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EFECTOS DE LA CONVERSIÓN DEL BOSQUE TROPICAL CADUCIFOLIO A MOSAICOS AGRÍCOLAS SOBRE ENSAMBLAJES HERPETOFAUNISTICOS

TESIS

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PRESENTA

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"***Después de todo un sapo es puro corazón***"

Juan José Arreola

DEDICATORIA

Al Dr. Miguel Martínez Ramos, mi guía y formador académico

A mis padres, hermanos y hermanas, sus hijos e hijas y Javier Alvarado por ser mi luz y mis compañeros en esta vida

A mis amigos, por ser mi alegría

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Contenido

RESUMEN

El Disturbio antrópico puede modificar la estructura del hábitat y tiene el potencial de alterar la organización y distribución espacial de las comunidades. En esta tesis se evalúan los efectos del disturbio ocasionado por las actividades agrícolas y ganaderas sobre la herpetofauna en la región de Chamela, Jalisco, México con el fin de: 1) identificar cambios en la organización de las especies; 2) evaluar cambios en la distribución espacial de las especies en el gradiente ripario-laderas adyacentes; 3) identificar los atributos de las especies sensibles a la perturbación; y 4) generar propuestas para su conservación. Durante 2 años se muestrearon 6 cuencas pequeñas, 3 conservadas y 3 perturbadas, en la Reserva de la Biósfera Chamela-Cuixmala y áreas aledañas. Las cuencas perturbadas se caracterizaron por un mosaico de pastizales y campos cultivados (maíz, frijol, calabaza) entremezclados con parches de Bosque Tropical Caducifolio en diferentes etapas sucesionales. En general se encontró que: 1) la riqueza de especies, la diversidad y la abundancia de lagartijas fueron mayores en los bosques perturbados mientras que las tortugas respondieron de manera inversa; 2) la diversidad y riqueza de especies de anuros fueron menores en el bosque perturbado pero la abundancia fue similar en ambas condiciones; 3) la estructura y la composición de los ensambles de serpientes no difirieron entre las condiciones de bosque; 4) cuatro (22%) especies de anuros, 2 (11%) de lagartijas y 3 (100%) de tortugas fueron sensibles a la perturbación, ninguna especie de serpiente fue sensible; 5) la declinación en la abundancia de especies sensibles a la perturbación se asoció con la reducción de los siguientes elementos del hábitat: cobertura del dosel, tallos leñosos, raíces y hojarasca; 6) la abundancia y diversidad de lagartijas y serpientes disminuyó de las áreas riparias a las zonas altas de las laderas tanto en la estación de lluvias como la estación de secas y en las dos condiciones de conservación del bosque. Los anfibios siguieron la misma tendencia sólo en el bosque conservado durante la estación de lluvias; 7) independientemente de la distancia al arroyo, la abundancia y la diversidad de anfibios disminuyó marcadamente durante la estación seca del año mientras que en las serpientes y lagartijas se incrementaron; 8) las especies de anuros de cuerpo pequeño y desarrollo embrionario directo fueron especialmente sensibles a la perturbación del bosque, mientras que en relación a la dieta al parecer las especies generalistas no se ven afectadas, tal es el caso del bufo marmoleado (*Incilius marmoreus = Bufo marmoreus*) que tiene la capacidad de cambiar su dieta dependiendo de la disponibilidad de sus presas. Para la conservación exitosa de la herpetofauna en los paisajes transformados por las actividades agrícolas y ganaderas se sugiere: 1) desarrollar estrategias de conservación a escala local y regional que incorporen el ordenamiento regional en la conversión del bosque; 2) asegurar la permanencia de fragmentos de bosque maduro y bosque secundario en diferentes estadios de regeneración; 3) mantener una red de vegetación riparia y 4) mantener una elevada conectividad entre todos los elementos estructurales del paisaje. Finalmente, tanto los bosques tropicales secos, como las especies sensibles al disturbio deberán ser cuidadosamente monitoreados, pues la batalla actual en contra de la extinción de especies se ganará o perderá en los paisajes modificados.

ABSTRACT

The anthropogenic disturbance can alter habitat structure and may disturb the organization and spatial distribution of natural communities. In this thesis the effects of disturbance associated to agricultural and cattle ranching activities on the herpetofauna are evaluated in the region of Chamela, Jalisco, México with the purpose of: 1) identify changes in species organization; 2) evaluate changes in the spatial distribution of species in a riparian-upland gradient; 3) identify attributes of species sensitive to disturbance; and 4) generate conservation strategies. For 2 years, 6 small watersheds, 3 conserved and 3 disturbed were sampled in the Biosphere Reserve of Chamela-Cuixmala and adjacent areas. Disturbed watersheds presented a mosaic of pastures and cultivated fields (corn, beans, and squash) intermingled with patches of Dry Tropical Forest in different succession stages. In general it was found that: 1) lizard species richness, diversity and abundance were greater in disturbed forest, whereas turtles presented greater values of these community attributes in conserved forest; 2) anuran diversity and species richness were lower in disturbed forest, but abundance was similar in both forest conditions; 3) structure and composition of snake assemblages were similar in both forest conditions; 4) four (22%) anuran, 2 (11%) lizard and 3 (100%) turtle species were sensitive to disturbance, no snake species was disturbance sensitive; 5) decline of abundance of sensitive species was associated to a reduction of the following habitat attributes: canopy cover, woody stems, roots and leaf litter; 6) lizard and snake abundance and diversity decreased from riparian areas to uplands in both rainy and dry season and in both forest conservation conditions. Amphibians presented the same tendency but only in conserved forest during the rainy season; 7) regardless of the distance from stream edge, abundance and diversity of amphibians markedly decreased during the dry season, whereas those of lizards and snakes increased; 8) anuran species with small body size and direct development were especially sensitive to forest disturbance, whereas in relation to diet generalist species were not affected, such is the case of the toad *Incilius marmoreus* = *Bufo marmoreus*) that changes its diet according to changes is prey availability. For the successful conservation of the herpetofauna in landscapes transformed by agricultural and cattle ranching activities it is suggested that: 1) develop conservation strategies at a local and regional scale that incorporate regional ecological planning in forest conversion; 2) insure permanence of patches of old growth forest and secondary forest in several succession stages; 3) maintain a network of riparian vegetation and 4) maintain a high connectivity between all structural elements of the landscape. Finally, both dry tropical forests and disturbance sensitive species must be carefully monitored considering that the present struggle against species extinction will be won or lost in modified landscapes.

INTRODUCCIÓN GENERAL

A pesar de que la cobertura forestal está aumentando en varios países del mundo, a través de la regeneración de bosques secundarios y plantaciones forestales (Chazdon 2008), la modificación del hábitat sigue siendo la principal huella ecológica de las actividades humanas. Tales modificaciones son causadas por el cambio de uso del suelo que buscan aumentar la productividad primaria sin considerar los efectos negativos sobre la biodiversidad y el funcionamiento de los ecosistemas (Gascón et al. 2007). Estos efectos han sido reconocidos profusamente (Gibbons et al. 2000; Collins y Storfer 2003; Cushman 2006; Gallant et al. 2007), sin embargo, aún existen grandes vacíos de información sobre la respuesta de los diferentes ensamblajes de especies a la alteración del hábitat. Estos son particularmente evidentes en los grupos de anfibios y reptiles que paradójicamente son dos de los grupos que se encuentran en mayor peligro de extinción (Gibbons et al. 2000; Houlahan et al. 2000; Roelants et al. 2007; Gascon et al. 2007; Stuart et al. 2004, 2008).

La pérdida y fragmentación del hábitat afectan de manera directa a las especies (Collins y Storfer 2003; Gardner et al. 2007). La sobreexplotación de especies (e.g. cacería excesiva), contaminación, enfermedades y cambio climático son factores indirectos que afectan también a las especies sin modificar necesariamente la estructura del hábitat (Gardner et al. 2007). Debido a que la pérdida del hábitat sigue siendo la principal amenaza para la diversidad biológica, es prioritario realizar estudios sobre la respuesta de las especies a tal pérdida, en particular, de los grupos de especies y ecosistemas más amenazados (Sala et al. 2000). Tal es el caso de los anfibios y reptiles y el de los bosques tropicales caducifolios (Gibbons et al. 2000; Collins y Storfer 2003; Cushman 2006; Gallant et al. 2007; Quesada et al. 2009).

En México, los bosques tropicales caducifolios cubren el 60% del área ocupada por los bosques tropicales del país y se caracterizan por su importancia en términos de riqueza y endemismo de especies animales y vegetales (Trejo-Vazquez y Dirzo 2000; Trejo-Vazquez 2005; García 2006). En el caso de la herpetofauna estos bosques albergan casi un tercio de los anfibios y reptiles registrados y un cuarto de las especies endémicas a México (Flores–Villela y Goyenechea 2003; García 2006; Ochoa–Ochoa y Flores–Villela 2006). En la actualidad y a pesar de su importancia biológica, únicamente el 27% de estos bosques permanece intacto (Trejo-Vazquez y Dirzo 2000), por lo que no es de extrañar que el 73% de la superficie del país ocupada originalmente por este tipo de bosque, sea una mezcla de mosaicos agrícola-ganaderos y bosques secundarios en diferentes estadios sucesionales. Tal situación conlleva a la urgente necesidad de realizar estudios encaminado a entender los procesos que influyen sobre la abundancia y distribución de las especies en estos nuevos paisajes agroforestales (Chazdon et al. 2008). Así mismo, es urgente entender cuáles son los atributos estructurales del bosque que favorecen la permanencia de las especies en estos paisajes transformados.

En el contexto anterior, el objetivo general de la presente tesis fue el de evaluar la respuesta de la herpetofauna a la perturbación del bosque tropical caducifolio producida por la conversión del bosque a mosaicos agrícolas y ganaderos. Para cumplir con este objetivo se desarrollan 4 capítulos que se describen a continuación.

En el capítulo I. Se presenta una síntesis de la información publicada sobre los efectos de los cambios del hábitat causados por la actividad humana en ensambles herpetofaunísticos, especialmente en ecosistemas de bosque tropical seco. Específicamente, se abordan tres aspectos: 1. los cambios estructurales del hábitat que con mayor frecuencia pueden afectar a los anfibios y reptiles; 2. como los anfibios y reptiles que son afectados por estos cambios; y 3. los vacios de conocimiento sobre estos dos temas. Así mismo, se vislumbran perspectivas de investigación y conservación de anfibios y reptiles en paisajes transformados por actividades agropecuarias en regiones tropicales secas.

Las especies pueden variar en su respuesta al disturbio antrópico del hábitat. En el Capítulo II (Suazo-Ortuño et al. 2008) se explora el efecto de la conversión del bosque tropical seco a mosaicos agrícolas sobre los ensambles herpetofaunísticos. Se identificaron las especies sensibles al disturbio que requieren esfuerzos de conservación, y se relacionaron los cambios observados en los ensamblajes y la sensibilidad de las especies con la modificación del hábitat y las características de vulnerabilidad de las mismas.

Los cambios antrópicos producidos sobre el bosque en cuencas pequeñas puede generar gradiente ambientales de los bordes de los arroyos hacia las zonas más alejadas. En el Capítulo III (Suazo-Ortuño et al. enviado Agosto 2009) se presenta un estudio que explora si éstos gradientes afectan la distribución de los ensamblajes de anfibios y reptiles a lo largo del gradiente ripario-zonas aledañas de ladera en áreas conservas y perturbadas por actividades agrícolas y ganaderas. En particular probamos las siguientes hipótesis (1) la abundancia y diversidad de la herpetofauna es mayor en las zonas riparias que lejos de ellas, (2) la composición y dominancia de las especies en las zonas riparias difieren de las zonas aledañas, (3) las zonas riparias presentan un mayor efecto positivo durante la época de sequía ya que funcionan como refugios para muchas especies y (4) el efecto positivo sobre los ensamblajes de anfibios y reptiles de las zonas riparias es mayor en los sitios con perturbación humana que en las áreas conservadas.

La alteración del hábitat puede generar cambios en la disponibilidad de alimento para las especies e incidir en su rendimiento. En el capítulo IV (Suazo-Ortuño et al. 2007), se presenta un estudio que analiza este aspecto a través del análisis de la dieta del bufo marmoleado (*Incilius marmoreus = Bufo marmoreus*) en hábitats conservados y modificados por las actividades humanas. Finalmente en el capítulo V se presenta una discusión general que integra los resultados de los estudios incluidos en la tesis.

Durante el transcurso del presente trabajo, y a partir de los trabajos de Faivovich et al. (2005) y Frost et al. (2006) la taxonomía mundial de los anfibios sufrió cambios abruptos a nivel de familia, género y especie, por lo que con excepción del capítulo IV la nomenclatura utilizada para anfibios en esta tesis es la nueva nomenclatura oficial utilizada por la Amphibian species of the world 5.3 del American Museum of Natural History.

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CAPÍTULO I

Efectos de la perturbación del hábitat sobre la herpetofauna en bosques tropicales caducifolios: una revisión y perspectivas

Efectos de la perturbación del hábitat sobre la herpetofauna en bosques tropicales caducifolios: una revisión y perspectivas

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Resumen

Las actividades humanas como la agricultura, la ganadería y la explotación forestal están modificado los hábitats naturales en el que se desarrollan las especies. En este trabajo se hace una revisión de los factores de disturbio de origen antrópico que modifican la estructura física del hábitat y se revisa la respuesta de la herpetofauna a estos cambios con énfasis en los bosques tropicales caducifolios. El objetivo final es, por un lado, analizar el estado actual del conocimiento sobre los diferentes factores que afectan la estructura del hábitat y su efecto sobre los ensambles herpetofaunísticos y, por otro lado, identificar los vacíos de información sobre este tema en México. Se sugieren enfoques de estudio que pueden proveer conocimientos y acciones efectivas para la conservación de la herpetofauna en paisajes que están experimentando una acelerada modificación del hábitat.

1. Introducción

1.1. Tasas de extinción y herpetofauna

Actualmente nuestro planeta está enfrentando las más altas tasas de extinción de los últimos 65 millones de años (Vitousek et al. 1997; Wilson 1999; Balmford et al. 2003). La pérdida de diversidad biológica representa una tasa de extinción global de especies hasta de cuatro órdenes de magnitud en relación al registro fósil (May y Tregonning 1998; Kerr y Cihlar 2004) e incluso la tasa de desaparición de poblaciones a escala regional puede ser de mayor magnitud que la desaparición de especies a nivel global (Ehrlich y Daily 1993).

