely surrounded by pasture and in which at least one temporal stream cross the interior-edge-pasture ecotone to avoid changes in amphibian and reptile composition due to the absence of water bodies. There were no standing bodies of water (not lakes, neither rivers) near the study ecotones. According to the owners and farm keepers these fragments have not been altered extensively for more than 15 years. The study sites ranged in elevation from 30 and 275 m, and slopes of the terrain ranged from 1 % and 44 %. Although elevation and slope always decreased in a gradient from forest interior to pasture, when taking into account all the studied ecotones there were no differences on this variables between edge and interior. In the same way distance to streams that potentially confuses true edge effects were adequately controlled for by the sampling design in this study (e.g. there were no difference between edge and interior; Urbina-Cardona et al. 2006).

Research design

Within each fragment there were two rectangular 50 X 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. Within each plot, we install several 50-m permanent line transects (three on each habitat type: pasture, forest edge and forest interior) located at standard distances from, and parallel to the rainforest edge (Fig 3). Following Williams-Linera et al. (1998), the forest edge habitat were delimited within the first 20 m of forest, where major changes in the vegetation structure and density occur. The forest interior habitat 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 (Williams-Linera et al., 1998). This study reports seasonality and orientation effects on the amphibian and reptile's abundance and composition based on

the survey of 14 ecotones containing 126 transects with a total of 1008 man hours of sampling effort.

Amphibian and Reptile survey

The study area was visited on six occasions: June-July and September-October 2003, February-March, May and September 2004, and April 2005. During each visit, all permanent transects were surveyed two times by two observers during six hours (1100 to 1400 h and 2100 to 2400 h). The first transect of the ecotone to be sampled was randomly chosen to avoid bias related to species activity patterns confusing true edge effects. Sampling was restricted to the understory, recording all visual encounters of amphibians and reptiles found within one meter on either side of the transect and up to two meters above the ground. We did not mark individuals, but overestimation of abundance by recapture was not considered 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). On a previous study Urbina-Cardona et al. (2006) determined that for amphibian and reptile composition there was no difference between ecotones demonstrating that the effect of habitat heterogeneity between study ecotones were adequately controlled by the sampling design and that there was no differences in species composition between the six evaluated fragments. During this study we don't search for fragment-area effects, so we included ecotones from various fragments to increase sample sizes (*following* Schlaepfer & Gavin 2001).

To identify species, we created a field guide using photographic files of voucher specimens collected during April 2003 and referred to the 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, organisms difficult to identify were preserved for later comparison with specimens in the Colección Nacional de Anfibios y Reptiles of the Instituto de Biología, Universidad Autónoma de México (UNAM) in Mexico City.

Statistical Analysis

Precipitation and air temperature data were gathered from the meteorological station at the Los Tuxtlas Tropical Biology Station, Instituto de Biología (UNAM).

To evaluate seasonality, habitat and edge orientation effects on reptiles and amphibians, we analyzed reptile and amphibian's abundance per transect ($n = 126$) per season ($n = 2$) by analysis of variance in JMP version 4.0.2 (SAS Institute 2000) after Box Cox transformation (SAS Institute 2000). When analyzing the models, all residuals accomplished normality and homoscedasticity of variance. To test for differences between factors we used the LSMeans contrast test (SAS Institute 2000).

To detect spatial differences in amphibian and reptile composition we used a non-parametric two-way analysis of similarity (ANOSIM subroutine; PRIMER software, Clarke and Gorley 2001). Before the analysis we generated Bray-Curtis similarity matrices of amphibian and reptile data, using normalized relative abundance of species in each transect. We used the ANOSIM procedure applying a permutation-based test to habitat types (e.g. pasture, edge or interior) nested within seasons (wet V.S. cold; hot V.S. dry); and orientations (north faced edges V.S. south oriented edges) nested within habitats (e.g. pasture, edge or interior). We tested the null hypotheses that within-season (and within-orientation) and within-habitat similarity were equal to between-season (and between-orientation) and between-habitat similarity.

4. Results

We registered 1111 individuals of 41 reptile species and 2265 individuals of 23 amphibian species. The surrounding pasture matrix was dominated by the rose-belly lizard *Sceloporus variabilis* (82.7% of the total reptile captures), Rio grande leopard frog *Lithobates berlandieri* (34.5% of the total amphibian captures), the white-lipped frog *Leptodactylus fragilis* (14% of the total amphibian captures) and the leprus chirping frog *Syrnhophus leprus* (11% of the total amphibian captures). The forest edge and interior was dominated by the lesser scaly anole *Anolis uniformis* (62% and 65.3% of the total reptile

captures respectively) and by the polymorphic robber frog *Craugastor rhodopsis* (90.5% and 86% of the total amphibian captures respectively).

At the north faced ecotones we captured 589 individuals of 31 reptile species and 1493 individuals of 21 amphibian species, and at the south faced ecotones we captured 522 individuals of 31 reptile species, and 772 individuals of 18 amphibian species. North faced ecotones were dominated by the reptiles *Anolis uniformis* and *Sceloporus variabilis* (48.2% and 20.2% of the total reptile captures respectively), and by the amphibians *Craugastor rhodopsis*, and *Ollotis valliceps* (83.5%, and 3.5% of the total amphibian captures respectively). South faced ecotones were dominated by *Anolis uniformis* and *Sceloporus variabilis* (52% and 18.3% of the total reptile captures respectively), and *Craugastor rhodopsis*, *Lithobates berlandieri*, and *Ollotis valliceps* (77.7%, 5.4% and 3.1% of the total amphibian captures respectively).

Hot and cold season effects

Reptiles:

During hot season we captured 595 individuals of 29 reptile species and during cold season we captured 516 individuals of 32 reptile species. During hot and cold seasons reptiles were dominated by *Anolis uniformis* (49.1% and 50.7% of the total reptile captures respectively) *Sceloporus variabilis* (17.5% and 21.5% of the total reptile captures respectively), and *Scincella cherriei* (5.5% and 4.6% of the total reptile captures respectively).

We founded effects of seasonality, habitat and the interaction between those factors on reptile's abundance, but no effects were detected in relation to orientation (Table 1). The reptile's abundance was significantly higher during hot season, and on forest interior habitat (Fig. 1). Forest edge was different between cold and hot seasons, and the same pattern has been observed for forest interior habitat (Fig. 1). Reptiles' abundance was no different on pasture along cold and hot seasons (Fig. 1). All habitats were different between them during hot season, but during cold season pasture and forest edge were not different (Fig. 1).

Amphibians:

During hot season we captured 1063 individuals of 20 amphibian species and during cold season we captured 1202 individuals of 20 amphibian species. During hot season amphibians were dominated by *Craugastor rhodopis*, *Lithobates berlandieri* and *Ollotis valliceps* (74.3%, 5.8% and 5.5% of the total amphibian captures respectively). During cold season amphibians were dominated by *Craugastor rhodopis* (88% of the total amphibian captures).

We founded effects of habitat, orientation, the interaction between those factors, and the interaction between habitat and seasonality on amphibian's abundance, but no direct effects were detected in relation to seasonality (Table 1). In general the amphibian's abundance was significantly higher in both forest edge and interior, but there was no difference between edge and interior (Fig. 2a).

Pasture habitat exhibited critical minor abundance and there were different along cold and hot seasons. Amphibians' abundance on pasture habitat was significantly higher during hot season contrary to our expectations (Fig 2a.). Forest edge was no different during cold and hot seasons, and the same pattern has been observed for forest interior habitat (Fig 2a.). During cold and hot seasons, both forest edge and forest interior were not different (Fig 2a.).

Amphibian's abundance was significantly higher in north-faced ecotones because of almost the double number of individuals than in south-faced ecotones. North-faced forest edge and interior were different from south-faced ones, but there was no difference between northern pastures and southern ones (Fig 2b,c). Pasture habitat were different from forest edge and interior habitats in both orientations, and there was no difference between forest edge and interior habitats in both orientations.

Dry and wet season effects

Reptiles:

During dry season we captured 620 individuals of 29 reptile species and during wet season we captured 491 individuals of 30 reptile species. During dry and wet seasons reptiles were dominated by *Anolis uniformis* (59.3% and 37.8% of the total reptile captures

respectively) and *Sceloporus variabilis* (15.2% and 24.6% of the total reptile captures respectively). During dry season *Scincella cherriei* abundance were 7.5%, and during wet season *Plestiodon sumichrasti* were 7.1% of the total reptile captures.

We founded effects of seasonality, habitat and the interaction between those factors on reptile's abundance, but no effects were detected in relation to orientation (Table 2). The reptile's abundance was significantly higher during dry season, and on forest interior habitat (Fig. 3). Forest edge was different between dry and wet seasons, and the same pattern has been observed for forest interior habitat (Fig. 3). Reptiles' abundance was no different on pasture along dry and wet seasons (Fig. 3). All habitats were different between them during dry season, but during wet season forest edge and forest interior were not different (Fig. 3).

Amphibians:

During dry season we captured 1451 individuals of 22 amphibian species and during wet season we captured 814 individuals of 21 amphibian species. During dry season amphibians were dominated by *Craugastor rhodopis*, and *Lithobates berlandieri* (81.3%, and 3.8% of the total amphibian captures respectively). During wet season amphibians were dominated by *Craugastor rhodopis*, *Nanotriton rufescens* and *Syrrhophus leprus* (82%, 3.2%, and 3.1% of the total amphibian captures respectively).

We founded effects of seasonality, habitat, orientation, and the interaction between those factors on amphibian's abundance, but no effects were detected in relation to the interaction between seasonality and habitat (Table 2). In general the amphibian's abundance was significantly higher during wet season and in both forest edge and forest interior, but there were no differences between edge and interior habitat (Fig. 4a). Pasture habitat exhibited critical minor abundance when compared to forest edge and interior (Fig. 4a).

Amphibian's abundance was significantly higher in north-faced ecotones because of almost the double number of individuals than in south-faced ecotones (Fig. 4b,c). North-faced ecotones were different during dry and wet season, but south-faced ecotones were not different during seasons (Fig 4b,c). North-faced ecotones were different than south-faced

ecotones during both dry and wet season. At north-faced oriented ecotones, forest edge and forest interior habitat were different during dry and wet seasons, and on south-faced oriented ecotones, pasture and forest interior were different between dry and wet seasons (Fig 4b,c).

Effects on amphibian and reptile composition

Reptiles:

ANOSIM determined that for reptile composition there was no difference between seasons ($p=0.913$), but between habitat nested within seasons ($p=0.001$). All habitat were different from each other ($p=0.024$ for all possible combinations). There was no difference on reptile composition between orientation nested within habitat ($p=0.571$).

Amphibians:

ANOSIM determined that for amphibian composition there was no difference between seasons ($p=0.687$), but between habitat nested within seasons ($p=0.001$). Pasture habitat were different from both forest edge and interior ($p=0.024$ for each combination), but there were no difference between forest edge and interior ($p=0.057$). There was a difference on amphibian composition between orientation nested within habitat ($p=0.002$), but no differences was detected between habitat ($p=0.999$).

5. Discussion

Due to highly dynamic temporal and spatial patterns on edge effects, different approaches are needed when trying to understand this complex and multidimensional process. On a previous study herpetofauna diversity and microenvironment correlates along pasture-edge-interior ecotone at Los Tuxtlas were reported (Urbina-Cardona et al. 2006). During this study we used a different approach focusing on direct biological responses such as abundance and species composition along seasonal and spatial gradients. Together, these approaches will provide important information to understanding edge effect dynamics on tropical herpetofauna at Los Tuxtlas region.

As a general pattern, reptile's abundance and composition exhibited simpler habitat-seasonality relationships than amphibians do. For the reptiles abundance a strong edge effect was detected and the edge influence changed with cold-hot season with a great

amount of species composition exchange between habitats. For the amphibians we couldn't detect a direct and strong edge effect, and orientation effects were the most important to define edge and interior habitat patterns on amphibians' abundance and composition, principally during dry and wet seasons with a great increase of the abundance during dry seasons.

We wouldn't be able to test diurnal versus nocturnal patterns (Daily and Elrich 1996) on edge effects on amphibians and reptiles due to some diurnal cryptic species are more prone to be detected at night when they are inactive at exposed leafs and branches and vice versa (Urbina-Cardona and Reynoso 2005) increasing biases related to visual encounters reflecting the abundance of this organisms.

Hot and cold season effects

Reptiles:

Due to ecophysiological constraints, reptiles require hot habitats to thermoregulate (Zug 2001). Although reptile's abundance and composition are expected to vary to seasonal temperature changes in their microhabitat (Schlaepfer and Gavin 2001) we wouldn't be able to find studies that reported examples of cold-hot contrasts on edge effects. We founded that reptiles were more abundant during hot season, and seasonality (when comparing hot and cold seasons) had an effect on reptiles' abundance inhabiting forest (both edge and interior habitats) but not pasture. During hot season all habitat were different, showing a clear habitat differentiation and a strong edge effect, but during cold season pasture and forest edge presented the same reptile abundance, suggesting seasonal (when comparing hot and cold seasons) changes on edge effect over reptiles' abundance.

During our study it seemed that pasture habitat was a good place to live during cold season maybe because of absence of canopy and understory cover, which offered more places to thermoregulate. Another possibility could be that pasture dominant species (such as *S. variabilis*) could stand more efficiently cold-hot changes along seasons, showing high abundance at pasture, but no edge and interior where is more abundant during hot season (APENDIX A). In this sense, human perturbation instigates ideal environments to thermoregulate and could influence changes in reptile abundance patterns in anthropogenic landscapes.

Amphibians:

It is known that, amphibians need cold habitats to avoid desiccation due to ecophysiological requirements (Zug 2001). We founded that amphibians were more abundant at the forest (both edge and interior) principally on north-faced ecotones, but not on pasture. So orientation has no effects on pasture species maybe due to more similar and simpler microhabitats (*sensu* Urbina-Cardona et al. 2006) or to specific species identity, such as reproductive mode, size and habit (Urbina-Cardona & Reynoso 2005).

We hypothesized that south faced edges had more sun exposition and desiccation and this could be the reason for an abrupt increase of amphibians' abundance on north-faced borders. We founded that hot-cold seasonality *per se* had no direct effects on amphibian's abundance but their effect appeared when comparing different habitat types such as pasture, forest edge and forest interior. As a general fact, we founded strong differences between pasture and forest habitat, but no between edge and interior habitat along seasons. We have to take into accounts that pasture species exhibits less dominance than forest species does, amphibian composition is different at pasture, and forest species dominance showed more seasonality effects, so abundance patterns could be obscured by species-specific responses (APENDIX B).

We concluded that there was no true edge effect on amphibian's abundance (*sensu* differences between forest edge and interior), and it seemed that amphibians abundance and composition responded to absence of canopy and undestory cover on their habitat but no to edge-interior ecotone, and the real strong effects appear when comparing north-faced ecotones with south-faced ones. Until now orientation effects on tropical amphibians haven't included into "edge effect studies". We recommend including this variable into future research designs and description on study site, to find (if exist) a general pattern on tropical amphibians.

Dry and wet season effects

Reptiles:

We founded that reptiles were more abundant during dry season, and seasonality (when comparing dry and wet seasons) had an effect on reptiles' abundance inhabiting forest edge and forest interior. Seasonal effects along edge-interior habitat on tropical lizards could be explained by seasonal parasitism rates, predation and prey abundance dynamics (Schlaepfer and Gavin 2001). During dry season all habitats were almost different showing a clear habitat differentiation on reptiles' abundance and a strong edge effect, but during wet season forest edge and forest interior presented the same reptile abundance, suggesting a decrease on edge effect impact due maybe to a most homogeneous moist gradient along the ecotone. Urbina-Cardona et al. (2006) founded that during dry season canopy cover was important in structuring reptile's ensembles while during dry season distance to temporal water bodies was important. This could explained the dry-wet dynamics on reptiles' abundance revealed on this study.

During our study it seemed that forest interior habitat was a good refuge for some forest affine reptiles principally during dry season (sensu *Anolis uniformis*, and *Scincella cherrieri*). While other lizards, such as *Anolis barkeri*, *Anolis lemurinus*, and *Plestiodon sumichrasti* preferred forest interior habitat during wet season (APENDIX A). In contrast pasture dominant specie (*S. variabilis*) uses indifferently the surrounding matrix during dry and wet seasons, and *Anolis sericeus* was more abundant during wet seasons. So edge effect on the reptile's abundance are highly dynamic and has different effects depending on the species identity, the habitat type and the dry-wet seasons. Schlaepfer and Gavin (2001) reported for Costa Rica moist forest, that two *Norops* lizard species (similar to Los Tuxtlas *Anolis* lizards) were generally more abundant at the edge during the end of dry season, while during wet season *Norops* species were more abundant at the interior. A similar pattern was exhibited by two *Anolis* species (*A. barkeri*, *A. lemurinus*), but we couldn't generalize this pattern to all Family Polychrotidae species due to other species such as more abundant lizard at the forest (*A. uniformis*) shower the opposite pattern.

Amphibians:

Perhaps relative humidity is the most important variable affecting amphibians' abundance and distribution. So it's logical that dry-wet dynamic effects were the most

complex at all, and that seasonality were related to orientation, habitat and almost all possible combinations between those three factors.

We founded that orientation effects were stronger than edge effects on amphibians' abundance and composition. North-faced ecotone patterns define general patterns on amphibian's abundance, because exhibit the double number of organisms than south-faced ecotones.

But amphibian's abundance increased during wet season and on the forest habitat (both edge and interior). More complex patterns appear when comparing north-faced to south-faced ecotones: North-faced ecotones showed differences between dry and wet seasons; however south-oriented ecotones did not, principally at the forest edge. South oriented forest edges bordering open habitat exhibit stronger edge effect because of increased exposure to sunlight (Ries et al 2004). Amphibian species inhabiting south faced edges had to be adapted to more sun exposition and desiccation, and because of that we have founded an increase on amphibian species abundance such as *Chaunus marinus*, *Lithobates berlandieri*, and *Leptodactylus melanonotus* (APENDIX C), which are highly known to inhabit anthropogenic disturbed habitats, contradicting general and north-faced ecotones pattern on amphibians. Amphibian abundance at North faced ecotones could be explained by the increased number of individuals of *Craugastor rhodopis*, *Craugastor berkenbuschi*, *Ollotis valliceps* *Craugastor vulcani*, and *Pseudoeurycea orchimelas* (APENDIX C). Those last three species are considered as forest interior species which are reported to be highly vulnerable to habitat loss and edge effects (Urbina-Cardona et al. 2006). Although a great uncertainty degree remains, it seems that north faced ecotones are important for amphibian conservation due to support more species richness (70% of all amphibian species), and more forest interior affine species which are highly known to be more vulnerable.

Local versus Tropical implications

During the years when field work was conducted, the climate was warmer and wetter when compared to last 24 years at Los Tuxtlas region (Fig 1 and 2), and there was less contrast between wet and dry, and hot and cold seasons. Reported amphibian and

reptile's abundance patterns could be a response of synergistic relations between long-term seasonal changes (such as more rainfall during last months of the year) and actual loss of habitat and edge effects.

No significant differences in amphibian composition were detected between edge and interior. This could be due to our studied fragments presented old borders that have not been altered extensively for more than 15 years. So studied borders at Los Tuxtlas must be at post-closure phase when edge-related changes are almost stabilized (*sensu* Laurance et al. 2002). Orientation had a strong influence on amphibian composition leading us to think that at old tropical edges, the edge effect *per se* (*sensu* differences between forest edge and interior) is not important for this group but edge orientation does. Although, reptile composition exhibit the opposite pattern, being influenced by habitat type (pasture, edge or interior), and showing that perhaps for the reptiles' old-edges are not old enough. This is a strong evidence of the highly dynamic mechanisms on edge and matrix effects over different organisms such as amphibians and reptiles, which lead us to different management strategies.

Although the great regeneration capacity at the evergreen forest, recent land use (e.g. extensive pastures for cattle) don't give a chance to secondary regrowth and has generated heavily fragmentation rates in which 40 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). Current landscape structure has caused top predator's extinction and understory and canopy mammal impoverishment (Dirzo and Miranda 1991), which could include non reported secondary extinction cascades at the region (*sensu* Laurance et al. 2000) Rarity and commonness of amphibian and reptile species inhabiting Los Tuxtlas' rainforest have been changed during last decades (Urbina-Cardona and Reynoso 2005). This could be a resilience response of the herpetofauna to actual forest disturbance, degradation and loss such as reported by Laurance et al. (2001).

On this study seasonal and edge-orientation effects on amphibians and reptiles across pasture-forest ecotones are reported, but more studies are required to determine seasonality and orientation effects on the dispersal of amphibians and reptiles between forest patches along pasture matrix using secondary regrowth forest, cultivated fields, live

fences, riparian vegetation and body waters. This information could guide insights to land managers working on restoration plans, by stimulating forest regrowth at strategic dispersal places enhancing economic viable and organized connectivity arrangements across the landscape.

We have to keep in mind that reported patterns of amphibian and reptile's abundance and composition are based on the survey of six forest fragments at Los Tuxtlas region, on 14 ecotones containing 126 transects along 1008 man hours of sampling effort. Results most due restricted to this region but we suggest that in further studies about edge effect on tropical herpetofauna, the concomitant effects of habitat type, season and orientation must be included in order to reduce the uncertainty and the synergistic effects (*sensu* Murcia 1995).

Extrapolation of this study to other regions should be viewed with caution due to Los Tuxtlas region has exhibited different anthropogenic activities since 4000 years ago, and actual biodiversity (3356 plant species and 851 vertebrate species) had to bear with different deforestation and reforestation rates and intensities (Laborde 2004, Guevara et al. 2004a). Tropical rainforest at Los Tuxtlas is the northernmost limit of the distribution in the entire continent (Dirzo and Miranda 1991) and this latitudinal position far away from the Equator could lead to a forest with mixed characteristics of tropical and temperate regions. Those characteristics determined the influence of seasonality and edge-orientation effects on amphibians and reptiles, which could imprint high resilience capacity to local biodiversity and lead to differences with other studies on lowland tropical landscapes (e.g. Amazon rainforest; Gascon 1993, Pearman 1997).

The strength and nature of edge effects on tropical herpetofauna may vary among altitudinal and latitudinal gradients. Contrary to that proposed by Toral et al. (2002) for tropical highlands, we founded that edge effect on tropical lowlands had more effects (through orientation for the amphibians, and through habitat type for the reptiles) than fragmentation-area *per se* (e.g, no differences in species composition between the six evaluated fragments).

One big difference between tropical lowland and highland is the amount of frog species inhabiting, crossing or breeding at matrix habitat. At the wet Andean forest 95% of

studied species were at forest transects (Marsh and Pearman 1997, Toral et al. 2002), while at the Amazonia 40% of frog species (Tocher et al 2001) and 80% of nominally primary forest species (Gascon et al. 1999) were registered at pasture. At this study we registered at pasture the 30% of total reptile and 52% of total amphibian species richness. This suggests that for lowland edge and matrix tolerant species conservation (*sensu* Urbina-Cardona et al. 2006), linear remnants along water courses could improve species reproduction and dispersal between forest patches (de Lima and Gascon 1999). While forest interior species require “edge management” to ensure forest fragments with high habitat quality to reproduce and survive (Urbina-Cardona et al. 2006).

On the other hand seasonality apparently has more effects on tropical herpetofauna edge effects when analyzing faunas regions from the Equator. On the Andean forest of Ecuador (lat. 0° 28'N, long. 78° 33'W; Toral et al. 2002) and Colombia (lat. 6° 77'N, long. 75° 03'W; Osorno 1999) authors didn't find differences on *Eleutherodactylus* species between census period; on a premontane wet forest at Costa Rica (lat. 8° 47'N, long. 82° 59'W), Schlaepfer and Gavin (2001) founded seasonality effects on frog (*Eleutherodactylus*) and lizard (*Norops*) species; during this study (lat. 18° 32'N, long. 95° 6'W) seasonality influenced amphibian and reptile's abundance; and on conifer plantations at Maine (lat. 45° 06'N, long. 68° 53'W) seasonality explain salamander's abundance. This give us an insight that edge effects on tropical herpetofauna is not just dynamic at time and local space scales, but seasonality and orientation effects changes depending on altitude, and latitude of the study region. So conservationists should use this information to complement management plans of their particular region of interest and make decisions depending on the study region's latitude, altitude, edge orientation and seasonality effects, between other factors.

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FIGURE LEGENDS

Figure 1. Mean daily temperatures at the study site. Dotted-lines represent maximum and minimum temperatures, and solid line represents mean temperatures, all during 24 years period (1982-2004). Horizontal dotted line represents total mean temperature during 24 years period. And the line with filled circles represent mean daily temperatures during the study period. The arrows behind the x axis indicate the times at which amphibians and reptiles surveys were conducted. It's important to note here that there's a relative marked cold-hot period and that mean daily temperatures during the study period are warm than mean temperatures during 24 years.

Figure 2. Mean daily rainfall at the study site. Solid line represents mean rainfall during 24 years period (1982-2004). Horizontal dotted line represents total mean rainfall during 24 years period. And the line with filled circles represent mean daily rainfall during the study period. The arrows behind the x axis indicate the times at which amphibians and reptiles surveys were conducted. It's important to note here that there's a relative marked dry-cold period and that mean daily rainfall during the study period are wetter than mean temperatures during 24 years.

Figure 3. Diagram of study site in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Rectangular 50 x 250 m ecotones were situated along the pasture-edge-interior gradient. Lines represent the 50 x 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.

Figure 4. Comparisons of mean (and SD) number of reptiles per habitat during hot (□) and cold (■) seasons. The asterisks indicate a significant difference ($P < 0.05$).

Figure 5. Comparisons of mean (and SD) number of amphibians per habitat during hot (□) and cold (■) seasons. (a) General model, (b) north-faced ecotones, and (c) south-faced ecotones. The asterisks indicate a significant difference ($P < 0.05$).

Figure 6. Comparisons of mean (and SD) number of reptiles per habitat during dry (□) and wet (■) seasons. The asterisks indicate a significant difference ($P < 0.05$).

Figure 7. Comparisons of mean (and SD) number of amphibian per habitat during dry (□) and wet (■) seasons. (a) General model, (b) north-faced ecotones, and (c) south-faced ecotones. The asterisks indicate a significant difference ($P < 0.05$).

APPENDIX A. Number of individuals of reptile species recorded during hot and cold seasons, and on dry and wet seasons at the pasture, edge, and interior habitats of the tropical rainforest at Los Tuxtlas, Veracruz, Mexico.

	Pasture				Edge				Interior			
	H ot	Col d	Dr y	W et	H ot	Col d	Dr y	W et	H ot	Col d	Dr y	W et
SAURIA												
<i>Ameiva undulata</i>	2	4	0	6	10	6	6	10	1	1	1	1
<i>Anolis barkeri</i>	0	0	0	0	6	0	0	6	6	2	1	7
<i>Anolis biporcatus</i>	0	0	0	0	0	0	0	0	1	0	1	0
<i>Anolis cf.</i>												
<i>duellmani</i>	0	0	0	0	0	1	0	1	0	1	0	1
<i>Anolis lemurinus</i>	0	0	0	0	0	4	0	4	0	6	0	6
<i>Anolis pentaprion</i>	0	0	0	0	5	2	5	2	1	1	2	0
<i>Anolis petersi</i>	2	0	0	2	1	0	0	1	1	1	0	2
<i>Anolis rodriguezii</i>	1	0	0	1	3	3	4	2	6	0	2	4
<i>Anolis sericeus</i>	8	17	6	19	6	1	4	3	2	0	0	2
					11		14		18		22	10
<i>Anolis unifomis</i>	0	0	0	0	2	117	8	81	0	145	0	5
<i>Basiliscus vittatus</i>	0	0	0	0	2	0	2	0	0	2	0	2
<i>Corytophanes</i>												
<i>hernandezii</i>	0	0	0	0	11	6	11	6	12	10	11	11
<i>Ctenosaura</i>												
<i>acanthura</i>	0	0	0	0	0	0	0	0	0	1	0	1
<i>Iguana iguana</i>	0	0	0	0	0	1	1	0	0	2	0	2
<i>Lepidophyma</i>												
<i>pajapanensis</i>	0	0	0	0	0	0	0	0	1	0	1	0
<i>Lepidophyma</i>												
<i>tuxtlae</i>	0	1	0	1	5	3	5	3	8	5	9	4
<i>Plestiodon</i>												
<i>sumichrasti</i>	0	0	0	0	14	3	4	13	19	7	4	22
<i>Sceloporus salvini</i>	0	0	0	0	0	0	0	0	1	0	0	1
<i>Sceloporus</i>				10								
<i>variabilis</i>	92	109	92	9	8	1	2	7	4	1	0	5
<i>Scincella cherriei</i>	1	0	1	0	9	4	9	4	23	20	36	7
<i>Sphaerodactylus</i>												
<i>glaucus</i>	0	0	0	0	0	1	0	1	0	0	0	0
SERPENTES												
<i>Boa constrictor</i>	0	0	0	0	0	0	0	0	1	1	1	1
<i>Bothrops asper</i>	1	0	0	1	5	4	5	4	2	3	3	2
<i>Clelia scylatina</i>	0	0	0	0	0	0	0	0	0	1	1	0
<i>Coniophanes</i>	0	0	0	0	0	0	0	0	1	0	1	0

bipunctatus												
Coniophanes												
fissidens	0	0	0	0	2	0	1	1	0	1	1	0
Coniophanes												
imperialis	0	0	0	0	1	1	1	1	1	0	1	0
Coniophanes												
quinquevittatus	0	0	0	0	0	1	1	0	0	0	0	0
Dryadophis												
melanolomus	0	0	0	0	0	0	0	0	0	0	0	0
Ficimia publia	1	1	2	0	0	0	0	0	0	0	0	0
Imantodes cenchoa	0	0	0	0	2	2	3	1	6	6	5	7
Leptodeira												
septentrionalis	0	1	0	1	3	0	1	2	0	0	0	0
Leptophis												
mexicanus	0	0	0	0	0	0	0	0	0	0	0	0
Micrurus diastema	1	0	1	0	0	1	0	1	0	0	0	0
Ninia sebae	0	1	0	1	0	0	0	0	0	0	0	0
Oxyrhopus petola	0	0	0	0	0	1	0	1	0	0	0	0
Pseustes												
poecilonotus	0	0	0	0	1	0	1	0	0	0	0	0
Rhadinaea decorata	0	0	0	0	1	0	1	0	0	1	1	0
Stenorrhina												
degenhardti	0	0	0	0	1	0	0	1	0	0	0	0
Tantilla sp.	0	0	0	0	0	0	0	0	1	0	0	1
Tropidodipsas												
sartorii	0	0	0	0	0	1	1	0	0	0	0	0

APPENDIX B. Number of individuals of amphibian species recorded during hot and cold seasons, and on dry and wet seasons at the pasture, edge, and interior habitats of the tropical rainforest at Los Tuxtlas, Veracruz, Mexico.

	Pasture				Edge				Interior			
	H ot	Col d	Dr y	W et	H ot	Col d	Dr y	W et	H ot	Col d	Dr y	W et
CAUDATA												
Bolitoglossa alberchi	0	0	0	0	3	1	1	3	1	0	0	1
Bolitoglossa platydactyla	1	0	0	1	0	0	0	0	0	0	0	0
Nanotriton rufescens	0	0	0	0	11	11	8	14	9	9	6	12
Pseudoeurycea orchimelas	0	0	0	0	0	0	0	0	1	2	1	2
ANURA												
Chaunus marinus	8	0	3	5	0	0	0	0	0	0	0	0
Ollotis valliceus	2	0	0	2	21	2	19	4	36	5	30	11
Craugastor alfredi	0	0	0	0	4	10	5	9	7	6	5	8
Craugastor berkenbuschi	0	0	0	0	0	2	1	1	11	15	26	0
Craugastor rhodopis	4	17	7	14	37	51	56	33	41	52	61	32
Craugastor vulcani	0	0	0	0	3	0	0	3	3	6	2	7
Dendropsophus ebraccatus	0	0	0	0	0	1	0	1	3	2	3	2
Dendropsophus microcephala	0	0	0	0	0	1	0	1	1	1	1	1
Ecnomiohyla cf. valancifer	0	0	0	0	3	0	3	0	0	1	0	1
Gastrophryne elegans	2	0	2	0	2	0	1	1	4	0	4	0
Gastrophryne usta	0	0	0	0	0	0	0	0	0	1	1	0
Leptodactylus fragilis	7	20	23	4	1	2	3	0	0	0	0	0
Leptodactylus melanonotus	11	4	14	1	0	0	0	0	0	0	0	0
Lithobates berlandieri	62	5	55	12	0	0	0	0	0	0	0	0
Lithobates vaillanti	15	0	15	0	0	1	0	1	0	0	0	0
Smilisca baudini	4	5	6	3	2	1	3	0	7	5	11	1
Smilisca cyanosticta	0	0	0	0	0	0	0	0	0	1	1	0
Syrhophus leprus	16	5	5	16	7	3	5	5	5	6	7	4
Tlalocohyla loquax	0	6	0	6	0	1	0	1	0	4	1	3

APENDIX C. Number of individuals of amphibian species recorded along north faced and south faced ecotones at the pasture, edge, and interior habitats of the tropical rainforest at Los Tuxtlas, Veracruz, Mexico.