En el caso de los anfibios, el 32% de las aproximadamente 6000 especies existentes corresponde a taxa en riesgo. En otros grupos de vertebrados la proporción de taxa en riesgo es menor, por ejemplo el 12% de especies de aves y 33% de mamíferos están amenazadas (Gascon et al. 2007). Se calcula que 122 especies de anfibios se han extinguido entre 1980 y 2005 y el tamaño poblacional está declinando en cuando menos el 43% de las especies (Roelants et al. 2007). En las últimas décadas del siglo XX la tasa de extinción de anfibios excedió la tasa de extinción promedio de los últimos 350 millones de años por cuando menos 200 veces (Houlahan et al. 2000; Roelants et al. 2007; Gascon et al. 2007). Los reptiles también están experimentando un declive global (Shine 1991; Nilson et al. 1999; Gibbons et al. 2000) y aunque escasamente estudiados, están en igual o mayor peligro que los anfibios (IUCN 2006), y frecuentemente enfrentan las mismas amenazas (Gibbons et al. 2000).

1.2. Vulnerabilidad de anfibios y reptiles

Siendo los únicos tetrápodos ectotérmicos, anfibios y reptiles ocupan hábitats similares y son igualmente vulnerables a la alteración del hábitat (Gibbons et al. 2000). Sin embargo, los anfibios y reptiles actuales son producto de linajes independientes, separados en los últimos 300 millones de años (Pough et al. 1998) y por lo tanto presentan diferencias sustanciales en aspectos como tolerancia fisiológica, biología reproductiva, ecología y comportamiento (Gibbons et al. 2000). Los anfibios presentan un ciclo de vida complejo con una fase larvaria con requerimientos de hábitat y nutricionales diferentes al adulto, diversidad de modos reproductivos, huevo anamniótico, piel permeable, ámbitos hogareños reducidos y en general reducida tolerancia a modificaciones de las condiciones del hábitat. En contraste, los reptiles presentan desarrollo directo, solamente 2 modos reproductivos, piel impermeable cubierta de escamas, huevo amniótico, ámbitos hogareños de hasta cientos de kilómetros cuadrados y en general una mayor tolerancia a las condiciones del hábitat (Pechmann y Wilbur 1994).

El efecto que diversas amenazas tienen sobre reptiles y anfibios puede ser atenuado o intensificado por las características particulares que cada uno de estos linajes presenta, por ejemplo, la reducida movilidad, una tolerancia fisiológica estrecha y la piel delgada y altamente permeable de los anfibios (una característica a la que frecuentemente se asocia la sensibilidad ambiental de este grupo a sustancias tóxicas tanto en el medio acuático como terrestre, Vitt et al. 1990) magnifican los efectos de la pérdida y modificación del hábitat (Sinsch 1990; Findlay y Houlahan 1997; Gibbs 1998; DeMaynadier y Hunter 2000; Semlitsch 2000; Houlahan y Findlay 2003; Bowne y Bowers 2004), mientras que en los reptiles la modificación del hábitat puede tener efectos negativos o positivos dependiendo de la movilidad y tamaño del ámbito hogareño de las especies o de sus rangos de tolerancia fisiológica (Buhlmann 1995; Burke y Gibbons 1995; Dorcas et al. 1998). En los reptiles hay especies con amplia tolerancia (Suazo-Ortuño et al. 2008) y especies con reducida tolerancia a las condiciones del hábitat (Ballinger y Congdon

1996; Suazo-Ortuño et al. 2008). La piel con escamas y prácticamente impermeable confiere a los reptiles mayor resistencia a cambios ambientales asociados a presencia de contaminantes y a fluctuaciones de temperatura y humedad, sin embargo, la evidencia empírica con tortugas de agua dulce sugiere que los efectos de modificaciones de los patrones de temperatura asociados al cambio climático global incrementará las tasas de crecimiento en juveniles y reducirá la edad a la madurez sexual (Frazer et al. 1993), mientras que taxa con determinación sexual dependiente de la temperatura (i.e. algunas especies de tortugas y todas las especies de cocodrilos) podrán sufrir alteraciones en las proporciones sexuales naturales y por lo tanto en la demografía poblacional (Janzen y Morjan 2001).

1.3. Factores asociados al declive poblacional de anfibios y reptiles

Estudios recientes identifican una serie de amenazas implicadas en el declive de poblaciones de anfibios y reptiles (Alford y Richards 1999; Gibbons et al. 2000; Blaustein y Kiesecker 2002; Semlitsch 2000, 2003; Collins y Storfer 2003; Beebee y Griffiths 2005). Collins and Storfer (2003) clasifican estas amenazas en dos grandes grupos: 1) factores directos, que incluyen pérdida y fragmentación del hábitat, sobreexplotación, e introducción de especies exóticas; y 2) factores indirectos tales como cambio climático, acidificación del ambiente, contaminación y enfermedades infecciosas. Gardner et al. (2007a) clasifican las amenazas en aquellas que implican cambios estructurales del hábitat como deforestación y fragmentación y aquellas que afectan a las poblaciones de anfibios y reptiles sin modificar necesariamente la estructura del hábitat como sobreexplotación, contaminación, enfermedades y cambio climático.

En esta revisión sigo la propuesta de Gardner et al. (2007a) para analizar el papel de los cambios estructurales del hábitat sobre las comunidades herpetofaunísticas. Los cambios estructurales del hábitat se consideran la causa principal del declive de la mayoría de las poblaciones de vida silvestre y de la pérdida de la diversidad biológica (Czech y Krausman 1997; Wilcove et al. 1998; Sala et al. 2000; Ashton et al. 2006). Y aunque la respuesta de los vertebrados a la modificación del hábitat ha sido ampliamente explorada (Lynam y Billick 1999; Escamilla et al. 2000; Daily et al. 2003; Lindenmayer et al. 2003; Hill y Hamer 2004; Driscoll y Weir 2005), los estudios están sesgados en más de un orden de magnitud hacia aves y mamíferos (Fazey et al. 2005; Gardner et al. 2007a), por lo que los resultados no necesariamente aplican para otros grupos de vertebrados menos estudiados como anfibios y reptiles (McGarigal y Cushman 2002).

El propósito de ésta revisión es integrar una síntesis del estado actual del conocimiento sobre la respuesta de los ensamblajes herpetofaunísticos a los cambios estructurales del hábitat con énfasis en los bosques tropicales caducifolios. La mayoría de las revisiones de los efectos de la pérdida del hábitat sobre los anfibios y reptiles se han limitado a estudios realizados en las zonas templadas, especialmente de Norte América (DeMaynadier y Hunter 1995; Gibbons et al. 2000; Cushman 2006) y a los subtrópicos Australianos (Hazell 2003), o a evaluar las consecuencias de la fragmentación (Cushman 2006). Pocos son los trabajos que han abordado revisiones que incluyan la información global existente de las consecuencias de los cambios estructurales del hábitat sobre las comunidades de anfibios y reptiles (ver Gardner et al. 2007a).

Específicamente se abordan tres aspectos: 1. identificar los cambios estructurales del hábitat que con mayor frecuencia afectan a los anfibios y reptiles; 2. identificar como los anfibios y reptiles son afectados por estos cambios; y 3. identificar los vacios de conocimiento sobre el tema. El objetivo principal es resaltar las líneas de investigación necesarias para el conocimiento y la conservación efectiva de anfibios y reptiles en paisajes que están experimentando marcados cambios estructurales.

2. Cambios estructurales del hábitat y su efecto en las comunidades herpetofaunísticas

2.1. Fragmentación del hábitat

La fragmentación implica una reducción de la cantidad total de hábitat original en el paisaje. Adicionalmente, implica que el hábitat remanente está dividido en fragmentos de varios tamaños, formas y grados de aislamiento inmersos en una matriz de hábitat modificado (Laurance 2008). El paisaje se fragmenta a diferentes escalas para diferentes especies, dependiendo de las barreras de la matriz ambiental (ambiente modificado entre los fragmentos) para el movimiento y dispersión de los individuos (Wind 2000). Los efectos de la fragmentación del hábitat sobre la biota pueden ser muy variables, y dependen de multitud de factores como son: las características del taxón, la escala espacial, el tipo de hábitat, las características del paisaje, el tiempo de retardo en la respuesta de las poblaciones a la fragmentación y la aparición de sinergias entre diferentes procesos (Benitez-Malvido y Arroyo-Rodríguez 2008), y aunque los efectos de la fragmentación no pueden ser generalizados, ya que cada especie responde de manera individual dependiendo de sus propios requerimientos (e. i. alimentación, refugio, espacio, condiciones climáticas adecuadas, etc.) en general las especies de plantas y animales en los trópicos presentan tres tipos de respuesta a la fragmentación de su hábitat: 1) una respuesta positiva (e.g., incremento del tamaño poblacional de especies de plantas pioneras, algunos invertebrados y roedores en fragmentos comparados con áreas de bosque continuo); 2) una respuesta negativa (e.g., disminución en el tamaño poblacional de muchas especies de primates, mortalidad de árboles grandes, y extinción local de algunos escarabajos peloteros y de carroña); y 3) una respuesta neutral (e.g., el tamaño poblacional de algunas especies de plantas en 1000 m^2 de bosque continuo no difieren de 1000 m^2 de un paisaje fragmentado en los Tuxtlas, México; Benitez-Malvido y Arroyo-Rodríguez 2008).

En el caso de los anfibios, la mayoría de los estudios realizados sobre la respuesta de este grupo a la fragmentación sugieren que frecuentemente las poblaciones de anfibios quedan fácilmente aisladas dentro de los paisajes fragmentados debido a su baja movilidad, alta filopatría a sitios húmedos y especialmente porque encuentran la matriz ambiental inhóspita sin las condiciones microclimáticas que favorecen su permanencia y dispersión (e.g., Pough et al. 1987; Bury y Corn 1988; Petranka et al. 1994; Dupuis et al. 1995; Waldick 1997; Pineda y Halffter 2004), sin embargo también existen trabajos que reportan que los fragmentos de bosque no son verdaderas islas para los anfibios, pues muchas especies pueden utilizar y migrar a través de la matriz que rodea a los fragmentos (e.g., anfibios en fragmentos de bosque tropical en Manaus, Brazil; Tocher et al. 1997) . La riqueza y abundancia de anfibios también puede ser afectada positiva o negativamente por el tamaño y grado de conectividad del fragmento (Rosenberg y Raphael 1986; Dupuis y Bunnell 1999).

Los reptiles por su parte, presentan diferencias entre especies dependiendo del tamaño y grado de conectividad del fragmento, así como de la distancia del fragmento a áreas continuas del hábitat original (MacNally y Brown 2001). En general, los reptiles no están limitados por los requerimiento de humedad como los anfibios, y muchas especies de lagartijas no se ven afectadas por la fragmentación (Jellinek et al. 2004), aunque también se han registrado especies sensibles (e.g., Cosson et al. 1999; MacNally y Brown 2001; Driscoll 2004) como la lagartijas *Amphibolurus muricatus* y el sincido *Egernia whitii* que desaparecen de los fragmentos en un bosque de Eucaliptos de Australia (MacNally y Brown 2001). También se ha documentado que las serpientes de tamaño grande son más vulnerables a la fragmentación que las especies de menor tamaño (Luiselli y Capizzi 1997).

La fragmentación del hábitat también potencia el efecto negativo de las enfermedades infecciosas y parasitarias asociadas con el declive de muchas especies de anfibios y reptiles (Daszak et al 1999; Smith et al. 1998; Gibbons 2000). En el caso de los anfibios y reptiles, donde los hábitats son fragmentados y las poblaciones son disminuidas existe mayor susceptibilidad de una epidemia (e.g., la enfermedad emergente por Chytriodimycosis en anfibios o enfermedades bacterianas en el caso de los reptiles; Gibbons 2000; Gascon et al 2007).

Como se puede observar, en los anfibios y reptiles los efectos de la fragmentación del hábitat son variables, no actúa directamente sobre el ensamblaje completo de especies, sino más bien de manera particular sobre cada especie (específicamente sobre cada población) de una manera independiente, de tal manera que los cambios en el número de especies de cada ensamblaje es el resultado acumulativo de una serie de eventos específicos (Pineda y Halffter 2004).

2.2. Efecto de borde

El efecto de borde se define como la variedad de fenómenos físicos y biológicos asociados con el ecotóno entre los fragmentos del hábitat y la matriz circundante (Laurance 2008). Algunos autores consideran el efecto de borde como una consecuencia de la fragmentación del hábitat y coinciden en que la biota en los fragmentos está influenciada únicamente por las fuerzas opuestas de colonización y extinción (MacArthur y Wilson 1967, Gardner et al. 2007a), mientras que para otros, su efecto sobre las comunidades biológicas es lo suficientemente significativo como para considerarlo un elemento importante en los hábitats fragmentados, ya que puede alterar aspectos de la estructura, microclima, dinámica, y composición de especies de los ecosistemas fragmentados (Lovejoy et al. 1986, Laurance et al. 2002, Lehtinen et al. 2003, Ries et al. 2004). Un ejemplo son los más de 30 diferentes efectos de borde -y las diferentes distancias del borde al interior del fragmento a las que se registran sus efectos- documentados en la región Amazónica (Laurance 2008).

En el caso de los anfibios y reptiles, hasta ahora no se ha encontrado evidencia contundente del efecto de borde sobre éstas comunidades. Por ejemplo los estudios de Gascon (1993), Biek et al. (2002) y Toral et al. (2002) no reportaron efectos de borde, mientras que DeMaynadier y Hunter (1995) sólo registraron un débil efecto, distinguiendo entre especies de anfibios que evaden los bordes (principalmente las salamandras sin pulmones cuya respiración es más eficiente en lugares húmedos con temperaturas ambientales frías, características de los sitios alejados de los bordes) y especies que los prefieren. Por su parte Urbina-Cardona y Reynoso (2005) y Urbina-Cardona et al. (2006) encontraron un aumento en la riqueza de anfibios y reptiles en el borde en comparación con el interior de la selva tropical, aunque hacia el interior incrementaron las especies de reptiles arborícolas y aquellos de tamaño grande, así como de anfibios pequeños con desarrollo directo y con preferencia por hábitats fosoriales y arborícolas.

En general, los estudios del efecto de borde sobre los ensambles de anfibios y reptiles arrojan resultados contradictorios, por lo que quizá sea más importante evaluar el efecto de borde a nivel específico, considerando además su efecto en los diferentes paisajes y ambientes climáticos (Demaynadier y Hunter 1995) ya que en el caso de los anfibios y reptiles las especies presentan un amplio rango de tolerancia ecofisiológica dentro de los ensambles y responden diferencialmente al rango de variables ambientales que ocurren en los bordes, influyendo a su vez en las afinidades de las especies a las diferentes condiciones del hábitat (Urbina-Cardona et al. 2006).

2.3. Aprovechamiento forestal y corte selectivo de los bosques

El aprovechamiento forestal y el corte selectivo de los bosques es probablemente uno de los usos más extendidos y lucrativos de los bosques en todo el mundo (Johns 1996) y es también en la mayoría de las ocasiones el detonador en la pérdida y fragmentación de los hábitats debido en gran parte a que los caminos forestales comúnmente son construidos por los madereros para tener acceso a árboles valiosos, sin embargo, la población rural aprovecha esos caminos para colonizar y abrir nuevas tierras a otras actividades.

El efecto del aprovechamiento forestal sobre las comunidades herpetofaunísticas es poco conocido. Existe una gran variabilidad de estudios que abordan este tema en términos de tiempo desde el aprovechamiento, intensidad y método del aprovechamiento y taxa estudiado, por lo que resulta difícil generalizar la información, pero se ha encontrado que la riqueza y composición de anfibios y reptiles difieren poco entre bosques primarios y bosques bajo aprovechamiento forestal tanto en zonas templadas como tropicales (Greenberg et al. 1994, Goldingay et al. 1996, Pearman 1997, Vitt et al. 1998, Lima et al. 2001, Fredericksen y Fredericksen 2004, Vallan et al. 2004) aunque también se ha reportado en algunos casos una pérdida significativa de especies de salamandras en áreas taladas de bosques templados (Vesely y McComb 2002) y en anfibios lóticos (Ashton 2006).

Frecuentemente la abundancia de la herpetofauna incrementa en las áreas taladas (Goldingay et al. 1996, Fredericksen and Fredericksen 2002) observándose que las especies generalistas o comunes en los bordes o en los claros de los bosques son las especies que tienden a incrementar sus abundancias después del aprovechamiento, como es el caso de algunos anfibios generalistas (hylidos y bufonidos) y lagartijas heliotérmicas como las del género *Mabuya* (Pearman 1997, Vitt et al. 1998, Lima et al. 2001, Fredericksen y Fredericksen 2004). Sin embargo al parecer no todas las especies y poblaciones de anfibios y reptiles sufren el mismo efecto. Por ejemplo, se ha demostrado que en algunas especies de anfibios (pletodóntidos y algunos eleutherodactylidos) y de lagartijas no heliotérmicas la abundancia tiende a ser más baja en claros y en rodales en regeneración que en los bosques maduros (e.g., Pough et al. 1987, Bury y Corn 1988, Petranka et al. 1994, Dupuis et al. 1995, Waldick 1997, Pearman 1997, Vitt et al. 1998, DeMaynadier y Hunter 1995).

2.4. Fuego

El fuego representa un componente importante en los paisajes tropicales del mundo (Cochran 2003), principalmente como resultado de la sinergia entre el crecimiento poblacional, las técnicas utilizadas en el cambio de uso de suelo y el cambio climático global inducido por las actividades humanas, lo que incrementa la probabilidad de fuegos catastróficos (Kinnaird y O'Brien 1998, Laurance 2003). Por ejemplo se ha documentado que los fuegos inducidos por el fenómeno de El Niño (ENSO) representa uno de los mayores peligros para los bosques tropicales húmedos (Barlow et al. 2002, 2003, Fredericksen y Fredericksen 2002, Cleary 2003, Cochran 2003, Laurance 2003, Cleary y Genner 2004). En el caso de los bosques tropicales secos este peligro se incrementa por su propia naturaleza estacional y por el uso generalizado en actividades agrícolas como la roza- tumba y quema. Dentro de los ecosistemas el fuego puede alterar y modificar la estructura del hábitat y la composición de las comunidades vegetales y animales (Robbins y Myers 1992).

La respuesta de la herpetofauna al fuego está documentada con mayor claridad en zonas donde los fuegos son recurrentes y comunes (Wilgers y Horne 2006), en estos sitios se ha observado un amplio rango de tolerancia a los regímenes de fuego por parte de las especies (Braithwaite 1987). En áreas, donde el fuego es común, la herpetofauna y otros animales evaden su efecto negativo a través de adaptaciones morfológicas y de comportamiento (Morin 2005). Generalmente la mortalidad después de la quema es muy baja en lagartijas y serpientes ya que estos son capaces de alejarse del fuego refugiándose en sitios húmedos, cuerpos de agua o bien usan refugios en el subsuelo hasta que pasa el peligro (Komarek 1969). También se ha observado que muchas especies exhiben preferencias por zonas sujetas a regímenes intensos de fuego (e.g. *Eumeces obsoletus*, *Phrynosoma cornutum* y *Cnemidophorus sexlineatus* en E.E.U.U. (Wilgers y Horne 2006) mientras que otras son sensibles a ello (*Carlia amax, Heteronotia binoei* y *Carlia gracilis* en Australia; Braithwaite 1987). Por sus características fisiológicas los anfibios son más sensibles al fuego, y también se han observado agregaciones de anfibios alrededor de cuerpos de agua inmediatamente después de la ocurrencia del fuego (Morin 2005). El efecto del fuego sobre la herpetofauna en los bosques tropicales secos no es muy claro. Pero las especies de lento movimiento o que no pueden refugiarse profundamente en el suelo durante los incendios son más susceptibles.

2.5. Bosques secundarios

Los bosques secundarios o “acahuales” producto de la alteración del estado original de los bosques son sin duda el paisaje que domina en la superficie arbolada del planeta (Stokstad 2008). La ganadería y la agricultura se consideran como las actividades humanas que más han contribuido a la formación de estos bosques (Bowen et al. 2007). Generalmente, cuando el disturbio humano desaparece sobre estas tierras, la regeneración natural de los bosques secundarios ocurre en un proceso estocástico que sigue distintas e impredecibles rutas de sucesión dependiendo de la historia de uso de los sitios (Walker 2007).

Aún cuando la deforestación de los bosques primarios continúa siendo alta (13 millones de ha/año) la cobertura forestal en por lo menos 18 países del mundo se ha incrementado ya sea por plantaciones forestales o por la regeneración de bosques secundarios (FAO 2005), por lo que la importancia de los bosques secundarios como facilitadores de la restauración pasiva del paisaje y la recuperación de las comunidades faunísticas en los paisajes fragmentados por las actividades agrícolas y ganaderas es cada vez más reconocida (Walker et al. 2007, Bowen et al. 2007, Chazdon 2008, Stokstad 2008). Recientemente, muchos trabajos de investigación se han enfocado a evaluar la importancia de estos bosques para diferentes ensambles faunísticos. En el caso de las especies de anfibios y reptiles la mayoría de los estudios realizados en áreas de regeneración de bosques tropicales y templados encuentran consistentemente una riqueza menor de especies que en los bosques primarios (Crump 1971, Lieberman 1986, Bowman et al. 1990, Heinen 1992, Petranka et al. 1993, Herbeck y Larsen 1999, Tocher et al. 2002, Vallan 2002, Ashton et al. 2006, Gardner et al. 2007b).

Las diferencias en las condiciones locales del hábitat y la historia del disturbio confunden las comparaciones entre sitios (Chazdon 2003) pero algunos autores predicen que la riqueza de especies de bosques en regeneración puede llegar a ser similar a la de los bosques maduros entre los 20 y 40 años (Dunn 2004). En el caso de los anfibios y reptiles existen muy pocos estudios a largo plazo para apoyar esta predicción y es muy probable que se requieran escalas de tiempo mayores (Petranka et al. 1993, 1994, Pawar et al. 2004). Por otro lado no existen estudios que indiquen si los bosques secundarios más viejos proveen hábitats exitosos para las especies especialistas de bosques primarios o si los rodales de bosque secundario pueden sostener poblaciones y comunidades viables en ausencia de bosques primarios vecinos (Gardner et al. 2007a), por lo que la investigación sobre el papel de los bosques secundarios en la permanencia de los ensamblajes de especies requiere aún de un amplio debate e investigación.

3.- Investigaciones en México sobre los cambios estructurales del hábitat y su efecto sobre anfibios y reptiles

México es considerado uno de los de los países con mayor diversidad biológica a nivel mundial (Mittermeier 2004). Dentro de ésta diversidad, los anfibios y reptiles contribuyen con una gran cantidad de especies. De hecho, México ocupa el primer lugar a nivel mundial en reptiles y el cuarto lugar en anfibios. En la actualidad se conocen en México 1164 especies (360 anfibios y 804 reptiles) de las cuales aproximadamente 60% son endémicas al país (Flores-Villela y Canseco-Márquez 2004).

A pesar de la importancia de los anfibios y reptiles tanto a nivel de la diversidad biológica mexicana como a nivel de los procesos biológicos que ocurren dentro de los ecosistemas, existen muy pocos estudios en el país que aborden el efecto de los cambios estructurales del hábitat sobre la comunidad herpetofaunística. Además de que cada uno de los estudios aborda diferentes factores asociados a los cambios en la estructura del hábitat. Así, por ejemplo, a la fecha solamente se encuentran publicados en revistas arbitradas y/o indizadas nacionales e internacionales los trabajos de Pineda y Halffter (2004) quienes evalúan el efecto de la fragmentación del hábitat y de los hábitats transformados por actividades humanas (pastizales y cafetales) sobre el ensamble de anfibios en un Bósque Mesófilo de Montaña. Encontrando que ni los fragmentos ni los hábitats transformados por si solos son capaces de preservar la diversidad de especies registrada a nivel de paisaje, existiendo una interdependencia de los diferentes hábitats en la preservación de las especies. Los trabajos de Urbina-Cardona y Reynoso (2005) y Urbina-Cardona et al. (2006) evalúan el efecto del ecotono (pastizal-borde-interior del bosque) sobre la comunidad herpetofaunística en fragmentos de bosque tropical lluvioso en la región de Los Tuxtlas y reportan que aunque no existe un efecto claro sobre la diversidad de especies, sí ocurre un cambio en la composición de especies en los diferentes hábitats. Registran también mayor número de especies de anfibios y reptiles en el borde de selva seguido por el sitio de interior de selva y un mayor recambio de especies de anfibios y reptiles entre potrero e interior de selva, seguido por el potrero y el borde de la selva. Macip-Ríos y Muñoz-Alonso (2008) reportan que en el caso de las lagartijas agroecosistemas como los cafetales presentan mayor diversidad de especies que los sitios de vegetación primaria como la selva mediana y el bosque mesófilo.

Por último, Suazo-Ortuño et al. (2008; Capítulo II), al evaluar el efecto de la conversión del bosque tropical caducifolio de Chamela, Jalisco, a mosaicos agrícolas y ganaderos sobre los ensambles herpetofaunísticos, encuentran tres tipos de respuesta de la herpetofauna a la perturbación del hábitat: 1) negativa, en anfibios y tortugas; 2) positiva, en lagartijas; y 3) neutra, en serpientes. Suazo-Ortuño, Alvarado y Martínez-Ramos (ver Capítulo III) al abordar la importancia de las zonas riparias para los anfibios y reptiles en los paisajes transformados por las actividades agrícolas encuentran que en general la abundancia y diversidad de las lagartijas y serpientes disminuyen de las zonas riparias a las partes altas de las cuencas en lluvias y secas tanto en sitios conservados como perturbados, mientras que los anfibios siguen esta tendencia únicamente en los sitios conservados durante la época de lluvias.

Además de las publicaciones mencionadas, existen una serie de trabajos que se han realizado a nivel de tesis de licenciatura y maestría que también abordan el efecto de los cambios estructurales del hábitat sobre los anfibios y reptiles. En general los estudios realizados se limitan a la selva tropical lluviosa de México y en su mayoría concluyen que no existen diferencias significativas entre en la riqueza y abundancia de los anfibios y reptiles entre la selva y los fragmentos estudiados (Carmona-Torres 2005, Salvatore 2006, Machuca-Barbosa 2007, Mena 2008) con excepción de fragmentos < 9 ha (Cabrera-Guzmán 2005). Por su parte Calderón-Mandujano et al. (2008) y Hernández-Ordóñez (2009) encuentran que en general la riqueza y la diversidad de especies de anfibios y reptiles aumentan con la edad de la cronosecuencia de los bosques secundarios.

Existen también algunos trabajos que reportan el efecto de los cambios en la estructura del hábitat sobre especies particulares, por ejemplo, se ha documentado que la pérdida de bromelias (*Aechmea bracteata*) por las prácticas de roza-tumba y quema, y por la explotación selectiva, tiene como consecuencia la pérdida de refugios para las ranas arbóreas en la selvas tropicales estacionales de sur de México (Galindo-Leal et al. 2003). Así mismo, Suazo-Ortuño et al. (Capítulo IV) evaluaron cambios en la composición y diversidad de la dieta de *Bufo marmoreus* en áreas conservadas y perturbadas del bosque tropical seco de Chamela, Jalisco encontrando que la diversidad de la dieta fue significativamente menor en el área perturbada aunque la disponibilidad de las presas no fue afectada por la perturbación.

5.- Implicaciones de los cambios estructurales del hábitat para la conservación de la Herpetofauna en los Bosques Tropicales Secos

Como se observa en esta revisión, a pesar de que a nivel mundial se pueden encontrar una gran cantidad de trabajos que han aportado información valiosa sobre las consecuencias de los cambios estructurales del hábitat para los anfibios y reptiles, la mayoría de estos trabajos están orientados hacia los anfibios y reptiles de Norte América (45% de los estudios, Gardner et al. 2007a). Aún cuando este cuerpo de conocimiento es importante para entender implicaciones generales de la perturbación del hábitat sobre las especies, es preocupante el reducido número de estudios que sobre este tema se han desarrollado en México, dada la importancia que tiene el país a nivel de la diversidad de anfibios y reptiles y de las elevadas tasas de deforestación y degradación de los hábitats que presenta.