	North faced ecotone			South faced ecotones		
	Pasture	Edge	Interior	Pasture	Edge	Interior
CAUDATA						
<i>Bolitoglossa alberchi</i>	0	2	1	1	1	0
<i>Bolitoglossa platydactyla</i>	0	1	0	0	0	0
<i>Nanotriton rufescens</i>	0	14	2	0	9	15
<i>Pseudoeurycea orchimelas</i>	0	0	3	0	0	0
ANURA						
<i>Chaunus marinus</i>	0	0	0	8	0	0
<i>Ollotis valliceps</i>	2	20	30	1	3	10
<i>Craugastor alfredi</i>	0	4	9	0	8	6
<i>Craugastor berkenbuschi</i>	0	0	25	0	2	1
<i>Craugastor rhodopis</i>	11	613	623	10	281	309
<i>Craugastor vulcani</i>	0	2	7	0	0	3
<i>Dendropsophus ebraccatus</i>	0	0	6	0	0	0
<i>Dendropsophus microcephala</i>	0	0	1	0	1	1
<i>Ecnomiohyla cf. valancifer</i>	0	0	0	0	4	0
<i>Gastrophryne elegans</i>	0	2	3	2	0	1
<i>Gastrophryne usta</i>	0	0	1	0	0	0
<i>Leptodactylus fragilis</i>	20	3	0	7	0	0
<i>Leptodactylus melanonotus</i>	5	0	0	10	0	0
<i>Lithobates berlandieri</i>	25	0	0	42	0	0
<i>Lithobates vaillanti</i>	13	0	0	2	1	0
<i>Smilisca baudini</i>	6	2	3	3	1	9
<i>Smilisca cyanosticta</i>	0	0	1	0	0	0
<i>Syrhophus leprus</i>	15	4	4	6	6	7
<i>Tlalocohyla loquax</i>	6	1	3	0	0	1

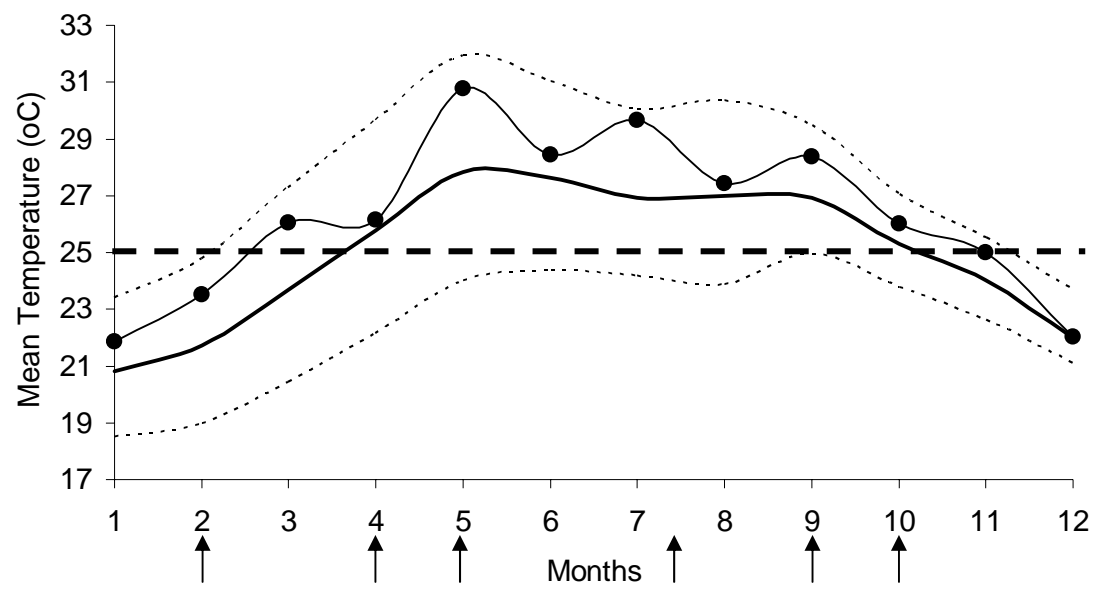


Fig 1.

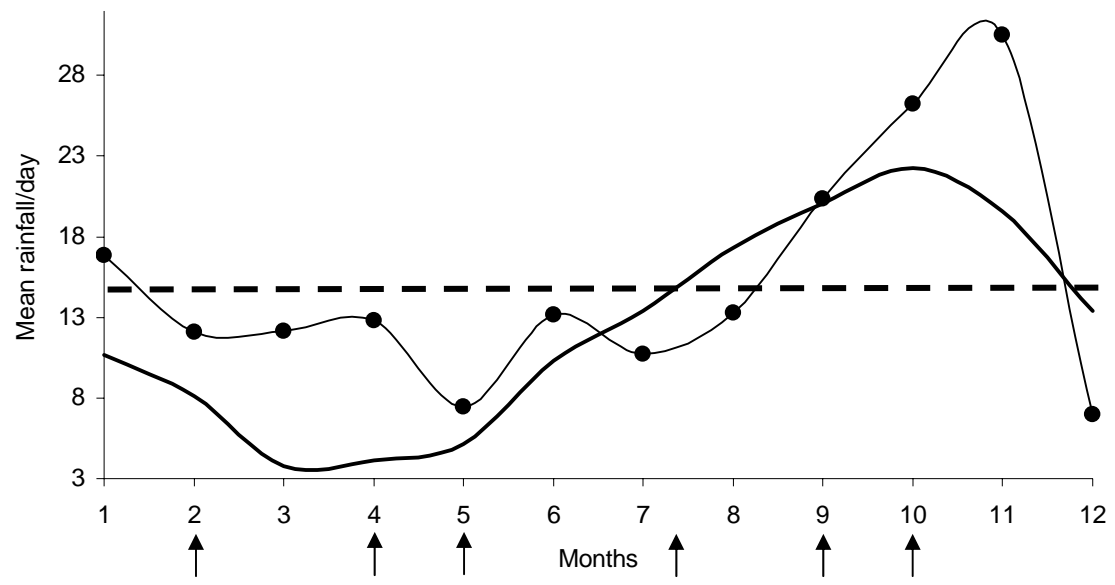


Fig 2.

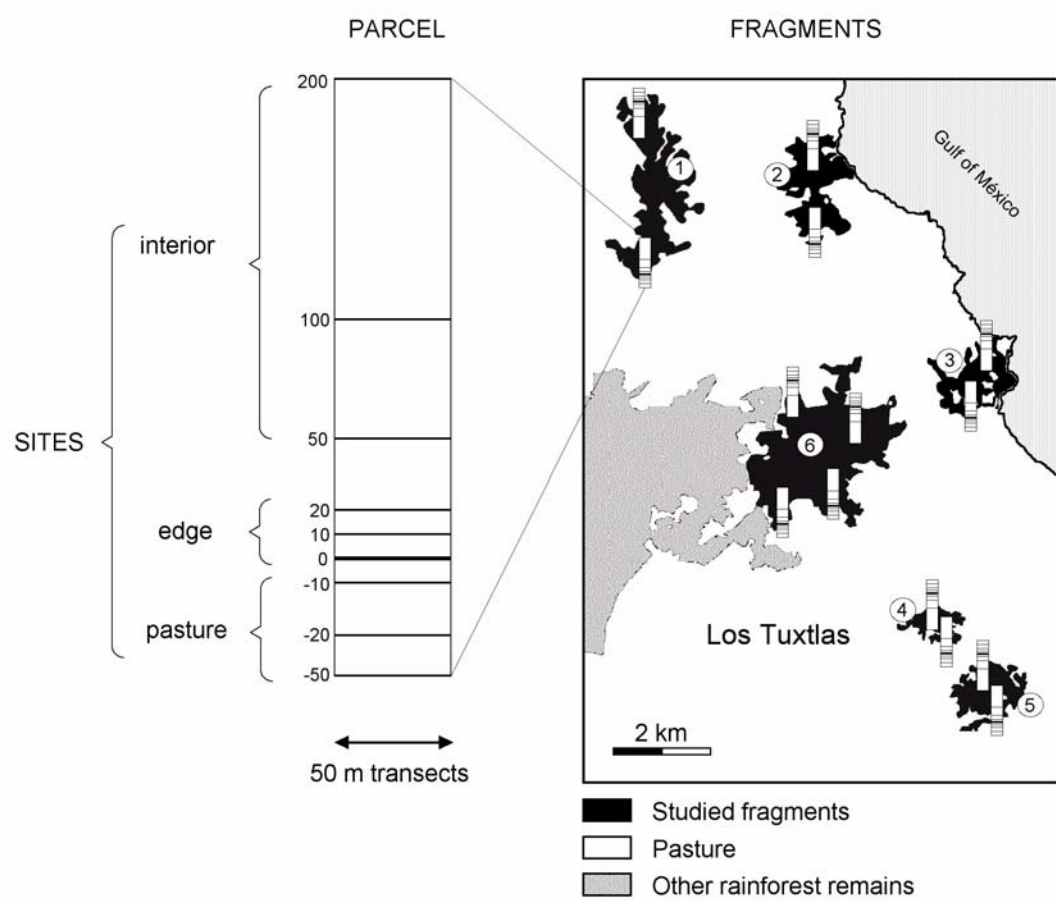


Fig 3.

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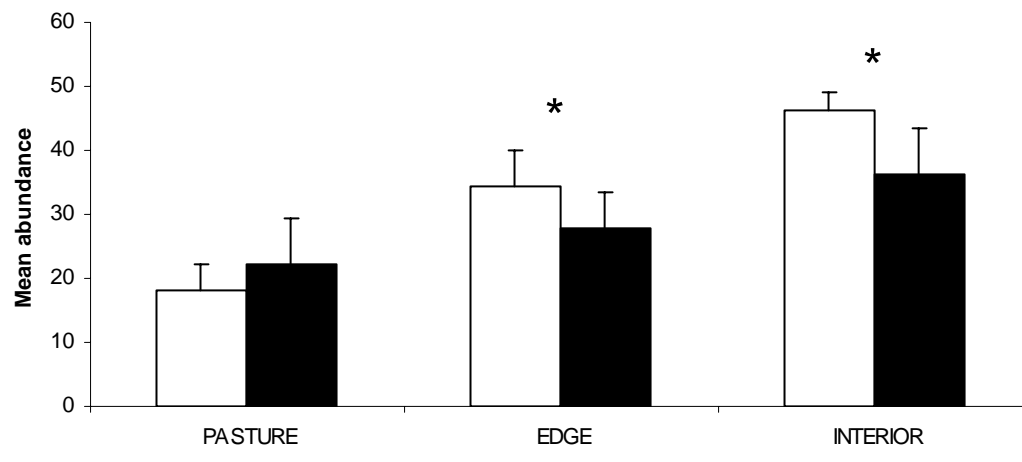


Fig 4.

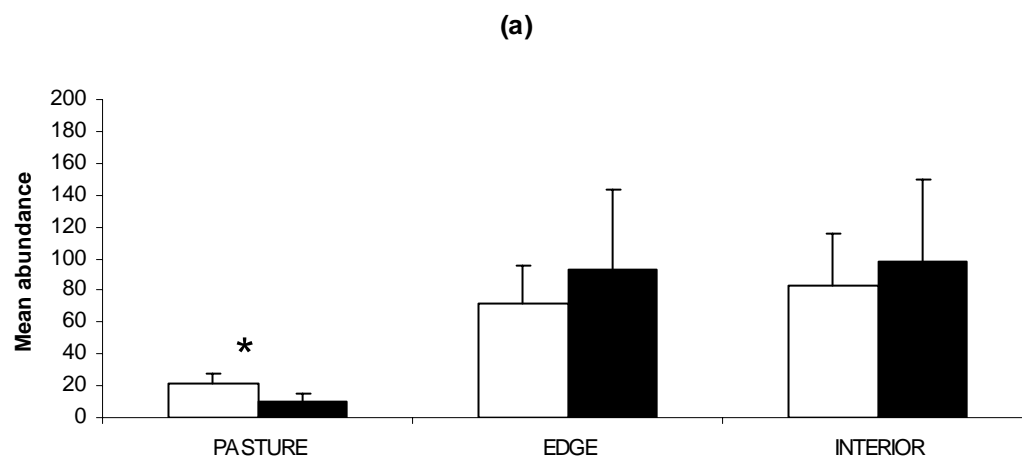


Fig 5a.

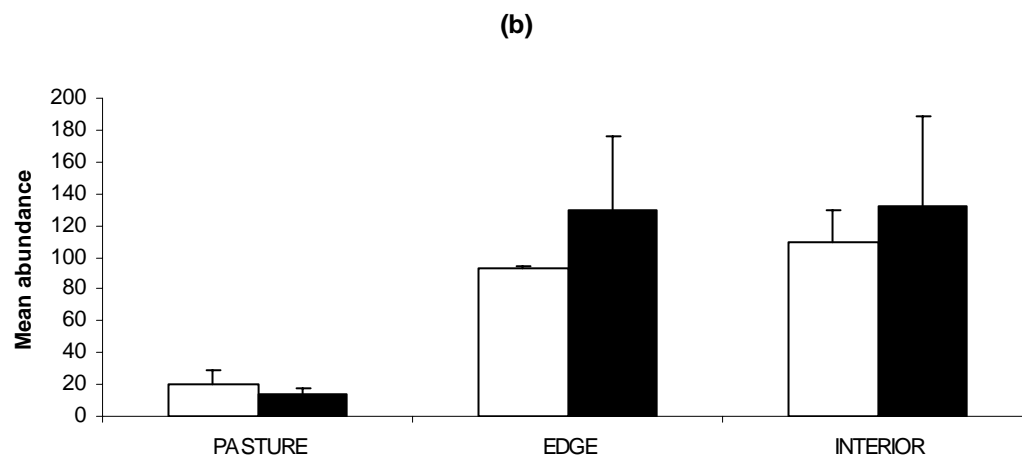


Fig 5b.

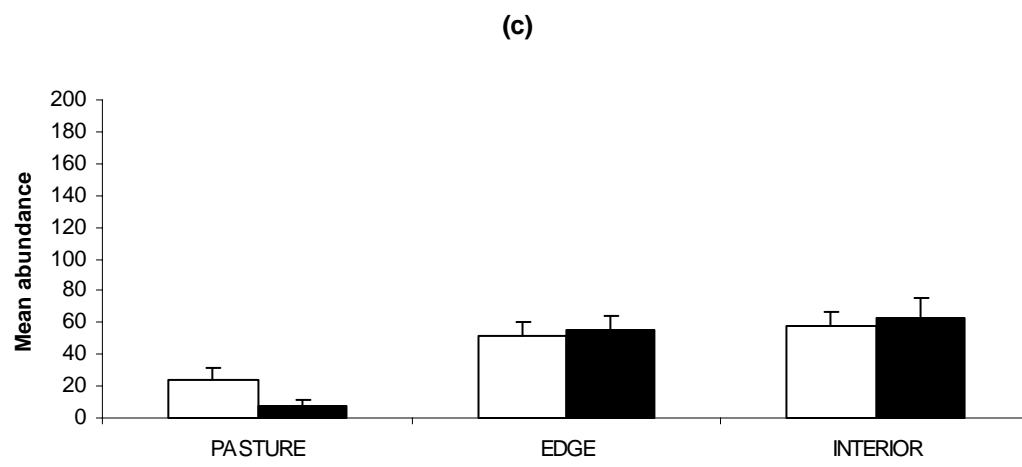


Fig 5c.

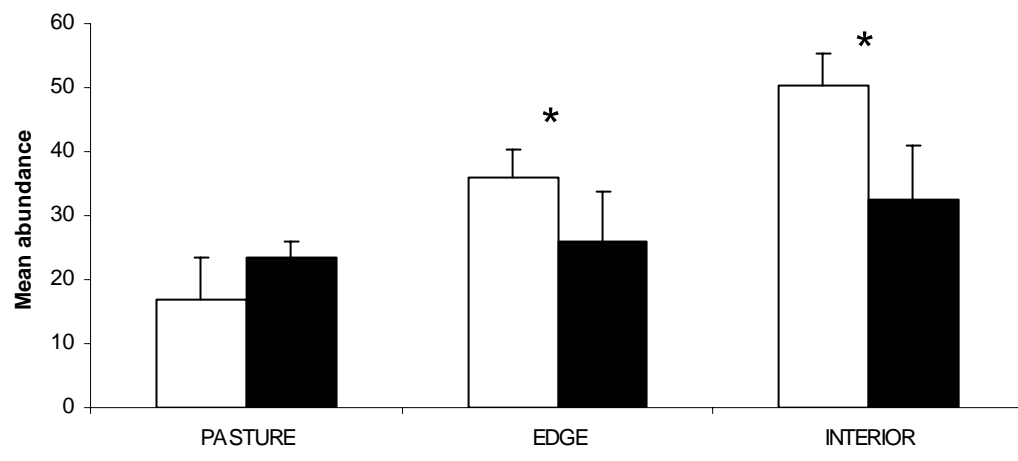


Fig 6.

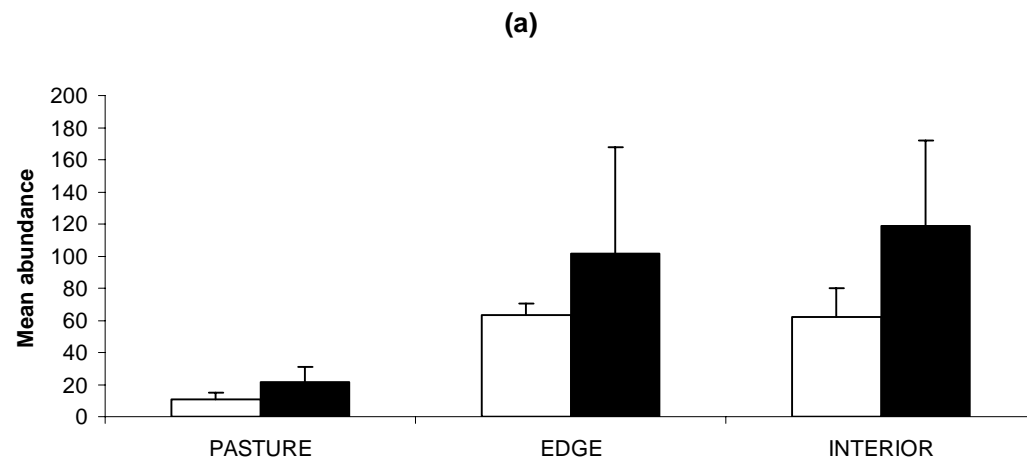


Fig 7a.

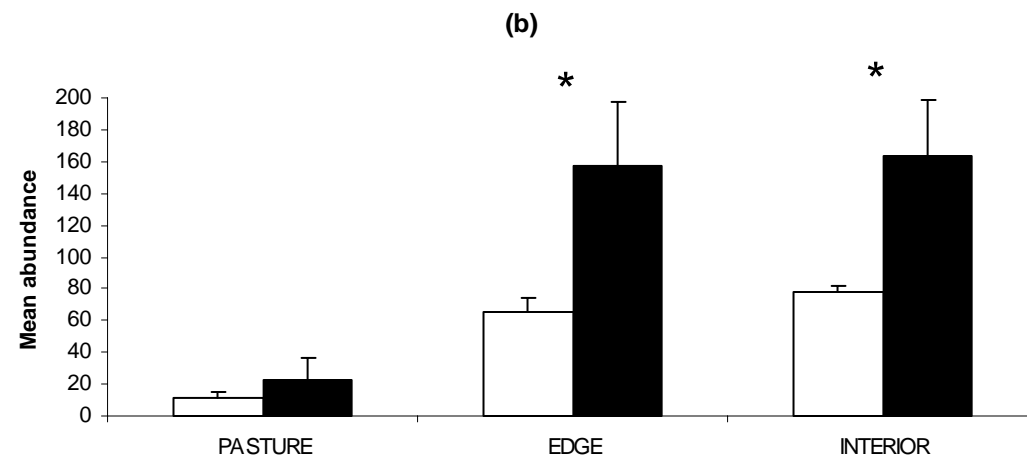


Fig 7b.

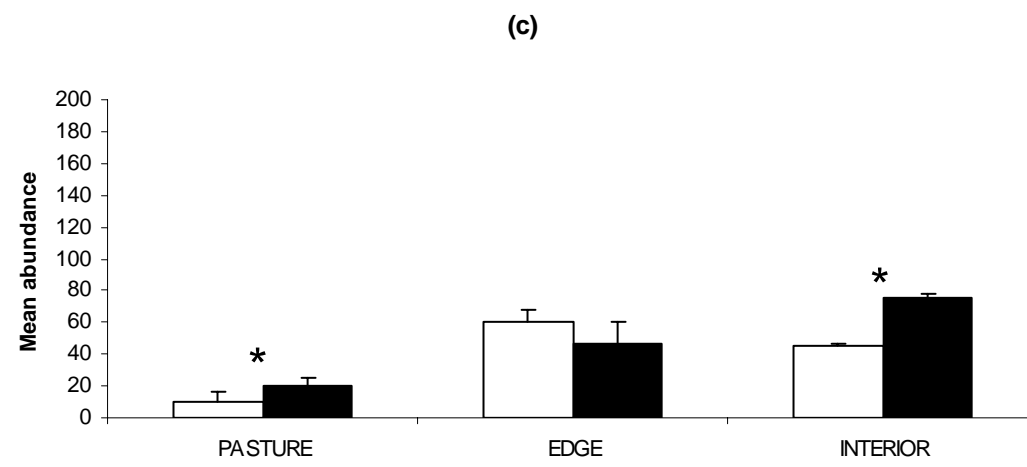


Fig 7c.

Table 1. Results of ANOVA for the effects of seasonality (cold and hot seasons), habitat, orientation and combinations on the abundance of reptiles and amphibians. Bold types indicates that the effect is significant ($P < 0.05$).

Effect	Reptiles			Amphibians		
	d.f.	F	P	d.f.	F	P
Model	11	10.09	<0.0001	11	27.66	<0.0001
Seasonality	1	4.88	0.0368	1	1.02	0.321
Habitat	2	44.44	<0.0001	2	120.39	<0.0001
Orientation	1	3.95	0.0584	1	34.51	<0.0001
Seasonality*Habitat	2	5.53	0.0106	2	7.93	0.0023
Seasonality*Orientation	1	0.23	0.63	1	2.89	0.1019
Habitat*Orientation	2	0.06	0.9362	2	3.78	0.0373
Seasonality*Habitat*Orientation	2	0.91	0.4124	2	0.85	0.4368
Error	24			24		

Table 2. Results of ANOVA for the effects of seasonality (dry and wet seasons), habitat, orientation and combinations on the abundance of reptiles and amphibians. Bold types indicates that the effect is significant ($P < 0.05$).

Effect	Reptiles			Amphibians		
	d.f.	F	P	d.f.	F	P
Model	11	9.29	<0.0001	11	35.72	<0.0001
Seasonality	1	8.618	0.0072	1	40.02	<0.0001
Habitat	2	32.84	<0.0001	2	131.88	<0.0001
Orientation	1	3.15	0.0882	1	44.02	<0.0001
Seasonality*Habitat	2	11.2	0.0004	2	1.65	0.2124
Seasonality*Orientation	1	1.38	0.2507	1	11.94	0.0021
Habitat*Orientation	2	0.14	0.868	2	7.94	0.0022
Seasonality*Habitat*Orientation	2	0.32	0.7278	2	6.99	0.004
Error	24			24		

**FROGS AND LIZARDS INHABITING FORESTS AND PASTURES IN A HIGHLY
FRAGMENTED TROPICAL LANDSCAPE: AN INFORMATION-THEORETIC
APPROACH**

José Nicolás Urbina-Cardona¹, Leonardo Chapa-Vargas² and Víctor Hugo Reynoso*¹

¹ Colección Nacional de Anfibios y Reptiles, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México. C.P. 04510 México, DF, México.

² Instituto Potosino de Investigación Científica y Tecnológica A.C. División de Ingeniería Ambiental y Manejo de Recursos Naturales. Camino a la Presa San José 2055 Lomas 4^a Sección, CP 78216 San Luis Potosí SLP MEXICO.

* Corresponding author. Telephone +52 (55) 5622 8222- Ext. 47865. Fax: +52 (55) 5550 0164. *E-mail address:* vrey noso@ibiologia.unam.mx (V.H. Reynoso)

Key words: Frogs and lizards, vegetation structure, landscape composition, forest isolation, fragmentation, habitat loss, edge effect, Akaike's information criterion

Abstract: Recent herpetological studies have demonstrated that at least some populations and communities respond to environmental factors ranging from topography to habitat fragmentation, as well as to more traditionally measured microhabitat and microclimatic variables. The effects of multiple factors, however, have not been studied simultaneously. We used information-theoretic approaches to simultaneously evaluate the relative influences of topography, vegetation structure, landscape composition within habitat types, distance from different edge types, habitat loss, and habitat isolation on the occurrence of one lizard and one frog species that use pastures primarily but enter the forest occasionally, as well as two frogs and one lizard that use the forest habitat. We sampled six forest fragments that ranged in area from 27 ha to 472 ha at a highly fragmented landscape at the “Los Tuxtlas” tropical moist forest in central Veracruz, Mexico. Our sampling design included eighteen plots that contained pasture, secondary forest, forest edge, and forest interior. Within each of these plots we established several transects (three in each habitat type) located at increasing distances from and parallel to the forest edge. We recorded occurrence of our study species within each of these transects. There was a great deal of variation among species on their responses to the variables that we measured, suggesting that sound management approaches will only be those that simultaneously address the needs of multiple species. In general, our results suggested that probabilities of occurrence of pasture species increased with increasing distance from the nearest forest fragment, probabilities of occurrence of forest species increased with increasing canopy cover, understory density, and percentages of forest within 10-m of our transects, and probabilities of occurrence of the most abundant species were unrelated to any of the variables that we measured. Our results showed that variables at the scales that we studied may act in combination with the already documented effects of microhabitat and microclimate at least on some of the species that we studied.

INTRODUCTION

Studies of environmental factors and their effects on amphibian and reptile species abundance and distribution constitute robust tools for the conservation and management of these species in tropical fragmented forests (Pineda and Halffter 2004, Urbina-Cardona et al. 2006). One kind of habitat fragmentation is the transformation of a large expanse of original contiguous habitat into a number of smaller patches (Wilcove et al. 1986). The remaining patches have smaller total areas, and are isolated from each other by a matrix that consists of habitats other than the original. Habitat fragmentation has the potential to create large changes on the physical environment, which in turn may dramatically influence the biota within remnant forests, especially near boundaries between forest patches and the surrounding matrix (Saunders et al. 1991, Murcia 1995, Urbina-Cardona et al. 2006). The effects of habitat modification on species diversity are heavily scale-dependent (Hamer and Hill 2000, Stoddard and Hayes 2005). Habitat fragmentation and its effects may also act at different scales and may create increased distance from edges, habitat loss, patch isolation, and changes on landscape configuration (Saunders et al. 1991, Hammer and Hill 2000, Fahrig 2003, Guevara et al. 2004b). In addition to the effects of habitat fragmentation, environmental variables that act at other spatial scales also influence populations of some organisms such as amphibians (e.g., Mazerole et al. 2005, Stoddard and Hayes 2005, Van Buskirk 2005) due to the ecophysiological needs of these organisms and the idiosyncrasies of their life cycles. Traditionally measuring habitat associations of species at different scales on fragmented landscapes has been logistically and conceptually difficult (Fahrig 2003). Recent studies, however, have successfully applied information-theoretic approaches (reviewed by Burnham and Anderson 2002, Johnson and Omland 2004) to these types of situations (e.g., Weyrauch and Grubb 2004, Welch and Mac Mahon 2005). These techniques allow researchers to simultaneously test several biological meaningful *a priori* hypotheses related to the effects of independent factors such as topography, vegetation structure, landscape composition of habitat types, edge effects, and habitat loss and isolation on response variables related to species occurrence, abundance, and population demographics. These approaches also allow researchers to explore multiple associations among independent factors and identify hypotheses that receive the most support from the data for different species. Information-theoretic approaches also enable scientists to identify interactions among different factors that confound true effects on focal species, or detect co-varying factors that simultaneously influence organisms in special ways.

Species composition, richness, and structure of tropical and temperate amphibian and reptile communities have been found to vary through, and to be influenced by gradients in **topography** (Pearman 1997, Pineda and Halffter 2004, Jellinek et al. 2004, Funk et al. 2005, Urbina-Cardona et al 2006), **vegetation structure** (Ildos and Ancona 1994, Pearman 1997, deMaynadier and Hunter 1998, Urbina-Cardona and Pérez-Torres 2002, Urbina-C and Londoño-M 2003, Jellinek et al. 2004, Parris 2004, Pineda and Halffter 2004, Bragg et al. 2005, Mazerolle et al. 2005, Welch and MacMahon 2005, Urbina-Cardona et al. 2006), **landscape composition** (Burbrink et al. 1998, Gibbs 1998a, Conroy 1999, de Lima and Gascon 1999, Gascon et al. 1999, Knutson et al. 1999, Greenberg 2001, Weyrauch and Grubb 2003, Willson and Dorcas 2003, Jellinek et al. 2004, Neckel-Oliveira 2004, Parris 2004, Mazerolle et al. 2005), **distances from edges** (Gambold and Woinarski 1993, Gascon 1993, Marsh and Pearman 1997, Pearman 1997, deMaynadier and Hunter 1998, Osorno 1999, Schlaepfer and Gavin 2001, Toral et al. 2002, Lehtinen et al. 2003, Mazerolle 2003, Weyrauch and Grubb 2003, Bragg et al. 2005, Urbina-Cardona et al. 2006), **habitat loss** (Gambold and Woinarski 1993, Marsh and Pearman 1997, Tocher et al. 1997, Schlaepfer and Gavin 2001, Weyrauch and Grubb 2003, Pineda and Halffter 2004), and **isolation** (Vos and Stumpel 1995, Marsh and Pearman 1997, Gibbs 1998a, Tocher et al. 2001, Weyrauch and Grubb 2003, Pineda and Halffter 2004).

Studies that investigated the effects of some variables related to habitat fragmentation on amphibian and reptile species have revealed inconsistent results for different species and habitats probably because of differences in disturbance regimes and management plans (Murcia 1995, Toral et al. 2002). Edge effects on amphibian and reptile species may vary in strength among land use types (deMaynadier and Hunter 1998, Gascon et al. 1999, Toral et al. 2002), and could be more influential for lowland (Gascon 1993, Pearman 1997, but see Jellinek et al. 2004) than highland species (Marsh and Pearman 1997, Osorno 1999, Toral et al. 2002, Urbina-Cardona *unpublished data*). Some studies suggest that large fragments support larger amphibian species richness and abundance than small fragments, and amphibian communities in small fragments consist mainly of species typical of the matrix habitat (Culotta 1995, Marsh and Pearman 1997, Tocher et al. 1997, Pineda and Halffter 2004). Other studies, however, showed that fragment size did not influence amphibian and reptile richness and abundance (Gambold and Woinarski 1993, Schlaepfer and Gavin 2001). Concerning landscape connectivity, Tocher and collaborators (2001) found that numbers of species of amphibians that reproduce in water were independent of distance from nearest fragment, whereas Marsh and Pearman (1997) found that distance effects depend on species

vagility (ability to move large distances). In conclusion, some amphibian and reptile species tolerate induced grasslands, have great dispersal abilities, and apparently tolerate habitat fragmentation to some extent, whereas others are more vulnerable (Gibbs 1998a, Gascon et al. 1999, Lehtinen et al. 2003).

Some researchers have recorded significant negative correlations of amphibian and reptile diversity with slope probably because at steep slopes, landslides remove vegetation (Geissert 2004), and positive correlations with altitude (Urbina-Cardona et al. 2006). In addition, differences in amphibian species composition and exchange increase with increasing differences in altitude (Pineda and Halffter 2004), but genetic variation within frog populations decrease (Funk et al. 2005a).

Vegetation structure (e.g., canopy cover and understory density) may also positively influence total amphibian and reptile species richness and distribution (e.g., Pearman 1997, deMaynadier and Hunter 1998, Urbina-C and Londoño-M 2003, Pineda and Halffter 2004, Urbina-Cardona et al. 2006) but could negatively influence density and richness of some species from open habitats (e.g., pasture or sand dunes) that depend on heat to thermoregulate (Conroy 1999, Bragg et al. 2005, Urbina-Cardona et al. 2006). In addition, because within habitat types there is also some heterogeneity caused by elements such as canopy openings, streams, bodies of water, etc, landscape composition within habitat types could also influence herpetofauna in different ways; it may constitute a barrier to dispersal through direct mortality (e.g., roads; Fahrig et al 1995, Ashley and Robinson 1996, Gibbs 1998b, Lehtinen et al. 1999, Hels and Buchwald 2001), negatively influence reptile richness in habitats with exotic plant species (Jellinek et al. 2004), facilitate recolonization and genetic exchange on secondary regrowth portions of forests (Burbrink et al. 1998, de Lima and Gascon 1999, Gascon et al. 1999, Knutson et al. 1999, Neckel-Oliveira 2004), influence negatively relative abundance of salamanders on watersheds with disturbed habitats (Willson and Dorcas 2003), generate increases on reptile abundance and richness on canopy gaps (Sartorius et al. 1999, Greenberg 2001), and increase amphibian and reptile species richness due to local habitat heterogeneity (Burbrink et al. 1998, Sartorius et al. 1999).

The relative and simultaneous influences of all these factors on frog and lizard occurrence, however, have not been previously evaluated. Because the effects of habitat transformations on species diversity vary with spatial scale (Hamer and Hill, 2000), the mechanisms that determine frog and lizard occurrence at Los Tuxtlas are predicted to vary with factors at broad spatial scales. These organisms have poor dispersal capabilities, are limited by physiological constraints due to thermal requirements, have different

ecophysiological responses to small scale environmental changes (Zug 2001, Weyrauch and Grubb 2003), have different microhabitat requirements, and respond in different ways to edge effects (Urbina-Cardona et al. 2006). Lizards have a scaled skin that protects their body from environmental conditions and require the direct sun light to maintain their body temperatures at a level that allows them to accomplish their physiological requirements (Zug 2001). Frogs, on the other hand, have a permeable skin and a variety of reproductive modes that influence their microhabitat use (Crump 1974).