Por otro lado, la distribución de la herpetofauna en México no es homogénea (García et al. 2007). El occidente de México y en particular las tierras bajas de la costa del Pacífico y valles interiores albergan a casi un tercio de las especies de la herpetofauna mexicana y a un cuarto de los especies endémicas (Flores–Villela y Goyenechea 2003, García 2006, Ochoa–Ochoa y Flores–Villela 2006). Los Bosques Tropicales Secos son el tipo de vegetación dominante en estas tierras (Trejo-Vazquez y Dirzo 2000, García 2006) y a pesar de su importancia para la conservación de la biodiversidad mexicana estos bosques se encuentran en alto riesgo ya que presentan las más altas tasas de deforestación anual en México 2% y únicamente el 27% del bosque original permanece intacto (Trejo-Vazquez y Dirzo 2000, Trejo-Vázquez 2005, García 2006). De acuerdo con lo anterior, es de esperarse que el 73% de la superficie ocupada por los bosques tropicales secos en el país estén constituidos por una mezcla de mosaicos agrícola-ganaderos y bosques secundarios en diferentes estadíos sucesionales. Por ello, los estudios encaminados a entender de los procesos que subyacen en la abundancia y distribución de la diversidad biológica en estos paisajes agroforestales son prioritarios. Así mismo dado que los anfibios y reptiles representan al grupo de vertebrados terrestres con mayor sensibilidad a los cambios estructurales del hábitat (Shine 1991, Nilson et al. 1999, Gibbons et al. 2000, Roelants et al. 2007, Gascon et al. 2007) es menester entender lo siguiente: a) ¿qué tanto las especies de anfibios y reptiles tienen éxito en estos hábitats modificados por las actividades agrícolas y ganaderas del trópico seco? b) ¿cuál es el cambio en la riqueza, composición y abundancia de las especies de la herpetofauna una vez que los bosques maduros son sustituidos por los paisajes modificados? c) ¿pueden estos hábitats sostener poblaciones viables de anfibios y reptiles especialistas de bosques maduros? d) ¿qué elementos estructurales del paisaje modificado pueden favorecer una estructura de la comunidad de anfibios y reptiles similar a la encontrada antes del disturbio? e) ¿qué atributos en la historia de vida de las especies de anfibios y reptiles son más sensibles a los cambios estructurales del hábitat y como pueden ser enriquecidos los paisajes agrícola-ganaderos para la permanencia de estas especies? f) ¿qué tipo de reglas pueden seguirse en la dinámica de cambio de uso de suelo para recuperar y mantener una biodiversidad similar a la encontrada en los bosques maduros .

Cada una de estas preguntas representa un reto de investigación que conlleva dificultades tanto logísticas como de financiamiento. Sin embargo, a pesar de las dificultades es vital que enfoquemos nuestros esfuerzos para mejorar nuestro entendimiento de las consecuencias del cambio del hábitat para los anfibios y reptiles en particular y para la biodiversidad en general en una de las ecorregiones más importantes de México por su diversidad y endemismo de especies.

6. Conclusiones

Los anfibios y reptiles están experimentado un declive global. Ambos comparten similitudes fisiológicas, ocupan hábitats similares y son igualmente vulnerables a la modificación del hábitat. A pesar de esto, el efecto que diversas amenazas tienen sobre ellos es mediado por las características particulares que presenta cada uno de estos grupos. La fragmentación del hábitat, el aprovechamiento forestal, el fuego y la formación de bosques secundario son factores que inciden directamente en el cambio estructural del hábitat en el que se desarrollan las especies y han sido asociados al declive poblacional de anfibios y reptiles. Los estudios que se han realizado para evaluar el efecto de estos factores sobre las especies sugieren que la respuesta de los ensamblajes y de las especies es diferencial, siendo negativa, neutra o positiva dependiendo del factor que incide en la estructura del hábitat y los atributos de la historia de vida de las especies. A pesar de la importancia de los anfibios y reptiles para la diversidad biológica de México existen muy pocos estudios que abordan los cambios estructurales del hábitat debido a las actividades humanas y con excepción de los trabajos realizados por Suazo et al. (2007, 2008, 2009) no existen trabajos de este tipo en los bosques tropicales secos de México.

En este contexto, se requieren de manera urgente estudios encaminados a evaluar el efecto de la conversión de bosque a mosaicos agrícolas sobre los ensambles herpetofaunísticos a nivel nacional y mundial.

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CAPÍTULO II

Effects of conversion of dry tropical forest to agricultural mosaic on herpetofaunal assemblages

Contributed Paper

Effects of Conversion of Dry Tropical Forest to Agricultural Mosaic on Herpetofaunal Assemblages

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Abstract: *We explored the impact of forest conversion to agricultural mosaic on anuran, lizard, snake, and turtle assemblages of Neotropical dry forests. Over 2 years, we sampled 6 small watersheds on the west coast of Mexico, 3 conserved and 3 disturbed. The disturbed watersheds were characterized by a mosaic of pastures and cultivated fields (corn, beans, squash) intermingled with patches of different successional stages of dry forest. In each watershed, we conducted 11 diurnal and nocturnal time-constrained searches in 10 randomly established plots. We considered vulnerability traits of species in relation to habitat modification. Eighteen anuran, 18 lizard, 23 snake, and 3 turtle species were recorded. Thirty-six species (58%) occurred in both forest conditions, and 14 (22%) and 12 species (19%) occurred only in the conserved and disturbed sites, respectively. Assemblages responded differently to disturbance. Species richness, diversity, and abundance of lizards were higher in disturbed forests. Anuran diversity and species richness were lower in disturbed forest but abundance was similar in both forest conditions. Diversity, richness, and abundance of turtles were lower in disturbed forest. The structure and composition of snake assemblages did not differ between forest conditions. We considered species disturbance sensitive if their abundance was significantly less in disturbed areas. Four anuran (22%), 2 lizard (11%), and 3 turtle (100%) species were sensitive to disturbance. No snake species was sensitive. The decline in abundance of disturbance-sensitive species was associated with the reduction of forest canopy cover, woody stem cover, roots, and litter-layer ground cover. Anuran species with small body size and direct embryonic development were especially sensitive to forest disturbance. An important goal for the conservation of herpetofauna should be the determination of species traits associated with extinction or persistence in agricultural mosaics.*

Keywords: agricultural mosaic, habitat modification, herpetofaunal assemblages, tropical dry forest, vulnerability traits

Efectos de la Conversión de Bosque Tropical Seco a Mosaico Agrícola sobre Ensambles Herpetofaunísticos

Resumen: *Exploramos el impacto de la conversión de bosques a mosaico agrícola sobre ensambles de lagartijas, serpientes y tortugas de bosques Neotropicales secos. Durante 2 años muestreamos 6 cuencas pequeñas, 3 conservadas y 3 perturbadas, en la costa occidental de México. Las cuencas perturbadas se caracterizaron por un mosaico de pastizales y campos cultivados (maíz, frijol, calabaza) entremezclados con parches de bosque seco en diferentes etapas sucesionales. En cada cuenca, realizamos 11 búsquedas diurnas y nocturnas en 10 parcelas establecidas aleatoriamente. Consideramos los atributos de vulnerabilidad de especies en relación con la modificación del hábitat. Registramos 18 especies de lagartijas, 23 de serpientes y 3 de tortugas. Treinta y seis especies (58%) ocurrieron en ambas condiciones de bosque, y 14 (22%) y 12 (19%) especies solo ocurrieron en los sitios conservados y perturbados, respectivamente. Los ensambles respondieron a la perturbación de manera diferente. La riqueza de especies, la diversidad y la abundancia de lagartijas fueron mayores en los bosques perturbados. La diversidad y riqueza de especies de anuros fueron menores*

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en el bosque perturbado pero la abundancia fue similar en ambas condiciones de bosque. La diversidad, riqueza de especies y abundancia de tortugas fueron menores en el bosque perturbado. La estructura y la composición de los ensambles de serpientes no difirieron entre condiciones de bosque. Consideramos que las especies eran sensibles a la perturbación si su abundancia fue significativamente menor en las áreas perturbadas. Cuatro (22%) especies de anuros, 2 (11%) de lagartijas y 3 (100%) de tortugas fueron sensibles a la perturbación. Ninguna especie de serpiente fue sensible. La declinación en la abundancia de especies sensibles a la perturbación se asoció con la reducción en la cobertura del dosel, de tallos leñosos, raíces y hojarasca. Las especies de anuros de cuerpo pequeño y desarrollo embrionario directo fueron especialmente sensibles a la perturbación del bosque. La determinación de atributos de las especies asociadas con su extinción o persistencia en mosaicos agrícolas debería ser una meta importante para la conservación de la herpetofauna.

Palabras Clave: atributos de vulnerabilidad, bosque tropical seco, ensambles herpetofaunísticos, modificación del hábitat, mosaico agrícola

Introduction

Loss and alteration of tropical forest habitat due to deforestation, fragmentation, and land use represent a serious threat to global biodiversity (Vitousek et al. 1997). Although the response of vertebrates to habitat modification has been the focus of extensive research, much of what is known is biased toward birds and mammals and may not be representative of other threatened vertebrate groups (McGarigal & Cushman 2002).

Amphibians and reptiles occur at high density and diversity levels in tropical forests and play important ecological roles as primary, midlevel, and top consumers (Whitfield & Donnelly 2006). Amphibians and reptiles are experiencing widespread global decline (Lips et al. 2005; Araujo et al. 2006) associated with habitat loss and modification, climate change, invasive species, environmental pollution, epidemic diseases, and unsustainable harvest (Bell & Donnelly 2006). Habitat attributes and traits of species associated with their vulnerability to disturbance (i.e., vulnerability traits) influence the response of herpetofaunal assemblages to forest disturbance (Brown 2001). Structural aspects of habitat, forest canopy cover and heterogeneity and physical characteristics influence the structure and composition of herpetofaunal assemblages (Urbina-Cardona et al. 2006). Habitat attributes influence critical components of species biology, such as habitat selection and the availability of fundamental resources such as food, oviposition sites, or refuge from predators (Conroy 1999). To thoroughly assess the effects of forest disturbance on herpetofaunal assemblages, it is important to define and measure relevant habitat attributes.

Not all species are equally influenced by the same habitat modifications (Brook et al. 2003). Species vulnerability to disturbance depends on a suit of taxon-related traits (Hooper et al. 2005). Two important traits are body size and diet breadth (Lunney et al. 1997). Under desiccating conditions, rates of water loss are higher in small-sized ectotherm vertebrates than in larger species (Nagy 1982; Duellman & Trueb 1994). Conversely, species with narrow diet breadth are prone to negative demographic effects if disturbances diminish the availability of specific prey (Rodríguez-Robles 2002). Reproductive mode and foraging strategy are also useful for assessing the response of herpetofaunal assemblages to disturbance (Reed & Shine 2002; Trenham & Shaffer 2004).

Neotropical dry forests, which support high biodiversity and host many amphibian and reptile species are threatened by deforestation and land-use change and are considered one of the most threatened types of tropical habitats (Primack 1998). For example, 18 species of amphibians and 91 species of reptiles have been registered in the tropical dry forests of Mexico (Flores & Gerez 1994). In Mexico only 27% of the original cover remained as intact forest by 1990 (Trejo & Dirzo 2000). The special significance of Mexican dry forests in terms of richness and endemism of terrestrial vertebrates is highlighted by Ceballos and García (1995), who report that dry-forest vertebrate species represent 80% of all orders, 73% of all families, and 51% of all genera from Mexico. Our current understanding of the response of herpetofaunal assemblages to human disturbance is based almost entirely on studies of lowland rainforests (Tocher et al. 1997). The loss of Neotropical dry forest has presumably resulted in a decline of vertebrate abundance and diversity, but the degree to which this has affected the composition and structure of amphibian and reptile assemblages is unknown. In addition, the response of herpetofaunal assemblages to disturbance based on attributes of their habitat and the vulnerability traits of species has not been explored. Furthermore, most studies of tropical dry forest biodiversity conservation focus on forest loss and fragmentation (Turner 1996). Fewer researchers have explored the consequences of agricultural activities in landscapes that are a mixture of dry tropical forest, pastures, cultivated fields, and secondary forests (Hill & Hamer 2004). Given that agricultural landscapes now form an increasingly large proportion of tropical areas (Daily et al. 2001), it is important to investigate the response of faunal assemblages to such a landscape mosaic.

We explored the response of herpetofaunal assemblages to deforestation and agricultural disturbance in a dry Neotropical forest. Our objectives were to (1) compare the structure and composition of anuran, lizard, snake, and turtle assemblages in conserved and human disturbed forest areas, (2) identify disturbance-sensitive species that might need special conservation efforts, and (3) relate assemblage changes and species sensitivity to habitat modification and species' vulnerability traits.

Methods

Study Area

The study was conducted in the Chamela Biosphere Reserve and in surrounding agricultural areas along the coast of Jalisco state (19°30′N, 105°03′W), Mexico. Mean annual temperature is 24.6° C with an average annual rainfall of 788 mm, 80% of which falls in the rainy season (July–October) after a 7- to 8-month dry season (Lott 1993). The dominant vegetation type is tropical dry forest with strips of semideciduous forest along riparian areas. The average forest canopy height is about 7 m. The conserved forest is highly diverse with more than 200 tree species (Lott 1993). Dominant plant families are Leguminosae-Papilionoideae and Euphorbiaceae. Human development in the area began in the 1960s. Presently, the area is characterized by subsistence cultivation, small pastures for cattle, and selective extraction of trees for firewood. This has resulted in a landscape mosaic of pastures (45% of the area) with sparse shrubs; isolated trees; fields cultivated with a mixture of corn, squash, and beans; and secondary forest in different stages of succession (moderate undergrowth and sparse to moderate canopy). Hereafter we refer to these landscapes as disturbed-forest mosaic.

We sampled 6 independent, small watersheds (about 1 km^2), 3 with disturbed and 3 with conserved forest (Fig. 1). The availability of suitable amphibian reproductive habitat was similar between conserved and disturbed watersheds (each contained a single seasonal stream). The 3 watersheds with conserved forest were in the reserve (conserved watershed, CW1-CW3) and were completely surrounded by continuous undisturbed forest. The 3 disturbed forest watersheds were outside the reserve (disturbed watershed DW1-DW3) and were completely surrounded by disturbed forest mosaic. Conserved and disturbed watersheds were 15–25 km apart and were similar in terms of original forest type, elevation, climate, and topography. There was probably little herpetofaunal beta diversity between watersheds prior to the onset of human forest modification in the area.

Sampling Protocol

Eleven times from November 2000 to November 2002, we surveyed 10 randomly established temporary plots in each of the 6 watersheds. Five surveys were made in the dry season (November–June) and 6 in the rainy season. For each of the 11 survey periods, each temporary plot was surveyed twice, once diurnally (09:30–16:00) and once nocturnally (21:00–04:00). Each temporary plot was 100 × 10 m and was located parallel to the stream and watershed crest (Fig. 1). On each survey date the perpendicular distance of each temporary plot from the stream and the distance from the mouth of the stream were selected at random.

During each survey period a crew of 6 people (the same crew throughout the study) surveyed the temporary plots in time-constrained searches. Plots were surveyed

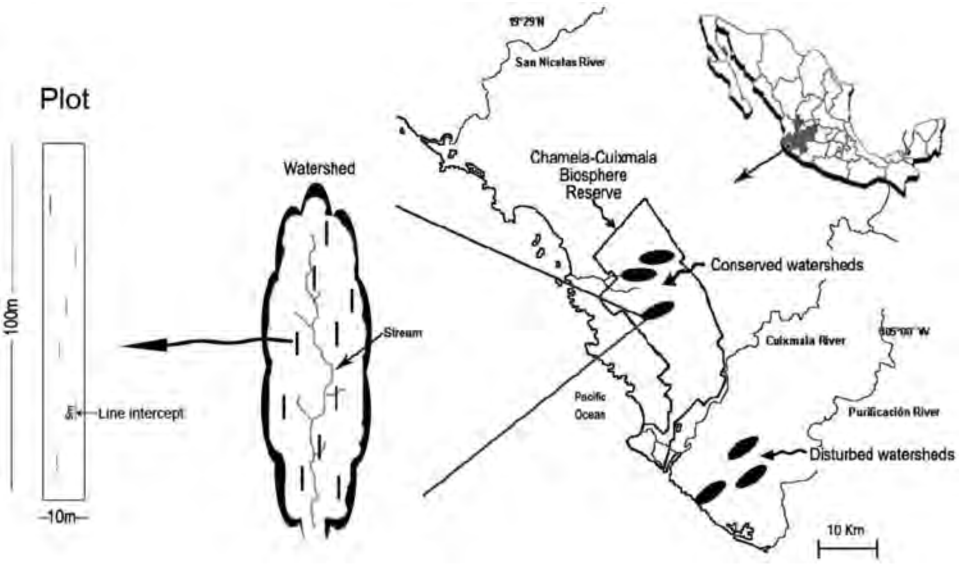

Figure 1. Site map and plot deployment scheme in a study of the effects of forest conversion on herpetofaunal assemblages. Gray section on inset of Mexico is Jalisco, and ovals are watersheds.

visually by searching vegetation and the ground surface for reptiles and amphibians, including lifting cover objects (rocks, logs, and debris). All encountered individuals were captured, identified to species, measured, and released. To avoid counting the same individual more than once during the 2-year study period, we clipped frogs and lizards' toes and snakes' ventral scales and notched turtles' carapaces.

The sampling effort was measured in person-hours. Over 2 years the total search effort for each watershed was 330 person-hours, for a grand total of 1980 person-hours across the 6 watersheds. During each survey period, the elapsed time between sampling the conserved and disturbed areas was no more than 72 h.

Habitat Attributes

One person (the same person throughout the study) measured vegetation structure, ground cover, and microclimatic variables at each plot after each diurnal search. At 6 randomly placed points within each plot, we measured tree height with a clinometer and shrub and herb height with a metric ruler. We visually estimated number of canopy layers by counting the number of shrub and tree crowns intercepting an imaginary vertical line. We quantified the percentage of canopy openness with a spherical concave densiometer (Model C, Forest Densiometers, Bartlesville, Oklahoma). At each point, 1 reading was taken in each of the 4 cardinal directions. These values were then averaged to obtain a single mean value of canopy openness per plot. Soil moisture and temperature and air relative humidity and temperature were measured with a thermohygrometer after 30 seconds of exposure. Slope was measured with a clinometer (average 6 readings per plot). We used the line-intercept method (Krebs 1999) to evaluate ground structure as percent cover of the following attributes: rocks, litter layer, burrows, dry branches, roots, woody stems and shrubs, herbs, lianas, stumps, grasses, and standing dead trees.

Vulnerability Traits

We evaluated body size, habits, foraging strategy, and reproductive mode for anurans; habits, foraging strategy, and body size for lizards; and body size, habits, activity, diet breadth, and foraging strategy for snakes. Body size for each species was assigned according to the maximum body size we recorded in this study. Body size of lizards, snakes, and anurans was measured as snout-vent length (SVL). Turtle size was measured as curve carapace length. We classified habits as terrestrial or arboreal. With respect to diet breadth, animals were classified as specialists (feeding on ≤ 2 kinds of prey within a particular order or suborder) and generalists (feeding on > 2 kinds of prey within 1 or more orders or suborders). The period of activity was classified as diurnal or nocturnal based on species' natural history. Animals were classified as sit-and-wait (ambush) foragers or active foragers. In anurans reproduction was classified into four modes: (1) eggs deposited in water and free aquatic larvae, (2) eggs deposited above water, suspended on vegetation, and with free aquatic larvae, (3) eggs deposited in foam nests on or near water and free aquatic larvae, and (4) eggs deposited in moist soil and direct embryonic development (Duellman & Trueb 1994).

Data Analysis

To test differences in species richness and diversity (Shannon–Winner index) of herpetofaunal assemblages between conserved and disturbed forest, we used the rarefaction approach proposed by Sanders (1968) and implemented by the Species Diversity Module of EcoSim (Gotelli & Entsminger 2001). Rarefaction uses probability theory to derive expressions for the expectation and variance of species richness for a sample of a constant size (Heck et al. 1975).

To quantify species density (the recorded number of species per sampling effort), we used species accumulation curves. The observed species density was compared with the expected real number, estimated through 4 nonparametric indices: incidence-based coverage estimator (ICE); abundance-based coverage estimator (ACE); Chao2; and bootstrap (EstimateS, Colwell 2005). We assessed sampling completeness by calculating the percent value of the observed species density with respect to the estimated real species density (Soberón & Llorente 1993).

To evaluate whether assemblage structure was affected by disturbance, we constructed species rank-abundance curves for each herpetological assemblage in each forest condition. We pooled data from the 3 watersheds per forest condition and then plotted the relative abundance of species (on a logarithmic scale) against the rank of the species, from the most abundant to the rarest species (Magurran 2004).

Species sensitivity to disturbance was evaluated with an index of sensitivity (IS) (Cosson et al. 1999): $IS = (CR_{cf} - CR_{df})/(CR_{cf} + CR_{df})$, where CR_{cf} is the capture rate (total individuals recorded in 2 years) in the conserved forest and CR_{df} is the capture rate in the disturbed forest. The index ranged from -1 (lowest sensitivity) to $+1$ (highest sensitivity). Species with IS values close to zero were considered neutral in their response to disturbance. To assess the statistical significance of the species disturbance-sensitivity values, we used a simple 2×2 chi-square contingency table analysis. In the chi-square tests, for each species the observed abundance in conserved and disturbed forests was contrasted with a null hypothesis of equal abundance. We used only species with a total abundance of more than 6 individuals. We applied Yate's correction when needed (Sokal & Rohlf 1995).

For each of the 22 habitat attributes, we averaged all measurements in a given watershed to estimate the average for the habitat attribute per watershed over 2 years. For each attribute we then had 3 values per forest condition. We used 2-sample *t* tests to evaluate differences between conserved and disturbed forest for continuous variables. These variables were log transformed to meet homoscedasticity requirements. To test for differences in proportional and count habitat attributes, we used nonparametric Mann–Whitney *U* tests.

We used canonical correspondence analysis (CCA, Pcord4) to identify associations of anuran, lizard, and snake species with forest condition and habitat attributes (turtles were excluded owing to small sample size). Each herpetofaunal assemblage was analyzed separately. The main CCA matrix consisted of the species abundances in each of the 6 watersheds. The second CCA matrix was the habitat matrix. We used principal component analysis (PCA) to reduce the 22 habitat attributes to a composite variable for each site and then used the loading factors from the first 2 principal components of the PCA (orthogonal habitat variables) as the habitat matrix. Pearson correlation was used to identify the habitat attributes significantly associated with each of the first 2 principal components.

A simple 2-sample *t* test was performed to assess species segregation between forest conditions. Scores for the conserved and disturbed forest sites were in the first and second CCA axes. The similarity of assemblages between conserved and disturbed forest was assessed with Morista-Horn's index of community similarity in the program EstimateS 7.5 (Colwell 2005). Morista-Horn's index is zero when no species are shared between sites and one when there is a complete species similarity.

To test for differences in habits, foraging strategy, reproductive mode, diet breadth, and period of activity of herpetofaunal assemblages between conserved and disturbed forest, we used general linear models in GLIM 3.77 (Crawley 1993). The frequency of species in each trait category per watershed was used as the response variable. Forest condition (conserved and disturbed) and vulnerability trait (different levels depending on the trait) were the independent variables. In all cases, because of the count nature of the response variable, we used a log-link function and a Poisson error. The deviance explained by the interaction between the forest condition and vulnerability trait was used to assess the significance of trait differences between forest conditions. The explained deviance approximates chi-square values with degrees of freedom equal to the number of forest conditions minus one times the number of trait categories minus one (Crawley 1993). A rescaling procedure was applied when overdispersion problems were detected. To test for differences in body size between forest conditions, we used Mann–Whitney *U* tests for amphibians, lizards, and snakes separately.

Results

Assemblage Structure

We registered 1655 individuals representing 62 species of anurans and reptiles (see Supplementary Material). Of these, about 80% were lizards, 11% anurans, 6% snakes, and 1% turtles. Pooling watersheds, 779 individuals representing 50 species were recorded in conserved forest. In disturbed forest, 876 individuals representing 48 species were recorded (Supplementary Material). Fourteen of the total recorded species (23%) were exclusively found in the conserved forest. Twelve species (19%) were exclusively found in disturbed forest. Thirty-six species (58% of all species) were recorded in both forest conditions (Supplementary Material). Significantly higher numbers of lizards were recorded in the disturbed forest (735) than in conserved forest (630; $\chi^2 = 8.1$, df $= 1$, $p < 0.001$), but the contrary was found for turtles (1 vs. 15). Abundance of anurans (89 vs. 92) and snakes (48 vs. 43) was similar in both forest conditions.

Sampling completeness per watershed varied from above 17% for snakes at DW1 to 100% for lizards at DW3. Pooling all 6 watersheds, the inventory was complete for turtles (100%), followed by lizards (above 95%), frogs (above 90%), and snakes (above 82%; Table 1). Species accumulation curves were not asymptotic for frogs and snakes, indicating that the inventories were incomplete. In lizards and turtles, the curves were almost asymptotic (Fig. 2).

Assemblage structure, analyzed with species-rank curves, changed differentially between conserved and disturbed forest, depending on the taxonomic group. In the conserved forest, anuran relative abundance decreased exponentially with species rank. In the disturbed forest, the anuran species-rank curve followed a log-log power trend, indicating the strong dominance of a few species (Fig. 3a). In the disturbed forest, *Ollotis marmorea* was clearly the dominant species, accounting for 54% of recorded frog individuals. In the conserved forest this species was also dominant, although its relative abundance was <20%. Rarefied diversity values indicated higher anuran species evenness, richness, and diversity in the conserved forest (Table 2).

In both forest conditions lizards exhibited exponential species-rank curves (Fig. 3b). Nevertheless, there was higher species evenness, richness, and diversity in the disturbed than in the conserved forest (Table 2). Although *Aspidocelis lineattissimus* was dominant in the disturbed forest (20% relative abundance), *Sceloporus utiformis* was dominant in conserved forest (25%). For snakes species-rank curves (exponential) and species evenness, richness, and diversity were similar in both forest conditions (Fig. 3c; Table 2). The dominant snake species differed between forest conditions. *Micrurus distans* (17% relative abundance) dominated in the conserved and

Table 1. Observed and expected species density in herpetological assemblages at watershed and landscape levels in conserved and disturbed forest at Chamela, Jalisco, Mexico.

Assemblage and watershed[a]	*Number of observed species*	*ACE*[b]	*ICE*[c]	*Chao 2*	*Bootstrap*	*Completeness*[d]
Anurans						
CW1	4	57	67	100	80	57–100
CW2	11	92	58	69	85	58–92
CW3	13	76	54	65	81	54–81
DW1	7	64	70	78	88	64–88
DW2	6	86	46	75	75	46–75
DW3	8	47	42	57	80	42–57
conserved	15	94	79	88	88	79–88
disturbed	11	73	73	85	85	73–85
entire landscape	18	100	90	90	90	90–100
Lizards						
CW1	11	73	85	69	92	73–92
CW2	12	86	86	86	92	86–92
CW3	12	80	86	92	92	86–92
DW1	17	81	81	74	89	74–89
DW2	13	76	93	72	93	72–93
DW3	13	100	100	100	100	100
conserved	14	93	93	100	93	93–100
disturbed	17	85	89	77	94	77–94
entire landscape	18	100	100	100	95	95–100
Snakes						
CW1	9	33	32	45	75	32–75
CW2	9	36	20	38	75	20–75
CW3	14	52	52	70	78	52–78
DW1	14	33	17	34	88	17–88
DW2	15	56	45	58	83	45–83
DW3	5	100	100	100	83	83–100
conserved	18	75	75	82	82	75–82
disturbed	19	73	73	83	83	73–83
entire landscape	23	88	82	85	88	82–88
Turtles						
CW1	2	100	50	100	100	50–100
CW2	2	67	67	100	100	67–100
CW3	2	67	67	100	100	67–100
DW3	1	50	50	50	100	50–100
conserved	3	75	75	100	100	75–100
disturbed	1	50	50	50	100	50–100
entire landscape	3	75	75	100	100	75–100

[a] *Abbreviations: CW, watersheds with conserved forest; DW, watersheds with disturbed forest.*

[b] *Abundance-based coverage nonparametric richness estimator.*

[c] *Incidence-based coverage nonparametric richness estimator.*

[d] *Percentage of expected richness covered by sampling effort (range: minimum-maximum).*

Oxybelis aeneus (18% relative abundance) dominated the disturbed forest. Of the 3 turtle species recorded in the conserved forest, only the dominant *Rhinoclemmys rubida* (73% relative abundance) was found in the disturbed forest, with just one individual recorded.

Species Sensitivity to Disturbance

Ten anuran species had positive IS values (≥ 0.3), indicating they could be sensitive to disturbance. Of these, 4 species, *Exerodonta smaragdina*, *Craugastor hobartsmithi*, *Leptodactylus melanonotus*, and *Hypopachus variolosus* were significantly more abundant in conserved forest. Eight species had negative IS values (≤ -0.2), indicating they could be positively affected by disturbance; however, only 2 species, *O. marmorea* and *Smilisca fodiens*, were significantly more abundant in the disturbed forest and 1 species, *Pachymedusa dacnicolor*, was practically absent from the conserved forest.