For each vertebrate group we chose the most abundant species of the ensemble. Two species, the Rio Grande leopard frog (*Rana berlandieri*) and rosebelly lizard (*Sceloporus variabilis*), use the pasture and enter occasionally into the forest. The remaining species: lesser scaly anole (*Anolis uniformis*), polymorphic robber frog (*Eleutherodactylus rhodopis*) and Golf coast frog (*Bufo valliceps*), use the forest habitat preferentially (Urbina-Cardona et al. 2006). For Los Tuxtlas region, studies have previously reported relationships within tropical evergreen forest for these frog and lizard species (Urbina-Cardona and Reynoso 2006) at the microhabitat scale (e.g., temperature, relative humidity, leaf litter cover and depth, and herbaceous cover) but not at larger scales. Our approach allowed us to propose conservation actions that may help local persistence of the herpetofauna of a highly fragmented landscape at Los Tuxtlas tropical forest, southern Veracruz state, Mexico. Our objective was to test if incorporating factors at large spatial scales could add information to the already documented effects of microhabitat variables on the presence of lizard and reptile species at Los Tuxtlas fragmented landscape (Urbina-Cardona and Reynoso 2006). We used a small-sample bias-corrected version of Akaike's information criterion (*AICc*) and Akaike weights (w_i) to evaluate support for several candidate *a priori* hypotheses related to the influences of factors on the occurrence of two lizard and three frog species. Our *a priori* hypotheses included effects of 1) topography, 2) vegetation structure, 3) landscape composition within habitat types, 4) distances from edge types, 5) habitat loss, 6) isolation, and combinations of vegetation structure, landscape composition within habitat types, distance from edge types, habitat loss, and isolation. A test of these hypotheses is relevant for a tropical fragmented forest in which the combination of several factors such as isolation and habitat loss (Guevara et al. 2004b, Mendoza et al. 2005), several transitions on habitat heterogeneity (Williams-Linera et al. 1998, Guevara et al. 2004a) and large elevation gradients (Geissert 2004) complicate the analysis of factors associated to presence and absence of particular organisms.

METHODS

Study area and sampling design

From June 2003 through May 2005 we recorded presence and absence of two lizard (rosebelly lizard - *Sceloporus variabilis*, and lesser scaly anole - *Anolis uniformis*) and three frog species (Rio Grande leopard frog - *Rana berlandieri*, polymorphic robber frog - *Eleutherodactylus rhodopis*, and Golf coast frog - *Bufo valliceps*) on 162 linear transects at the Los Tuxtlas tropical rainforest reserve and adjacent areas (18°32'N, 95°6'W). Mean annual temperature at Los Tuxtlas is ≥ 22 °C and annual precipitation fluctuates from ≤ 60 mm to 4959 mm with marked wet and dry seasons (wet from June to February, and dry from March to May) (Soto 2004).

Los Tuxtlas is located in southern Veracruz, Mexico, along the Mexican Gulf coastal plain (Geissert 2004). Altitude at Los Tuxtlas ranges from sea level to 900 m (Geissert 2004, Laborde 2004). The region has been occupied by humans since 2000 B.C. Through this time human population density fluctuations have generated dramatic deforestation (Laborde 2004), which transformed 84 % of the original tropical rain forest into pasture (Dirzo and García 1992), the current dominant land use type (Guevara et al 2004b, Laborde 2004). Los Tuxtlas is the northernmost limit of the distribution of the tropical rainforest in the entire continent (Dirzo and Miranda 1991, Vázquez et al. 2004). According to these authors the larger forest fragments showed a clear deviation from ideal circular shapes and fragment size decreased with increasing distance from the largest forest tract, resulting on considerable fragmentation and isolation. The region currently consists of a mosaic landscape composed of primary forest fragments (e.g., tropical evergreen forest, also known as “selva alta perennifolia”) interspersed with several habitat types which include internal canopy openings, secondary forest, riparian vegetation along rivers, lakes and streams, cultivated tree areas (with *Citrus* spp., *Psidium guajava* and *Byrsonima crassifolia*), live fences (*Bursera simaruba*, *Gliricidia sepium* and *Erythrina folkersii*), and isolated trees immersed in a larger pasture matrix with native (*Paspalum conjugatum*, *Axonopus compressus*, *Setaria geniculata*, *Panicum* spp. and *Digitaria* spp.) and cultivated (*Cynodon plectostachyus* and *Panicum maximum*) grasses, and dissected by additional anthropogenic elements that include roads, farms, and villages (Ibarra-Manríquez et al., 1997, Guevara et al. 2004a). This habitat heterogeneity led us to test our hypothesis concerning topography, vegetation structure, landscape composition within habitat types, distance from edges, habitat loss and isolation, and their effects on the presence of two lizard and three frog species.

Our study sites included six forest fragments surrounded by pasture that ranged in area from 27 ha to 472 ha. Within these fragments we established fourteen 50 X 250 m plots that included three habitat types: pasture, forest edge, and forest interior. In our largest fragment, four additional plots containing secondary forest, forest edge, and forest interior sites were also established (Ecological Archives Supplement). Within each plot, we set several 50-m transects (three on each habitat type: pasture, secondary forest, forest edge and forest interior) located at standard distances from, and parallel to the rainforest edge (Fig 1). In all, our design accounts for 18 land plots containing 162 transects for the entire study. A detailed description of the criteria for fragment selection, research design, survey techniques and microhabitat measurement methods is provided by Urbina-Cardona and collaborators (2006).

Frog and lizard survey

The study area was visited on six occasions: June-July and September-October 2003, February-March, May and September 2004, and April 2005. During each visit, all permanent transects were surveyed two times by two observers during six hours (three hours at day and three hours at night) for a total effort of 1296 man-hours. Sampling was restricted to the understory, recording all visual encounters of frogs and lizards found within one meter on both sides of the transect and up to two meters in height.

Vegetation structure and topography characteristics

Several environmental variables were measured on each of the 162 transects; slope and altitude (height above the sea level) were measured with a clinometer and altimeter respectively by averaging the values obtained at three random points along each transect. Canopy cover was obtained by analyzing pictures taken with a 180° hemispherical lens in a camera during high luminosity days. For these measurements we placed the camera at a height of 0.5 m and used a diaphragm aperture of f 11, an obturation speed of 1/125, and ASA 100 film. The negatives were scanned, and the percentage of canopy cover was calculated with the Winphot 5 software (Ter Steege, 1996) as an average value obtained from two pictures randomly located on each transect. Relative understory density was obtained by averaging the number of contacts of the vegetation (branches, stumps, and leafs) with a 3.5 cm diameter and 2 m high stick, placed perpendicular to the ground at five random places within the transect. The distance to nearest flowing stream was measured with a Geographic Global Positioning System (GPS, Table 1).

Habitat loss and isolation

A Landsat-7 image (pixel size of 30 x 30 m) from 2000 and digital georeferenced aerial photos (2003 year) with pixel sizes of 1.5 x 1.5m were used to identify different

habitats in our study area. The outer borders of forest sites could be easily distinguished on both the Landsat image and on aerial photos as the borders between the forest and the external agricultural matrix. We displayed the Landsat images and aerial photos using ArcView 3.3 (Environmental Systems Research Institute, ESRI 2002) and digitized a polygon for each forest fragment. Inner polygons were created for each study site by generating internal buffers of 30 m using ArcInfo 8.1 (ESRI 2001), these buffers represented edge habitats. We used 30 m as our buffer distance because previous studies at Los Tuxtlas suggest that edge effects on microclimatic conditions and vegetation structure go as far as 30 m into the forest interior (Williams-Linera 1998, Mendoza *et al.* 2005).

Using ArcView 3.3 (ESRI 2002) we calculated for each of our study forest fragments: area, perimeter, mean distance from the nearest four fragments, area of the 30 m edge, and area of forest interior (> 30 m from the external edge). Then we used these measures to calculate shape, percentage of edge, and percentage of forest interior (>30 m from edge). Shape was calculated using the Patton's Diversity Index (Patton, 1975) as $sh = P / 2\sqrt{\pi A}$ where P is the perimeter of the fragment, and A is the area. Shape equals one when the site is a perfect circle, and its value increases as the perimeter increases in relation to area.

Distance from different edge types

We used a Geographic Information System (GIS, Arc View Version 3.3, ESRI 2002), the Arc View extension "Nearest features, v3.7a" (Jenness 2004), and previously digitized maps of transect locations (see above), to measure the distance of each transect from the nearest sea, lake, and road.

Landscape composition within habitat types

We used a GIS-based technique to measure landscape composition within habitat types (e.g., Chapa and Robinson 2006). Habitat and disturbance types within study sites were digitized for each transect. Habitats were grouped into two main habitat types (forest for forest – inhabiting species, and pasture for pasture – inhabiting species). We also identified adjacent habitats (pasture for forest – inhabiting species, and forest for pasture – inhabiting species), natural disturbances (river), anthropogenic disturbances (roads), within-pasture disturbances (live fences and/or isolated trees), and within-forest disturbances (secondary forest and canopy openings). The main habitat and disturbance categories that we used could be easily discriminated on digital aerial photos because they have different textures and grey

tones. Using these categories of habitats and disturbances is unlikely to reduce our ability to detect statistical significance because habitats that were grouped in the same category were structurally similar (J.N.U-C pers. obs.). Therefore, their influences on amphibian and reptile occurrence are similar.

Using a GIS (ArcInfo 8.1, ESRI 2001), we built 10m radius buffers centered on each transect location. We used these buffers to clip the previously digitized habitat map. Finally, within these clipped habitat maps we measured percentages of main habitats, and presence/absence of each type of disturbance. We used presence/absence of different types of disturbances because using percentages of these habitat types within 10-m of transects would generate a large number of zeros on our data matrix, and would greatly reduce our ability to detect effects of these disturbances. We used the 10m radius because lizard and frog species have low vagilities (i.e., they do not move large distances from their microhabitat).

Statistical analyses

We used logistic regression to analyze the presence/absence of each focal species as our response variables. Using regression analysis with abundances for each transect as a response variable instead, would generate a large number of zeros and would greatly reduce our ability to statistically detect any trends. In addition, not using abundances is more appropriate because the species that we studied show aggregated distribution patterns, therefore they are abundant in their microhabitats when present. We used PROC LOGISTIC in SAS 8.0 (SAS institute, 1999 Cary, North Carolina) to fit several competing logistic regression models (see Appendices A and B) to evaluate the effects of factors related to topography, vegetation structure, landscape composition within habitat types, distances from different edge types, habitat loss patterns, and isolation on the occurrence of two lizard and three frog species. We verified the fit of our global model (see below) with Hosmer and Lemeshow's (2000) goodness-of-fit test.

We used a small sample bias-corrected version of Akaike's information criterion (AIC_c) and Akaike weights (w_i , e.g., Burnham and Anderson 2002, 2004) to evaluate the support for competing *a priori* models about several factors influencing occurrence of three frog and two lizard species. Our set of *a priori* hypotheses were that the occurrence of the Rio Grande leopard frog (*Rana berlandieri*), rosebelly lizard (*Sceloporus variabilis*), lesser scaly anole (*Anolis uniformis*), polymorphic robber frog (*Eleutherodactylus rhodopis*), and Gulf coast frog (*Bufo valliceps*) at Los Tuxtlas region, Veracruz, Mexico, are influenced by effects of: 1) topography, 2) vegetation structure, 3) landscape composition within habitat

types, 4) distance from edge types (water bodies and anthropogenic edge), 5) habitat loss patterns, 6) isolation, and combinations of vegetation structure, landscape composition within habitat types, distance from edge types, and habitat loss and isolation. For pasture affine species there were a total of 9 competing hypotheses (candidate models) and for forest affine species there were 17 hypotheses because of higher complexity of vegetation structure and combinations with other factors (see Appendices A and B for a full description of explanatory variables on models representing each of our *a priori* hypotheses).

Our criteria to include variables in models of our *a priori* hypotheses included; knowledge of the effects of these factors at Los Tuxtlas on lizard and frog abundance from previous studies (Urbina-Cardona and Reynoso 2005, Urbina-Cardona and Reynoso 2006, Urbina-Cardona et al. 2006), that suggested that slope, altitude, canopy cover, understory density, distance from forest edge, and distance from streams might influence presence of lizards and frogs in their microhabitats. In addition, for each lizard and frog species we built a global model with all parameters that was used to assess model fit (e.g., Burnham and Anderson 2002, 2004), and a null model with only an intercept estimated iteratively by the method of maximum likelihood in SAS using data of lizard and frog occurrence from the entire data set. This model was used to determine if a constant presence model would receive more support from the data than one including any of the remaining variables. We used Akaike's information criterion (Burnham and Anderson 2002, 2004) to rank models from most to least supported given the data on the basis of Akaike differences (ΔAIC = the difference in $AICc$ between the model with the smallest $AICc$ value and the current model) and Akaike weights (w_i). We only provide interpretation for models that had ≤ 2 ΔAIC units distance from the best – supported model (e.g., Burnham and Anderson 2002, 2004). Following Burnham and Anderson's (2002, 2004) recommendation, we used a small sample version of Akaike's Information Criterion because the number of K parameters in our global model (14 for pasture focal species and 17 for forest focal species) was larger than the sample size divided by 40 ($162/40 = 4.05$). Akaike weights (w_i) are measures of support for each model based on ΔAIC that add to 1 across all models. These values provide direct interpretation of the relative likelihood of a model given the data and the set of candidate models; a given w_i is considered as the weight of evidence in favor of its corresponding model. To account for model-selection uncertainty, we calculated model-averaged weighted parameter estimates and their associated standard errors using w_i as weights as suggested by Burnham and Anderson (2002, 2004). Finally, we used these weighted parameter estimates

and standard errors to calculate odd-ratios (OR) and their associated 95 % confidence intervals (CI). Odd-ratios provide a direct interpretation (e.g., Hosmer and Lemeshow 2000). For instance, for categorical independent variables an OR > 1 for a given category would indicate that presence of a given species was more likely than for the comparison category. For numerical independent variables, an OR > 1 would indicate that the probability of occurrence would decrease with increasing values of the independent variable, whereas an OR < 1 would indicate that the probability of occurrence would decrease with decreasing values of the independent variable. We interpreted only OR's whose CI's did not include 1 (e.g., Peak et al 2004).

RESULTS

We monitored occurrence of two lizard and three frog species along 162 transects (42 in pasture, 12 in secondary forest, 54 in forest edge and 54 in forest interior). Overall we recorded 4333 individuals. The rosebelly lizard occurred on 58 transects for a total of 260 individuals, the Rio Grande leopard frog was present on 21 transects for a total of 92 individuals, the lesser scaly anole occurred on 110 transects for a total of 762 individuals, the polymorphic robber frog occurred on 128 transects for a total of 2270 individuals, and the Golf coast frog occurred on 37 transects for a total of 86 individuals.

Rosebelly lizard - Hosmer and Lemeshow (2000) goodness-of fit test indicated that the global model fit the observed values ($X^2 = 1.081$; $df = 8$; $P = 0.9977$). Our landscape composition within habitat types, distance effects, and isolation hypothesis received the most support from the data (LAND_COMP_DIST_EF_ISOL; Table 1). The best-fitting model (estimated standard errors are shown in parentheses below parameter estimates, predictor variables codes as in Appendix A) was as follows (coefficients for dichotomic variables represent absence of the focal element, whereas presence of the focal element is the comparison category, coefficients and standard errors for the categorical variable “de” , distance categories as in Table 2, are $de1 = 3.7 / 29.28$; $de2 = 5.03 / 29.28$; $de3 = 4.04 / 29.27$; $de4 = 1.94 / 29.26$; $de5 = -1.22 / 29.27$; $de6 = -12.2 / 234$; $de7 = -1.1 / 29.27$; $de8 = -0.08 / 29.7$; $de9 = 0 / 0$):

$$\text{Log}(Sv/[1-Sv]) = -3.35 + 0.02 \times ht + 0.87 \times ah - 0.88 \times nd + 0.21 \times ad - 0.54 \times wfd$$

(29.35) (0.021) (0.66) (0.81) (0.75) (0.68)

$$- 0.03 \times wpd + de - 0.0004 \times ds + 0.0036 \times dr - 0.0006 \times dl - 0.0003 \times dro + 0.002 \times dnf$$

(0.53) (0.0003) (0.0017) (0.0006) (0.0016) (0.0014)

Our landscape composition within habitat types and distance effects hypothesis (LAND_COMP_DIST_EF), and landscape composition within habitat types and isolation hypothesis (LAND_COMP_ISOL) also received some support from the data (Table 1). Odd ratios and confidence intervals suggested that probabilities of presence of this species increased, but only slightly, with mean distance from four nearest forest fragments (dnf). Confidence intervals on odd ratios for all other variables overlapped one (Table 2, Figure 2).

Rio Grande leopard frog - Hosmer and Lemeshow (2000) goodness-of fit test indicated that the global model fit the observed values ($X^2= 0.1299$; $df = 7$; $P = 0.2851$). Our distance effects hypothesis received the most support from the data (DIST_EF; Table 1). The best-fitting model (estimated standard errors are shown in parentheses below parameter estimates, predictor variables codes as in Appendix A) was as follows (coefficients for dichotomic variables represent absence of the focal element, whereas presence of the focal element is the comparison category, coefficients and standard errors for the categorical variable “de” are $de1 = 6.51 / 40.9$; $de2 = 5.3 / 40.9$; $de3 = 5.78 / 40.9$; $de4 = 2.46 / 40.91$; $de5 = -8.41 / 189.3$; $de6 = 2.45 / 40.91$; $de7 = -8.4 / 191$; $de8 = 2.51 / 40.91$; $de9 = 0 / 0$):

$$\text{Log}(R_b/[1-R_b]) = -5.26 + de + 0.0004 \times ds + 0.0016 \times dro - 0.0032 \times dr - 0.0016 \times dl$$

(40.93) (0.0004) (0.002) (0.0023) (0.0005)

Our landscape composition within habitat types and distance effects hypothesis (LAND_COMP_DIST_EF), landscape composition within habitat types, distance effects and isolation hypothesis (LAND_COMP_DIST_EF_ISOL, and landscape composition within habitat types and isolation hypothesis (LAND_COMP_ISOL) also received some support from the data (Table 1). Odd ratios on all independent variables, however, suggested that their effects were negligible. Moreover, confidence intervals on odds ratios for these independent variables overlapped one (Table 2).

Lesser scaly anole - Hosmer and Lemeshow (2000) goodness-of fit test indicated that the global model fit the observed values ($X^2= 1.844$; $df = 3$; $P = 0.605$). Our vegetation structure hypothesis received the most support from the data (VEG_STR; Table 3). The best-fitting model (estimated standard errors are shown in parentheses below parameter estimates; predictor variables codes as in Appendix B) was:

$$\text{Log (Au/[1-Au])} = -4.238 + 0.14 \times \%c + 0.364 \times ud$$

$$(1.221) \quad (0.023) \quad (0.125)$$

No additional models received substantial support from the data (Table 3). Odd ratios and confidence intervals suggested that probabilities of presence of this species increased slightly, with percentage of canopy cover (%c) and with understory density (ud, Table 4, Figs. 3a,b). No additional variables had odd ratios whose confidence intervals did not overlap one (Table 4).

Polymorphic robber frog - Hosmer and Lemeshow (2000) goodness-of fit test indicated that the global model fit the observed values ($X^2 = 0.528$; $df = 3$; $P = 0.912$). Our vegetation structure hypothesis received the most support from the data (VEG_STR; Table 3). The best-fitting model (estimated standard errors are shown in parentheses below parameter estimates; predictor variables codes as in Appendix B) was:

$$\text{Log (Er/[1-Er])} = -0.34 + 0.44 \times \%c + 0.12 \times ud$$

$$(0.335) \quad (3.72) \quad (0.064)$$

Our landscape composition within habitat types and isolation hypothesis also received some support from the data (LAND_COMP_ISOL; Table 3). Odd ratios on all independent variables, however, suggested that their effects were negligible. Moreover, confidence intervals on odd ratios for these independent variables overlapped one (Table 4).

Golf coast frog - Hosmer and Lemeshow (2000) goodness-of fit test indicated that the global model fit the observed values ($X^2 = 7.378$; $df = 7$; $P = 0.391$). Our landscape composition within habitat types and isolation hypothesis received the most support from the data (LAND_COMP_ISOL; Table 3). The best-fitting model (estimated standard errors are shown in parentheses below parameter estimates; predictor variables codes as in Appendix B) was:

$$\text{Log (Bv/[1-Bv])} = -0.85 + 0.03 \times ht - 0.23 \times ah - 0.54 \times nd + 0.23 \times wfd + -0.002 \times dnf$$

$$(0.77) \quad (0.01) \quad (0.36) \quad (0.36) \quad (0.284) \quad (0.0005)$$

No additional hypotheses received substantial support from the data compared to our best-supported model. Odd ratios and confidence intervals suggested that probabilities of presence of this species increased, but only slightly, with percentage of forest within ten

meters of transects (ht; Table 4). Confidence intervals on predicted probabilities of occurrence for this species as a response to proportions of forest within ten meters of transects were large (Fig. 4). No additional variables had odd ratios whose confidence intervals did not overlap one (Table 4).

DISCUSSION

In order to determine if lizard and frog occurrence respond to factors at scales larger than the microhabitat scale (e.g., Hamer and Hill, 2000), we tested for the effects of competing hypotheses related to: a) habitat-effects (topography, vegetation structure, and landscape composition within habitat types), b) effects at the patch scale (habitat loss patterns), and c) landscape-scale effects (distance from different edge types and isolation). In addition, to determine if probabilities of species occurrences were influenced simultaneously by different types of effects (i.e., cascade effects, Urbina-Cardona et al. 2006) we tested for combinations of some of our individual hypotheses. Urbina-Cardona et al. (2006) suggested that there may be edge cascade effects based on the observation that there were high correlations of distance to forest edge with temperature, understory density, canopy cover, and leaf litter cover and depth, and a strong relationship between changes on these environmental variables and the composition of amphibian and reptile species.

Our results suggest that at least for some species (*Bufo valliceps* and *Sceloporus variabilis*), factors including topography, vegetation structure, landscape composition within habitat types, distance from different edge types, habitat loss patterns, isolation, and interactions between these factors, did actually add information to effects of microhabitat and microclimate previously reported by Urbina-Cardona and Reynoso (2006). For some other species including *Anolis uniformis*, *Eleutherodactylus rhodopis* and *Rana berlandieri*, however, the factors that we measured had negligible effects. These results illustrate the importance of analyzing the effects of environmental factors on lizard and frog occurrences on a species-by-species basis. These groups of organisms show clear differences in microhabitat use patterns, abilities to face environmental changes, and abilities to use and tolerate the matrix habitat (Urbina-Cardona and Reynoso 2005, Urbina-Cardona et al 2006).

Within the highly fragmented landscape that we studied, patterns of occurrence varied among species depending on the types of habitats that they use. Unfortunately, for the current study we could not incorporate effects of variables related to microhabitats and microclimates because these variables fluctuate greatly within transects (J.N. Urbina-Cardona, Pers. Obs.). Factors at small scales may obscure important species-habitat associations at larger scales (Debinski et al. 2001). A previous study on the same region,

however, suggested that microhabitat and microclimate greatly influence reptile and amphibian assemblages (Urbina-Cardona et al. 2006, a), and reported that from the variables measured, canopy cover, understory density, leaf litter depth, and temperature influenced amphibian and reptile distribution the most. The same authors also reported significant pearson correlation coefficient (r) values for some microhabitat and microclimate variables with variables at larger scales (e.g., distance from edge vs. temperature $r = 0.17$, $p < 0.001$, distance from edge vs. leaf litter cover $r = 0.49$, $p < 0.001$, distance from edge vs. leaf litter depth $r = 0.75$, $p < 0.001$, distance from edge vs. canopy cover $r = 0.58$, $p < 0.001$, distance from edge vs. understory density $r = 0.74$, $p < 0.001$, distance from edge vs. precipitation $r = 0.06$, $p < 0.001$, slope vs. temperature $r = -0.06$, $p < 0.01$, slope vs. relative humidity $r = 0.07$, $p < 0.01$, slope vs. grass cover $r = -0.06$, $p < 0.05$, slope vs. relative humidity $r = 0.07$, $p < 0.01$, and altitude vs. understory density $r = 0.07$, $p < 0.01$). Because the values of some of these correlation coefficients are not too large, it is likely that the effects that we report may act in conjunction with microhabitat scale effects. In addition, knowing that some microhabitat and microclimate variables are somewhat tied to factors at larger scales may be helpful for management purposes because strategies implemented adequately at the large scales could influence microhabitat and microclimate in such a way that these populations may become more viable.

Probabilities of occurrence of one pasture species increased with increasing distance from the nearest forest fragment. Rosebelly lizard occurrence increased with increasing mean distance from the four nearest forest patches. Therefore, this pasture species tend to be present in portions of the landscape that are isolated from the forest. Urbina-Cardona and Reynoso (2006), however, found that this diurnal lizard uses high temperature (26 to 32 °C) microhabitats and intermediate levels of canopy cover and additional microhabitat variables such as temperature, relative humidity and grass cover had positive effects, and leaf litter cover had negative effects on the occurrence of this species. Although microhabitat variables influence occurrence of this species, at least one landscape-level variable is also important. Therefore, to understand probabilities of occurrence of this species, it is important to consider landscape configuration and microhabitat changes simultaneously.

Probabilities of occurrence of forest species, varied with some of the vegetation structure variables that we measured and with proportions of forest within 10-m of our transects.

Probabilities of occurrence of the lesser scaly anole increased with increasing complexity of vegetation structure (e.g., canopy cover and understory density), suggesting that this forest

species uses dense microhabitats. This finding contrast with those reported by Villareal and Heras (1997), these authors suggest that the lesser scaly anole cues on the light entrance and vegetation structure because these variables influence their visual communication. Urbina-Cardona and Reynoso (2006) found that additional microhabitat variables such as leaf litter depth, temperature and herbaceous cover, had positive effects on lesser scaly anole occurrence, whereas relative humidity had negative effects. Therefore, this is another example of a species influenced not only by the structure of microhabitat and microclimate, but also by variables at larger scales. These results suggest that in order to survive at Los Tuxtlas, this species requires complex vegetation structure that provides substrate to search for food and refuges. The lesser scaly anole uses preferentially microhabitats such as leaf litter, trunks and branches (J.N.U-C pers. obs.) and is dominant on abundance over other forest reptile species that inhabit both forest edge and forest interior (Urbina-Cardona et al. 2006).

The occurrence of the Golf coast frog increased with increasing percentages of forest within 10-m of transects, indicating that this forest species tends to be present in highly covered habitats without any additional landscape composition elements. Urbina-Cardona and Reynoso (2006) found that this diurnal frog uses microhabitats with intermediate temperatures (19 to 28 o C) and high percentages of canopy cover and that microhabitat variables such as relative humidity and herbaceous cover had positive effects on probabilities of occurrence of the Golf coast frog, whereas temperature and leaf litter depth had negative effects. This is our last species whose probabilities of occurrence were influenced by both microhabitat and environmental factors at larger scales. This species occurs on leaf litter microhabitats (Urbina-Cardona and Reynoso 2006) embedded within the forest interior (Urbina-Cardona et al. 2006). Viable populations of this species require an area of forest interior with complex vegetation structure, otherwise they could become locally extinct (Urbina-Cardona et al. 2006).

Probabilities of occurrence of the most abundant species such as the Rio Grande leopard frog were independent from any of the variables that we measured. Individuals of this species were recorded by Pineda and Halffter (2004) in tropical montane cloud forests and shaded coffee plantations in ponds of every study site independently of canopy cover or patch size. This frog is commonly associated with mud banks and open areas and it's population numbers are influenced by river depths as well as air and water temperatures (Jung et al. 2002). We recorded this species on both open pastures and tropical evergreen forests. Therefore, the evidence suggests that this is a generalist species that occupies a

variety of environmental gradients and uses a great diversity of microhabitats. In general, individuals of the Rio Grande leopard frog are generalist, and opportunistic predators whose diet is mostly influenced by prey availability (Parker and Goldstein 2004). At Los Tuxtlas this species inhabits preferentially open habitats but could make some active migrations from pastures to forests during the rainfall season (López-Luna com. pers). For this reason, it is likely that this species is not greatly influenced by the surrounding variables from tropical fragmented landscapes. The key factor for this species is likely the presence of bodies of water more than forest fragments *per se*. This result is also consistent with those of Pineda and Halffter (2004). The effects of the factors that we measured on probabilities of occurrence of the polymorphic robber frog were also negligible. Urbina-Cardona and Reynoso (2006), however, found that microhabitat variables that include relative humidity, herbaceous cover, and leaf litter depth had negative effects on polymorphic robber frog occurrence. The polymorphic robber frog is a terrestrial species that uses preferentially the leaf litter to forage and to deposit its eggs. This specie is the most abundant amphibian, and possibly the most abundant vertebrate at Los Tuxtlas, it inhabits both forest edge and forest interior (Urbina-Cardona et al. 2006). At the microhabitat scale this species uses preferentially the leaf litter and also uses wide gradients in temperature, relative humidity, herbaceous cover, leaf litter cover and depth, canopy cover, understory density, and slope available throughout the forest (Urbina-Cardona and Reynoso 2006). In order to survive, this species needs forest habitats but has no additional specific requirements as far as we know. For this most abundant species group there are two possible explanations for the lack of effects of the independent variables that we measured on their probabilities of occurrence: a) they are generalist species with a wide range of environmental tolerances and could occupy a great diversity of microhabitats, or b) their probabilities of occurrence could depend on factors such as temperature, relative humidity, leaf liter and herbaceous cover operating at smaller spatial scales than the ones that we studied.

Amphibian and reptile species have poor dispersal capabilities and their movements are limited by the characteristics of their microhabitats due to the physiological constrains that their thermal requirements impose on them (Zug 2001, Weyrauch and Grubb 2003). Some works, however, have demonstrated that frogs and snakes could have exceptionally high dispersal rates depending their habitat use and seasonality (Webb and Shine 1997, Seebacher and Alford 1999, Funk et al. 2005b, Webb and Shine 2005) and maintain high gene flow over long distances (more than 5 km), large elevation gradients (more than 750 m) and steep slopes (Funk et al. 2005b). Webb and Shine (1997) found that broad-headed snake

movements were more frequent and extensive when they were in woodland habitats (mean displacement per movement = 159 m) than in rock-open areas (mean displacement per movement = 37 m). Seebacher and Alford (1999) found that toads remained under canopy cover during the drier months, but increasingly moved into the open grass as humidity increased. Species with high dispersal behaviors that move long distances to forage could be vulnerable, especially on highly fragmented landscapes such as Los Tuxtlas where microclimatic conditions fluctuate tremendously, exposing these organisms to higher mortality than sedentary ambush foragers (Bonnet et al. 1999).

Our study provided further support for the idea that probabilities of species occurrence can change at more than one spatial scale (e.g., Hamer and Hill, 2000, Stoddard and Hayes 2005) with landscape composition within habitat types (e.g., Golf coast frog), vegetation structure (e.g., lesser scaly anole) and landscape isolation (e.g., rosebelly lizard). Guevara and collaborators (2004d) demonstrated that rain forest regenerates after three years under the canopy of fig trees isolated in pastures of Los Tuxtlas to a degree in which more than 95 plant species, and 46 tree species with canopies taller than four meters establish. They found that under this type of canopy, herbaceous plants characteristic of pastures disappear letting forest regeneration find its way. On the other hand, isolated trees on pastures modify microclimatic conditions, stabilizing fluctuations in temperature and relative humidity, and promoting water retention (Holl 1999). These elements of the landscape may act as “steep stones” between forest patches for animals that cannot tolerate pasture microclimates. We recorded some individuals of forest species such as the Golf coast frog and the polymorphic robber frog under the canopy of isolated trees on pastures. Maintaining connectivity elements, such as isolated trees, riparian vegetation, live fences and secondary forest at Los Tuxtlas could increase animal movements between fragments and increase viability for a large proportion of the biota without completely stopping agricultural and cattle activities (Guevara et al. 2004c).

High rates of deforestation and fragmentation at Los Tuxtlas may affect more than 3356 plant and 851 vertebrate species (Guevara et al. 2004c). Los Tuxtlas has suffered from loss of top predator species (e.g., jaguar), impoverishment of forest floor-dwelling vertebrates, and absence of some understory and canopy mammals (Dirzo and Miranda 1990). Therefore, a strategy that attempts to preserve middle size bird, mammalian, snake, and lizard predator species, and small predator species such as frogs and some lizards through maintenance of connectivity elements would help preserve areas of conservation importance

and protect several species considered important (Peterson et al. 2000). This would also allow maintenance of the genetic flux between forest patches and biotic interactions.

Conclusion

The occurrence of some frog and lizard species could be influenced in part by factors that operate at spatial scales larger than the microhabitat including habitat composition, patch structure, and patterns of landscape configuration resulting from habitat loss. Studies that investigate factors influencing reptile and amphibian species occurrences should integrate information pertaining to microhabitat effects such as topography, vegetation structure, habitat composition, edge effects, habitat loss, and isolation. These studies should include information from a variety of species because their individual responses may vary depending on species tolerances, microhabitat, and microclimate requirements. At least a number of species that represent the entire community should be considered. Information theoretic approaches that simultaneously study several biological meaningful *a priori* hypotheses could benefit these types of studies. These approaches will allow researchers to explore multi-scale associations among independent factors and to identify real causative factors (e.g., Burham and Anderson 2001). Therefore, reliable conservation strategies could be designed.