Six lizard species had positive IS values (>0.2), but only *Ameiva undulata* and *S. utiformis* were significantly more abundant in the conserved forest. Eleven species had negative IS values (<-0.1), but only 7 showed significantly more abundance in the disturbed forest. Most snake species did not show significant differences in abundance between forest conditions, except *Imantodes*

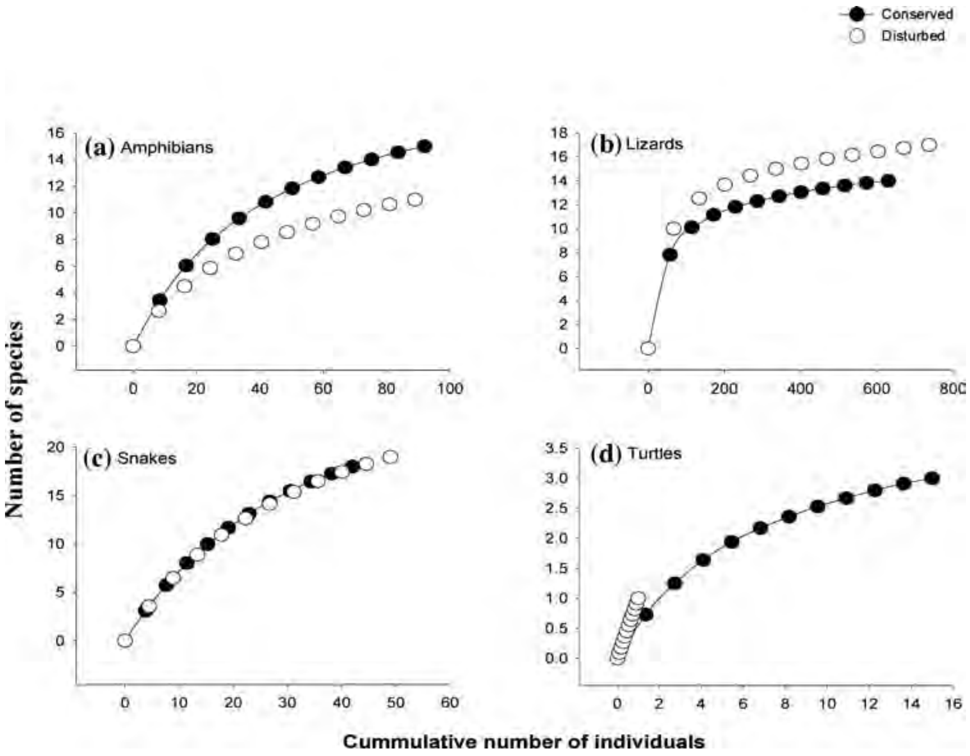

Figure 2. Species accumulation curves for (a) amphibians, (b) lizards, (c) snakes, and (d) turtles in conserved and disturbed forest at Chamela, Jalisco, Mexico.

gemmistratrus, which was marginally more abundant in disturbed forest. The 3 turtle species had positive IS values, but only *R. pulcherrima* exhibited significantly lower abundance in disturbed forest.

Habitat Attributes

Of the 22 habitat attributes, only 11 were significantly different between conserved and disturbed forest. As expected, most structural forest variables, except canopy openness and grass ground cover, were significantly higher in conserved forest. Air and soil temperature and stump ground cover were higher in disturbed forest (Table 3). The PCA of habitat attributes differentiated conserved from disturbed forest sites along the first component (PC1), which explained 61% of total intersite variance. Conserved forest sites were similar in habitat attributes, whereas disturbed forest sites were heterogeneous. Conserved forest had lower canopy openness, air and soil temperatures, and grass and shrub ground cover than disturbed forest, but higher woody stem cover, root ground cover, and taller herb strata. The second principal component (PC2; 23% of total variance) separated disturbed forest sites based on liana and dead-branch ground cover (Fig. 4a).

Species Similarity between Forest Conditions

Lizard assemblages showed the highest similarity between conserved and disturbed forest (Morisita-Horn's index = 0.87), followed by snake (0.60) and anuran assemblages (0.57). The first 2 axes of the CCA analysis explained 42.4% of intersite variation in anurans and 64.5 and 42.8% of intersite variation in lizards and snakes, respectively. Axis 1 of the CCA significantly separated the species assemblages of conserved and disturbed forest sites (Student's $t > 4.5$, df = 2, $p < 0.05$ in all assemblages; Fig. 4).

The first CCA axis was positively correlated with PC1 of the habitat matrix ($r > 0.99$, df = 4, $p < 0.05$). Abundance variation of *O. marmorea* and *P. dacnicolor* was significantly correlated with site scores of the PC1 ($r > 0.81$, $n = 6$, $p \leq 0.05$), indicating the species positively responded to canopy openness, air and soil temperature, and shrub and grass cover. In contrast, *C. hobartsmithi* showed the opposite trend ($r = 0.89$, $n = 6$, $p < 0.05$). In lizards intersite variation in abundance of *Urosaurus bicarinatus* ($r = 0.95$, $n = 6$, $p < 0.01$), *S. melanorhinus* ($r = 0.87$, $n = 6$, $p < 0.05$), and *Anolis nebulosus* was positively associated with PC1 ($r = 0.80$, $n = 6$, $p < 0.056$). No snake species was significantly correlated with PC1.

Vulnerability Traits

Frog body size was significantly greater in disturbed than conserved forest ($U = 9$, $p < 0.05$, one-tailed test; disturbed and conserved medians were 44 and 75 mm, respectively). Species with small body size were infrequent in disturbed forest. Anuran's reproductive mode was significantly different between forest conditions ($\chi^2 = 44.22$, df = 4, $p < 0.001$): there were more species with reproductive modes 1 and 2 in disturbed forest and more species with mode 4 in conserved forest. Lizards, snakes, and turtles did not have significantly different functional traits between forest conditions.

Discussion

Assemblage Structure

ANURANS

Our results concur with previous studies documenting negative effects of habitat modification on the species diversity and composition of anuran assemblages (Pineda & Halffter 2004). Nevertheless, we observed a neutral rather than negative effect on species total abundance. *O. marmorea*, *S. fodiens*, and *P. dacnicolor* abundance increased notably in the disturbed forest, explaining why anuran abundance did not differ between forest conditions even though species richness declined. Although 4 species, *E. smaragdina*, *C. hobartsmithi*, *L. melanonotus*, *H. variolosus*, were significantly more abundant in

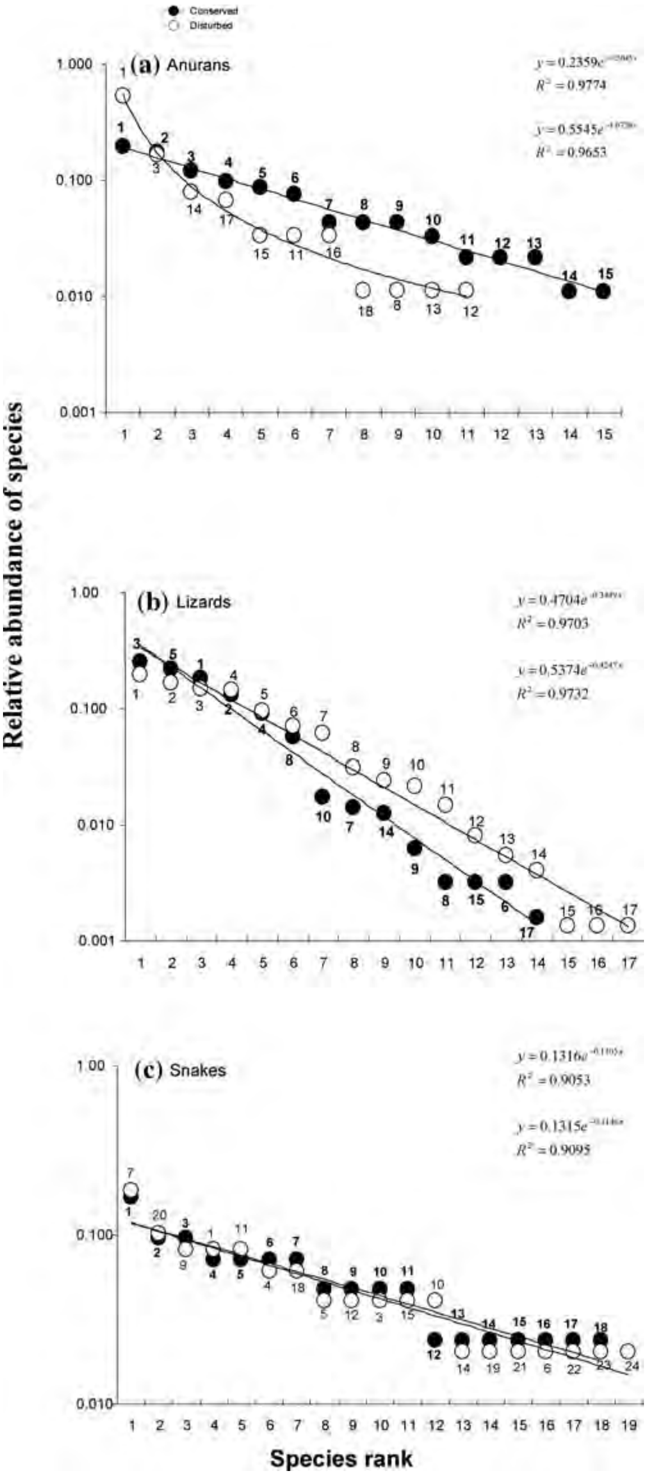

*Figure 3. Species-rank plots for anuran, lizard, and snake assemblages from conserved and disturbed forest at Chamela, Mexico. Species rank is ordered from the most to the least abundant species. Anurans: 1, Olma (*Ollotis marmorea*); 2, Crbo (*Craugastor hobartsmithi*); 3, Smba (*Smilisca baudinii*); 4, Leme (*Leptodactylus melanonotus*); 5, Hyva (*Hypopachus variolosus*); 6, Exsm (*Exerodonta smaragdina*); 7, Gaus (*Gastrophryne usta*); 8, Elni (*Eleutherodactylus nitidus*); 9, Crme (*C. mexicanus*); 10, Elmo (*Eleutherodactylus modestus*); 11, Lifo (*Lithobates forreri*); 12, Trve (*Trachycephalus venulosus*); 13, Tlsm (*Tlalocohyla smithii*); 14, Pada (*Pachymedusa dacnicolor*); 15, Chma (*Chaunus marinus*); 16, Trsp (*Triprion spatulatus*); 17, Smfo (*S. fodiens*); 18, Olmz (*Ollotis mazatlanensis*); lizards: 1, Asli (*Aspidoscelis lineattissimus*); 2, Anne (*Anolis nebulosus*); 3, Scut (*Sceloporus utiformis*); 4, Asco (*Aspidoscelis communis*); 5, Amun (*Ameiva undulata*), 6, Urbi (*Urosaurus bicarinatus*); 7, Scme (*S. melanorhinus*); 8, Phla (*Phyllodactylus lanei*); 9, Coel (*Coleonyx elegans*); 10, Ctpe (*Ctenosaura pectinata*); 11, Scho (*S. horridus*); 12, Mabr (*Mabuya brachypoda*); 13, Igig (*Iguana iguana*); 14, Plpa (*Plestiodon parvulus*); 15, Hebo (*Heloderma horridum*); 16, Phas (*Phrynosoma asio*); 17, Scas (*Scincella assata*); 18, Geli (*Gerrhonotus liocephalus*); snakes: 1, Midi (*Micrurus distans*); 2, Drma (*Drymobius margaritiferus*); 3, Lema (*Leptodeira maculata*); 4, Boco (*Boa constrictor*); 5, Crba (*Crotalus basiliscus*); 6, Ledi (*Leptophis diplotropis*); 7, Oxae (*Oxybelis aeneus*); 8, Mapu (*Manolepis putnami*); 9, Mame (*Masticophis mentovarius*); 10, Psur (*Pseudoleptodeira uribei*); 11, Taca (*Tantilla calamarina*); 12, Diga (*Dipsas gaigeae*); 13, Drme (*Dryadophis melanolomus*); 14, Drco (*Drymarchon corais*); 15, Lobi (*Loxocemus bicolor*); 16, Setr (*Senticolis triaspis*); 17, Sine (*Sibon nebulata*); 18, Trbi (*Trimorphodon biscutatus*); 19, Hyto (*Hypsiglena torquata*); 20, Imge (*Imantodes gemmistratus*); 21, Latr (*Lampropeltis triangulum*); 22, Lehu (*Leptotyphlops humilis*); 23, Psla (*Pseudoleptodeira latifasciata*).*

Table 2. Observed and rarefied species richness and species diversity for the 6 watersheds sampled for anurans and reptiles in conserved and disturbed forest at Chamela, Jalisco, Mexico.

	Conserved					*Disturbed*					
	CW1[a]	*CW2*[a]	*CW3*[a]	*average*	*SE*	*DW1*[b]	*DW2*[b]	*DW3*[b]	*average*	*SE*	U (p)
Anurans											
abundance	9	46	37	30.7	11.1	40	23	26	29.7	5.2	0.83
species richness	4	11	13	9.3	2.7	7	6	8	7	0.6	0.51
species richness rarefied	4	5.8	6.5	5.4	0.7	3.5	3.2	3.5	3.4	0.1	0.05
H′	1.1	2.1	2.3	1.9	0.4	1.3	1.4	1.4	1.4	0.03	0.51
H′ rarefied	1.2	1.7	1.8	1.5	0.2	1.1	1	0.9	1	0.05	0.05
evenness	0.83	0.9	0.92	0.88	0.03	0.68	0.78	0.66	0.7	0.03	0.05
Lizards											
abundance	213	262	155	210	30.9	290	216	231	245.7	22.6	0.27
species richness	11	12	12	11.7	0.3	17	13	13	14.3	1.3	0.04
species richness rarefied	5.2	5.2	5.3	5.3	0.04	5.9	6.5	6	6.1	0.2	0.03
H′	1.9	1.9	1.9	1.9	0.01	2.1	2.2	2.1	2.2	0.03	0.05
H′ rarefied	1.5	1.5	1.5	1.5	0.02	1.6	1.7	1.6	1.7	0.03	0.03
eveness	0.77	0.76	0.77	0.77	0.03	0.76	0.87	0.82	0.82	0.03	0.34
Snakes											
abundance	12	11	19	14	2.6	14	22	13	16.3	2.8	0.27
species richness	9	9	14	10.7	1.7	12	14	5	10.3	2.7	1.00
species richness rarefied	4.5	4.6	4.7	4.6	0.06	4.8	4.5	3.6	4.3	0.4	0.65
H′	2.1	2.1	2.6	2.3	0.17	2.4	2.5	1.5	2.2	0.3	0.82
H′ rarefied	1.5	1.5	1.5	1.5	0	1.5	1.5	1.2	1.4	0.1	0.31
eveness	0.95	0.98	0.98	0.97	0.01	0.98	0.95	0.95	0.96	0.01	0.45
Turtles											
abundance	8	3	4	5	1.53	0	0	1	0.33	0.33	0.04
species richness	2	2	2	2	0	0	0	1	0.33	0.33	0.03
species richness rarefied	1	1	1	1	0	0	0	1	0.33	0.33	0.10
H′	0.56	0.27	0.56	0.46	0.09	0	0	0	0	0	0.03
H′ rarefied	0	0	0	0	0	0	0	0	0	0	1.00
eveness	0.81	0.92	0.81	0.85	0.03	0	0	0	0	0	0.34

[a] *Watersheds with conserved forest.*
[b] *Watersheds with disturbed forest.*

conserved forest, dominance of these species was not as strong as those of disturbed forest. Thus, the overall effect of forest disturbance on the anuran assemblage was a rearrangement of dominance among species and the loss of some species. These changes were due to the differential effects of forest disturbance on 2 relevant vulnerability traits, body size and reproductive mode.