From the ten existing reserves at Veracruz, Los Tuxtlas is predicted to be the richest in bird and mammal endemic species, and therefore was the first to enter the state reserve system (Peterson et al. 2000). In this landscape, 88% of the land is ancestral property of the community (e.g., “terreno ejidal”), 5.5% is private property, and 6.5% is property of the “Universidad Nacional Autónoma de México” (UNAM). In 1966 the UNAM created the Tropical Biology Station, and since that year research has directed efforts to promote conservation biology. Currently Los Tuxtlas is one of the most studied tropical rainforest regions around the world (Laborde 2004). Although the Los Tuxtlas Biosphere Reserve was created in 1998, its management plan is still being designed and different sectors of the society such as authorities and local land owners may participate (Laborde 2004). It is currently unknown if preservation of the large forest fragments at Los Tuxtlas alone is sufficient to guarantee the survival of lizard and frog species that inhabit the forest. Under poor management practices such as extensive conversion of the tropical evergreen forest and live fences into lands for agriculture and cattle grazing (e.g., Scott et al 1993), even common species such as the lesser scaly anole, the polymorphic robber frog, and the Golf coast frog could become extinct at Los Tuxtlas. Because some of these species are restricted to isolated forest patches, they are prone to enter genetic bottlenecks (e.g., Saunders et al. 1991). Moreover, a change in the population structure of these five most abundant vertebrate species

at Los Tuxtlas region could cause fatal changes on biotic interactions in both forest and pasture habitats. The local extinction of one of these species could cause the disruption in the food chain. Because at Los Tuxtlas these are the most abundant vertebrate species, and because of their dietary habits, they control a large proportion of the invertebrate community. Besides, they are also important as a source of food for several lizard, snake and bird species. Preservation of large forest fragments is the management strategy most likely to benefit at least some reptiles and amphibians because it would provide greater habitat heterogeneity. This type of action is likely to also benefit other organisms such as primates, birds, and mammals that operate at larger scales and are known to be influenced by the effects of distances from edges, and habitat fragmentation in the region (Estrada et al. 1996, 2000, 2001, 2002). Adequate complementary management strategies would include maintaining the already existing isolated trees and live fences on abandoned pastures. These elements could help increase connectivity on the landscape and would promote migration and dispersal of organisms among habitat patches. Finally, promoting the creation of buffer zones for the Reserve in which alternative practices such as sustainable harvest of bromeliads (Ticktin et al. 2002) were implemented, could simultaneously promote local economic development and the connectivity within the landscape (Laborde 2004).

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Table 1. *A priori* candidate models explaining occurrence of two pasture species: rosebelly lizard (*Sceloporus variabilis*) and Rio Grande leopard frog (*Rana berlandieri*) at Los Tuxtlas region, Veracruz state, Mexico, 2003–2005. Number of parameters (K) in each model included the intercept and each explanatory variable. Models with lower ΔAICc and a greater Akaike weight (w_i) values have more support. Values for the model with the most support are in bold. Model abbreviations as in Appendix A.

Model	K	<i>Rosebelly lizard</i>		<i>Rio Grande leopard frog</i>	
		ΔAICc	w_i	ΔAICc	w_i
GLOB_MOD	22	4.89137673	0.03885767	5.51711608	0.0608165
DIST_EF	13	2.61312874	0.12139255	0	0.95950662
LAND_COMP_DIST_EF_ISOL	20	0	0.44835882	1.10798735	0.55138072
LAND_COMP_DIST_EF	19	0.38566588	0.36972552	0.78665322	0.64748304
LAND_COMP_ISOL	8	1.00472967	0.27130103	1.65071701	0.42033865
LAND_COMP	7	10.1788259	0.00276262	23.0748133	0
TOPOG	3	92.7134519	0	28.0574393	0
ISOL	2	95.1480249	0	29.5870122	0
NULL_MOD	1	98.6060532	0	45.8165405	0

Table 2. Odd ratios and 95% confidence intervals (CI) for explanatory variables based on model-averaged coefficients from 9 *a priori* candidate models of the occurrence of two pasture species: rosebelly lizard (*Sceloporus variabilis*) and Rio Grande leopard frog (*Rana berlandieri*) in Los Tuxtlas region, Veracruz state, Mexico, 2003–2005. Values for the variables whose CI's did not include 1 are in bold. Variable abbreviations as in Appendix A.

Variable	<i>Rosebelly lizard</i>			<i>Rio Grande leopard frog</i>		
	Odds ratio	CI		Odds ratio	CI	
al	1.00095696	1.00213843	0.99977548	1.00160046	1.00573785	0.997463065
sl	0.9996608	1.00434764	0.99497396	0.99388857	1.00924707	0.978530067
ht	1.00087532	1.00299861	0.99875204	1.0016007	1.00703447	0.996166935
ah (no vs yes)	1.04002614	1.10519376	0.97485852	1.10045917	1.3879194	0.81299893
nd (no vs yes)	0.96507119	1.04824004	0.88190234	0.51747305	10.6228609	-9.58791477
ad (no vs yes)	1.01262463	1.08556107	0.93968819	1.08453079	1.31360712	0.855454447
wfd (no vs yes)	0.98144727	1.0469997	0.91589484	1.10825809	1.30215919	0.914356996
wpd (no vs yes)	0.99813573	1.05211926	0.9441522	1.03809985	1.18817785	0.88802186
de1	1.31362629	4.79019529	-2.16294271	2.7497101	14.3651321	-8.86571188
de2	1.41595699	4.89350626	-2.06159228	2.33127776	13.9484968	-9.28594132
de3	1.32935043	4.80550823	-2.14680737	2.89812793	14.5109167	-8.71466081
de4	1.13017455	4.60473402	-2.34438492	0.75461266	14.1783441	-12.6691188
de5	0.90759683	4.38436363	-2.56916997	0.23424201	34.5961422	-34.1276581
de6	0.45133709	28.2299619	-27.3272877	0.71625252	14.1391692	-12.7066642
de7	0.90655451	4.38363154	-2.57052252	0.26626828	34.314831	-33.7822945
de8	0.97990735	4.45573067	-2.49591597	2.15049776	13.7621788	-9.4611833
ds	0.99997455	1.0000186	0.99993049	1.00007347	1.00021747	0.999929475
dro	0.99993429	1.00013745	0.99973113	1.00008949	1.00079381	0.999385165
dr	1.00012336	1.00037317	0.99987355	0.99936258	1.00026125	0.998463899
dl	0.99995314	1.00002493	0.99988134	0.99959809	1.00004322	0.999152953
dnf	1.00026474	1.00050122	1.00002827	1.00069537	1.0018886	0.999502142

1 Table 3. *A priori* candidate models explaining occurrence of three forest species: lesser scaly anole (*Anolis uniformis*), polymorphic robber frog
2 (*Eleutherodactylus rhodopis*), and Golf coast frog (*Bufo valliceps*) at Los Tuxtlas region, Veracruz state, Mexico, 2003–2005. Number of
3 parameters (*K*) in each model included the intercept and each explanatory variable. Models with a lower ΔAICc and a greater Akaike weight (*wi*)
4 have more support. Values for the model with the most support are in bold. Model abbreviations as in Appendix B.

Model	K	<i>Lesser scaly anole</i>		<i>Polymorphic robber frog</i>		<i>Golf coast frog</i>	
		ΔAICc	<i>wi</i>	ΔAICc	<i>wi</i>	ΔAICc	<i>wi</i>
VEG_STR	3	0	0.96785963	0	0.52261353	20.7309633	0
LAND_COMP_ISOL	6	15.0340367	0.00052628	1.78303675	0.21428863	0	0.98301625
LAND_COMP_VEG_STR	7	7.18037399	0.02670632	2.48337399	0.15098119	17.3863372	0.00016488
LAND_COMP	5	20.2747167	0	3.09271665	0.11132835	13.2216799	0.00132285
LAND_COMP_DIST_EF_ISOL	17	20.4721013	0	14.3631013	0.00039744	18.0020645	0.00012119
DIST_EF_HAB_LOSS	16	18.9308254	0	16.4188254	0.00014219	15.7087887	0.00038145
DIST_EF	12	21.338061	0	17.583061	0	22.2800242	0
LAND_COMP_DIST_EF	16	18.6838254	0	17.6448254	0	26.4587887	0
DIST_EF_HAB_LOSS_ISOL	17	21.4461013	0	18.3711013	0	8.59106452	0.01339784
DIST_EF_VEG_STR	14	10.8092441	0.00435126	19.7362441	0	23.5642074	0
LAND_COMP_DIST_EF_VEG_STR	18	17.345318	0.0001657	22.177318	0	28.4342813	0
GLOB_MOD	25	18.0909248	0.00011413	23.7929248	0	14.186888	0.00081643
TOPOG	3	138.321	0	88.132	0	16.4909633	0.00025798
ISOL	2	149.591573	0	94.481573	0	17.2805362	0.00017384
NULL_MOD	1	149.951301	0	94.9470013	0	20.4486799	0

HAB_LOSS	5	154.606717 0	99.3257167 0	34.7879645 0	
HAB_LOS_ISOL	6	156.747037 0	101.274037 0	16.503	0.00025644

5

6 Table 4. Odds ratios and 95% confidence intervals (CI) for explanatory variables based on model-averaged results from 17 *a priori* candidate
7 models of the occurrence of three forest species: lesser scaly anole (*Anolis uniformis*), polymorphic robber frog (*Eleutherodactylus rhodopis*)
8 and Golf coast frog (*Bufo valliceps*) in Los Tuxtlas region, Veracruz state, Mexico, 2003–2005. Values for the variables whose CI's did not
9 include 1 are in bold. Variable abbreviations as in Appendix B.

Variable	<i>Lesser scaly anole</i>			<i>Polymorphic robber frog</i>			<i>Golf coast frog</i>		
	Odds ratio	CI		Odds ratio	CI		Odds ratio	CI	
Intercept	0.80711873	1.03450087	0.5797366	0.93054332	1.60005966	0.26102697	2.13541543	5.03022133	-0.75939047
al	0.99999822	1.00000066	0.99999579	0.99999998	1	0.99999996	0.99999967	1.00000084	0.99999851
sl	0.99999861	1.00000171	0.99999551	0.99999997	1.00000001	0.99999994	0.99999498	0.99999897	0.99999099
%c	1.0083641	1.01129428	1.00543392	1.0222461	1.32001334	0.72447887	0.99999919	1.00000255	0.99999583
ud	1.02162672	1.03615963	1.00709381	1.00374945	1.01008677	0.99741213	0.99997859	1.00001236	0.99994483
ht	0.99999659	1.00011465	0.99987854	1.00168391	1.00462538	0.99874244	1.00197812	1.0030859	1.00087035
ah (no vs yes)	0.99948658	1.00120526	0.9977679	1.03390265	1.07221719	0.99558812	0.98646048	1.02722384	0.94569711
nd (no vs yes)	0.9991259	1.00148972	0.99676207	1.07899047	1.72320217	0.43477878	0.96874043	1.01021226	0.92726859
wfd (no vs yes)	0.99972489	1.00208582	0.99736395	1.00110854	1.023186	0.97903107	1.0134592	1.0457124	0.98120599
de1	0.99956681	1.02549088	0.97364274	0.99941456	1.00489591	0.99393321	0.9991618	1.00535097	0.99297263
de2	0.99930833	1.02524643	0.97337022	0.99935968	1.00484117	0.99387818	0.99335152	1.04017525	0.94652779
de3	0.99977582	1.02575648	0.97379517	0.99943148	1.00491188	0.99395108	0.99913641	1.00531758	0.99295524
de4	0.99884916	1.02447509	0.97322323	1.00039516	1.01477097	0.98601935	1.00110448	1.00708159	0.99512738
de5	1.00186892	1.12432592	0.87941192	1.00032993	1.01489809	0.98576177	1.00077587	1.00675561	0.99479613
de6	0.99851788	1.02429659	0.97273917	1.00035513	1.0154386	0.98527167	1.0017203	1.00769207	0.99574853

de7	0.99847291	1.02416981	0.97277601	1.00036055	1.01511408	0.98560701	1.00175523	1.00772571	0.99578475
de8	0.99881442	1.10974201	0.88788682	1.00017374	1.01602328	0.98432419	1.00148231	1.00744862	0.995516
ds	0.99999997	1.00000003	0.99999964	0.99999997	1.00000001	0.99999993	1.00000051	1.00000119	0.99999983
dr	0.99999888	1.00000046	0.99999731	1.00000001	1.00000017	0.99999985	0.99999842	1.00000115	0.99999568
dl	0.99999969	1.00000026	0.99999912	1.00000001	1.00000007	0.99999996	0.99999998	1.00000108	0.99999853
a	0.99995278	1.0000418	0.99986376	0.99999998	1.00000808	0.99999189	0.99889591	1.00265709	0.99513473
p	1.00187981	1.00527904	0.99848058	1.00001928	1.00018368	0.99985489	1.04719042	1.20420171	0.89017912
ip	0.9996798	1.0002557	0.99910389	0.99999383	1.00002393	0.99996373	0.99209168	1.01928262	0.96490074
s	0.90213616	1.08711654	0.71715578	0.99866156	1.00727845	0.99004468	0.0719498	9.10281683	-8.95891723
dnf	1.00000333	1.00000914	0.99999752	0.9999835	1.00000161	0.9999654	0.99999145	1.00040046	0.99958243

11 **Figure legends**

12 **Fig. 1.** Diagram of a study plot of 250 m in length and 50 m in width along the pasture-edge-
13 interior gradient. Horizontal lines represent 50 x 2 m transects parallel to the forest edge.

14 Negative distances represent distances from pasture transects to the forest-pasture edge.

15 Positive distances represent distances from forest transects to the forest-pasture edge.

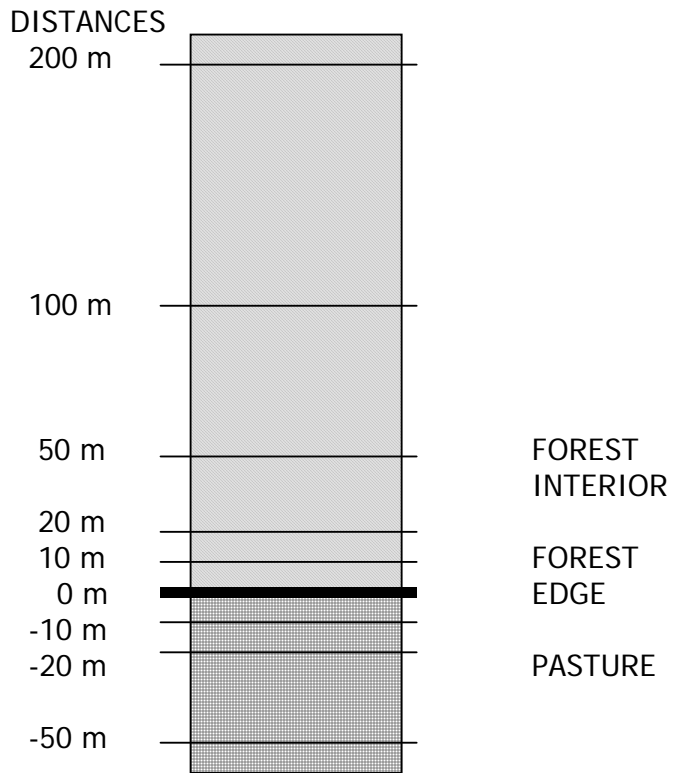
16 **Fig. 2.** Effects of distance from nearest rainforest fragment (mean \pm 95% confidence
17 intervals) on probabilities of occurrence of rosebelly lizards (*Sceloporus variabilis*) at Los
18 Tuxtlas region, Veracruz state, Mexico, 2003 – 2005. Probabilities of occurrence of forest
19 species presence were estimated from model-averaged coefficients of the best supported
20 logistic regression model. Dotted lines indicate 95 % confidence intervals.

21 **Fig. 3.** Effects of (a) canopy cover and (b) understory density (mean \pm 95% confidence
22 intervals) on probabilities of occurrence of lesser scaly anoles (*Anolis uniformis*) at Los
23 Tuxtlas region, Veracruz state, Mexico, 2003–2005. Probabilities of forest species presence
24 were estimated from model-averaged coefficients of the best supported logistic regression
25 model. Dotted lines indicate 95 % confidence intervals.

26 **Fig. 4.** Effects of percentage of forest within 10 m of transects on probability of occurrence
27 of Gulf coast frogs (*Bufo valliceps*) at Los Tuxtlas region, Veracruz state, Mexico, 2003–
28 2005. Probabilities of forest species presence were estimated from model-averaged
29 coefficients of the best supported logistic regression model. Dotted lines indicate 95 %
30 confidence intervals.

31

32

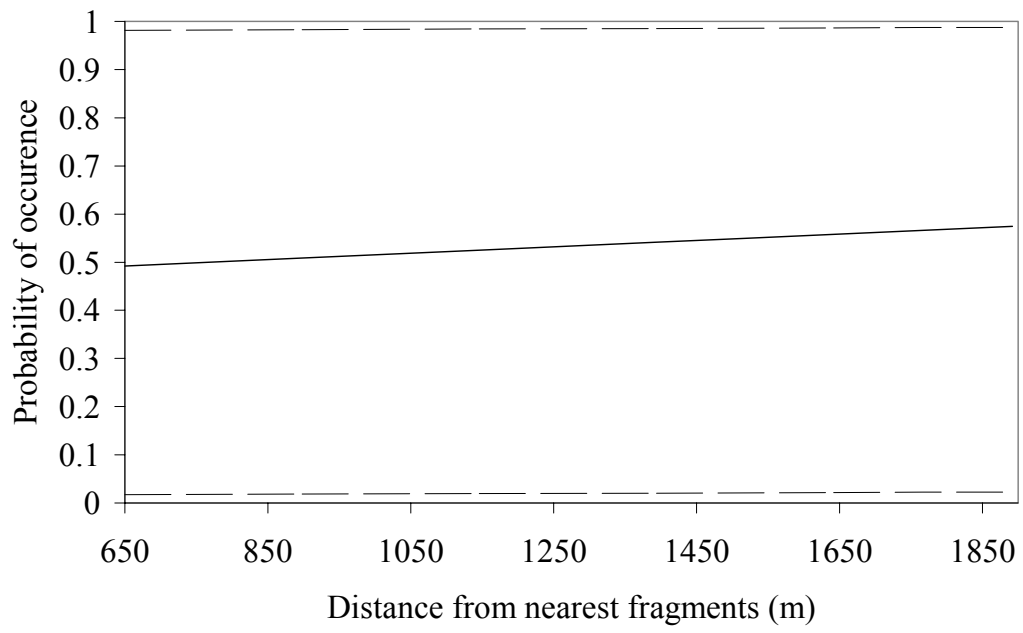


33

34 Fig. 1

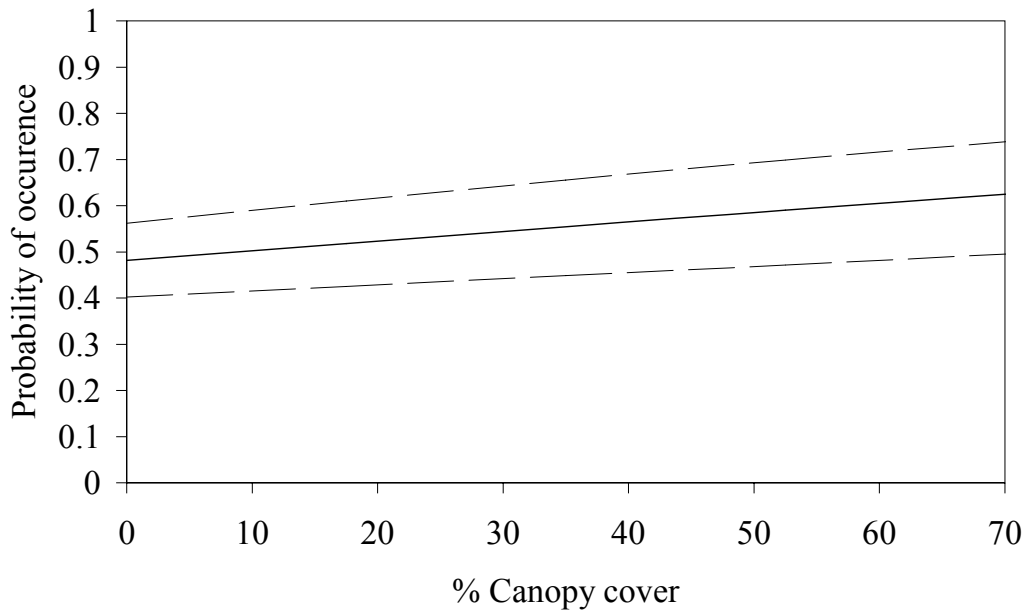
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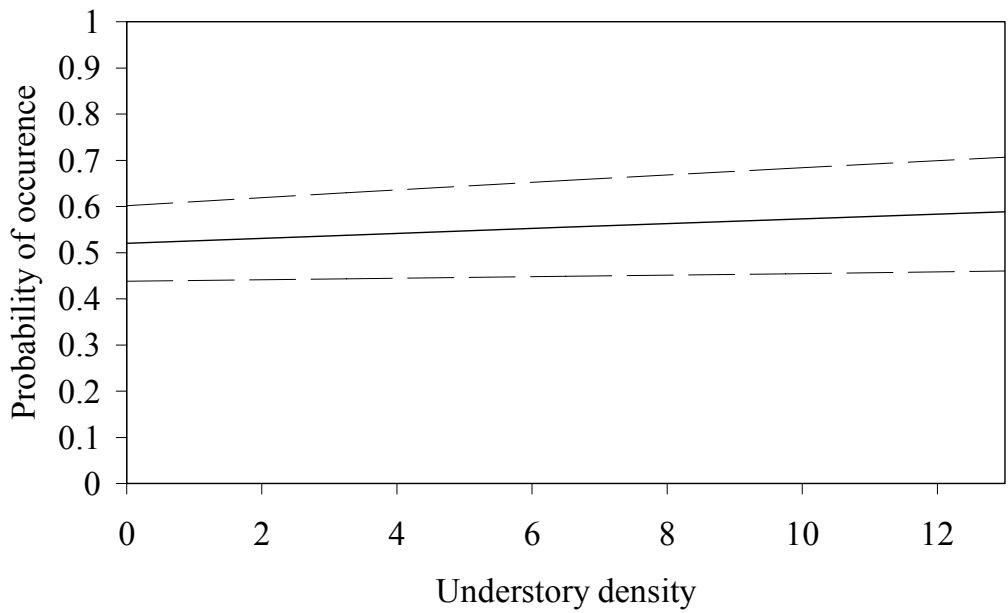
37

38 Fig 2.



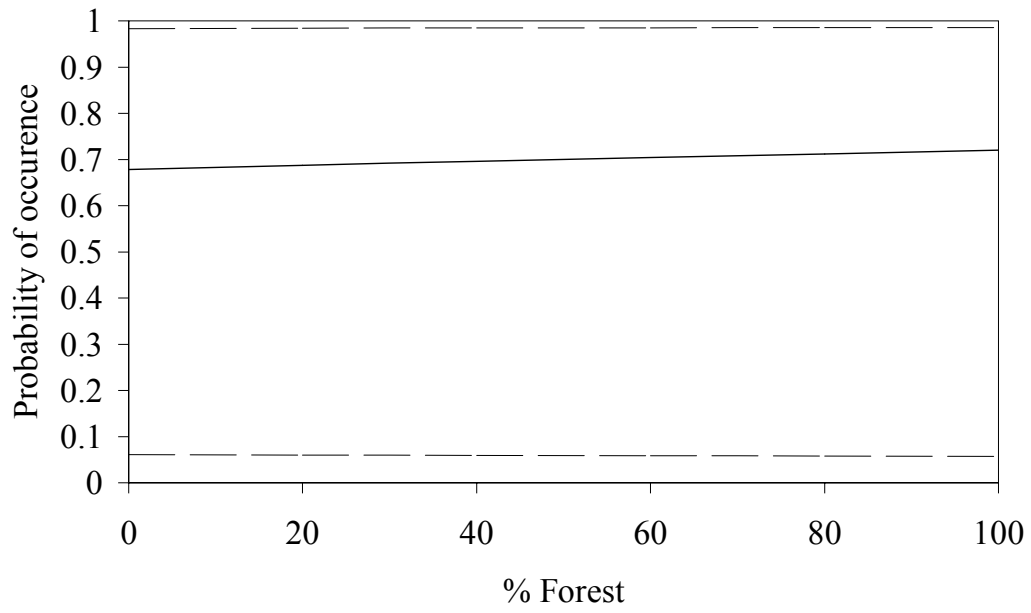
39

40 Fig 3 a



41

42 Fig 3 b



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44 Fig. 4

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47

48 **Appendix A.** Set of competing candidate *a priori* hypotheses explaining the presence of two
 49 pasture affine species, Rio Grande leopard frog (*Rana berlandieri*) and rosebelly lizard
 50 (*Sceloporus variabilis*) at Los Tuxtlas region, Veracruz, México. Response variables: Rb =
 51 occurrence of *Rana berlandieri* (n= 92 individuals), and Sv = occurrence of *Sceloporus*
 52 *variabilis* (n= 260 individuals). Predictor variables (n = 14): *al* = altitude, *sl* = slope, *ht* = %
 53 pasture within 10m of each transect, *ah* = adjacent habitat type (presence / absence of forest
 54 edge and forest interior within 10m of each transect), *nd* = natural disturbance (presence /
 55 absence of river within 10m of each transect), *ad* = anthropogenic disturbance (presence /
 56 absence of roads within 10m of each transect), *wfd* = within-forest disturbance (presence /
 57 absence of secondary forest and canopy openings), *wpd* = within-pasture disturbance
 58 (presence / absence of life fences and/or isolated trees within 10m of each transect), *de* =
 59 distance from nearest edge (categorical variable that ranges from 1 at pasture to 9 at forest
 60 interior), *ds*, *dr*, *dl*, *dro* = distance from nearest sea, river, lake, and road; *dnf* = mean
 61 distance to four nearest forest fragments.

- 62 1) Effects of topography (TOPOG); Rb, Sv = $al + sl$
- 63 2) Effects of landscape composition within habitat types (LAND_COMP); Rb,
 64 Sv = $ht + ah + nd + wfd + ad + wpd$
- 65 3) Effects of distances from edge types such as water bodies and anthropogenic edge
 66 (DIST_EF); Rb, Sv = $de + ds + dr + dl + dro$
- 67 4) Effects of isolation (ISOL); Rb, Sv = dnf
- 68 5) Effects of landscape composition within habitat types and isolation
 69 (LAND_COMP_ISOL); Rb, Sv = $ht + ah + nd + wfd + ad + wpd + dnf$
- 70 6) Effects of landscape composition within habitat types and distances from edge types
 71 (LAND_COMP_DIST_EF); Rb, Sv = $ht + ah + nd + wfd + ad + wpd + de + ds + dr + dl +$
 72 dro
- 73 7) Effects of landscape composition within habitat types, distances from edge types, and
 74 isolation (LAND_COMP_DIST_EF_ISOL); Rb, Sv = $ht + ah + nd + wfd + ad + wpd + de +$
 75 $ds + dr + dl + dro + dnf$
- 76 8) Global model (GLOB_MOD); Rb, Sv = all variables from previous models.
- 77 9) Null model (NULL_MOD); Rb, Sv = intercept.

78 **Appendix B.** Set of competing candidate *a priori* hypotheses explaining the presence of
79 three forest affine species, lesser scaly anole (*Anolis uniformis*), polymorphic robber frog
80 (*Eleutherodactylus rhodopis*) and Golf coast frog (*Bufo valliceps*) at Los Tuxtlas region,
81 Veracruz, México. Response variables: Au = occurrence of *Anolis uniformis* (n= 765
82 individuals), and Er = occurrence of *Eleutherodactylus rhodopis* (n= 2270 individuals), Bv =
83 occurrence of *Bufo valliceps* (n= 86 individuals). Predictor variables (n = 17): *al* = altitude,
84 *sl* = slope, *%c* = % canopy cover, *ud* = understory density, *ht* = habitat type within 10m of
85 each transect (%forest), *ah* = adjacent habitat type (presence / absence of pasture within 10m
86 of each transect), *nd* = natural disturbance (presence / absence of river within 10m of each
87 transect), *wfd* = within forest disturbance (presence / absence of canopy openings and
88 secondary forest within 10m of each transect), *de* = distance from nearest edge (categorical
89 variable that ranges from 1 at pasture to 9 at forest interior), *ds*, *dr*, *dl* = distance from nearest
90 sea, river, lake; *a*, *p*, *s*, *ip* = forest fragment area, perimeter, shape (Patton's diversity index)
91 and proportion of interior habitat; *dnf* = mean distance to four nearest forest fragments.

92 1) Effects of topography (TOPOG); Au, Er, Bv = *sl* + *al*
93 2) Effects of vegetation structure (VEG_STR); Au, Er, Bv = *%c* + *ud*
94 3) Effects of landscape composition within habitat types (LAND_COMP); Au,
95 Er, Bv = *ht* + *ah* + *nd* + *wfd*
96 4) Effects of distance from edge types such as water bodies and anthropogenic edge
97 (DIST_EF); Au, Er, Bv = *de* + *ds* + *dr* + *dl*
98 5) Effects of habitat loss (HAB_LOSS); Au, Er, Bv = *a* + *p* + *s* + *ip*
99 6) Effects of isolation (ISOL); Au, Er, Bv = *dnf*

100 7) Effects of distances from edge types and habitat loss patterns (DIST_EF_HAB_LOSS); Au, Er, Bv
101 = *de* + *ds* + *dr* + *dl* + *a* + *p* + *s* + *ip*
102 8) Effects of habitat loss patterns and isolation (HAB_LOSS_ISOL); Au, Er, Bv = *a* + *p* + *s* +
103 *ip* + *dnf*
104 9) Effects of landscape composition within habitat types and isolation
105 (LAND_COMP_ISOL); Au, Er, Bv = *ht* + *ah* + *nd* + *wfd* + *dnf*
106 10) Effects of landscape composition within habitat types and distances from edge types
107 (LAND_COMP_DIST_EF); Au, Er, Bv = *ht* + *ah* + *nd* + *wfd* + *de* + *ds* + *dr* + *dl*
108 11) Effects of landscape composition within habitat types, distances from edge types, and
109 isolation (LAND_COMP_DIST_EF_ISOL); Au, Er, Bv = *ht* + *ah* + *nd* + *wfd* + *de* + *ds* + *dr*
110 + *dl* + *dnf*

111 12) Effects of distances from edge types, habitat loss patterns, and isolation (DIST_EF
112 HAB_LOSS_ISOL); Au, Er, Bv = de + ds + dr + dl + a + p + s + ip + dnf
113 13) Effects of landscape composition within habitat types, distances from edge types, and
114 vegetation structure (LAND_COMP_DIST_EF_VEG_STR); Au, Er, Bv = ht + ah + nd +
115 wfd + de + ds + dr + dl + %c + ud
116 14) Effects of distances from edge types and vegetation structure (DIST_EF_VEG_STR);
117 Au, Er, Bv = de + ds + dr + dl + %c + ud
118 15) Effects of landscape composition within habitat types and vegetation structure
119 (LAND_COMP_VEG_STR); Au, Er, Bv = ht + ah + nd + wfd + %c + ud
120 16) Global model (GLOB_MOD); Au, Er, Bv = all variables from previous models.
121 17) Null model (NULL_MOD); Au, Er, Bv = intercept
122

DISCUSION GENERAL

A partir de este trabajo se determinó que la magnitud del efecto de borde sobre los anfibios y reptiles tropicales covaría, no siempre de una manera directa, con las variables del microhábitat, la estacionalidad, la orientación del borde y la composición del paisaje entre tipos de hábitat. Además, las respuestas de la herpetofauna varían ampliamente al comparar diferentes tipos de ensamblajes y especies, dependiendo de su afinidad o tolerancia por el potrero, borde o interior de la selva.

Diversidad herpetofaunística de las tierras bajas de Los Tuxtlas

En los Capítulos 1 y 2 se reporta la diversidad de anfibios y reptiles en el gradiente potrero-borde-interior con base en los registros obtenidos durante cuatro salidas al campo (672 horas hombre). Se observó que los patrones de riqueza de anfibios y reptiles reportados inicialmente (Urbina-Cardona y Reynoso 2005, Urbina-Cardona *et al.* 2006) se mantienen al culminar la fase de campo. Al culminar las seis salidas al campo se determinó que el hábitat con mayor riqueza de anfibios y reptiles fue el interior del selva (20 anfibios y 32 reptiles) seguido por el borde de la selva (19 anfibios y 31 reptiles) sin embargo, éstas diferencias entre hábitat no son significativas. A pesar de incrementar el esfuerzo de muestreo en el potrero, la riqueza de anfibios se mantuvo constante (12 especies) y el número de reptiles aumentó en una sola especie (12 especies). Los hábitat donde se incrementó en mayor medida el número de especies durante las dos últimas salidas fueron el borde (5 anfibios y 6 reptiles nuevos en el listado) e interior de selva (7 anfibios y 10 reptiles nuevos en el listado) aumentando aun más las diferencias en diversidad y composición con el potrero.

Si bien los patrones en el efecto de borde se mantuvieron constantes durante las últimas salidas, el incremento de esfuerzo de captura sirvió para aumentar la representatividad en el muestreo (*sensu* completeness, Soberón y Llorente 1993). Al acumular seis salidas al campo, el presente trabajo reporta una representatividad promedio de 98.6% para los anfibios (entre 94.3% con Jack1, y 100% con Chao 1 y 2) y de 72.5% para los reptiles (entre 65.3% con Jack2, y 87% con Bootstrap).

De las 86 especies reportadas a lo largo de 93 años (iniciando con Ruthven 1912, 1913) para las tierras bajas (de 0 a 600 msnm) cercanas a la Estación de Biología Tropical Los Tuxtlas (Pérez-Higareda *com. pers.* 2003) este trabajo registró el 88.8% de los anfibios, y el 71.2% de los reptiles. Si se tiene en cuenta que el presente trabajo no exploró microhábitat como dosel, cuerpos de agua y construcciones humanas, una cifra por encima del 70% del total de las especies representa una diversidad bastante alta. Dado que la herpetofauna de Los Tuxtlas es uno de los grupos mejor estudiados en el país, el presente estudio no se enfocó en determinar la diversidad gamma de anfibios y reptiles.

En general la selva alta perennifolia estuvo dominada por especies de ranas del género *Craugastor* (anteriormente *Eleutherodactylus*) y lagartijas del género *Anolis*. Este patrón ya había sido reportado anteriormente para otros bosques tropicales en México (bosque mesófilo de montaña: Pineda y Halfpeter 2004, selva: Luna 1997), en el bosque de montaña de Costa Rica (Schlaepfer y Gavin 2001), en bosque de niebla en Colombia (Arroyo *et al.* 2003, Suárez-Badillo y Ramírez-Pinilla 2004), en el choco colombiano (Urbina y Londoño 2003) y en la amazonia ecuatoriana (Pearman 1997) y brasilera (Tocher *et al.* 1997).

Efecto de borde

El Capítulo 1 resalta la importancia de tener en cuenta la historia natural de la especies (e.g. hábitat, habito, talla y modo reproductivo) al evaluar la diversidad de anfibios y reptiles a lo largo del potrero, borde e interior de selva. Zimmerman y Bierregard (1986) sugieren que es importante determinar la autoecología de las especies a conservar. Esta es la primera vez que se analiza el efecto de borde bajo este enfoque y se encontraron patrones interesantes tales como un aumento de especies terrestres en el potrero, y un aumento de especies arborícolas en la selva debido a la diferencia en estructura vegetal de ambos hábitat. Respecto al modo reproductivo en anfibios, las especies de potrero tienden a presentar huevos y larvas en el agua, mientras que en la selva tienden a presentar un desarrollo directo fuera de cuerpos de agua (Urbina-Cardona y Reynoso 2005). Finalmente se determinó que las especies de talla pequeña tienden a estar confinadas al interior de la selva y podrían verse afectadas por cambios en el

microhábitat dado que pueden llegar a desecarse más fácilmente. El modo reproductivo y el hábitat preferencial de las especies de anfibios y reptiles deben considerarse formalmente en estudios que pretendan evaluar la diversidad de estos organismos a lo largo de gradientes ambientales y espaciales.

El Capítulo 2 permitió validar que existe un fuerte efecto de borde sobre la herpetofauna que habita tierras bajas tropicales (en contraste con el descrito para tierras altas, Toral *et al.* 2002). Sin embargo, esta es la primera vez que se demuestra y describe de manera robusta los “efectos cascada” (*sensu* Murcia 1995) al estudiar el efecto de borde sobre la herpetofauna y su relación con las condiciones del microhábitat (variables ambientales). Se resalta la importancia de agrupar las especies según su afinidad por (o tolerancia a) la matriz, el borde o el interior de la selva, generando entidades que requieren diferentes estrategias de manejo y conservación. Este enfoque permitió evidenciar que el ensamble de especies más vulnerables al efecto de borde y la pérdida de hábitat (e.g. especies de interior) presenta un alto grado de complejidad en su relación con el microhábitat. Se determinó que *Pseudoeurycea orchimelas*, *Ollotis valliceps*, *Craugastor vulcani*, *Imantodes cenchoa*, *Scincella cherriei* y *Plestiodon sumichrasti* son especies típicas de interior. Pueden indicar la calidad del hábitat del interior de selva, y su desaparición puede demostrar la degradación del hábitat en el fragmento o que el área del mismo es insuficiente para excluir los efectos del borde.

En el Capítulo 3 se demostró que a partir de un diseño riguroso en campo y numerosos transectos replicados a lo largo del paisaje y temporadas de muestreo, es posible hacer inferencias sobre la presencia de ranas y lagartijas a diferentes escalas espaciales. De esta manera se encontró que en general las especies de potrero estudiadas se ven afectadas positivamente por el aislamiento (reflejado por la distancia entre parches), mientras que las especies de selva se ven afectadas positivamente por la cobertura de dosel, la densidad de sotobosque y la heterogeneidad (reflejada como la proporción de diversos tipos de hábitat alrededor del transecto). Estos patrones indican que la pérdida y aislamiento de hábitat, y el efecto de borde no se manifiestan de la misma manera en todas las especies y que depende en gran medida de la escala a la que se evalúen estos efectos. Para las especies dominantes de ranas y lagartijas no se encontró relación con las variables medidas. Esto puede ser debido a que a) son generalistas y

poseen un amplio espectro en sus tolerancias ecofisiológicas, o b) su presencia puede estar determinada por variables microclimáticas no incluidas en el análisis (e.g. temperatura, humedad relativa).

En el Capítulo 4 se demostró que existe un fuerte efecto del hábitat en relación con la estacionalidad para la abundancia y composición de reptiles. Por primera vez se expone que la orientación tiene un gran efecto sobre la composición y abundancia de anfibios tropicales en estrecha relación con la estacionalidad. Se concluye que la fuerte influencia de la estacionalidad en la herpetofauna confiere a Los Tuxtlas características de ambientes templados en conjugación con el entorno tropical.

A partir del estudio del uso del hábitat se pudo determinar que no existe una sobreposición de nicho espacial en la selva de Los Tuxtlas, reflejando que el uso de los recursos disponibles en los remanentes son explotados de manera óptima para reducir la competencia inter-específica y la distribución diferencial de las especies en el entorno (Apéndice I) en el cual la composición de anfibios y reptiles en la selva remanente de tierras bajas en Los Tuxtlas son una subserie predecible de las especies presentes en lo que originalmente pudo haber sido la “fuente de especies” en la región (e.g. la Reserva de la Estación). Debido a la alta dominancia de *C. rhodopis* y *A. uniformis* algunas especies de abundancia media pueden estar desplazadas a lugares subóptimos de su nicho reflejando el alto grado de perturbación en la selva remanente (Apéndice II).

Efectos de matriz

Actualmente se sabe que los cambios sucesionales y en general la ecología de los bosques tropicales se ven influenciados en gran medida por el tipo de matriz circundante (Laurance *et al.* 2002). Estudios recientes han considerado a la matriz de potrero como un sitio idóneo para la reproducción de los anfibios tropicales (Gascon *et al.* 1999) llevando a peligrosas inferencias hacia la conservación de los ambientes fragmentados. En el presente trabajo (Capítulo 2, Urbina-Cardona *et al.* 2006) se demuestra que el potrero no es un lugar idóneo para la reproducción y supervivencia de los anfibios dado que presenta la menor riqueza, abundancia y proporción de organismos juveniles al compararlo con los ambientes de selva. Así mismo se pone en duda la utilidad de las cercas vivas, y los corredores de vegetación ribereña como herramienta de conectividad entre fragmentos,

dado que estos elementos actúan como bordes de selva permitiendo solo la dispersión de especies de potrero (que en teoría no necesitan corredores para desplazarse de un fragmento a otro) y aquellas que toleran la interfaz potrero-borde de bosque.

Se detectaron dos lagartijas típicas de matriz (*Sceloporus variabilis* y *Ameiva undulata*), que pueden invadir el interior de la selva (a 200 m del borde) haciendo uso del microhábitat generado por las aperturas en el dosel (Urbina-Cardona *et al.* 2006). Estas especies de áreas abiertas pueden competir con las especies de la selva por alimento, llegando incluso a cambiar su dieta insectívora y depredando algunas ranas y lagartijas. En el Apéndice II se determinó que las especies de áreas abiertas que invaden la selva no compiten por el microhábitat dado que se encuentran en condiciones ambientales muy particulares en la selva. La intrusión de estas especies a la selva puede ser controlada manteniendo microhábitat con alta densidad de sotobosque, cobertura de hojarasca y de dosel, y baja cobertura herbácea que provean ambientes húmedos y fríos (Urbina-Cardona *et al.* 2006).

Perspectivas para el manejo y conservación local de la herpetofauna

México es uno de los países con mayor diversidad de reptiles, más del 45% de los vertebrados mexicanos son serpientes y esa riqueza representa el 13.5 % del total mundial (Sánchez 1998). Esta alta diversidad confiere una obligación a México hacia la conservación de estos organismos símbolo carismático de las raíces históricas y ancestrales (Sánchez 1998). La reserva de Los Tuxtlas protege el 12% de la herpetofauna mexicana (Santos-Barrera *et al.* 2004) pero sus remanentes se encuentran amenazados por la deforestación (Mendoza *et al.* 2005) siendo la pérdida de hábitat, una de las principales causas de extinción de especies de anfibios y reptiles a nivel global (Gibbons *et al.* 2000, Semlitsch 2003).

Una gran cantidad de especies de reptiles se encuentran amenazadas directamente por el hombre dado que algunas son temidas y eliminadas, y otras son sobre explotadas para el comercio ilegal, su potencial uso en la medicina tradicional y la confección de prendas para vestir (Castaño-Mora 2002, Urbina-Cardona *et al.* 2006). Es imperante realizar talleres de sensibilización con la población de las comunidades aledañas a la reserva de Los Tuxtlas para determinar la percepción que tienen hacia los anfibios y

reptiles, y modificar las actitudes de rechazo y aversión al mostrarles la importancia de estos organismos para la “salud” de la selva y como indirectamente representan beneficios para ellos como el control de plagas.

Es importante mantener la heterogeneidad y conectividad en la región de Los Tuxtlas promoviendo el mantenimiento y creación de cercas vivas, vegetación ribereña, árboles inmersos en potreros, y acahuales en diferentes estadios de regeneración que permitan el flujo de especies de matriz y de borde de selva. Los fragmentos de tierras bajas son los más amenazados por la deforestación (Mendoza *et al.* 2005) por lo cual es importante mantener los escasos remanentes que aun conserven un hábitat de interior y hacer un manejo de los bordes para asegurar la calidad de hábitat para las especies de interior y mantener la representatividad de estos organismos en tierras bajas (Urbina-Cardona *et al.* 2006) dado que existen diferencias en diversidad y composición con las especies de tierras altas (*sensu* Hernández-Ordóñez 2005).

Los Tuxtlas: ¿conservación o restauración?

Veracruz es el estado que presenta mayores tasas de deforestación en el país (Aguilar *et al.* 2000). Las selvas mexicanas son la cuarta formación vegetal con mayor superficie (15.83%) en el territorio nacional (Velásquez *et al.* 2002); sin embargo, la Selva Alta Perennifolia se encuentra entre los siete tipos de vegetación más degradados en el país (Aguilar *et al.* 2000). Específicamente para la región de Los Tuxtlas, el 84% de la selva original ha sido transformada en áreas de potrero y cultivos (Dirzo y García 1992). Por ello la conservación y restauración de la mayor cantidad de remanentes de Selva Alta Perennifolia en el estado de Veracruz constituye una prioridad.

El aprovechamiento, la conservación y el manejo de especies silvestres, y la reintroducción de especies extintas localmente constituyen alternativas complementarias a la restauración ecológica entendida como el reestablecimiento de las comunidades destruidas o deterioradas (Martínez-Romero 2000). Sin embargo, dirigir el ecosistema para estimular una recuperación en la composición de especies y sus interacciones, para obtener un funcionamiento similar a la comunidad original (Martínez-Romero 2000) no siempre es posible o económicamente viable. Debido a la alta degradación en diversos aspectos físicos, ecológicos y culturales que explicaré a continuación, la restauración de

Los Tuxtlas es cada vez un sueño más lejano y las estrategias de conservación deben ser enfocadas a controlar la deforestación, preservar los remanentes y manejar las zonas que aun conecten gradientes altitudinales entre diversos tipos de vegetación.

El uso intensivo del suelo por parte de los habitantes de Los Tuxtlas (e.g. ganadería y cultivo de maíz), y la degradación de los fragmentos remanentes por el uso ilegal de la selva remanente (e.g. cacería de fauna y entresaca de árboles para aprovechamiento de madera) hace cada vez mas apremiante tomar medidas políticas y económicas viables para evitar su completa destrucción.

Se sabe que los potreros abandonados de Los Tuxtlas tienen el potencial de regenerarse en menos de tres años a un acahual diverso (95 especies de plantas de las cuales 46 son árboles que pueden llegar hasta los 4 metros de altura; Guevara *et al.* 2004a). Sin embargo, la selva de Los Tuxtlas puede haber perdido su capacidad de autosostenibilidad (*i.e.* capacidad de autopropagación sin ayuda del hombre; Martínez-Romero 2000) dado que las actividades antropogénicas durante las últimas cinco décadas han deteriorado la productividad del suelo y no ha permitido una regeneración significativa de la selva (Laborde 2004, Guevara *et al.* 2004b, Mendoza *et al.* 2005). Así mismo la interrupción de las interacciones bióticas por pérdida de mamíferos grandes y medianos (Dirzo y Miranda 1990) puede haber generado cambios en la polinización, dispersión y predación, cambiando la estructura y composición de la selva a un estado difícil de recuperar. En este estudio se demuestra que la estructura y composición actual de la herpetofauna en la selva remanente de Los Tuxtlas refleja un ambiente perturbado y se plantea que la comunidad puede haber perdido la capacidad de recuperar su configuración original, previa al disturbio. A pesar de la gran cantidad de inventarios y estudios herpetofaunísticos realizados en la región durante casi un siglo, quedará la incógnita acerca de cual fue la estructura de los anfibios y reptiles antes de que la mano del hombre deforestara esta región de manera tecnificada y masiva.

La región de Los Tuxtlas es uno de los bosques tropicales mas estudiados en el planeta y sus enseñanzas podrán evitar la toma de decisiones erróneas en otros ambientes tropicales; sin embargo, seguirá siendo el laboratorio natural de estudios de fragmentación de hábitat por excelencia ante la imposibilidad de generar una alta

conectividad entre parches y restaurar la estructura y composición de especies así como los procesos, mecanismos e interacciones originales.

Alternativas sociales para la conservación en Los Tuxtlas

Las comunidades rurales han perdido cada vez mas su conocimiento de la flora, la fauna y la medicina tradicional con las generaciones jóvenes, dado que la meta actual de los adolescentes es buscar un nuevo futuro en Estados Unidos y muchas mujeres jóvenes migran a las ciudades para trabajar como empleadas del servicio. Antagónicamente muchas personas ajenas a la comunidad han llegado a la región para refugiarse y esconderse en los ejidos, tratando de escapar de cuentas pendientes en las grandes ciudades. Esta cruda realidad lleva a una descomposición social en las comunidades aledañas que desconocen cada vez más sus raíces, su sentido de pertenencia por la selva y su conciencia de conservación por la vida.

A nivel global, la naturaleza tiende a ser administrada y controlada por las comunidades locales (Ramírez y Eccardi 2005) por lo cual la conservación de la biodiversidad dependerá en gran medida de los “stakeholders” que viven en las áreas de amortiguamiento de las reservas. En México la reapropiación del territorio puede desarrollar esquemas administrativos, técnicos y organizativos que permitan aprovechar sustentablemente los bosques y selvas (Ramírez y Eccardi 2005). El deseo del cambio de actividades rurales tradicionales (agricultura y ganadería) por parte de los habitantes de Los Tuxtlas ha llevado a algunas comunidades como la de Montepío a aprovechar el auge del ecoturismo. El alto potencial de la región por la convergencia de playas y selva, y la fácil observación de la fauna por su aglutinamiento en los remanentes, representan atractivos valiosos para la gente de las ciudades. Sin embargo, la identificación y apoyo de líderes comunitarios por parte de la Reserva de la Biosfera y autoridades municipales debe ser una prioridad para generar grupos locales de conservación que vigilen los fragmentos de selva remanente e informen a los visitantes sobre las actividades permitidas en la zona. Así mismo, es importante realizar talleres de sensibilización ambiental abarcando temas como la diversidad biótica de la selva, y los servicios que nos presta, y enfocar el conocimiento científico disponible para determinar y esclarecer el posible impacto ambiental de las actividades turísticas, la capacidad de carga para

soportar cierto número de visitantes, el manejo de basuras en los sitios de campamento y el diseño de senderos que no involucren áreas vulnerables, inestables o de alta importancia para la conservación (e.g. sitios de reproducción de especies, sitios específicos de alimentación o refugio).

El ecoturismo sustentable en Los Tuxtlas podría enfocarse en actividades recreativas, de apreciación de la naturaleza y educación ambiental mediante el contacto directo con la selva y sus habitantes (Gómez-García y Dredge 2003). Este tipo de actividades puede reducir la deforestación en la medida que promueve la conservación, y sustentabilidad, le agrega un valor económico a la naturaleza y reorienta la política del gasto público (Gómez-García y Dredge 2003), siempre y cuando se fortalezcan las comunidades en sus capacidades técnicas, administrativas, organizativas, financieras y legales (Ramírez y Eccardi 2005). Se debe tener en cuenta que el ecoturismo puede ser una herramienta autosuficiente para la conservación y una alternativa para el progreso económico de las comunidades a largo plazo, en la medida en que venga acompañado por un manejo sustentable planificado, riguroso, cuidadoso y respetuoso del medio natural (Gómez-García y Dredge 2003). Una experiencia local del éxito del ecoturismo comunitario se encuentra en Peña Hermosa, (Veracruz) donde se vinculan actividades recreativas, educativas con la naturaleza y la comunidad aledaña (*citado en* Gómez-García y Dredge 2003).

Otras dos alternativas económicas viables y sostenibles para las comunidades de la región, son el cultivo de especies no convencionales (Ticktin *et al.* 2002) y el manejo en cautiverio de algunas especies animales con potencial para la comercialización. Para esta última alternativa es necesario determinar la factibilidad de zootecnia de especies como *Iguana iguana*, *Boa constrictor*, *Chaunus marinus*, *Lithobates berlandieri*, *Bothrops asper* y *Micrurus* spp. que podrían ser comercializadas para el consumo de huevos y carne, el uso de pieles para la confección de prendas de vestir, el uso para medicina tradicional y brujería, y la extracción de venenos para la fabricación de sueros antiofídicos.

En la medida que las comunidades rurales actuales y futuras de Los Tuxtlas puedan vivir del redescubrimiento de la selva, volverán a encontrar sus raíces, rescatarán el conocimiento tradicional, la conservación se realizará por convicción y no por

obligación. De esta manera los usos y costumbres podrán apoyar al conocimiento científico abstracto con un mismo fin, proteger la vida.

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APÉNDICE I

USO DEL HÁBITAT POR PARTE DE LOS ANFIBIOS Y
REPTILES DE LA SELVA DE LOS TUXTLAS, VERACRUZ.

TITLE PAGE

Microhabitat use of amphibians and reptiles in a highly fragmented tropical rainforest at Los Tuxtlas, Eastern México

J. Nicolás Urbina-Cardona

Víctor Hugo Reynoso

Colección Nacional de Anfibios y Reptiles, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México. C.P. 04510 México, DF, Mexico

Running title: Microhabitat use by tropical amphibians and reptiles

Corresponding author: Victor H. Reynoso. Telephone +52 (55) 5622 9153.

Fax: +52 (55) 5550 0164 E-mail address: vreynoso@ibiologia.unam.mx

Abstract

Habitat use of tropical amphibians and reptiles could be affected in highly fragmented landscapes reflecting how different organisms take advantage of physical or biological resources in disturbed environments. We determined patterns of spatial niche overlap and nested distribution in a tropical rainforest herpetofauna at Los Tuxtlas region, Veracruz, Mexico. After 576 man-hours we recorded 1484 amphibians of 18 species and 636 reptiles in 34 species. The greatest diversity of amphibians was found on horizontal branches, leaves, and vertical trunks, while the greatest reptiles' diversity was found on bare soil and leaf litter. Using null model analysis we found that amphibian and reptile distribution was not different from that expected by chance, concluding that there is no spatial overlap. Although the observed variances were significantly lower than expected by chance, showing some internal guild structure in resource use. The analysis of nested subset patterns indicated that at Los Tuxtlas, frog, lizard and snake assemblages exhibited a nested distribution within microhabitat types driving two possibilities: nestedness at microhabitat level evidence high degree of disturbance in forest remnants or could just indicate a lack of environmental heterogeneity at the forest remnants. Additional data for tropical highly fragmented landscapes describing species activity in each microhabitat, in relation to diet, sex, age and body size overlap needs to be gathered in the future.

Key words: Amphibians, Reptiles, microhabitat, species diversity, Null model, Spatial Niche Overlap, Nestedness.

INTRODUCTION

Habitat is defined as the site holding necessary resources and conditions that permits the presence of a given species, its survival and reproduction (Hall et al. 1997). Habitat selection is a hierarchical process that involves innate and learned decisions about how physical and biological resources of the habitat are used at different environmental scales (Krausman 1999, Hofer et al. 2004). The spatial distribution of the amphibian and reptile species is given by the interaction between species, the physiological requirements of the organisms, the availability of resources (e.g. food, refuges, reproduction, thermoregulation sites, escape routes, among others) and the physical features of the habitat (Zug et al. 2001). Factors such as the reproductive condition, sex, digestive and foraging state, ecdysis, social relationships, learning, effect of diseases, injuries and parasites, affect the use of habitat in animals such as snakes (Reinert 1984). Hofer et al. (2004) determined that at undisturbed sub-montane forest at Cameroon, reptiles tend to reduce potential interspecific competition, while amphibians may be more constrained by resource requirements (e.g. breeding sites) than by competition. Species coexistence can reflect spatial and temporal niche partitioning at different scales (Albrecht and Gotelli 2001). Actually there is no basic reference information on the habitat use of herpetofauna assemblages inhabiting Neotropical fragmented landscapes.

Due to habitat fragmentation and their consequent disturbance, affects species composition at tropical forest remnants (Laurance et al. 2002), we hypothesize that the herpetofauna inhabiting Los Tuxtlas rainforest remnants is a subset of the richer original “undisturbed” community (sensu nestedness; Atmar and Patterson, 1993) and if these are highly nested, it is an indication of extensive fragmentation and human disturbance at the region. We compared amphibian and reptile species abundance, richness and diversity among different microhabitat types at the Los Tuxtlas tropical rainforest. We identify non-random distribution patterns in the composition of amphibian and reptile assemblages. Finally we generated null models to test which is the probability that spatial niche overlap pattern were produced by chance alone, and to detect internal guild structure in resource use. This study aims to contribute to a better understanding of

microhabitat use on amphibians and reptiles inhabiting in a highly fragmented tropical rainforest at Los Tuxtlas lowlands.

METHODS

Study site

The study was carried out between 35 and 300 m of elevation in the tropical rainforest at the Biosphere Reserve Los Tuxtlas, in the state of Veracruz, situated on the southwestern coast of the Gulf of México (N 18°32' to N 18°38'; W95°03' to W95°06'). The mid annual temperature is about 27 °C, fluctuating between 35 °C in May to 13 °C in February (Soto and Gama 1997). The annual mean precipitation is 4964 mm (SD 862, n = 20 years) showing a marked dry season from March to May.

The study site was selected analysing digital aerial photographs with direct corroboration in the field. We identified six fragments between 26 to 420 ha of well preserved tropical rainforest surrounded by induced pasture. According to owners and farm keepers the fragments do not have perturbation since 15 years ago. These forest fragments are some of the last lowland faunal refuges at Los Tuxtlas since lowland rainforest has been largely eradicated reflecting a considerable fragmentation of the forest between 0 and 330 m of elevation (Mendoza et al., 2005). Each selected fragment had at least one stream to prevent that water absence bias results as a limiting factor to strong water dependence organisms (i.e. amphibians for reproduction). Twelve transects of 50 m length were placed in each fragment with the exception of the largest fragment where 48 transects were placed, giving a total of 108 transects of 50 x 2 m in the whole study. A detailed description of the criteria for fragment selection, research design, survey method and the relationship between herpetofauna diversity and microenvironment variables is provided by Urbina-Cardona et al. (2006).

Amphibian and Reptile survey

Four field seasons searching throughout all transects were completed in June-July and September-October, 2003, February-March and May, 2004. Each transect was surveyed by two persons 20 minutes day and 20 minutes night, accumulating 576 man-

hours total. The transects were surveyed walking along the 50 m recording visual encounters of all amphibians and reptiles observed within a meter on each side of the transect and up to 2 meters high only, for a high efficiency in detecting organisms along the forest understory (Urbina-Cardona and Reynoso 2005).

To describe the microhabitat use of the amphibian and reptile species we recorded the number of individuals of each species, separating juvenile and adult stage categories. On each observed organism we annotated first encounter substrate (leaves, leaf litter, branch, rock, vertical trunks, or bare soil) and day or night temporality. We analyze total abundance of each species on each substrate (microhabitat type), without separating juvenile and adult stages, to gain robustness when working with rare species such as snakes.

Data Analysis

To describe the composition and microhabitat use structure of amphibian and reptiles species we used the number of species (specific richness) and the proportional distribution of the importance value of each species in the community (equitability). The equitability was determined by using natural Logarithm based Shannon diversity index, with values ranging between zero and the logarithm of maximum richness when all species are represented by the same number of individuals (Magurran, 2004). It expresses the uniformity of the important values throughout all founded species (Magurran 1988) and measures the degree of uncertainty to predict to which species an individual of the collection would belong (Pielou 1977, Magurran 1988), raising the importance of rare species in the sample (Brower et al. 1998). This index assumes that all species are represented in a homogeneous sample and that all individuals are randomly sampled (Pielou 1975, Magurran 1988, Zar 1999). This index permits to subdivide the scale analysis within the community and to work with additive components such as the microhabitat diversity (Pielou 1977). We assume that when a substrate has high species diversity it supports more available niches for the herpetofauna. Bootstrap analysis and the Solow (1994) index were used to detect differences in diversity index among two microhabitat combinations. Bootstrap analysis estimates 95% confidence intervals to compare graphically between Shannon indexes, and Solow index resample 10000 times

from a distribution of species abundance produced by a summation of the two samples (two compared microhabitat). In the Solow index, the difference between the Shannon index in two microhabitat is called delta. To determine whether the differences between the observed indexes values of two samples were generated randomly, the observed values are compared against the distribution of delta values generated randomly (Henderson and Seaby 2002).

We report the dispersion model for each species (whether the organisms are distributed at random, aggregated or uniform through the samples, Brower et al. 1998) based on the variance of the number of individuals in the six evaluated microhabitat (leaves, leaf litter, branch, rock, vertical trunks, or bare soil), Chi-squared tests were used to measure patchiness in species populations using the Species Diversity and Richness 3.02 software (Henderson and Seaby 2002).

We compared the species abundance among different substrate types using non-parametric Kruskal-Wallis test, and differences were detected using the Fisher LSD test (Zar 1999). All, data were analyzed using Statistica 6.0 software (StatSoft, 2001).

To quantify patterns of spatial niche overlap between a given pair of species, we calculated the Pianka's (1973) niche overlap index. This index measures the relative amount of habitat overlap between each pair of species and ranges from a minimum of zero if no shared habitat, to a maximum of one if an identical habitat use. In this analysis a separate index is calculated for each pair of species in the assemblage. So, if we have 52 species in the assemblage, there will be $52(52-1)/2$ unique pairwise indices calculated. We obtained a symmetric matrix of 1326 pairwise niche overlaps, calculated using Pianka's (1973) niche overlap index. To determine which is the probability that a given ecological pattern is produced by chance alone, we generated null models by randomizing the utilization of real data according to algorithm RA2 with Niche breadth relaxed and Zero States retained, and created 1000 null assemblages in EcoSim software (Gotelli 2001, Gotelli and Entsminger 2001). In this way we ensure that the utilization of levels are equiprobable for any microhabitat, and that zeroes in the observed matrix is maintained in each simulated matrix (Gotelli and Entsminger 2001). Thus for example, exclusive terrestrial species will not appear using arboreal microhabitat (e.g. leaves, branches or vertical trunks) in the simulation matrices, and vice versa. We calculated the

mean and variance niche overlap of all possible species pairs and compared the observed mean and variance to the distribution of the simulated ones. We calculated the two-tailed probability values by tabulating the number of simulated niche overlaps that were greater or less than the observed overlap. Interspecific competition should cause mean niche overlap to be less than expected by chance; whereas environmental constraints on activity, might cause all species to have similar microhabitat use patterns, so that observed niche overlap would be greater than expected (Albrecht and Gotelli 2001). Inger and Colwell (1977) showed that if there is a guild organization within the species assemblage, the variance in niche overlap will be greater than expected. Finally to graphically describe the similarity of niche overlap index of Pianka (1973) for amphibian and reptile species we used the symmetric matrix of 1326 pairwise niche overlaps and we constructed a cluster using UPGMA algorithm in Statistica 6.0 software (StatSoft, 2001). The UPGMA niche-overlap dendrogram is useful to describe the ecological similarities of species and the pattern of relative abundances (Sugihara et al. 2003).

Finally, we used an analysis of nestedness to identify a non-random distribution patterns in the composition of amphibian and reptile assemblages within microhabitat types, where species assemblages of sites with lower richness are subsets of the biota at the richer sites (Wright and Reeves 1992, Higgins et al. 2006). We prepared data by constructing presence/absence matrices where columns were species and rows were microhabitat. To quantify nestedness of assemblages we used the nested temperature (T) method (Atmar and Patterson, 1993) calculated with the Nestedness Temperature Calculator computer program (Atmar and Patterson, 1995) which measures the deviation of an observed presence-absence matrix from a perfectly nested one of equal size (Pineda and Halffter 2004). Values for T range from 0o for perfectly nested assemblages showing a maximum order on the presence/absence matrix structure; to 100o for completely randomly ordered assemblages indicating matrix disorder. Because the degree of nestedness in a system differ among taxa orders (anuran, salamanders, lizard and snake species; Hecnar et al. 2002) we calculated T metric for each order at all microhabitat. To determine the significance of T observed temperature, it is compared with the distribution of simulated temperatures produced by 1000 randomizations of the presence/absence matrix in Monte Carlo simulations.

RESULTS

Species Diversity

After 576 man hours we recorded more amphibians (1484 individuals) than reptiles (636 individuals); and in both taxa more adults (884 amphibians and 436 reptiles) than juveniles (600 amphibians and 200 reptiles). The diversity and richness of reptiles ($H' = 1.87$; 34 species) was significantly larger ($\Delta = 0.4$) than that of amphibians ($H' = 0.78$; 18 species) (Table 1). Amphibian ($\Delta = 0.37$) and reptile ($\Delta = 0.45$) diversity was significantly larger in adult organisms when compared to juveniles.

We found that the anuran *Craugastor rhodopis* is the most abundant amphibian species in the Los Tuxtlas rainforest. Among 18 species of amphibians, *C. rhodopis*, were the only species to be uniformly distributed. Eight amphibian species were randomly distributed, indicating that each organism has the same probability to occupy a given place and that the presence of an individual does not affect the distribution of another (Brower et al. 1998). Finally, nine amphibian species were aggregated (Table 2) meaning that once an individual of a given species is found there is an increased probability of finding another one of the same species nearby. Of the 1484 amphibians total captures, 1301 captures were of the family Brachycephalidae while the remaining captures were represented by Leptodactylidae, Microhylidae and Ranidae. The dominant amphibian species were *C. rhodopis* with 84.3% of all amphibians captures, followed by *Ollotis valliceps* and *Nanotriton rufescens* with 4 and 3.5% of the entire amphibian captures respectively. *Chaunus marinus*, *Craugastor berkenbuschi*, *Dendropsophus microcephala* and *Lithobates vaillanti*, were the rarest species in the tropical rainforest with less than two captured individuals (Table 2).

Of the 34 species of reptiles, 24 were randomly distributed, 10 aggregated and none with uniform distribution (Table 2). Of the 636 total reptile captures, the family Polychrotidae was the most abundant with 422 individuals while the least abundant were Elapidae and Gekkonidae. The dominant species were the anole *Anolis uniformis* (57.2% of the total captures), followed by *Plestiodon sumichrasti*, *Corytophanes hernandezi* and *Scincella cherriei* (with 8.3, 5.5 and 4.2% of the total captures of the reptiles

respectively). Most of the species of the family Gekkonidae, Iguanidae, Elapidae, Boidae and Colubridae (but *Imantodes cenchoa*), were rare in the tropical rainforest (Table 1).

Habitat diversity and use

Most amphibians were recorded during day time (1005 individuals) but most amphibian species were recorded at night (16 species), increasing night diversity ($H' = 1.448$). The amphibian diversity was significantly larger at night ($\Delta = 1.15$). More reptiles were recorded at day time (495 individuals) same among reptile species (26 species), although night diversity was significantly higher ($H' = 2.32$; $\Delta = 0.83$). The amphibian and reptile diversity increased at night because of the reduction in counts of the most abundant amphibian (*C. rhodopis*) and reptile (*A. uniformis*) species (Table 1).

Most amphibians were recorded on the ground using leaf litter (1069 individuals of 12 species) and over the leaves above the ground (285 individuals of 11 species). Most diverse substrates used by amphibians were horizontal branches ($H' = 1.71$), leaves ($H' = 1.4$) and vertical trunks ($H' = 1.28$) because of the low abundance of the dominant species *C. rhodopis* (Table 2, Fig 1). Amphibian diversity on branches was significantly more diverse than diversity on the other substrates ($\Delta = 0.42$). The abundance of amphibians was not significantly different between the substrates used (Kruskal-Wallis test $H = 18.28$, $p = 0.26$). We recorded 12 in leaf litter, 11 species of amphibians in leaves, 7 in branches, 7 in trunks, 4 in bare soil and 2 in rocks. The use of leaves was dominated by *C. rhodopis* with 58% of the recorded amphibians in this substrate, followed by *N. rufescens* (17.5%), *Craugastor alfredi* (7%), *Tlalocohyla loquax* (5.2%) and *Syrrhophus leprus* (4.2%); leaf litter was dominated by *C. rhodopis* (92.9%) and by *C. valliceps* (4.4%); branches were dominated by *Smilisca baudini* (33.3%) and *C. rhodopis* (26.6%); rocks were dominated by *C. rhodopis* (85%); trunks were dominated by *C. rhodopis* (62.8%), *C. valliceps* (9.3%) and *S. leprus* (9.3%); and bare soil also was dominated by *C. rhodopis* (84.6%) (Table 2).