Anurans are vulnerable to direct solar radiation and have relatively narrow tolerances to changes in moisture and temperature (Duellman & Trueb 1994). In our study disturbed forest watersheds had significantly higher canopy openness and less litter, and concomitantly higher air and soil temperature than the conserved forest. Of the 10 disturbance-sensitive frogs, 7 were exclusively in conserved forest. Their absence in disturbed forest is not because of inherent rarity because they accounted for 48% of anuran species in the conserved forest. Because the entire region was forested recently, the abundance of species in the conserved forest may be a reasonable estimate of natural commonness and rarity. The disturbance-sensitive species had smaller body sizes than nonsensitive species. Small-sized amphibians have proportionately higher surface area with respect to body volume and therefore higher rates of water loss than larger species (Duellman & Trueb 1994). This may cause small amphibians to be intolerant of the desiccating conditions of the disturbed area. Furthermore, the small species have a reproductive mode particularly vulnerable to desiccation: encapsulated eggs laid on the ground in moist microsites (Hödl 1990). Our results suggest that the microclimatic conditions associated with removal of forest canopy and reduced moisture-retaining litter layer are critical habitat features that preclude the persistence of small frogs in disturbed forest.

The group of disturbance-tolerant anurans contained 8 frog species. Most were characterized by large body size and an aquatic larval stage in which eggs are laid in puddles. *Chaunus marinus* and several *Ollotis* species respond positively to habitat modification. A number of structural and physiological features allow toads to tolerate dry conditions (Duellman & Trueb 1994) and *O. marmorea* feeds on a wide range of prey including ants, termites, and beetles and may switch prey depending on availability (Suazo-Ortuño et al. 2007). This foraging ability may partially explain why toads became highly dominant in disturbed forest. Other tolerant species, such as

Table 3. Descriptive statistics of habitat and ground structure attributes in conserved and disturbed forest at Chamela, Jalisco, Mexico.[a]

		Conserved			*Disturbed*				
Variable	*Unit*	*mean*	*SD*	*range*	*mean*	*SD*	*range*	t *test (df)/*U *test*	p
Air temperature	°C	29.65	0.41	29.1-29.9	32.38	0.78	31.9-33.3	$t = 5.48$, (4)	0.005[b]
Canopy layers	number	4.94	0.12	4.8-5.1	1.87	0.4	1.4-2.2	$U = 9$	<0.05[b]
Canopy openness	%	26.39	0.75	25.6-27	70.83	7.07	66.2-79.0	$U = 9$	<0.05[b]
Herbs	height (m)	0.86	0.65	0.5-1.6	0.4	0.09	0.3-0.5	$t = 1.48$, (4)	0.21
Relative humidity	%	59.15	0.76	58.5-60	58.7	1.9	56.8-60.6	$U = 5$	0.827
Shrubs	height (m)	2.57	0.03	2.5-2.6	1.92	0.24	1.8-2.2	$t = 4.27$, (4)	0.013[b]
Slope	%	23.04	4.05	19.6-27.5	23.46	3.21	20.4-26.8	$U = 4$	0.82
Soil moisture	%	60.43	0.92	59.4-61	59.7	1.72	57.8-61.1	$U = 5$	0.83
Soil temperature	°C	29.72	0.34	24.4-30.1	33.13	0.96	32.6-34.3	$t = 6.05$, (4)	0.004[b]
Trees	height (m)	9.23	0.31	8.8-9.5	4.74	1.27	3.3-5.5	$t = 4.021$, (4)	0.016[b]
Burrows	% cover	0.04	0.07	0-0.1	0.09	0.09	0.01-0.20	$U = 2$	0.27
Standing dead trees	% cover	0.02	0.01	0.01-0.03	0.04	0.03	0.02-0.07	$U = 2$	0.27
Dry branches	% cover	5.24	0.12	5.1-5.4	5.56	2.44	4.1-8.4	$U = 6$	0.51
Grasses	% cover	0	0	0	45.96	8.22	41.0-55.5	$U = 9$	<0.05[b]
Herbs	% cover	7.01	0.7	6.4-7.7	8.98	1.59	7.2-9.7	$U = 1$	0.13
Lianas	% cover	0.79	0.16	0.6-7.7	0.78	0.58	0.2-1.4	$U = 4$	0.82
Litter layer	% cover	83.05	0.99	81.9-83.7	32.54	7.82	23.5-37.5	$U = 9$	<0.05[b]
Rocks	% cover	1.36	1.12	0.4-2.6	3.65	2.66	1.0-6.3	$U = 1$	0.13
Roots	% cover	0.38	0.2	0.2-0.5	0.07	0.09	0.01-0.20	$U = 8$	0.13
Shrubs	% cover	0.51	0.18	0.1-0.3	1.47	0.14	1.4-1.6	$U = 9$	<0.05[b]
Stumps	% cover	0.02	0.01	0.1-0.3	0.18	0.07	0.1-0.3	$U = 9$	<0.05[b]
Woody stem	% cover	1.47	0.2	1.3-1.6	0.69	0.17	0.5-0.8	$U = 9$	<0.05[b]

[a] *Variables were compared between conserved versus disturbed areas of forest.*

[b] *Significant difference.*

S. fodiens, burrow in the soil and form water-resistant cocoons, adaptations that reduce water loss (McDiarmid & Foster 1987). Furthermore, *Triprion spatulatus*, *P. dacnicolor*, and *S. baudini* are generalist species with wide distributions and adaptations to xeric conditions (Duellman & Trueb 1994).

LIZARDS, SNAKES, AND TURTLES

Lizards had higher abundance and species richness in the disturbed forest. This differs from previous observations in humid tropical areas that reptiles decrease in abundance from conserved forest to pastures (Urbina-Cardona et al. 2006). Nevertheless, the observed changes in our study area resulted from the increase in abundance of some lizard species but not from a reorganization of assemblage structure. Dominant species and species composition were similar in both habitats, resulting in high species similarity between forest conditions.

Reptiles are not as constrained by moisture requirements as amphibians (Jellinek et al. 2004). The higher species richness and abundance of lizards in disturbed forest could have been the result of increased food availability and thermoregulation microsites. These conditions are strongly related to lizard survival and reproduction (Parker 1994). In our study the more-open canopy of the disturbed forest undoubtedly increased the availability of basking sites. Various researchers have also registered an increase in insect diversity and abundance in disturbed habitats (Lenski 1982; Heliölä et al. 2001) and a higher turnover of insect species in areas with a mosaic of different degrees of disturbance intensity (Hill & Hamer 2004). The patchwork of disturbed habitats in our study area could result in a diverse array of microhabitats favoring the persistence of lizard species. Only 2 lizards, *S. utiformis* and *A. undulata*, were disturbance sensitive. Both are terrestrial and use the litter layer for cover or foraging. The reduction of this layer in the disturbed forest may be involved in the decline of these species.

The structure and composition of the snake assemblage did not change in disturbed watersheds, implying that snake species are flexible in their response to disturbance. Although 8 species were identified as disturbance sensitive, no species showed significant differences in abundance between forest conditions, but *I. gemmistratus* was present only in the disturbed sites. As with the disturbance-sensitive lizard species, all sensitive snake species, except *Leptophis diplotropis*, were terrestrial and used the litter layer.

Turtles were the only assemblage whose diversity and abundance diminished with disturbance, indicating that they are particularly disturbance sensitive. Plants, especially fallen fruits, are the main food source for these turtles (Alvarado-Diaz et al. 2003). Food availability may critically limit turtles in disturbed forests with reduced fruit crops. Other factors, such as predation may have also caused the decline in turtle numbers.

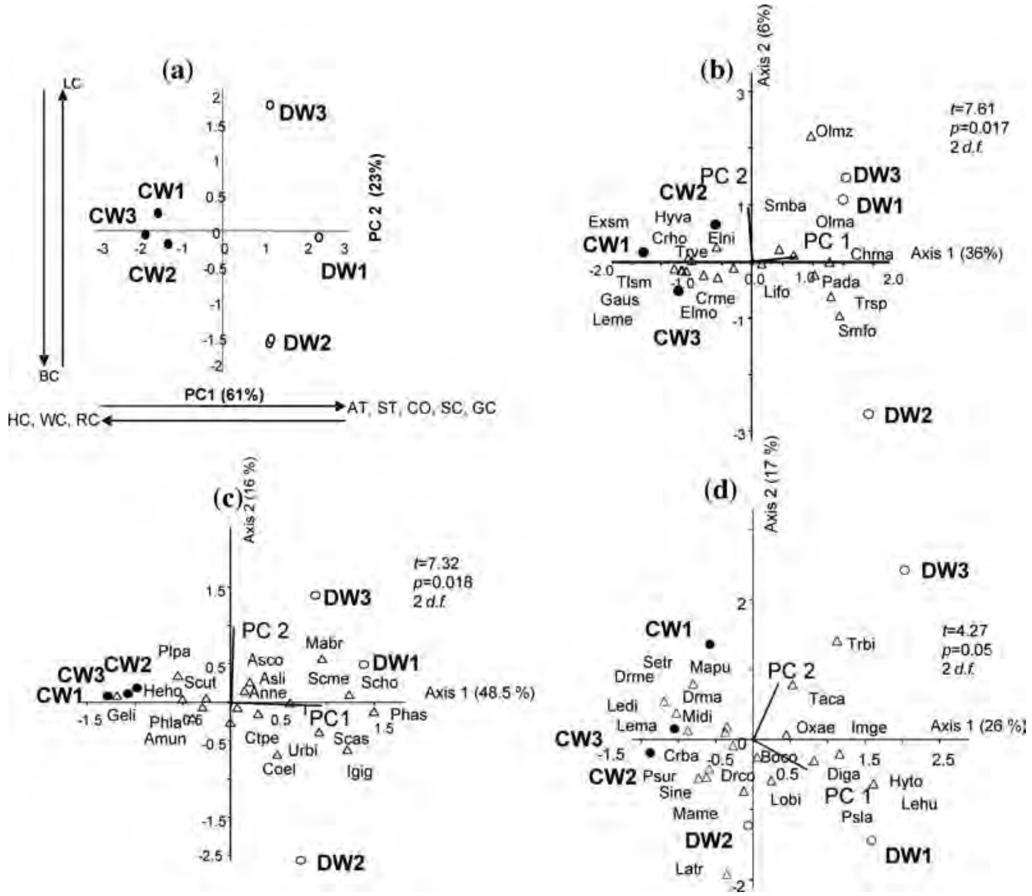

Figure 4. Ordination of anuran, lizard, and snake species recorded in conserved (CW1–CW3, black dots) and disturbed forest sites (DW1–DW3, open dots): (a) principal component analysis of watersheds by habitat variables (arrows indicate significant correlations [$p < 0.05$*] of PC 2 with different habitat attributes) (positively: AT, air temperature; ST, soil temperature; CO, canopy openness; SC, shrub cover; and GC grass cover; negative: HC, herb height cover; WC, woody stem cover, and RC, root cover) and (b–d) canonical correspondence analyses ordination of species assemblages and watersheds, anurans, lizards, and snakes, respectively. See Fig. 3 for definitions of species abbreviations.*

Conservation Implications

Our results indicate that the transformation of tropical dry forest to agricultural mosaic results in important structural and compositional changes of hepetofaunal assemblages that may imperil certain species of amphibians, turtles, and lizards. Our results support the prediction that 7 of the 60 species in conserved forest will be vulnerable to local extinction if the forest continues to be removed and modified. These species should be monitored carefully. The high degree of disturbance in the dry tropical forests of western Mexico suggests that the persistence of small isolated populations is critical for the survival of herpetofauna. Although environmental influences, such as climate, determine the broad distribution patterns of herpetofaunal species, forces operating at the population level, especially microhabitat suitability and availability, will determine the survival of amphibians and reptiles in modified agricultural landscapes.

Our results show that the response of herpetofaunal assemblages to disturbance is different among and within taxonomic groups. Although anuran and turtle assemblages decreased in diversity in the disturbed area, lizards benefited from the disturbed habitat mosaic. Small body size and a reproductive mode characterized by laying eggs on the ground may make some frog species especially prone to extinction.

An important goal for the conservation of herpetofauna should be the determination of species traits associated with extinction or persistence in disturbed forest patches. Although it is difficult to provide specific management guidelines for sensitive species, in the case of turtles (*Rhinoclemmys*), their frugivorous habits suggest that the permanence of fruit trees in forest patches will be important to prevent local extinction. The direct-development characteristic of most of the sensitive frog species makes them especially vulnerable to egg desiccation in the drying ambient conditions of modified forest;

therefore, the permanence of forest patches and thus the soil and air humidity associated with closed-canopy and litter-layer cover will be essential for the maintenance of these species in agricultural mosaics.

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Supplementary Material

Anuran, lizard, snake, and turtle species registered and species relative abundance and sensitivity values are available as part of the on-line article from http://www.blackwell-synergy.com/ (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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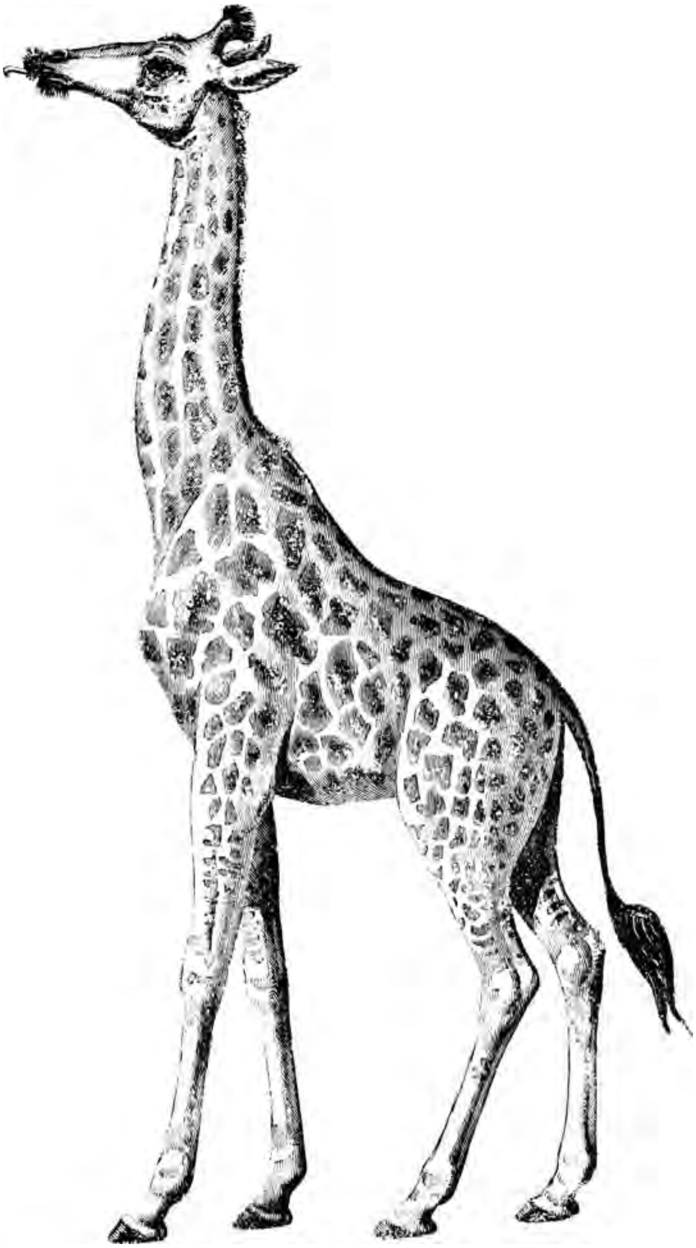

Appendix 1. Anuran, lizard, snake and turtle species registered in each watershed during 11 surveys in conserved and disturbed forests at Chamela, Jalisco, Mexico. Species relative abundance (percentage respect to total abundance per assemblage type) and sensitivity values (IS), X^2 and significance is provided for these species with total abundance higher than 6.