Most reptiles were recorded on leaf litter (347 individuals of 27 species) and in tree trunks (137 individuals of 17 species). As a general pattern, all substrates were highly diverse. The greatest diversity of reptiles was found in bare soil ($H' = 1.678$) and leaf litter ($H' = 1.662$) (Table 1, Fig 1), showing no statistical differences ($\Delta = -0.01$).

The abundance of reptiles was different among the used substrates (Kruskall-Wallis test $H = 40.18$, $p = < 0.005$). Differences were between use of leaf litter and leaves ($p = 0.032$); leaf litter and branches ($p = 0.018$), leaf litter and rocks ($p = 0.024$) and leaf litter and bare soil ($p = 0.013$). We recorded 27 species of reptiles on leaf litter, 17 on vertical trunks, 11 on leaves, 8 on branches, 7 on bare soil, and 6 on rocks. Leaves were dominated by *A. uniformis* and *I. cenchoa* with 54% and 19.6% respectively of all recorded reptiles in this substrate; leaf litter by *A. uniformis* (58.7%), *Plestiodon sumichrasti* (13.5%), *Scincella cherriei* (7.3%), *Ameiva undulata* (4.6%), and *Anolis barkeri* (2.3%); branches by *A. uniformis* (63.3%), *I. cenchoa* (10%), *Iguana iguana* (6.6%) and *A. sericeus* (6.6%); rocks by *Corytophanes hernandezi* (45.6%) and *A. uniformis* (34.7%); trunks by *A. uniformis* (66.4%), *Lepidophyma tuxtlae* (5.1%) and *C. hernandezi* (3.6%); and bare soil by *C. hernandezi* (40%), *L. tuxtlae* (20%) and *P. sumichrasti* (13.3%) (Table 2).

The amphibian and reptile mean overlap value obtained from the average of the pairwise values in the pairwise tab was 0.42, and the mean of simulated indices was 0.41. The simulation suggests that the observed mean were not statistically different from the null model (p for observed $<$ than expected = 0.68; p for observed $>$ than expected = 0.31), indicating that there is no spatial niche overlap. But the observed variance niche overlap were significantly lower than expected by chance (p for observed $>$ than expected < 0.0001), showing some internal guild structure in resource use, in which some species pairs are very similar in resource use and others are very dissimilar (Winemiller and Pianka 1990). We identified some species with most similar resource utilization (highest Pianka's pairwise overlap). *Ameiva undulata*, *Scincella cherriei*, *Plesiiodon sumichrasti*, *Anolis biporcatus*, *Anolis c.f. duellmani*, *Boa constrictor*, *Craugastor berkenbuschi*, *Ctenosaura acanthura*, *Ficimia publia*, *Gastrophryne elegans*, *Pseustes poecilonotus*, *Rhanidea decorata*, *Sphaerodactylus glaucus*, *Stenorhina degenhardti*, *Ollotis valliceps*, *Craugastor rhodopis*, and *Leptodactylus fragilis*, have an identical Pianka's spatial niche overlap value. At 0.5 linkage distance we identified six general clusters of species with the most dissimilar resource utilization (lowest Pianka's overlap) and shared microhabitat (Fig. 2).

The analysis of nested subset patterns indicated that frog assemblages in the tropical rainforest at Los Tuxtas exhibited a nested distribution ($T=12.570$, $p=<0.05$) as

oppose to salamanders ($T=56.340$, $p=0.95$). Nested subset analysis patterns indicated a nested distribution of lizard ($T=15.350$, $p<0.05$) and snake ($T=23.180$, $p<0.05$) assemblages.

DISCUSSION

Species Diversity and Composition

During this study, we captured 51% of all amphibian and 49.3% of all reptile species known in eastern Los Tuxtlas region (Perez-Higareda unpublished data) reported at low altitudes habitat (including elements such as forest fragments, riparian vegetation, body waters, cultivated tree areas, live fences crossing a larger pasture matrix and anthropogenic elements that include roads, farms, and villages). Current sampling did not record some amphibians and reptile species such as *Agalichnis callidryas*, *Tlalochoyla picta*, *Smilisca cyanosticta*, *Hemidactylus* spp., and *Lepidophyma pajapanensis*, *Leptodactylus melanonotus* and *Lithobates berlandieri*, that have been reported before as common and abundant along the Tropical rainforest areas in the region (Vogt 1997). This could be due to changes in rarity and commonness of amphibian and reptile species inhabiting Los Tuxtlas rainforest during last decades (Urbina-Cardona and Reynoso 2005). Another possibility is that some not registered species (or registered such as rare species) were not sampled during this study because they are associated to body waters (such as lakes) or disturbed habitats (such as pastures), not included in this study. Patterns of habitat use in some species such as *Agalichnis callidryas*, *Tlalochoyla picta*, *Lithobates vaillanti*, *Gastrophryne usta*, *Smilisca baudini*, *Leptodactylus labialis*, *Dendropsophus microcephala*, and *Dendropsophus ebraccatus* could be displaced to local streams, lakes and rivers because of the absence of suitable microhabitat to forage and reproduce inside and outside the remnant lowland rainforest at Los Tuxtlas.

Activity patterns and Diversity measurement

Effects of abundance reduction on most dominant species of the community is caused by the greater diversity of amphibians and reptiles found at night. The larger proportion of amphibians found during the day do not necessarily mean that the species of this group are diurnal. It is well known that amphibian species at Los Tuxtlas are

mostly nocturnal and reptile species are mostly diurnal (Vogt 1997, Urbina-Cardona and Reynoso 2005). If we eliminate data of *C. rhodopis*, the most abundant diurnal specie, 88.8% of the remaining amphibians were certainly captured at night showing true nocturnal habits for amphibians. It is important to take care when attributing day/night habit community patterns based exclusively in abundance values and ignoring activity patterns. Some diurnal cryptic organisms could be easily detected at night when they are exposed and inactive on more conspicuous substrates. So abundance data naïvely registered not necessarily reflects amphibian and reptile activity.

The Shannon index is an equitability value that relates the number of species with the abundance of each species (French, 1994). Because the information is thrown in a single value (H'), it is important to contrast the indexes against the abundance in the original data matrix. Our study supports a diversity decrement caused by an increment on the abundance of most dominant amphibian and reptile species. When *C. rhodopis* provides more than the 80% of the total amphibian individuals recorded in any substrate (e.g. leaf litter, rocks, and bare soil), the Shannon index in this microhabitat is reduced from values greater than 1, to values lower than 0.6 (Table 2). When *C. rhodopis* decreases their dominance in arboreal substrates such as leaves, branches and trunks (58%, 26%, and 63% of the total amphibians respectively) its Shannon index fluctuates between $H' = 1.28$ and $H' = 1.71$. This is good evidence that the Shannon diversity index is sensitive to species dominance, causing an abrupt decrease in its value because of species dominance.

In this study we reported Shannon index values to compare diversity between substrates, and to determinate some patterns of microhabitat use by amphibian and reptiles at Los Tuxtlas. However, we have to keep in mind that Shannon diversity index values are the synergistic result of several factors such as sample size, research design (response unit, sample unit, number of repetitions, and replicates) and habitat heterogeneity (Hayek 1994, Clarke and Warwick 2001). Extrapolation of diversity values driven from this study, to other regions or organisms should be done with caution.

Microhabitat use of Amphibians and Reptiles

The larger proportion of visual encounters (60% of the amphibians and 69% of the reptiles), species richness (18 amphibians and 32 reptiles), and diversity ($H' = 0.9$ amphibians and $H' = 1.985$ reptiles) was recorded in adult animals. The great proportion of adult organisms in all recorded species (with the exception of *Rhadinaea decorata* and *Coniophanes imperialis*) suggest the use of microhabitat relatively exposed by adults, while juveniles are kin to more secretive microhabitat or they have lower probability of detection. To detect rare and fossorial species it is important to complement visual encounter surveys with other techniques such as pitfall traps, frog vocalization registers, surveys on reproduction sites, among others. By using complementary techniques in the future we could be able to answer a question driven from this work: Are there fewer juveniles because of the effect of fragmentation on the breeding success of adult at Los Tuxtlas rainforest remnants?.

It is known that microhabitat is differentially used by amphibians and reptiles depending on stages (adults or juveniles), sexes, activity (territoriality, courtship, refuge, hibernation, feeding), staging (reproductive, ecdysis, diseases or injuries) or temporality (dry and rain season, or, diurnal or nocturnal activity) (Reinert 1984). Particularly for Los Tuxtlas, seasonality-habitat interactions have strong effects on amphibian and reptile composition (JNUC and VHR unpublished data) and herpetofauna structure pattern is explained during wet season by the combination of canopy cover, temperature, and leaf litter cover; while during dry season this structure pattern is explained by the combination of distance to streams, temperature, leaf litter depth and leaf litter cover (Urbina-Cardona et al. 2006). We expect that microhabitat use of amphibians and reptiles could change between seasons at the tropical rainforest at Los Tuxtlas. Patterns of microhabitat use shown in this study are a general but robust basis for later smaller scale analysis at the population level and spatio-temporal gradients at neotropical highly fragmented landscapes. With our survey we found that substrate mostly used by amphibians was leaf litter. This pattern is reflect of microhabitat use of the most dominant amphibian species (*C. rhodopis*) found showing a uniform distribution pattern in terrestrial habitats. Uniform distribution pattern is rare among animals and it is usually associated to territoriality, use of exclusive areas, and competition for food or space (Ludwig and

Reynolds 1988). When removing data of *C. rhodopis* from the analysis, leaf litter is used as much as bare soil or rocks over where land dweller species were found: *Pseudoeurycea orchimelas*, *Craugastor berkenbuschi*, *Craugastor vulcani*, *Leptodactylus fragilis*, *Ollotis valliceps*, *Chaunus marinus*, *Gastrophryne elegans* and *Lithobates vaillanti*, among others. On the other hand, most diverse substrates were arboreal substrates (e.g. leaves, branches and vertical trunks) dominated principally by *Smilisca baudin*. High diversity in arboreal substrates indicates that low abundances of *C. rhodopis* (which is assumed to compete hardly for space) allow more niches for other amphibians in the tropical rainforest. The diurnal species *C. rhodopis* uses the arboreal substrate occasionally to “sleep” at night without competing actively at this microhabitat for space or food with other species.

Reptiles were highly diverse in all microhabitat, but were more abundant in leaf litter (used by *A. uniformis*, *Plestiodon sumichrasti*, *Scincella cherriei*, *Ameiva undulada* and *Anolis barkeri*) and in trunks (used by *A. uniformis*, *Lepidophyma tuxtlae* and *Corytophanes hernandezi*). *A. uniformis*, the most abundant lizard among the reptile community, has densities of more than one individual per hectare (Villarreal and Heras 1997) but has a similar microhabitat use to other anole lizards (*A. petersi*, *A. lemurinus*, and *A. barkeri*). The dominance of this species is replaced by *C. hernandezi* in rocks and bare soil. This arboreal species inhabits medium stratum rainforest and during dry season can descent to leaf litter stratum (Vogt et al. 1997). Abundance patterns on amphibians and reptiles using different microhabitat, reflects a dynamic microhabitat use at Los Tuxtlas rainforest, with some exchange in composition and dominance among substrates.

Spatial Niche Overlap

Null model analyses of whole assemblage offer a rigorous alternative to investigate community properties that are difficult to reveal by experiments (Morin 1999, Gotelli 2001). Our study showed that amphibian and reptile distribution was not different to that expect by chance, suggesting that there was no spatial overlap. But the observed niche overlap variance was different to that expected by chance, indicating some internal guild structure in resource use (sensu Winemiller and Pianka 1990). In the neotropical rainforests such as Los Tuxtlas the population densities of some dominant frogs (*C.*

rhodopis) and lizards (*A. uniformis*) are maintained high. This could reflect a differential use of microhabitat, optimum exploitation of the available resources and less niche overlap, reducing the interspecific competition of species and allowing a differential distribution and use of the physical environment (MacArthur and Pianka 1966, MacArthur 1968, Shoener 1974).

If interspecific competition determines communities' structure, ecologically similar species should tend to have not overlapping spatial ranges at local scale (Gainsbury and Colli 2003, Hofer et al. 2004). At Los Tuxtlas, mean spatial niche imply that rainforest amphibian and reptile species may not exhibit high niche overlap (sensu Hofer et al. 2004). The spatial niche overlap at the highly fragmented region of Los Tuxtlas (0.42) is similar to that found in frogs (0.44) inhabiting the undisturbed submontane forest of Cameroon (Hofer et al. 2004). However, processes and mechanisms generating species low spatial niche overlap could be particular for each site (e.g. forest type, topography, elevation, management history, disturbance regimes, surrounding matrix type and use) and sampling (e.g. research design, survey technique, and area surveyed). Given the highly fragmented nature of Los Tuxtlas, we suggest that relative species overlap may not be suitable as a guide to perturbation or degree of conservation of a given site.

Species coexistence and habitat use is a widespread descriptor of niche partitioning at several spatial scales (Albrecht and Gotelli 2001). Linking species abundance and dendograms of spatial niche provides similarly a framework for understanding the effects of ecological factors on abundance distributions (Sugihara et al. 2003). Sugihara et al. (2003) suggested that species that are highly nested in the dendogram are on average less abundant than species from branches less subdivided. Contrary to Sugihara et al. (2003), we found that rare species such as *C. vulcani*, *L. vaillanti*, *I. iguana*, *Micrurus diastema* and *Dryadophis melanonotus* were on less subdivided branches (Fig. 3). While *C. rhodopis* and *C. valliceps* the most abundant species, were nested with *L. fragilis* one of the the least abundant species.

Sugihara et al. (2003) proposed that more equitable communities abundance are associated with more branched dendograms. Herpetofauna community inhabiting tropical rainforest lowlands at Los Tuxtlas do not follow this pattern, being dominated by one

frog (*C. rhodopis* representing 84.3% of all amphibians captures) and one lizard (*A. uniformis* representing 57.2% of all reptiles captures), and drive assemblages to low equitability values. The distribution of abundances of amphibian and reptile assemblages are disequitable and (following Sugihara et al. 2003) influenced by a single strong and dominating ecological pattern. Although to identify this pattern additional data for tropical highly fragmented landscapes describing species activity in each microhabitat, in relation to diet, sex, age and body size overlap, needs to be gathered in the future.

Amphibians and Reptiles distribution patterns and nestedness

The spatial pattern of animal species is an important characteristic of ecological communities (Ludwig and Reynolds 1988). We reported ten amphibian species and ten reptile species showing an aggregated spatial pattern at Los Tuxtlas tropical rainforest.

Aggregated distribution is a very common pattern for animals and it reflects an attraction of individuals to a common resource, a patchy resource distribution and environmental heterogeneity (Ludwig and Reynolds 1988, Brower et al. 1998). At Los Tuxtlas five species (*Ollotis valliceps*, *Craugastor vulcani*, *Plestiodon sumichrasti*, *Scincella cherriei*, and *Imantodes cenchoa*) show faunal agglutination in forest remnants and were reported as forest interior habitat quality indicators (Urbina-Cardona et al. 2006).

In this study a 70.6% of reptile species and 44.4% of amphibian species presented a random dispersion pattern. This distribution pattern implies environmental homogeneity and nonselective behavioral patterns (Ludwig and Reynolds 1988). Random placement of individuals predispose natural systems to show patterns of nestedness at the species level (Higgins et al. 2006). At Los Tuxtlas lowland rainforest fragments, we founded that frog, lizard and snake assemblages exhibited a nested distribution pattern. Nestedness occurs where assemblages in a series of depauperate sites are comprised of species that constitute subset of species that occurs in successively richer sites (Hecnar et al. 2002). Atmar and Patterson (1993) proposed a tendency in which species inhabiting fragmented landscapes exhibited patterns of pronounced nestedness, and, Fernandez-Juricic (2002) showed that human disturbance promote nestedness in highly disturbed fragments. This pattern was also found by Pineda and Halffter (2004) that found that anuran assemblages

in a fragmented landscape exhibited a nested distribution among the anthropogenic habitat (coffee plantations and pasture), but not in the tropical montane cloud forest at Veracruz, Mexico. If frog, lizard and snake nested distribution patterns are a strong evidence of the great degree of disturbance in forest remnants at Los Tuxtlas region, amphibian and reptile species local extinction and colonization maybe has been influenced by habitat fragmentation and now they could exhibit an extinction-driven community assembly pattern. At our knowledge this is the first study of microhabitat use and species diversity inhabiting a highly fragmented landscape. So, at the microhabitat level conclusions could be different... As demonstrated before there is no amphibian and reptile spatial niche overlap within microhabitat types, so nestedness between microhabitat could just indicate a lack of environmental heterogeneity and a resulting community of generalist species inhabiting the forest remnants.

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Table 1. Habitat diversity of amphibian and reptile species inhabiting the tropical rainforest of Los Tuxtlas, Veracruz.

ORDER	Variable	Total	Stage		Substrate*						Day	Night
			Juvenile	Adult	1	2	3	4	5	6		
Amphibians												
	Number of individuals	1484	600	884	285	1069	15	20	43	52	1005	479
	Species richness	18	8	18	11	12	7	2	7	4	11	16
	H' Shannon log e	0.78	0.525	0.9	1.4	0.36	1.71	0.42	1.28	0.58	0.3	1.45
Reptiles												
	Number of individuals	636	200	436	61	347	30	46	137	15	495	141
	Species richness	34	18	32	11	27	8	6	17	7	26	24
	H' Shannon log e	1.87	1.528	1.99	1.5	1.66	1.33	1.29	1.49	1.68	1.49	2.32

* Substrate type: 1. Leaves, 2. Leaf litter, 3. Branches, 4. Rock, 5. Vertical trunks, 6. Bare soil.

Table 2. Dispersion models (DM) and microhabitat use of amphibians and reptiles in the tropical rainforest of Los Tuxtlas, Veracruz.

ORDER Family	Species	Species codes	DM*	Stage		Substrate**						Day	Night
				Juvenile	Adult	1	2	3	4	5	6		
CAUDATA													
Plethodontidae	Bolitoglossa alberchi	Boli_al	R	0	4	2	0	2	0	0	0	0	4
	Nanotriton rufescens	Nano_ruf	A	32	20	50	1	1	0	0	0	0	52
	Pseudoeurycea orchimelas	Pseu_orc	R	1	3	0	0	0	3	1	0	3	1
ANURA													
Bufonidae	Chaurus marinus	Chau_mar	R	0	1	0	1	0	0	0	0	1	0
	Ollotis vallicept	Cran_val	A	28	32	5	47	1	0	4	3	40	20
Brachycephalidae	Craugastor alfredi	Crau_alf	A	10	15	20	4	0	0	1	0	1	24
	Craugastor berkenbuschi	Crau_ber	R	0	1	0	1	0	0	0	0	1	0
	Craugastor rhodopis	Crau_rho	U	526	725	166	993	4	17	27	44	946	305
	Craugastor vulcani	Crau_vul	A	1	3	0	0	0	0	0	4	0	4
	Syrrhophus leprus	Syrr_lep	A	1	19	12	4	0	0	4	0	1	19
	Leptodactylidae	Leptodactylus fragilis	Lept_fra	A	0	6	1	5	0	0	0	0	3
Microhylidae	Gastrophryne elegans	Gast_ele	A	0	5	0	5	0	0	0	0	0	5

Hylidae	Dendropsophus ebraccatus	Dend_ebr	A	0	6	5	1	0	0	0	0	2	4
	Dendropsophus microcephala	Dend_mic	R	0	2	2	0	0	0	0	0	0	2
	Ecnomiohyla cf. valancifer	Ecno_val	R	0	4	0	0	1	0	3	0	0	4
	Smilisca baudini	Smil_bau	R	0	20	7	5	5	0	3	0	6	14
	Tlalocohyla loquax	Tlal_loq	A	1	17	15	2	1	0	0	0	1	17
Ranidae	Lithobates vaillanti	Lith_vai	R	0	1	0	0	0	0	0	1	0	1
SAURIA													
Corytophanidae	Basiliscus vittatus	Basi_vit	R	0	3	0	2	1	0	0	0	2	1
	Corytophanes hernandezi	Cory_her	A	13	22	1	2	0	21	5	6	3	32
Gekkonidae	Sphaerodactylus glaucus	Spha_gla	R	0	1	0	1	0	0	0	0	1	0
Iguanidae	Ctenosaura acanthura	Cten_aca	R	0	1	0	1	0	0	0	0	0	1
	Iguana iguana	Igua_igu	R	0	2	0	0	2	0	0	0	2	0
Phrynosomatidae	Sceloporus salvini	Scel_sal	R	0	1	0	0	0	0	1	0	0	1
	Sceloporus variabilis	Scel_var	R	3	11	1	4	0	4	4	1	13	1

Polychrotidae	Anolis barkeri	Anol_bar	A	3	16	1	8	1	2	7	0	17	2
	Anolis biporcatus	Anol_bip	R	0	1	0	1	0	0	0	0	1	0
	Anolis cf. duellmani	Anol_due	A	1	2	0	3	0	0	0	0	1	2
	Anolis lemurinus	Anol_lem	A	4	7	0	6	0	1	4	0	11	0
	Anolis pentaprion	Anol_pen	R	0	3	2	0	0	0	1	0	1	2
	Anolis petersi	Anol_pen	R	0	4	1	2	0	0	1	0	2	2
	Anolis rodriguezi	Anol_pet	R	3	7	4	3	0	0	3	0	7	3
	Anolis sericeus	Anol_rod	R	1	6	3	1	2	0	1	0	4	3
	Anolis unifomis	Anol_ser	R	128	236	33	204	19	16	91	1	329	35
		Anol_unif	A										
	Scincidae	Plestiodon sumichrasti	Ples_sum	A	18	35	0	47	0	0	4	2	36
Scincella cherriei		Scin_che	A	6	21	0	25	0	0	2	0	25	2
Teiidae	Ameiva undulata	Amei_und	A	4	13	0	16	0	0	1	0	17	0
Xantusiidae	Lepidophyma tuxtlae	Lepi_tux	R	4	12	1	3	0	2	7	3	13	3
SERPENTES													
Boidae	Boa constrictor	Boa_con	R	0	2	0	2	0	0	0	0	1	1
Colubridae	Coniophanes bipunctatus	Coni_bip	R	0	1	0	1	0	0	0	0	0	1
	Coniophanes fissidens	Coni_fis	R	1	1	0	2	0	0	0	0	1	1
	Coniophanes imperialis	Coni_imp	R	2	0	0	2	0	0	0	0	2	0

	Dryadophis melanolomus	Drya_mel	R	0	1	0	0	1	0	0	0	0	1
	Ficimia publia	Fici_pub	R	0	1	0	1	0	0	0	0	1	0
	Imantodes cenchoa	Iman_cen	A	4	15	12	1	3	0	3	0	0	19
	Leptodeira septentrionalis	Lept_sep	R	1	2	2	0	0	0	1	0	0	3
	Oxyrhopus petola	Oxyr_pet	R	0	1	0	0	0	0	1	0	0	1
	Pseustes poecilonotus	Pseu_poe	R	0	1	0	1	0	0	0	0	1	0
	Rhadinaea decorata	Rhad_dec	R	1	0	0	1	0	0	0	0	1	0
	Stenorrhina degenhardti	Sten_deg	R	0	1	0	1	0	0	0	0	1	0
Elapidae	Micrurus diastema	Micr_dia	R	0	1	0	0	0	0	0	1	0	1
Viperidae	Bothrops asper	Both_asp	A	3	5	0	6	1	0	0	1	2	6

* Dispersion models (MD): R. Random, A. Aggregated, U. Uniform.

** Substrate type: 1. Leaves, 2. Leaf litter, 3. Branches, 4. Rock, 5. Vertical trunks, 6. Bare soil.

Figure 1. Species diversity along substrate types in the tropical rainforest of Los Tuxtlas. Amphibians (white bars), Reptiles (gray bars).

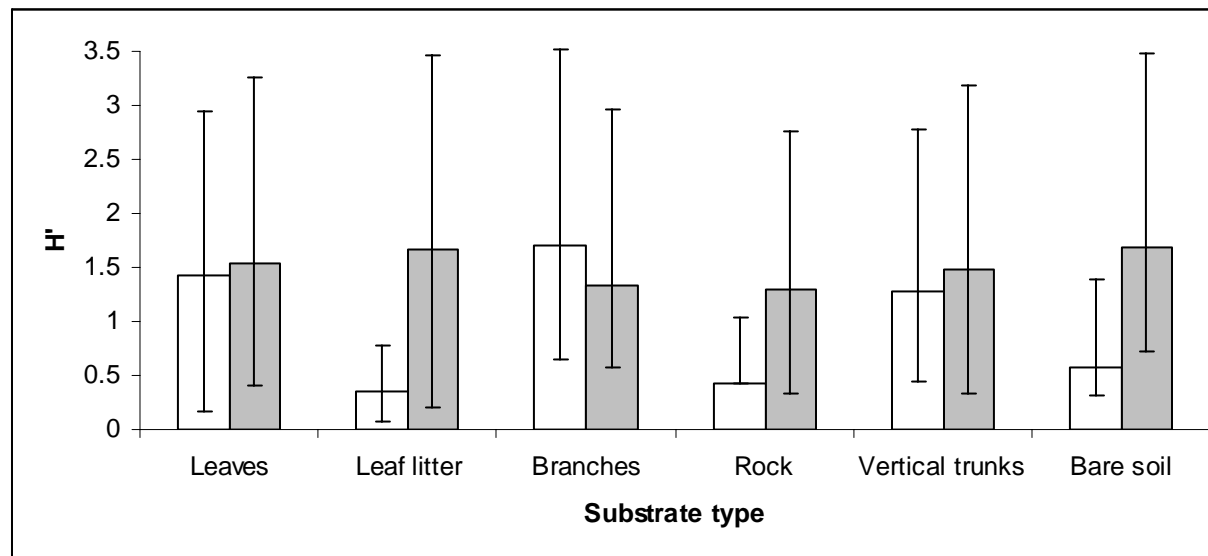
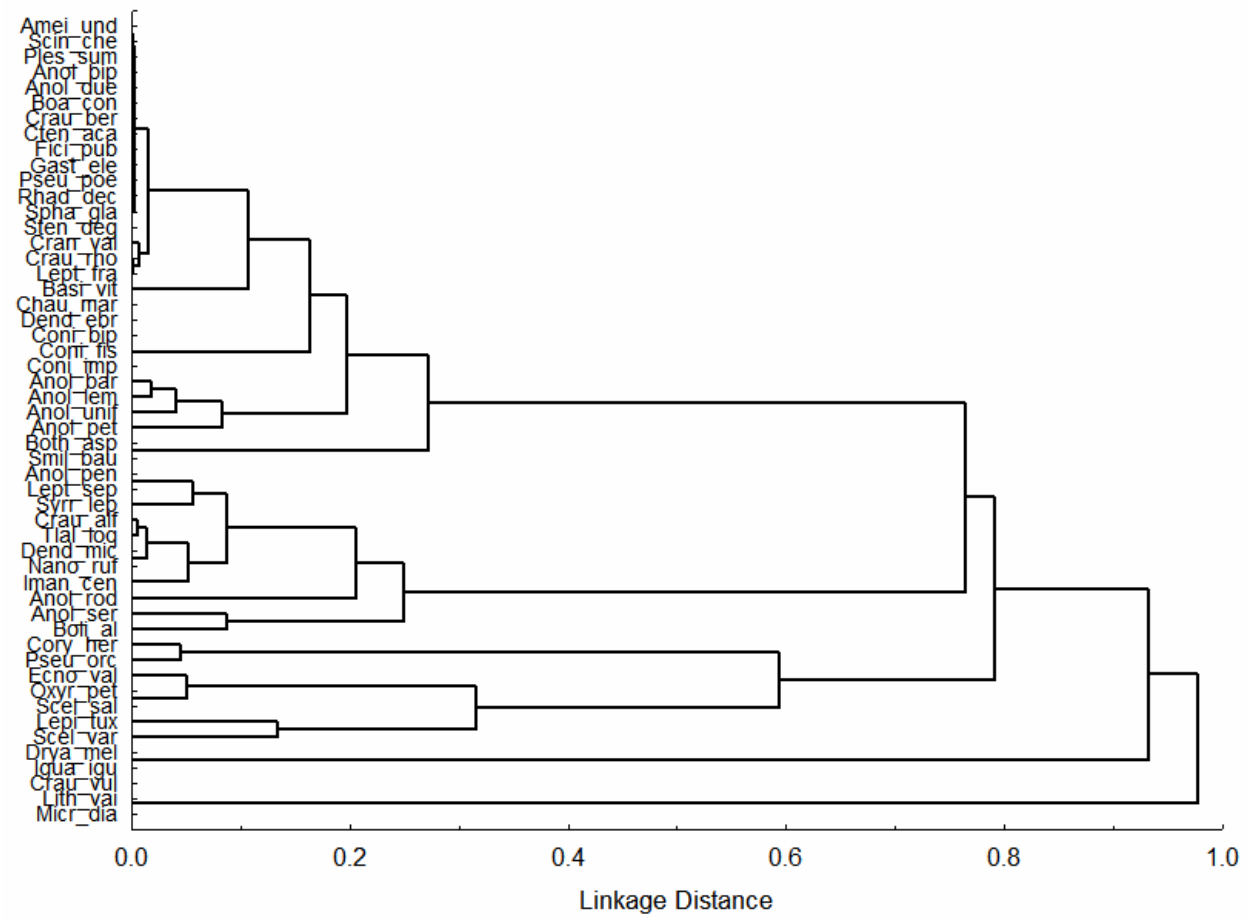


Figure 2. Similarity of Pianka's niche overlap index for amphibian and reptile species in the tropical rainforest of Los Tuxtlas.



APÉNDICE II

DESCRIPCIÓN Y MODELADO DEL MICROHÁBITAT DE
LOS ANFIBIOS Y REPTILES DE LA SELVA DE LOS TUXTLAS,
VERACRUZ.

DESCRIPCIÓN Y MODELADO DEL MICROHÁBITAT DE LOS ANFIBIOS Y REPTILES QUE HABITAN LA SELVA ALTA PERENNIFOLIA DE LOS TUXTLAS

José Nicolás Urbina-Cardona y Víctor Hugo Reynoso

Colección Nacional de Anfibios y Reptiles. Departamento de Zoología. Instituto de Biología. Universidad Nacional Autónoma de México. C.P. 04510 México, D.F.

1. INTRODUCCIÓN

El hábitat es el lugar donde un organismo vive y donde se encuentran los recursos y las condiciones que permiten su presencia, supervivencia y reproducción (Reinert 1984, Hall *et al.* 1997, Brower *et al.* 1998). Las dimensiones del hábitat son: temporal (cambios diarios y estacionales), espacial (topografía, tipo de hábitat y microhábitat, estratificación vegetal) y físico-química (ambiente y sustrato) (Lillywhite y Henderson 1993, Brower *et al.* 1998, Dodd y Smith 2003). A su vez, las condiciones del hábitat son el principal factor que influye el componente biótico como la presencia, la abundancia y la distribución de un organismo en el ambiente (Soutwood 1977).

Los organismos no se ubican aleatoriamente dentro de un paisaje, son sensibles a gradientes ambientales que determinan la disponibilidad de recursos y manifiestan una adaptación al medio (Begon *et al.* 1996, Krebs 1999, Zug *et al.* 2001). El establecimiento de los individuos en lugares óptimos o subóptimos depende de las tolerancias ecofisiológicas de la especie y también de sus interacciones con otros organismos (Whittaker *et al.* 1973). El nicho ecológico es definido por Hutchinson (1978) como un espacio abstracto determinado por la suma de los requerimientos de una especie y la interacción con otras especies en la comunidad; y por Odum (1959) como el status de un organismo al interior de la comunidad y ecosistema como resultado de sus adaptaciones estructurales, respuestas fisiológicas y comportamiento aprendido y heredado.

El uso es la manera en que el animal aprovecha los recursos físicos y biológicos presentes en el hábitat (Krausman 1999). El concepto de uso se encuentra relacionado con la teoría de nicho fundamental que se define como el conjunto total de las condiciones óptimas bajo las cuales un

organismo puede vivir y reemplazarse (Hutchinson 1978) y determina las condiciones bióticas y abióticas del hábitat a las cuales los organismos responden en un hiperespacio multidimensional (Whittaker *et al.* 1973, Begon *et al.* 1996, Brower *et al.* 1998, Pianka 2000, Dodd y Smith 2003). El uso espacial y temporal del hábitat afecta la estructura de la comunidad de acuerdo con las interacciones entre presas y depredadores potenciales (Lillywhite y Henderson 1993). Ese concepto de uso a su vez, se encuentra relacionado con la teoría del nicho realizado, definido como el uso de los recursos por parte de una especie teniendo en cuenta la competencia y otras interacciones biológicas (Hutchinson 1978).

La selección del hábitat es un proceso jerárquico que opera a nivel del organismo e involucra decisiones innatas y aprendidas acerca de que hábitat usar a diferentes escalas del ambiente, y se encuentra influenciado por factores evolutivos y conductuales (Krausman 1999, Krebs 2001). Como consecuencia de la selección y uso desigual de unos recursos sobre otros, se da la preferencia de hábitat (Hall *et al.* 1997). MacArthur y Pianka (1966) y Shoener (1974) sugieren que el uso diferencial del microhábitat es el principal mecanismo de disminución de la competencia interespecífica que permite una distribución y utilización diferente del ambiente físico. Así se mantiene alta densidad de población, explotación óptima de los recursos disponibles y menor sobreposición de nichos permitiendo mayor coexistencia de especies (MacArthur 1968, Krebs 2001).

Las diversas actividades que realiza un organismo requieren de componentes ambientales específicos y el organismo selecciona al hábitat con base en sus características para darle un uso específico (Krausman 1999). La distribución espacial de las especies de anfibios y reptiles está dada por la interacción entre los requerimientos fisiológicos de los organismos, la disposición de recursos (comida, refugio, reproducción, sitios para la termorregulación, rutas de escape, entre otros) y las características físicas del hábitat (Zug *et al.* 2001). Así mismo, dentro del microhábitat existen componentes críticos que proveen condiciones ecológicas ideales para procesos reproductivos, de alimentación, refugio, descanso y termorregulación (Zimmerman y Bierregard 1986, Gascon *et al.* 1999, Dickerson 2001, Castoe 2002, Brito 2003). De esta manera, conocer el ambiente físico es crucial para el entendimiento del éxito adaptativo y la ecología conductual de estos organismos (Lillywhite y Henderson 1993).

La influencia del ambiente determina la protección y reproducción de las especies y se basa principalmente en la regulación de los requerimientos fisiológicos mediante el

aprovechamiento de la temperatura (Beaupre 1995, McAllister 1995, Plummer 2002). Las variaciones en los rangos de temperatura en un ambiente determinado, afectan directamente la temperatura corporal, el comportamiento, las actividades diarias y los procesos metabólicos de los organismos ectotérmicos (Toft 1985, Gibbons y Semlitsch 1987, Beaupre 1995, Webb y Shine 1998). Este fenómeno determina en gran medida el aprovechamiento de la energía que incide sobre un lugar determinado (Beaupre 1995).

Estudios recientes han generado información para evaluar el hábitat potencial de los anfibios y reptiles como herramienta para su conservación a nivel local y regional (Zimmerman y Bierregard 1986, Cross y Petersen 2001, Martínez-Martínez 2004). El conocimiento de dicha información junto con la distribución de las especies es fundamental para predecir las respuestas de las poblaciones a cambios climáticos y ambientales (Beaupre 1995), y evitar la pérdida de hábitat críticos para las poblaciones de anfibios y reptiles (Keller y Heske 2000).

El presente estudio describe los rangos de tolerancia y modela la relación entre algunas variables ambientales (temperatura y humedad relativa), estructurales (cobertura de dosel, densidad de sotobosque), espaciales (altura sobre el nivel del mar, pendiente, distancia a ríos) y del microhábitat (altura sobre el suelo, porcentaje de cobertura herbácea, porcentaje de cobertura de hojarasca y espesor de la capa de hojarasca) con la presencia de las especies más abundantes de anfibios y reptiles que habitan la Selva Alta Perennifolia (SAP) de Los Tuxtlas, Veracruz, México.

2. ANTECEDENTES

Los estudios de herpetofauna realizados en los Tuxtlas datan desde 1910 (Ruthven 1912, 1913, citado por Vogt *et al.* 1997), año en el que se describieron las primeras especies con sus hábitat. Más adelante, entre 1945 y 1960, se actualizaron los listados de anfibios y reptiles, reconociendo algunos endemismos y hacia 1962 se iniciaron los primeros estudios en autoecología (Vogt *et al.* 1997). Pero fue realmente, hasta 1977, que Ramírez-Bautista publicó la primera lista de anfibios y reptiles, describiendo las características y hábitos de las especies, seguido por Pérez-Higareda *et al.* (1987), quien actualizó el listado diez años más tarde.

Durante las últimas décadas se han realizado, en la región, estudios más diversos cómo: el estudio comparativo de tres especies de tortugas (Guzmán 1984), la composición de anfibios y reptiles que habitan en las elevaciones (Hernández 1989), el uso del Sistema de Información Climático-Cartográfico aplicado a la herpetofauna (Pelcastre 1991), las ranas de la Laguna el

Zacatal (Vogt 1997a), la descripción de las comunidades de serpientes (Vogt 1997b), la comparación entre la diversidad herpetológica del interior y borde de la selva del Parque de Flora y Fauna Silvestre Tropical de la Universidad Veracruzana (Hernández-González 1996), el estudio de la ecografía de los anfibios y reptiles (Ramírez-Bautista y Nieto-Montes de Oca 1997), el estudio de la distribución altitudinal por tipo de vegetación de la herpetofauna (López y de la Torre 1998), la división de recursos en tortugas de agua dulce (Vogt y Guzman 1988), la dieta de dos salamandras (Anderson y Mathis 1999), la organización espacial y temporal de una comunidad de saurios (Lopez-Gonzalez *et al.* 1993), la diversidad Alfa y Beta de anfibios y reptiles en el gradiente potrero-borde-interior (Urbina-Cardona y Reynoso 2005), la relación entre la diversidad herpetofaunística y las variables del microhábitat a lo largo del gradiente potrero-borde-interior (Urbina-Cardona *et al.* *en prensa*), la comparación de las comunidades de anfibios y reptiles entre zonas altas y bajas dentro de la reserva (Hernández-Ordóñez 2005, Hernández-Ordóñez y Reynoso *en preparacion*), la estructura de las comunidades de anfibios y reptiles en fragmentos pequeños de selva (Cabrera-Guzmán 2005, Cabrera-Guzmán y Reynoso *en preparacion*) y algunos aportes a la historia natural y la ecología de algunas especies como *Sceloporus variabilis* (Benabib 1991, 1997), *Anolis barkeri* (Brit *et al.* 2001), *Anolis sericeus* (Heras-Lara y Villareal-Benitez 1997), *Anolis uniformis* (Villareal-Benitez y Heras-Lara 1997), *Bothrops asper* (Buttenhof y Vogt 1997), *Smilisca baudini* (Vogt 1997c), *Anolis spp.* (Villareal-Benitez 1997), entre otras.

Ramírez-Bautista y Nieto-Montes de Oca (1997) reportan para el área 43 especies de anfibios y 116 de reptiles. El número de especies endémicas de Los Tuxtlas es relativamente alto e incluye cuatro anfibios y 11 reptiles, lo que representa el 9.4% del total de la región. De los 11 tipos de vegetación en los cuales se encuentra distribuida la herpetofauna de la región, la Selva Alta Perennifolia, aloja la mayor riqueza de especies con 35 especies de anfibios y 102 reptiles (Ramírez-Bautista y Nieto-Montes de Oca 1997). Hasta el momento, no existen estudios que describan de manera sistemática y modelen el microhábitat de los anfibios y reptiles que habitan la SAP de la Reserva de los Tuxtlas.

3. MÉTODOS

3.1 Área de Estudio

El estudio fue llevado a cabo en el bosque tropical de la Reserva de la Biosfera de Los Tuxtlas en el Estado de Veracruz (N 18° 32' a N 18° 38'; W95° 3' a W95°6'), entre 35 y 300

metros sobre el nivel del mar (ANEXO 1). La temperatura media anual es ≥ 22 °C, fluctuando entre 35 °C hacia el mes de mayo y 13 °C en febrero (Soto y Gama 1997). La precipitación media anual fluctúa entre ≤ 60 mm y 4959 mm con una temporada de secas entre marzo y mayo, y una temporada de lluvias entre junio y febrero (Soto 2004).

La región de Los Tuxtlas representa el límite boreal de la selva tropical lluviosa en el continente americano, siendo además, uno de los último relictos del estado de Veracruz (Dirzo y Miranda 1991, Dirzo y García 1992, Torres-Orozco *et al.* 1997). El tipo de vegetación estudiada fue la Selva Alta Perennifolia (SAP). Este tipo de vegetación ocupa la mayor área en la región e históricamente estuvo en contacto amplio con la extensa área de bosque tropical perennifolio de la vertiente atlántica del sur de México (Rzedowski 1981). La SAP sobre suelos profundos se localiza en altitudes que oscilan entre los 0-350 m.s.n.m. y se caracteriza por tener un dosel entre 30 y 35 m, alcanzando hasta 40 m de altura en el caso de *Ficus yoponensis*, *F. tecolutensis* y *Ceiba pentandra*. El 50% de la flora pertenece a la familia *Palmae* con especies como *Astrocaryum mexicanum*, *Chamaedorea pinnatifrons* y *C. atterms* (Ibarra-Manríquez *et al.* 1997, Guevara *et al.* 2004). Debido a actividades antropogénicas como agricultura y ganadería, la SAP ha presentado una pérdida del 84% en la cobertura original (Dirzo y García 1992). Actualmente, en la zona se presentan diversos elementos arbóreos tales como fragmentos de selva, acahuals, corredores de vegetación ribereña, cercas vivas y árboles aislados inmersos en áreas de potrero, que generan un mosaico en el paisaje (Ibarra-Manríquez *et al.* 1997).

Las áreas de estudio fueron seleccionadas con base en el análisis de imágenes aéreas digitales y la corroboración directa en campo. Se identificaron seis fragmentos de selva entre 27 y 472 ha rodeados por potrero. Se entrevistaron a los propietarios y mayordomos de las fincas cercanas y se determinó que los fragmentos no presentan evidencias de perturbación hace más de 15 años. Se aseguró que todos los fragmentos muestreados presentaran por lo menos un río para asegurar que la ausencia de agua no fuera un factor limitante para los organismos que requieren cuerpos agua para su reproducción. En cada fragmento se ubicaron 12 transectos de 50 m de longitud, exceptuando el fragmento de mayor tamaño donde se ubicaron 48 transectos, para un total de 108 transectos en el estudio.

Para una explicación mas detallada de los parámetros de selección de áreas y ubicación espacial de los transectos en el paisaje remitirse a Urbina-Cardona *et al.* (*en prensa*).

3.2 Muestreo de los anfibios y reptiles

Las salidas al campo se hicieron en cuatro temporadas junio-julio y septiembre-octubre de 2003, febrero-marzo y mayo de 2004. Cada transecto fue muestreado por dos personas durante 20 minutos en el día y 20 minutos en la noche para un total de 576 horas-hombre. Los transectos se muestrearon caminando a lo largo de 50 m y registrando visualmente los anfibios y reptiles (Crump y Scott 1994). Se caracterizó el microhábitat de los anfibios y reptiles que habitan el sotobosque de la SAP a un metro a cada lado del transecto y hasta 2 m de altura (Urbina-Cardona y Reynoso 2005).

Los individuos no fueron marcados, debido a la baja tasa de recapturas encontrada en los anfibios y reptiles de Los Tuxtlas después de un mes (Vogt y López-Luna *datos no publicados*; Cabrera-Guzmán, *com. pers.* 2004), por lo cual la posibilidad de sobrestimar la abundancia es muy reducida. Para identificar rápidamente las especies en el campo se creó una compilación fotográfica basada en una colección de referencia con especímenes colectados durante abril de 2003. Estos fueron determinados hasta especie utilizando claves taxonómicas especializadas (Shannon y Werler 1955, Savage 1975, Flores-Villela *et al.* 1987, Flores-Villela *et al.* 1995, Lee 1996, Campbell y Savage 2000). Durante la fase de campo, los especímenes que presentaron dificultad para su determinación fueron fotografiados, sacrificados, montados, preservados en alcohol al 96% y depositados en la Colección Nacional de Anfibios y Reptiles, Instituto de Biología, UNAM en México D.F., para ser determinados taxonómicamente por un experto. El resto de los individuos fueron liberados en el mismo lugar de captura.

3.3 Medición del microhábitat

Algunas variables ambientales como altura sobre el nivel del mar, pendiente, distancia a ríos, cobertura de dosel y densidad de sotobosque, fueron tomadas para cada uno de los transectos (n=108). Otras variables como altura sobre el suelo, temperatura, humedad relativa, porcentaje de cobertura herbácea, porcentaje de cobertura de hojarasca y espesor de la capa de hojarasca, fueron tomadas en el lugar en que se observó por primera vez cada organismo (n= 2 120). Para todos los análisis se tuvieron en cuenta todas las observaciones n = 2 120 para cada variable, asumiendo que las variables tomadas por transecto influyen a los organismos a nivel del microhábitat.

Las variables por transecto se tomaron para cada uno de los 108 transectos. La altura sobre el nivel del mar fue medida con un altímetro, la pendiente con un clinómetro. La cobertura de dosel fue medida para cada transecto, tomando dos fotografías al azar dentro del transecto con

una cámara con lente hemisférico de 180° en días con alta luminosidad a una altura de trípode de 0.5 m, apertura de diafragma f 11, una velocidad de obturación de 1/125 segundos y ASA 100. Posteriormente los negativos fueron escaneados y el porcentaje de dosel cubierto en la fotografía, fue analizado con el programa WINPHOT 5 (ter Steege 1996), promediando los dos valores obtenidos por transecto. La densidad relativa del sotobosque se obtuvo ubicando una vara de madera de 3.5 cm de diámetro y 2 m de altura perpendicularmente al suelo y contando el número de contactos que hace la vara con la vegetación (ramas, troncos y hojas). En cada transecto se midió esta variable cinco veces de manera aleatoria y se promedió para obtener un solo valor. La distancia a ríos fue medida con un GPS, georeferenciando todos los transectos y haciendo uso de la función “Go To” desde el río mas cercano a cada transecto. La distancia a otros cuerpos de agua no fue tomada en cuenta debido a que la mayoría de los riachuelos y charcos permanecen secos la mayor parte del año, y las lagunas son escasas y quedan muy alejadas de los transectos de estudio.

Las variables por organismo se tomaron en el microhábitat, definido como los sitios particulares del hábitat en donde se encontró un individuo realizando sus actividades (*sensu* Inger 1994). Se evaluó un total de 2120 microhábitat con base en los siguientes parámetros: La temperatura y humedad relativa se midió situando en el microhábitat una sonda comunicada a un termohigrómetro durante 30 segundos. Tanto el porcentaje de cobertura herbácea como el porcentaje de cobertura de hojarasca fue medida colocando sobre el lugar de captura de cada organismo un marco de madera de 0.5 x 0.5 m con una cuadrícula de nylon dividiéndola en 4 cuadrantes. Finalmente, el espesor de la capa de hojarasca se midió enterrando una regla graduada en el suelo.

3.4 Análisis de Datos

Se establecieron los valores de tolerancia máximos, mínimos y promedio para las 11 variables ambientales y estructurales del microhábitat donde se capturaron los organismos de cada especie, y se compararon estas tolerancias respecto al gradiente total de microhábitat evaluados ($n = 2\ 120$).

Se usaron modelos de regresión múltiple por pasos (forward stepwise) en STATISTICA 6 (Statsoft 2000), para detectar las variables del microhábitat relacionadas con la presencia de los anfibios y reptiles más comunes (abundancia total $n > 5$) en los microhábitat evaluados en la SAP de Los Tuxtlas ($n = 2\ 120$). Las variables ambientales que presentaron una prueba de F no

significativa ($p < 0.05$) fueron eliminadas del modelo. Para cada modelo se evaluó la normalidad de los residuales de la regresión con una prueba de Shapiro-Wilk (W).

4. RESULTADOS

4.1 Diversidad taxonómica

Bajo este sistema de muestreo, en el sotobosque de la SAP se encontraron 17 especies de anfibios en 13 géneros y 6 familias. Los anuros estuvieron representados en mayor número de especies (14), géneros (10) y familias (5), mientras que las salamandras presentaron baja representación en las tres categorías (Tabla 1). El género más dominante de anuros fue *Eleutherodactylus* (Tabla 2).

Las familias y géneros representadas de anuros fueron: Bufonidae (*Bufo*), Leptodactylidae (*Eleutherodactylus*, *Leptodactylus* y *Syrrhophus*), Hylidae (*Dendropsophus*, *Tlalocohyla*, *Ecnomiohyla* y *Smilisca*), Microhylidae (*Gastrophryne*) y Ranidae (*Rana*), y de salamandras Plethodontidae (*Bolitoglossa*, *Nanotriton* y *Lineatriton*). La familia mejor representada fue la Leptodactylidae (con 6 especies) de la cuál el género *Eleutherodactylus* presentó 4 especies, seguida por la familia Hylidae con 5 especies (Tabla 1).

Los reptiles fueron el grupo taxonómico mejor representado en cuanto a especies (31), géneros (20) y familias (12). Las lagartijas estuvieron representadas en mayor número de especies y familias, mientras que las serpientes presentaron un mayor número de géneros (Tabla 1). El género más dominante de serpientes fue *Coniophanes* y de lagartijas *Anolis* (Tabla 2). Las familias y géneros representadas de lagartijas fueron: Corytophanidae (*Basiliscus* y *Corytophanes*), Gekkonidae (*Sphaerodactylus*), Iguanidae (*Iguana* y *Ctenosaura*), Phrynosomatidae (*Sceloporus*), Polychrotidae (*Anolis*), Scincidae (*Scincella* y *Plestiodon*), Teiidae (*Ameiva*), Xantusiidae (*Lepidophyma*); y de serpientes: Boidae (*Boa*), Colubridae (*Coniophanes*, *Imantodes*, *Leptodeira*, *Oxyrhopus*, *Pseustes*, *Stenorrhina*), Elapidae (*Micrurus*) y Viperidae (*Bothrops*). La familia mejor representada fue Polychrotidae (con 9 especies) de la cuál el género *Anolis* presentó 9 especies, seguida por Colubridae (con 8 especies) de la cuál el género *Coniophanes* presentó 3 especies.

4.2 Aportes a la autoecología de las especies

Nanotriton rufescens

Se registraron 52 individuos (61.5% juveniles y 38.5% adultos) entre 40 y 270 m.s.n.m. El 96% se encontraron sobre hojas ente 0 y 140 cm del suelo, aunque también se registraron en hojarasca y sobre ramas. Esta especie es exclusivamente nocturna. Se encontró haciendo uso de microhábitat con baja temperatura (entre 17 y 26 °C) y alta cobertura de hojarasca (promedio de 98%) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, la cobertura herbácea, la humedad relativa y la cobertura y espesor de hojarasca, y negativamente la temperatura y la pendiente (Tabla 2).

Ollotis valliceps

Se registraron 60 individuos (48% juveniles y 52% adultos) entre 130 y 265 m.s.n.m. El 78% se encontraron sobre hojarasca aunque también se registraron sobre hojas, troncos, tierra desnuda y ramas ente 0 y 40 cm del suelo. Esta especie puede encontrarse tanto de día cómo de noche (67% y 33% de individuos registrados respectivamente). Se encontró haciendo uso de microhábitat con temperaturas entre 19 y 28 °C y con alta cobertura de hojarasca (promedio de 95%; ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la humedad relativa, la cobertura herbácea y la altura sobre el nivel del mar, y negativamente la pendiente, la distancia a río, la altura sobre el suelo, la temperatura y el espesor de la capa de hojarasca (Tabla 2).

Eleutherodactylus alfredi

Se registraron 25 individuos (40% juveniles y 60% adultos) entre 35 y 275 m.s.n.m. El 80% se encontraron sobre hojas ente 0 y 140 cm del suelo, aunque también se registraron en hojarasca y sobre troncos. Esta especie es exclusivamente nocturna aunque un individuo fue encontrado inactivo durante el día. Los organismos hicieron uso de microhábitat con temperaturas entre 17 y 27 °C, alta cobertura de hojarasca (promedio de 95%), cobertura de dosel entre 32 y 70% y densidades de sotobosque intermedias (entre 4.4 y 7) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la cobertura herbácea, la altura sobre el suelo y la cobertura de dosel, y negativamente la temperatura (Tabla 2).

Eleutherodactylus rhodopis

Se registraron 1251 individuos (42% juveniles y 58% adultos) entre 35 y 300 m.s.n.m. El 79% se encontraron sobre la hojarasca aunque también se registraron sobre hojas, tierra desnuda, troncos, rocas y ramas ente 0 y 100 cm del suelo. Esta especie es exclusivamente diurna aunque el 24% de los individuos fueron encontrados inactivos durante la noche. Los organismos hicieron uso de todo el gradiente de variables ambientales medidas en los microhábitat evaluados (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el nivel del mar y la pendiente, y negativamente la altura sobre el suelo, la humedad relativa, la cobertura herbácea, el espesor de la capa de hojarasca, la cobertura de dosel y la densidad de sotobosque (Tabla 2).

Leptodactylus fragilis

Se registraron 6 individuos (100% adultos) entre 165 y 195 m.s.n.m. El 83% se encontraron sobre la hojarasca, aunque también se registraron en hojas ente 0 y 10 cm del suelo. Esta especie puede ser encontrada activa tanto de día cómo de noche. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 23 y 26 °C), alta humedad relativa (entre 83 y 95%), alta cobertura de hojarasca (100%), cobertura de dosel entre 40 y 46%, densidades de sotobosque intermedias (entre 4.8 y 7) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la humedad relativa y la cobertura herbácea, y negativamente la altura sobre el suelo, la pendiente y la distancia a río (Tabla 2).

Syrrhophus leprus

Se registraron 20 individuos (5% juveniles y 95% adultos) entre 60 y 265 m.s.n.m. El 60% se encontraron sobre la hojas ente 0 y 200 cm del suelo (aunque se registraron vocalizaciones a mas de 20 m de altura) y también se observaron sobre la hojarasca y troncos. Esta especie es exclusivamente nocturna aunque un individuo fue registrado durante el día. Los organismos hicieron uso de microhábitat con alto porcentaje (entre 78 y 100%) y espesor (entre 6 y 13 cm) de hojarasca y alejados de cuerpos de agua (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, la humedad relativa, la densidad de sotobosque y el espesor de la capa de hojarasca, y negativamente la temperatura (Tabla 2).

Gastrophryne elegans

Se registraron 5 individuos (100% adultos) entre 165 y 210 m.s.n.m. Todos los organismos se encontraron sobre la hojarasca. Esta especie es exclusivamente nocturna. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 24 y 26 °C), alta humedad relativa (entre 79 y 87%), alta cobertura de hojarasca (100%), coberturas de dosel intermedias (entre 44 y 57%) y baja densidad de sotobosque (entre 4.4 y 4.8) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fue la humedad relativa, y negativamente la densidad de sotobosque, la distancia a río y la pendiente (a un 94% de confianza; Tabla 2).

Dendropsophus ebraccatus

Se registraron 6 individuos (100% adultos) entre 35 y 180 m.s.n.m. El 83% se encontraron sobre la hojas ente 0 y 60 cm del suelo aunque también se registró un individuo sobre la hojarasca. Esta especie es exclusivamente nocturna aunque dos individuos fueron registrados inactivos durante el día. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 23 y 29 °C), alta cobertura de hojarasca (entre 78 y 100%), a niveles intermedios del gradiente de cobertura de dosel (entre 42 y 55%) y densidad de sotobosque (entre 4.4 y 5.6), cercanas a ríos; y no se registraron a menos del 20% de cobertura herbácea y humedad relativa (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo y la cobertura de dosel, y negativamente la humedad relativa, la altura sobre el nivel del mar, la densidad de sotobosque y la distancia a río (Tabla 2).

Tlalocohyla loquax

Se registraron 18 individuos (6% juveniles y 94% adultos) entre 155 y 300 m.s.n.m. El 83% se encontraron sobre hojas ente 0 y 80 cm del suelo aunque también se registraron haciendo uso de las ramas y la hojarasca. Esta especie es exclusivamente nocturna aunque un individuo fue registrado inactivo durante el día. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 21 y 25 °C) y alta cobertura de hojarasca (entre 70 y 100%) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la densidad de sotobosque, la pendiente, la altura sobre el suelo, la altura sobre el nivel del mar, la cobertura herbácea y la cobertura de hojarasca, y negativamente la temperatura y la distancia a río (Tabla 2).

Smilisca baudini

Se registraron 20 individuos (100% adultos) entre 55 y 275 m.s.n.m. Se encontraron individuos haciendo uso de hojas, ramas, troncos y hojarasca ente 0 y 200 cm del suelo. Esta especie es exclusivamente nocturna aunque seis individuos fueron registrados inactivos durante el día. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 24 y 30 °C), alta cobertura (entre 70 y 100%) y espesor (entre 4 y 30 cm) de hojarasca y pendientes altas (entre 11 y 43) (ANEXO 1)

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, el espesor de la capa de hojarasca, la pendiente, la densidad de sotobosque, la altura sobre el nivel del mar y la temperatura, y negativamente la distancia a río (Tabla 2).

Corytophanes hernandezi

Se registraron 35 individuos (37% juveniles y 63% adultos) entre 35 y 245 m.s.n.m. El 60% de los individuos se encontraron haciendo uso de rocas, aunque también se encontraron sobre troncos, tierra desnuda, hojarasca y hojas entre 0 y 200 cm del suelo. Esta especie es exclusivamente diurna aunque el 91% de los individuos se registraron durante la noche cuando se detectan con mayor facilidad inactivos sobre las ramas. Los organismos hicieron uso de todo el gradiente de variables en los microhábitat, prefiriendo aquellos con alta cobertura (entre 80 y 100%) y espesor (entre 5 y 14 cm) de hojarasca (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, la cobertura de hojarasca y la temperatura, y negativamente la altura sobre el nivel del mar y la pendiente (Tabla 2).

Sceloporus variabilis

Se registraron 14 individuos (21% juveniles y 79% adultos) entre 45 y 270 m.s.n.m. Se encontraron individuos haciendo uso de hojas, troncos, rocas, tierra desnuda y hojarasca ente 0 y 50 cm del suelo. Esta especie es exclusivamente diurna aunque un individuo fue registrado

inactivo durante la noche. Los organismos hicieron uso de microhábitat con temperaturas altas (entre 26 y 32 °C) y cobertura de dosel intermedia (entre 31 y 45) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la temperatura, la humedad relativa, la cobertura herbácea, la distancia a río, la densidad de sotobosque, la altura sobre el nivel del mar y la altura sobre el suelo, y negativamente la cobertura de hojarasca y la pendiente (Tabla 2).

Anolis barkeri

Se registraron 19 individuos (16% juveniles y 84% adultos) entre 75 y 260 m.s.n.m. El 79% de los individuos se encontraron haciendo uso de hojarasca y troncos ente 0 y 120 cm del suelo, aunque también frecuentaron hojas, ramas y rocas. Esta especie es exclusivamente diurna aunque dos individuos fueron registrados inactivos durante la noche. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 20 y 28 °C), alta cobertura (entre 50 y 100%) y espesor (entre 7 y 15 cm) de hojarasca (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, el espesor de la capa de hojarasca y la humedad relativa, y negativamente la pendiente (Tabla 2).

Anolis lemurinus

Se registraron 11 individuos (36% juveniles y 64% adultos) entre 35 y 260 m.s.n.m. El 54% de los individuos se encontraron haciendo uso de la hojarasca, aunque también se registraron en troncos y hojas ente 0 y 120 cm del suelo. Esta especie es exclusivamente diurna. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 23 y 30 °C), baja humedad relativa (entre 23 y 40%), alta cobertura (entre 67 y 95%) y espesor (entre 4 y 12 cm) de hojarasca, alta cobertura herbácea (entre 64 y 95%), baja densidad de sotobosque (entre 4 y 6.8) y pendientes altas (entre 11 y 33) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la cobertura de dosel y la altura sobre el suelo y negativamente la humedad relativa y la altura sobre el nivel del mar (Tabla 2).

Anolis rodriguezi

Se registraron 10 individuos (30% juveniles y 70% adultos) entre 110 y 260 m.s.n.m. Los individuos se encontraron haciendo uso de hojarasca, hojas y troncos entre 0 y 130 cm del suelo. Esta especie es exclusivamente diurna aunque tres individuos fueron registrados inactivos

de noche, cuando son más conspicuos descansando sobre hojas. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 24 y 31 °C), alta cobertura (entre 78 y 100%) y espesor (entre 6 y 15 cm) de hojarasca, cobertura de dosel intermedia (entre 33 y 60%), densidad de sotobosque intermedia (entre 4.2 y 7.2) y pendientes altas entre 18 y 36% (ANEXO 2).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, la altura sobre el nivel del mar, la temperatura, la pendiente y el espesor de la capa de hojarasca, y negativamente la cobertura de dosel, la densidad de sotobosque y la distancia a río (Tabla 2).

Anolis sericeus

Se registraron 7 individuos (14% juveniles y 86% adultos) entre 40 y 260 m.s.n.m. Los individuos se encontraron haciendo uso de hojarasca, hojas, ramas y troncos ente 0 y 120 cm del suelo. Esta especie es exclusivamente diurna aunque tres individuos fueron registrados de noche, cuando son detectados inactivos sobre el haz de las hojas. Los organismos hicieron uso de microhábitat con temperaturas altas (entre 26 y 32 °C), humedad relativa intermedia (entre 32 y 85%), alta cobertura (entre 66 y 100%) y espesor (entre 6 y 12 cm) de hojarasca, cobertura de dosel intermedia (entre 35 y 49%), densidad de sotobosque intermedia (entre 4.8 y 7.2) y pendientes altas (entre 12 y 30) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, la temperatura y la humedad relativa, y negativamente la altura sobre el nivel del mar (Tabla 2).

Anolis uniformis

Se registraron 364 individuos (35% juveniles y 65% adultos) entre 35 y 280 m.s.n.m. El 56% de los individuos se encontraron haciendo uso de la hojarasca aunque también fueron registrados en rocas, tierra desnuda, ramas, hojas y troncos ente 0 y 110 cm del suelo. Esta especie es exclusivamente diurna aunque el 10% de los individuos fueron registrados de noche, cuando son más conspicuos inactivos sobre hojas. Los organismos hicieron uso de todo el gradiente de variables medidas en los microhábitat de la SAP (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la cobertura de dosel, el espesor de la capa de hojarasca, la densidad de sotobosque, la distancia a río, la temperatura y la cobertura herbácea, y negativamente la altura sobre el nivel del mar y la humedad relativa (Tabla 2).

Plestiodon sumichrasti

Se registraron 53 individuos, (34% juveniles y 66% adultos) entre 35 y 265 m.s.n.m. El 89% de los individuos se encontraron haciendo uso de la hojarasca, aunque también se registraron sobre tierra desnuda y troncos ente 0 y 10 cm del suelo. Esta especie se registró principalmente durante la tarde y el 32% de los individuos fueron encontrados en las primeras horas de la noche por sus hábitos crepusculares. Los organismos hicieron uso de microhábitat por arriba de 40% de cobertura de hojarasca y 32% de cobertura de dosel y con alto espesor de hojarasca (entre 5 y 14 cm) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la cobertura herbácea, la humedad relativa, el espesor de la capa de hojarasca, la distancia a río y la temperatura, y negativamente la altura sobre el suelo, la altura sobre el nivel del mar y la densidad de sotobosque (Tabla 2).

Scincella cherriei

Se registraron 27 individuos (22% juveniles y 78% adultos) entre 40 y 275 m.s.n.m. El 92% de los individuos se encontraron haciendo uso de la hojarasca, aunque también se registraron sobre troncos ente 0 y 50 cm del suelo. Esta especie se registró principalmente durante el día aunque dos individuos fueron encontrados inactivos en la noche. Los organismos hicieron uso de microhábitat con alta temperatura (entre 21 y 31 °C), alta cobertura (entre 70 y 100%) y espesor (entre 5 y 13 cm) de hojarasca (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la pendiente, la humedad relativa, la cobertura de dosel y la cobertura y espesor de la capa de hojarasca, y negativamente la altura sobre el nivel del mar, la altura sobre el suelo y la distancia a río (Tabla 2).

Ameiva undulata

Se registraron 17 individuos (23% juveniles y 77% adultos) entre 40 y 245 m.s.n.m. El 94% de los individuos se encontraron haciendo uso de la hojarasca, aunque otros fueron registrados en troncos ente 0 y 5 cm del suelo. Esta especie es exclusivamente diurna. Los organismos hicieron uso de microhábitat con temperaturas altas (entre 25 y 31 °C), humedad relativa intermedia (entre 26 y 85%), alta cobertura (entre 71 y 100%) y espesor (entre 7 y 12 cm) de hojarasca, baja cobertura de dosel (entre 22 y 49%), alta densidad de sotobosque (entre 5 y 10) y pendientes altas (entre 12 y 39) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la densidad de sotobosque, la temperatura, la humedad relativa, la distancia a río, el espesor de la capa de hojarasca, y negativamente la altura sobre el nivel del mar, la altura sobre el suelo y la pendiente (Tabla 2).

Lepidophyma tuxtlae

Se registraron 16 individuos (25% juveniles y 75% adultos) entre 75 y 280 m.s.n.m. Los individuos se encontraron haciendo uso de la hojarasca, rocas, tierra desnuda, hojas y troncos ente 0 y 40 cm del suelo. Esta especie es exclusivamente nocturna aunque el 81% de los individuos fueron registrados durante el día, inactivos bajo troncos. Los organismos hicieron uso de microhábitat con temperaturas entre 18 y 28 °C, alta cobertura (entre 60 y 100%) y espesor (entre 5 y 13 cm) de hojarasca, cobertura de dosel intermedia (entre 29 y 60%), baja densidad de sotobosque (por debajo de 7.6) y pendientes altas (entre 7 y 39) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el nivel del mar y la cobertura herbácea, y negativamente la humedad relativa (Tabla 2).

Imantodes cenchoa

Se registraron 19 individuos (21% juveniles y 79% adultos) entre 35 y 250 m.s.n.m. El 63% de los individuos se encontraron sobre hojas entre 0 y 150 cm del suelo, aunque también hicieron uso de hojarasca, ramas y troncos. Esta especie es exclusivamente nocturna. Los organismos hicieron uso de microhábitat con temperaturas entre 17 y 29 °C, alta cobertura (entre 78 y 100%) y espesor (entre 5 y 16 cm) de hojarasca y coberturas de dosel por encima de 32% (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la altura sobre el suelo, la cobertura herbácea y la cobertura y el espesor de la capa de hojarasca, y negativamente la distancia a río y la temperatura (Tabla 2).

Bothrops asper

Se registraron 8 individuos (38% juveniles y 62% adultos) entre 65 y 270 m.s.n.m. El 75% de los individuos se encontraron haciendo uso de la hojarasca, aunque otros fueron registrados en tierra desnuda y ramas ente 0 y 50cm del suelo. Esta especie es nocturna aunque dos individuos fueron encontrados durante el día enroscados en el suelo bajo hojas de palma secas. Los organismos hicieron uso de microhábitat con temperaturas intermedias (entre 21 y 29

°C), humedad relativa intermedia (entre 23 y 86%), alta cobertura (entre 70 y 100%) y espesor (entre 4 y 13 cm) de hojarasca, cobertura de dosel intermedia (entre 31 y 44%), densidad de sotobosque intermedia (entre 4.8 y 7.2) y pendientes intermedias (entre 5 y 28) (ANEXO 1).

Las variables que determinaron positivamente la presencia de esta especie en los microhábitat evaluados fueron la cobertura herbácea y la altura sobre el nivel del mar, y negativamente la cobertura de dosel y la pendiente (a un 90% de confianza; Tabla 2).

5. DISCUSION

Para la mayoría de la herpetofauna el conocimiento acerca de la preferencia y uso del hábitat es mínima, y está basada en observaciones cualitativas y anecdóticas (Reinert 1993). Este trabajo provee un marco de referencia sólido para poder determinar a nivel general el uso del hábitat por parte de los anfibios y reptiles más comunes en la SAP en Los Tuxtlas.

5.1 Diversidad herpetofaunística de la SAP de Los Tuxtlas

En los listados más recientes para la herpetofauna de la Selva Alta Perennifolia de la Estación de Biología Tropical Los Tuxtlas y las zonas bajas (entre 0 y 600 metros sobre el nivel del mar) aledañas, Pérez-Higareda (*com. pers.* 2003) reporta un total de 27 especies de anfibios y 59 de reptiles. La riqueza encontrada en este estudio corresponde al 66.6% de los anfibios y 57.6% de los reptiles reportados en estos listados de especies. Se debe tener en cuenta que el presente estudio se enfocó en la búsqueda de la herpetofauna del sotobosque de la SAP a lo largo de transectos fijos, registrando el 96% de los individuos y 70% de las especies en microhábitat entre 0 y 50 m entre por encima del suelo (Urbina-Cardona y Reynoso 2005), sin contemplar ambientes fosoriales, dosel y cuerpos de agua. A pesar de las limitaciones de este método el presente estudio reporta un alto número de individuos y de especies colectadas, esto nos hace pensar que el uso de transectos fijos y replicados metódicamente a lo largo del paisaje (*sensu* Urbina-Cardona et al *en prensa*), es un método de colecta complementario a los recorridos aleatorios restringidos por tiempo (*sensu* Reynoso et al. 2005).

5.2 Uso del microhábitat, interacciones y perturbación antropogénica

En este estudio se determinó que la competencia por ocupación de microhábitat no se realiza intensamente entre especies de áreas abiertas y de selva. Las especies con preferencia por áreas de potrero como *L. fragilis*, *S. leprus*, *T. loquax*, *S. variabilis* y *A. sericeus* entran a la SAP pero se encuentran en microhábitat con rangos ambientales muy reducidos y no hacen uso de todo el gradiente de variables ambientales y estructurales disponibles en los microhábitat evaluados.

Esto determina que a nivel de nicho funcional estos organismos no ejercen mayor competencia por recursos con las especies de la selva y contrasta con la idea propuesta por Sartorius *et al.* (1999) acerca de la alteración de las interacciones al interior de la selva por parte de especies de áreas abiertas. Sin embargo, algunas especies de lagartijas típicas de bosque (*Anolis* spp.) pueden ser predadas por lagartijas de áreas abiertas como *Ameiva undulata* (Villareal-Benitez y Heras-Lara 1997), generando una interacción más compleja a nivel del nicho realizado.

Las especies de vertebrados más abundantes de la región de Los Tuxtlas son la rana *E. rhodopis* y la lagartija *A. uniformis*, estas ejercen su dominancia en la comunidad a través de la exclusión competitiva de otras especies de los microhábitat óptimos disponibles en la SAP. Teniendo en cuenta que en un mismo tiempo y espacio no pueden coexistir dos especies en completa competencia (principio de exclusión competitiva, Krebs 2001), es probable que en la SAP algunas especies se encuentren desplazadas a lugares subóptimos de su nicho de manera que una especie explote más eficientemente un gradiente que otra.

En el presente trabajo se reporta a *O. valliceps*, *N. rufescens*, *P. sumichrasti* y *C. hernandesi* como especies subdominantes en la herpetofauna de la región. Algunas especies dominantes pueden ser removidas de la comunidad siendo reemplazadas por especies subdominantes en ambientes perturbados, afectando en algunos casos la habilidad de la comunidad para recuperar su configuración original previa al disturbio (Krebs 2001). Dado que en la selva de Los Tuxtlas se han registrado actividades antropogénicas desde hace más de 4000 años (Laborde 2004), esto nos plantea algunos cuestionamientos: Cambió drásticamente la configuración de la herpetofauna después de la fragmentación y pérdida del hábitat en la SAP?, permitirán las estrategias de manejo y conservación propuestas (e.g. aumento de conectividad y manejo de potreros abandonados) mantener la estructura y composición de los anfibios y reptiles actuales?, o, se habrá afectado tan profundamente la estabilidad de esta comunidad que ya perdió su habilidad de recuperación (e.g. resiliencia)?. En tan solo tres décadas se han detectado cambios en la dominancia de algunos anfibios y reptiles que habitan la SAP de Los Tuxtlas (e.g. *C. hernandesi*, *Agalichnis callidyra*, *A. sericeus*, *Sphaerodactylus glaucus* y *A. uniformis*; Urbina-Cardona y Reynoso 2005). Por lo cual queda la incógnita acerca de cuáles de estas especies dominaron en la SAP cuando ésta era una gran franja que cubría parte de nueve Estados (San Luis Potosí, Veracruz, Hidalgo, Puebla Oaxaca, Chiapas, Tabasco, Quintana Roo y Campeche; Rzedowski 1981), y cuáles especies se han extinguido en el último milenio por causa directa o

indirecta de las actividades antropogénicas. Esta información sería de gran utilidad para entender las fluctuaciones poblacionales naturales y antropogénicas en los anfibios y reptiles, y predecir grupos con mayor vulnerabilidad a la extinción.

Algunas especies de anfibios pueden estar restringidas a microhábitat específicos que tienen profundas implicaciones desde el punto de vista de conservación dado que son indispensables para la reproducción de los organismos (Zimmerman y Bierregard 1986, Gascon *et al.* 1999). En el presente estudio se encontró que *L. fragilis*, *G. elegans*, *A. lemurinus*, *A. sericeus*, *T. loquax*, *D. ebraccatus*, *B. asper* y *L. tuxtlae* hicieron uso restringido de alguno de los gradientes ambientales descritos y podrían verse afectadas si este microhábitat desaparece de la selva. Por ejemplo, se encontró que *L. fragilis*, *G. elegans* y *T. loquax* toleran cambios en 5 grados de temperatura, y *L. fragilis*, *G. elegans* y *A. sericeus* no toleraron humedades relativas menores a 30%. A pesar que algunas de estas especies son consideradas como comunes en la región, estas se encuentran muy ligadas a cierto tipo de microhábitat, y pueden dejar de hacer uso de fragmentos que no proporcionen la suficiente heterogeneidad de hábitat.

5.3 Implicaciones en el uso diferencial de gradientes ambientales

A nivel global, los trópicos presentan mayor riqueza debido a que las especies presentan adaptaciones y especializaciones muy finas. Esto determina nichos más restringidos y más especies por unidad de área (Krebs 2001), generando alta sobreposición de nicho en ambientes como la SAP.

Puede darse el caso de especies que seleccionen diversos hábitat para darles diferentes usos como cortejo, copula, ovoposición, termorregulación, alimentación, refugio, ecdísis, entre otros (Reinert 1993, Dodd y Smith 2003). En este caso, la competencia por recursos podría aumentarse durante periodos de sequía y estos patrones sólo podrían elucidarse en monitoreos a largo plazo (Reinert 1993). Para futuros trabajos es importante explorar esta partición de recurso a nivel del mosaico en el paisaje (e.g. lagunas, ríos, charcas, cercas vivas, cultivos, potreros, acahuales, entre otros) y a la luz de las horas de actividad, migración entre hábitat acuáticos y terrestres, disponibilidad de presas y preferencias alimenticias.

De las 11 variables evaluadas en los 2120 microhábitat, las variable que afectaron a mayor cantidad de especies fueron la altura sobre el suelo (19 especies), altura sobre el nivel del mar (16 especies), humedad relativa (16 especies), temperatura (14 especies) y pendiente (14 especies). Sin embargo, la influencia de las variables ambientales puede cambiar dependiendo de las

condiciones climáticas y las temporadas. En Los Tuxtlas, Urbina-Cardona et al. (2006) encontraron que durante la temporada de lluvias la cobertura de dosel explica el patrón en la composición de anfibios y reptiles, mientras que en temporada de sequía el patrón es explicado por la distancia a ríos.

Las especies de anfibios que presentaron relación con la cercanía a ríos (*O. valliceps*, *L. fragilis*, *G. elegans*, *D. ebraccatus*, *T. loquax* y *S. baudini*) presentaron un modo reproductivo de huevos y larvas puestas en el agua que los relaciona con los cuerpos de agua disponibles en la selva. En contraste los anfibios que presentan desarrollo directo (huevos depositados en tierra) no exhibieron una relación significativa con la distancia a ríos, mostrando la independencia de este grupo a cuerpos de agua en la selva. De esta forma el modo reproductivo y la tolerancia a variables ambientales y estructurales del microhábitat determinan una división del recurso que media la competencia entre las especies. Este patrón refleja claramente la historia natural de los anfibios y explica en parte los cambios en la diversidad a lo largo de gradientes de hábitat (Urbina-Cardona y Reynoso 2005).

En general todos los *Anolis* se vieron influenciados por la altura sobre el nivel del mar determinando una estratificación en el gradiente altitudinal en la SAP de Los Tuxtlas. La coexistencia entre anolinos que ocupan nichos aparentemente similares es mediada por la separación de hábitat a partir del uso diferencial de la humedad relativa, altura sobre el suelo, cobertura de dosel, densidad de sotobosque. En los límites de los hábitat de *A. sericeus* y *A. rodriguezii* con *A. uniformis*, se han reportado interacciones interespecíficas fuertes y competencia por territorio y alimento (Villareal-Benítez y Heras-Lara 1997). Aparte de la competencia entre especies del mismo género, la presión de predación por parte de algunas serpientes puede determinar el desplazamiento y ocupación temporal de microhábitat más seguros para las lagartijas. Como ejemplo, durante el estudio se encontró *I. cenchoa* predando a *A. uniformis* y a *B. asper* alimentándose de *L. tuxtlae*.

De esta manera, el uso del hábitat por parte de la herpetofauna puede diferir a nivel poblacional dependiendo de la edad, sexo, morfotipo de coloración, condición reproductiva, ecdisis, relaciones sociales, aprendizaje, estado nutricional y de forrajeo, y efecto de enfermedades, heridas y parásitos (Reinert 1984, Toft 1985, Reinert 1993, Ford y Burghardt 1993, Krebs 2001). Es necesario realizar estudios, con diseños rigurosos y metódicos, que permitan evaluar el ámbito hogareño de las especies teniendo en cuenta el movimiento horizontal

y vertical en el hábitat, los patrones de uso a un nivel mas detallado en la población, sus preferencias alimentarias y su dinámica temporal (e.g. diferencias entre día y noche, entre estaciones y entre años). Estos estudios podrían revelar patrones específicos que difieran de las tendencias descritas y modeladas en el presente estudio. A medida que se esclarezcan este tipo de patrones, las hipótesis de investigación direccionadas a la conservación de los anfibios y reptiles de Los Tuxtlas (*sensu* Urbina-Cardona *et al. enviado*) se podrán ir refinando para incluir diferentes tipos de hábitat a diferentes escalas espaciales, e involucrando la variabilidad temporal y genética entre poblaciones. Cuando se incluyan todas estas variables en un concepto multidimensional del hábitat se constituirán los verdaderos límites dentro de los cuales los planes de manejo y conservación pueden hacerse tangibles (Dodd y Smith 2003).

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Tabla 1. Grupo de Anfibios y Reptiles registrados en la Selva Alta Perennifolia de Los Tuxtlas

Familia	Genero	Especies
CAUDATA		
Plethodontidae	3	3
ANURA		
Bufonidae	1	1
Leptodactylidae	3	6
Microhylidae	1	1
Hylidae	4	5
Ranidae	1	1
SAURIA		
Corytophanidae	2	2
Gekkonidae	1	1
Iguanidae	2	2
Phrynosomatidae	1	2
Polychrotidae	1	9
Scincidae	2	2
Teiidae	1	1
Xantusiidae	1	1
SERPENTES		
Boidae	1	1
Colubridae	6	8
Elapidae	1	1
Viperidae	1	1
Total Amphibia	13	17
Total Reptilia	20	31
Total Herpetofauna	33	48

ANEXO 1. Rangos de tolerancia a las variables ambientales medidas en el microhábitat de los anfibios y reptiles de la Selva Alta Perennifolia de Los Tuxtlas, Veracruz. *Temp*= temperatura del sustrato, *HR* = humedad relativa del sustrato, *%Her* = cobertura herbácea, *%Hoj* = cobertura de hojarasca, *EspHoj* = espesor de la capa de hojarasca, *hSue.* = altura sobre el suelo, *%Dos* = cobertura de dosel, *h.* densidad de sotobosque, *Pend* = pendiente, *hmsnm* = altura sobre el nivel del mar., *DisRio* = distancia a río

<i>Nanotriton rufescens</i> n= 52					<i>Ollotis valliceps</i> n=60					<i>Eleutherodactylus alfredi</i> n=25				
	X	Min	Max	DS		X	Min	Max	DS		X	Min	Max	DS
Temp	22.5	17.0	26.0	2.2	Temp	24.9	19.0	28.0	1.7	Temp	23.4	17.0	27.0	2.5
HR	75.8	21.0	90.0	19.5	HR	74.4	23.0	94.0	19.7	HR	66.5	23.0	92.0	27.6
%Her	70.0	10.0	100.0	26.2	%Her	53.3	5.0	100.0	29.9	%Her	69.9	10.0	100.0	28.4
%Hoj	98.2	50.0	100.0	7.3	%Hoj	94.9	0.0	100.0	14.7	%Hoj	94.7	60.0	100.0	10.1
EspHoj	8.8	5.0	15.0	2.5	EspHoj	7.7	0.0	13.0	2.8	EspHoj	8.8	4.0	13.0	2.0
hSue	50.7	0.0	140.0	38.3	hSue	3.3	0.0	40.0	9.2	hSue	47.5	0.0	140.0	36.7
%Dos	44.9	22.5	70.4	12.6	%Dos	46.8	22.5	71.0	10.1	%Dos	50.9	32.0	70.1	12.4
DenSot	5.8	3.8	10.0	1.3	DenSot	5.5	4.4	9.2	1.1	DenSot	5.5	4.4	7.0	0.7
Pend	19.6	1.0	43.0	8.7	Pend	15.0	1.0	34.0	9.2	Pend	21.2	7.0	39.0	7.9
hmsnm	188.1	40.0	270.0	45.3	hmsnm	188.3	130.0	265.0	25.6	hmsnm	168.4	35.0	275.0	65.3
DisRio	260.3	10.0	1270.0	353.7	DisRio	100.7	10.0	1270.0	187.3	DisRio	183.4	10.0	600.0	165.2

<i>Eleutherodactylus rhodopis</i> n=1275					<i>Leptodactylus fragilis</i> n=6					<i>Syrhophus leprus</i> n=20				
	X	Min	Max	DS		X	Min	Max	DS		X	Min	Max	DS
Temp	25.5	17.0	34.0	2.8	Temp	24.7	23.0	26.0	1.0	Temp	24.3	19.0	30.0	2.5
HR	68.2	20.0	97.0	22.1	HR	88.0	83.0	95.0	3.9	HR	78.7	24.0	97.0	19.3
%Her	47.7	0.0	100.0	31.6	%Her	58.3	10.0	90.0	29.3	%Her	57.0	0.0	100.0	29.3
%Hoj	94.0	8.0	100.0	12.9	%Hoj	100.0	100.0	100.0	0.0	%Hoj	98.2	78.0	100.0	5.7
EspHoj	8.1	0.0	30.0	3.0	EspHoj	7.7	5.0	10.0	2.3	EspHoj	9.5	6.0	13.0	2.0
hSue	2.9	0.0	100.0	9.0	hSue	1.7	0.0	10.0	4.1	hSue	55.5	0.0	200.0	59.2
%Dos	44.8	22.5	71.0	9.5	%Dos	44.4	40.1	46.5	2.6	%Dos	43.9	28.7	70.1	9.7
DenSot	5.4	3.8	10.0	1.1	DenSot	6.0	4.8	7.0	0.8	DenSot	6.1	4.6	8.2	1.1
Pend	20.5	1.0	43.0	9.6	Pend	11.5	1.0	18.0	6.0	Pend	20.4	1.0	40.0	11.5
hmsnm	180.6	35.0	300.0	67.2	hmsnm	188.3	165.0	195.0	11.7	hmsnm	171.5	60.0	265.0	61.5
DisRio	246.5	10.0	1270.0	286.6	DisRio	25.8	10.0	100.0	36.8	DisRio	260.5	30.0	1120.0	279.0

<i>Gastrophryne elegans</i> n=5					<i>Dendropsophus ebraccatus</i> n=6					<i>Tlalocohyla loquax</i> n=18				
	X	Min	Max	DS		X	Min	Max	DS		X	Min	Max	DS
Temp	24.6	24.0	26.0	0.9	Temp	26.3	23.0	29.0	2.9	Temp	23.1	21.0	25.0	1.0
HR	82.8	79.0	87.0	3.6	HR	39.3	23.0	61.0	17.5	HR	67.4	24.0	80.0	16.3
%Her	38.0	10.0	90.0	35.6	%Her	68.3	20.0	84.0	24.1	%Her	79.0	10.0	100.0	26.0
%Hoj	100.0	100.0	100.0	0.0	%Hoj	90.0	78.0	100.0	11.2	%Hoj	95.7	70.0	100.0	9.9
EspHoj	7.4	5.0	10.0	1.9	EspHoj	7.8	5.0	12.0	2.6	EspHoj	8.3	5.0	12.0	1.9
hSue	0.0	0.0	0.0	0.0	hSue	40.0	0.0	60.0	22.8	hSue	44.2	0.0	80.0	21.1
%Dos	49.2	44.0	56.9	7.0	%Dos	50.3	42.0	55.2	5.7	%Dos	45.9	22.5	70.4	16.6
DenSot	4.6	4.4	4.8	0.2	DenSot	5.2	4.4	5.6	0.5	DenSot	7.3	4.6	10.0	2.2
Pend	15.4	7.0	27.0	8.5	Pend	18.8	7.0	34.0	8.6	Pend	31.0	3.0	43.0	12.6
hmsnm	186.0	165.0	210.0	20.1	hmsnm	100.8	35.0	180.0	72.6	hmsnm	224.4	155.0	300.0	39.3
DisRio	82.0	10.0	150.0	76.6	DisRio	18.3	10.0	50.0	18.3	DisRio	36.4	10.0	185.0	55.3

<i>Smilisca baudini</i> n=20				
	X	Min	Max	DS
Temp	25.8	24.0	30.0	1.6
HR	69.0	24.0	86.0	23.7
%Her	68.5	10.0	100.0	30.6
%Hoj	94.0	70.0	100.0	10.0
EspHoj	10.0	4.0	30.0	5.5
hSue	47.0	0.0	200.0	59.4
%Dos	46.2	22.5	70.4	14.3
DenSot	6.2	3.8	10.0	1.8
Pend	25.1	11.0	43.0	12.2
hmsnm	195.0	55.0	275.0	53.7
DisRio	117.8	10.0	700.0	225.6

<i>Corytophanes hernandezii</i> n=35				
	X	Min	Max	DS
Temp	25.5	22.0	32.0	2.5
HR	64.0	23.0	95.0	27.4
%Her	66.1	10.0	100.0	27.1
%Hoj	95.9	80.0	100.0	6.5
EspHoj	8.7	5.0	14.0	2.3
hSue	80.9	0.0	200.0	60.3
%Dos	44.4	22.5	67.8	8.7
DenSot	5.7	4.0	9.2	1.2
Pend	19.6	3.0	40.0	8.0
hmsnm	136.4	35.0	245.0	69.0
DisRio	206.1	10.0	780.0	238.3

<i>Sceloporus variabilis</i> n=14				
	X	Min	Max	DS
Temp	28.9	26.0	32.0	2.1
HR	76.4	28.0	89.0	15.0
%Her	63.5	15.0	100.0	28.1
%Hoj	63.9	0.0	100.0	47.5
EspHoj	6.9	0.0	14.0	5.5
hSue	19.7	0.0	50.0	21.2
%Dos	41.4	31.6	45.7	4.1
DenSot	6.2	4.0	8.2	1.1
Pend	18.8	3.0	34.0	7.7
hmsnm	183.2	45.0	270.0	86.5
DisRio	693.2	30.0	1270.0	492.9

<i>Anolis barkeri</i> n=19				
	X	Min	Max	DS
Temp	25.8	20.0	28.0	1.9
HR	74.0	23.0	86.0	13.6
%Her	57.4	0.0	90.0	33.2
%Hoj	95.3	50.0	100.0	12.6
EspHoj	9.9	7.0	15.0	2.2
hSue	30.2	0.0	120.0	37.1
%Dos	46.5	22.5	71.0	12.3
DenSot	5.3	3.8	9.2	1.7
Pend	18.1	3.0	43.0	11.1
hmsnm	174.7	75.0	260.0	58.9
DisRio	186.3	10.0	690.0	244.5

<i>Anolis lemurinus</i> n=11				
	X	Min	Max	DS
Temp	25.9	23.0	30.0	2.5
HR	26.0	23.0	30.0	2.5
%Her	83.8	66.0	95.0	8.7
%Hoj	83.9	66.0	95.0	8.7
EspHoj	8.5	4.0	12.0	2.6
hSue	21.4	0.0	120.0	36.6
%Dos	48.0	33.6	69.6	9.5
DenSot	5.4	4.0	6.8	0.8
Pend	22.7	11.0	33.0	6.4
hmsnm	125.5	35.0	260.0	69.7
DisRio	265.5	10.0	1120.0	350.5

<i>Anolis rodriguezii</i> n=10				
	X	Min	Max	DS
Temp	27.0	24.0	31.0	2.2
HR	72.0	24.0	88.0	18.2
%Her	64.8	20.0	90.0	30.2
%Hoj	96.8	78.0	100.0	7.3
EspHoj	9.8	6.0	15.0	2.7
hSue	36.5	0.0	130.0	41.7
%Dos	42.8	32.7	60.2	9.7
DenSot	5.2	4.2	7.2	1.0
Pend	26.1	18.0	36.0	7.9
hmsnm	212.5	110.0	260.0	46.7
DisRio	137.5	10.0	350.0	128.2

<i>Anolis sericeus</i> n=7				
	X	Min	Max	DS
Temp	28.0	26.0	32.0	2.0
HR	71.4	32.0	85.0	18.1
%Her	57.3	10.0	100.0	33.4
%Hoj	95.1	66.0	100.0	12.9
EspHoj	9.3	6.0	12.0	2.1
hSue	50.7	0.0	120.0	49.2
%Dos	40.7	35.4	48.7	4.0
DenSot	5.4	4.8	7.2	0.8
Pend	21.7	12.0	30.0	7.5
hmsnm	90.7	40.0	260.0	76.0
DisRio	273.6	75.0	590.0	233.8

<i>Anolis unifomis</i> n=364				
	X	Min	Max	DS
Temp	25.7	17.0	32.0	2.7
HR	64.9	23.0	97.0	24.8
%Her	56.9	0.0	100.0	29.9
%Hoj	93.0	0.0	100.0	14.5
EspHoj	8.9	0.0	18.0	2.4
hSue	10.1	0.0	110.0	16.6
%Dos	46.2	22.5	71.0	10.4
DenSot	5.6	3.8	10.0	1.2
Pend	20.7	1.0	43.0	9.3
hmsnm	169.0	35.0	280.0	64.9
DisRio	246.8	10.0	1270.0	287.2

<i>Plestiodon sumichrasti</i> n=53				
	X	Min	Max	DS
Temp	26.2	22.0	34.0	2.3
HR	70.2	22.0	95.0	22.5
%Her	63.1	0.0	100.0	28.6
%Hoj	95.6	40.0	100.0	10.1
EspHoj	9.4	5.0	14.0	2.0
hSue	0.8	0.0	10.0	2.7
%Dos	44.1	32.0	70.1	10.5
DenSot	5.3	4.0	10.0	1.3
Pend	19.7	1.0	39.0	8.9
hmsnm	164.0	35.0	265.0	58.7
DisRio	295.8	10.0	710.0	268.1

<i>Scincella cherriei</i> n=27				
	X	Min	Max	DS
Temp	26.2	21.0	31.0	2.3
HR	75.0	23.0	92.0	13.6
%Her	50.0	0.0	100.0	33.2
%Hoj	97.6	70.0	100.0	7.3
EspHoj	9.3	5.0	13.0	2.1
hSue	2.1	0.0	50.0	9.8
%Dos	48.0	32.0	71.0	9.0
DenSot	5.5	3.8	10.0	1.3
Pend	23.3	1.0	43.0	10.7
hmsnm	156.9	40.0	275.0	66.8
DisRio	176.5	10.0	1120.0	253.4

<i>Ameiva undulata</i> n=17				
	X	Min	Max	DS
Temp	28.2	25.0	31.0	1.9
HR	61.1	26.0	85.0	20.1
%Her	80.0	20.0	100.0	23.9
%Hoj	93.1	71.0	100.0	10.2
EspHoj	9.6	7.0	12.0	1.2
hSue	0.3	0.0	5.0	1.2
%Dos	37.0	22.5	48.7	8.8
DenSot	7.0	5.0	10.0	1.5
Pend	16.5	12.0	39.0	7.1
hmsnm	116.8	40.0	245.0	78.0
DisRio	257.9	10.0	1080.0	320.8

<i>Lepidophyma tuxtlae</i> n=16				
	X	Min	Max	DS
Temp	24.6	18.0	28.0	2.4
HR	53.1	23.0	93.0	30.4
%Her	70.3	0.0	95.0	27.4
%Hoj	92.7	60.0	100.0	10.3
EspHoj	8.6	5.0	13.0	2.3
hSue	5.3	0.0	40.0	12.0
%Dos	45.8	29.6	60.6	8.6
DenSot	5.4	3.8	7.6	1.1
Pend	20.7	7.0	39.0	9.6
hmsnm	200.0	75.0	280.0	48.2
DisRio	224.7	10.0	1120.0	310.6

<i>Imantodes cenchoa</i> n=19					<i>Bothrops asper</i> n=8					Todos los microhabitats evaluados (n=2120)				
	X	Min	Max	DS		X	Min	Max	DS		X	Min	Max	DS
Temp	24.2	17.0	29.0	2.5	Temp	25.5	21.0	29.0	2.7	Temp	25.5	17.0	34.0	2.8
HR	62.4	22.0	91.0	28.6	HR	64.4	23.0	86.0	26.3	HR	67.8	20.0	97.0	22.9
%Her	81.3	20.0	100.0	25.8	%Her	69.3	40.0	100.0	25.9	%Her	53.2	0.0	100.0	31.6
%Hoj	96.5	78.0	100.0	6.2	%Hoj	92.4	70.0	100.0	13.0	%Hoj	93.9	0.0	100.0	13.4
EspHoj	9.4	5.0	16.0	2.6	EspHoj	8.8	4.0	13.0	2.9	EspHoj	8.4	0.0	30.0	2.9
hSue	43.6	0.0	150.0	37.4	hSue	6.3	0.0	50.0	17.7	hSue	10.5	0.0	200.0	26.3
%Dos	47.7	32.0	70.4	9.3	%Dos	39.2	31.6	44.0	5.1	%Dos	45.2	22.5	71.0	9.9
DenSot	5.7	4.2	10.0	1.3	DenSot	5.7	4.8	7.2	0.8	DenSot	5.5	3.8	10.0	1.2
Pend	19.1	3.0	43.0	10.7	Pend	16.1	5.0	28.0	8.1	Pend	20.4	1.0	43.0	9.6
hmsnm	189.7	35.0	250.0	46.0	hmsnm	196.3	65.0	270.0	65.1	hmsnm	176.2	35.0	300.0	65.9
DisRio	97.6	10.0	700.0	161.0	DisRio	223.8	10.0	1170.0	386.3	DisRio	238.2	10.0	1270.0	286.5

Tabla 2. Ecuaciones de regresión múltiple de las variables del microhábitat que determinan la presencia de anfibios y reptiles en la Selva Alta Perennifolia de Los Tuxtlas, Veracruz. *a.* temperatura del sustrato, *b.* humedad relativa del sustrato, *c.* cobertura herbácea, *d.* cobertura de hojarasca, *e* espesor de la capa de hojarasca, *f.* altura sobre el suelo, *g.* cobertura de dosel, *h.* densidad de sotobosque, *i* pendiente, *j* altura sobre el nivel del mar., *k.* distancia a río.

Especies	Modelo de regresión	R Multiple	Prueba F	gl	p
AMPHIBIA					
<i>Nanotriton rufescens</i>	$y= 0.1623 + f*0.213 - a*0.14 + c*0.067 + b*0.007 + d*0.036 - i*0.03 + e*0.025$	29%	28.6	7.2	≤ 0.005
<i>Ollotis valliceps</i>	$y=0.262 - i*0.1 - k*0.08 + b*0.06 - f*0.05 - a*0.04 - e*0.03 + c*0.026 + j*0.024$	16%	6.7	8.2	≤ 0.005
<i>Eleutherodactylus alfredi</i>	$y=0.031 + f*0.134 - a*0.06 + g*0.058 + c*0.03$	17%	16.2	4.2	≤ 0.005
<i>Eleutherodactylus rhodopis</i>	$y=1.064 - f*0.3 - c*0.16 - e*0.12 - b*0.08 - g*0.08 + j*0.079 - h*0.06 + i*0.04$	41%	54.2	8.2	≤ 0.005
<i>Leptodactylus fragilis</i>	$y=0.0092 + b*0.067 - k*0.04 + c*0.039 - i*0.03 - f*0.02$	8%	2.7	5.2	≤ 0.05
<i>Syrrhophus lepras</i>	$y= -0.0149 + f*0.152 + b*0.052 + h*0.038 + e*0.033 - a*0.03$	18%	13.5	5.2	≤ 0.005
<i>Gastrophryne elegans</i>	$y=0.0263 - h*0.04 - k*0.03 - i*0.03 + b*0.03$	6.56%	2.3	4.2	0.058
<i>Dendropsophus ebraccatus</i>	$y=0.02 - b*0.06 + f*0.058 - j*0.05 - k*0.04 - h*0.03 + g*0.023$	11.33%	4.6	6.2	≤ 0.005
<i>Tlalocohyla loquax</i>	$y= -0.142 + h*0.121 + i*0.099 + f*0.092 + j*0.051 - a*0.05 - k*0.05 + c*0.027 + d*0.025$	22.40%	14.0	8.2	≤ 0.005
<i>Smilisca baudini</i>	$y= -0.1 + f*0.133 + e*0.044 + i*0.04 + h*0.035 + j*0.033 - k*0.03 + a*0.028$	16.33%	8.3	7.2	≤ 0.005
REPTILIA					
<i>Corytophanes hermandezi</i>	$y= -0.003 + f*0.348 + d*0.37 - j*0.06 - i*0.03 + a*0.025$	35%	60.9	5.2	≤ 0.005
<i>Sceloporus variabilis</i>	$y= -0.005 - d*0.22 + k*0.153 + a*0.123 + b*0.121 + c*0.07 + h*0.05 + j*0.05 - i*0.03 + f*0.025$	29%	20.9	9.2	≤ 0.005
<i>Anolis barkeri</i>	$y=0.021 + f*0.072 + e*0.052 + b*0.03 - i*0.03$	10%	5.0	4.2	≤ 0.005
<i>Anolis lemurinus</i>	$y=0.028 - b*0.13 - j*0.03 + g*0.03 + f*0.027$	14%	10.8	4.2	≤ 0.005
<i>Anolis rodriguezi</i>	$y= -0.044 + f*0.077 + j*0.049 + a*0.047 - g*0.04 - h*0.04 + i*0.034 - k*0.03 + e*0.026$	11%	3.4	8.2	≤ 0.005
<i>Anolis sericeus</i>	$y= -0.02 + f*0.089 - j*0.07 + a*0.052 + b*0.023$	13%	8.4	4.2	≤ 0.005
<i>Anolis unifomis</i>	$y= -0.196 + g*0.076 + e*0.072 - j*0.05 + h*0.046 + k*0.04 + a*0.037 + c*0.037 - b*0.03$	13.6%	5.1	8.2	≤ 0.005
<i>Plestiodon sumichrasti</i>	$y= -0.073 + c*0.106 - f*0.08 + b*0.07 + e*0.058 - j*0.04 + k*0.036 + a*0.035 - h*0.03$	13.7%	5.0	8.2	≤ 0.005
<i>Scincella cherriei</i>	$y= -0.08 - j*0.06 + i*0.043 - f*0.04 + b*0.039 + e*0.032 - k*0.03 + g*0.027 + d*0.025$	9.9%	2.6	8.2	≤ 0.05
<i>Ameiva undulata</i>	$y= -0.893 + h*0.11 + a*0.08 - j*0.08 - f*0.06 + b*0.039 + k*0.037 + e*0.031 - i*0.02$	18.9%	8.7	9.2	≤ 0.005
<i>Lepidophyma tuxtlae</i>	$y=0.007 + j*0.42 - b*0.05 + c*0.026$	7%	3.9	8.2	≤ 0.05
<i>Imantodes cenchoa</i>	$y=0.001 + f*0.104 + c*0.059 - k*0.04 - a*0.03 + e*0.026 + d*0.025$	15%	7.8	6.2	≤ 0.005
<i>Bothrops asper</i>	$y=0.028 - g*0.03 - i*0.03 + c*0.03 + j*0.027$	6%	2.0	4.2	0.092