			Forest						Index of		
Family	Species	Acronym	Conserved	%	Disturbed	%	Total	%	sensivity	X^2	
Bufonidae	*Chaunus marinus*	Chma	1	1.1	3	3.4	4	0.2	-0.5		
	Ollotis marmorea	Olma	18	20	48	54	66	4	-0.5	12.7	****
	Ollotis mazatlanensis	Olmz	0	0	1	1.1	1	0.1	-1.0		
Hylidae	*Exerodonta smaragdina*	Exsm	7	7.6	0	0	7	0.4	1.0	5.1	**
	Tlalocohyla smithii	Tlsm	2	2.2	1	1.1	3	0.2	0.3		
	Pachymedusa dacnicolor	Pada	1	1.1	7	7.9	8	0.5	-0.8	3.1	*
	Trachycephalus venulosus	Trve	2	2.2	1	1.1	3	0.2	0.3		
	Smilisca fodiens	Smfo	0	0	6	6.7	6	0.4	-1.0	4.2	**
	Smilisca baudinii	Smba	11	12	15	17	26	1.6	-0.2	0.3	
	Triprion spatulatus	Trsp	0	0	3	3.4	3	0.2	-1.0		
Brachycephalidae	*Craugastor hobartsmithi*	Crho	16	17	0	0	16	1	1.0	14.1	****
	Craugastor mexicanus	Crme	4	4.3	0	0	4	0.2	1.0		
	Eleutherodactylus modestus	Elmo	3	3.3	0	0	3	0.2	1.0		
	Eleutherodactylus nitidus	Elni	4	4.3	1	1.1	5	0.3	0.6		
Leptodactylidae	*Leptodactylus melanonotus*	Leme	9	9.8	0	0	9	0.5	1.0	7.1	***
Microhylidae	*Gastrophryne usta*	Gaus	4	4.3	0	0	4	0.2	1.0		
	Hypopachus variolosus	Hyva	8	8.7	0	0	8	0.5	1.0	6.1	**
Ranidae	*Lithobates forreri*	Lifo	2	2.2	3	3.4	5	0.3	-0.2		
	TOTAL AMPHIBIANS		92	100	89	100	181	11			
Anguidae	*Gerrhonotus liocephalus*	Geli	2	0.3	0	0	2	0.1	1		
Eublepharidae	*Coleonyx elegans*	Coel	4	0.6	18	2.4	22	1.3	-0.64	7.7	***
Gekkonidae	*Phyllodactylus lanei*	Phla	36	5.7	23	3.1	59	3.6	0.22	2.4	
Helodermatidae	*Heloderma horridum*	Heho	2	0.3	1	0.1	3	0.2	0.33		
Iguanidae	*Ctenosaura pectinata*	Ctpe	11	1.7	16	2.2	27	1.6	-0.19	0.6	
	Iguana iguana	Igig	0	0	4	0.5	4	0.2	-1		

Phrynosomatidae	*Phrynosoma asio*	Phas	0	0	1	0.1	1	0.1	-1		
	Sceloporus horridus	Scho	0	0	11	1.5	11	0.7	-1	9.1	***
	Sceloporus melanorhinus	Scme	9	1.4	45	6.1	54	3.3	-0.67	23	****
	Sceloporus utiformis	Scut	159	25	110	15	269	16	0.18	8.6	***
	Urosaurus bicarinatus	Urbi	2	0.3	52	7.1	54	3.3	-0.93	45	****
Polychridae	*Anolis nebulosus*	Anne	83	13	123	17	206	12	-0.19	7.4	***
Scincidae	*Plestiodon parvulus*	Plpa	8	1.3	3	0.4	11	0.7	0.45	1.5	
	Mabuya brachypoda	Mabr	0	0	6	0.8	6	0.4	-1	4.2	**
	Scincella assata	Scas	1	0.2	1	0.1	2	0.1	0		
Teiidae	*Ameiva undulata*	Amun	140	22	70	9.5	210	13	0.33	23	****
	Aspidoscelis communis	Asco	57	9	107	15	164	9.9	-0.3	15	****
	Aspidoscelis lineattissimus	Asli	116	18	146	20	262	16	-0.11	3.2	
	TOTAL LIZARDS		630	100	737	100	1367	83			
Boidae	*Boa constrictor*	Boco	3	7.1	3	6.1	6	0.4	0		
Colubridae	*Dipsas gaigeae*	Diga	1	2.4	2	4.1	3	0.2	-0.33		
	Dryadophis melanolomus	Drme	1	2.4	0	0	1	0.1	1		
	Drymarchon corais	Drco	1	2.4	1	2	2	0.1	0		
	Drymobius margaritiferus	Drma	4	9.5	0	0	4	0.2	1		
	Hypsiglena torquata	Hyto	0	0	1	2	1	0.1	-1		
	Imantodes gemmistratus	Imge	0	0	5	10	5	0.3	-1		*
	Lampropeltis triangulum	Latr	0	0	1	2	1	0.1	-1		
	Leptodeira maculata	Lema	4	9.5	2	4.1	6	0.4	0.33		
	Leptophis diplotropis	Ledi	3	7.1	1	2	4	0.2	0.5		
	Manolepis putnami	Mapu	2	4.8	0	0	2	0.1	1		
	Masticophis mentovarius	Mame	2	4.8	4	8.2	6	0.4	-0.33		
	Oxybelis aeneus	Oxae	3	7.1	9	18	12	0.7	-0.5		
	Pseudoleptodeira latifasciata	Psla	0	0	1	2	1	0.1	-1		
	Pseudoleptodeira uribei	Psur	2	4.8	2	4.1	4	0.2	0		
	Senticolis triaspis	Setr	1	2.4	0	0	1	0.1	1		
	Sibon nebulata	Sine	1	2.4	1	2	2	0.1	0		
	Tantilla calamarina	Taca	2	4.8	4	8.2	6	0.4	-0.33		
	Trimorphodon biscutatus	Trbi	1	2.4	3	6.1	4	0.2	-0.5		
Elapidae	*Micrurus distans*	Midi	7	17	4	8.2	11	0.7	0.27		
Leptotyphlopidae	*Leptotyphlops humilis*	Lehu	0	0	1	2	1	0.1	-1		

Loxocemidae	*Loxocemus bicolor*	Lobi	1	2.4	2	4.1	3	0.2	-0.33	
Viperidae	*Crotalus basiliscus*	Crba	3	7.1	2	4.1	5	0.3	0.2	
	TOTAL SNAKES		42	100	49	100	91	5.5		
Kinosternidae	*Kinosternon integrum*	Kiin	3	20	0	0	3	3	1	
Bataguridae	*Rhinoclemmys rubida*	Rhru	11	73	1	100	12	12	0.83	***
	Rhinoclemmys pulcherrima	Rhpu	1	6.7	0	0	1	1	1	
	TOTAL TURTLES		15	100	1	100	16	1		
	TOTAL HERPETOLOGICAL ASSEMBLAGE						1655	100		

* = $p < 0.1$; ** = $p < 0.05$; *** = $p < 0.01$; **** = $p < 0.001$

CAPÍTULO III

Riparian Areas and Conservation of Herpetofauna in a Tropical Dry Forest in Western Mexico

LRH: Suazo-Ortuño, Alvarado-Díaz, Martínez-Ramos

RRH: Riparian-uplands gradients and herpetofauna

Riparian Areas and Conservation of Herpetofauna in a Tropical Dry Forest in Western Mexico

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Abstract: Studies that assess the importance of riparian habitats in maintaining diversity of herpetofaunal assemblages in tropical dry forests are limited. We examined changes in abundance, diversity and composition of anuran, lizard and snake assemblages along riparian-upland gradients in conserved and disturbed areas of a tropical dry forest on the Pacific coast of Mexico. We sampled 659 plots in six watersheds over two years. Two forest conditions (conserved and human disturbed, with three watersheds as replicates) were evaluated in the dry and rainy season. Within each watershed, plots were randomly located at three different distance categories from either stream edge: 0 – 10 m (riparian habitat), 30 – 40 m (middle habitat), and 50 – 60 m (upland habitat). Herpetofauna was surveyed by time-constrained searches with a sampling effort of 1980 person/hours. Eighteen anuran, 18 lizard, and 23 snake species were recorded. Overall, abundance and diversity of lizards and snakes decreased from riparian to upland areas in both forest conditions and seasons; while that of anurans followed this trend only for the conserved forest during the rainy season. Regardless of distance, abundance and diversity of anurans markedly decreased during the dry season, while that of snakes and lizards increased. Five of the most abundant species of amphibians and reptiles were only found in riparian areas (riparian-dependent species), 2 were significantly more abundant in such areas (riparian-facultative species), and another 25 species were evenly distributed along the riparian-upland gradient or were more abundant in uplands (riparian-independent species). Overall, our study shows that the importance of riparian areas for herpetofaunal conservation in dry tropical forests varies with forest condition and season.

Resumen: La importancia de los hábitats riparios para el mantenimiento de la diversidad herpetofaunistica en bosques tropicales secos ha sido escasamente evaluada. Examinamos cambios en abundancia, diversidad y composición de los ensambles de anuros, lagartijas y serpientes a lo largo del gradiente ripario-tierras de ladera en áreas conservadas y perturbadas del bosque tropical seco en la costa del Pacífico Mexicano. Muestreamos 659 cuadrantes dentro de seis cuencas durante dos años. Dos condiciones del bosque (conservado y perturbado, con tres cuencas como replicas) fueron evaluadas durante la estación de secas y lluvias. En cada cuenca los cuadrantes fueron establecidos al azar en tres diferentes categorías de distancia a partir del borde del arroyo: 0-10 m (hábitat ripario), 30-40 m (hábitat intermedio) y 50-60 m (laderas altas). Se utilizo el método de búsqueda intensiva con tiempo determinado con un esfuerzo de muestreo de 1980 horas/persona. En general, la abundancia y la diversidad de lagartijas y serpientes disminuyo de las áreas riparias a las laderas adyacentes en ambas condiciones del bosque y estaciones, mientras que los anuros siguieron la misma tendencia en el bosque conservado durante la estación de lluvias. Independientemente de la distancia, la abundancia y diversidad de anuros disminuyó durante la estación seca, mientras que las serpientes y las lagartijas aumentaron. Cinco de las especies más abundantes solo se encontraron en las áreas riparias (especies ripario-dependientes), 2 fueron significativamente más abundantes en éstas áreas (especies ripario-facultativas) y otras 25 especies estuvieron uniformemente distribuidas a lo largo del gradiente ripario-tierras de ladera o fueron más abundantes en las áreas de lasdera (especies ripario-independientes). En general, nuestro estudio sugiere que la importancia de las áreas riparias para la conservación de la herpetofauna en el bosque tropical seco varía con la condición del bosque y estación del año.

Key words: anurans, lizards, snakes; Chamela Jalisco; dry season-rainy season; forest disturbance; lizards; riparian-upland gradients; snakes

RIPARIAN AREAS FUNCTION AS ENVIRONMENTAL BUFFERS and/or core habitats for aquatic, semi-aquatic, and riparian-specialist species (Semlitsch & Bodie 2003, Lee *et al*. 2004). Riparian systems also expand the range of available microenvironments within the landscape (Naiman *et al*. 1998, Chen *et al*. 1999), and generally support high levels of biodiversity (Gregory *et al*. 1991, Ward 1998). The generally higher number of species in riparian areas may become more pronounced as anthropogenic disturbance of upland areas intensifies (Donald *et al.* 2006). Forested riparian areas may function as important ―habitat islands" for wildlife within areas of intensive agriculture. The herpetofauna that use riparian areas differ in their dependence upon such areas; some species are confined to them throughout their lives, whereas others may use it only occasionally or use a range of terrestrial habitats adjacent to wetlands and streams (*e.g.*, Madison 1997, Richter *et al*. 2001).

Considering that habitat use by riparian species often varies with climate, elevation, type of water body or adjoining land use (Petranka & Smith 2005), it is not surprising that many questions regarding the importance of riparian habitats for many taxa are poorly resolved, especially in tropical ecosystems. For example, in tropical dry forests where the dry season with its shortage of water and energy resources represents a particular challenging time of the year, especially for ground dwelling vertebrates, the role of riparian areas as faunal refuges for amphibians and reptiles has just recently begun to be explored (Gienger *et al.* 2002). The relevance of such studies is highlighted under the present scenario of deforestation and land use change to agriculture that tropical forest landscapes are undergoing (Chazdon *et al.* 2009). Riparian areas in tropical agricultural landscapes may play a critical role in biodiversity conservation, as shown for temperate systems (*e.g.*, Maisonneuve & Rioux 2001, Kluber *et al.* 2008). More studies are needed, however, to assess the ecological and conservation value of riparian areas in human disturbed tropical dry forests.

In this paper we assess changes in abundance, species diversity and composition of anuran, lizard and snake assemblages along riparian-upland gradients in conserved (covered with old-growth forest) and human disturbed tropical dry forest landscapes. Specifically, we tested the following hypotheses. (1) Herpetofaunal abundance and diversity is greater in riparian sites when compared to upland ones; it is expected that riparian sites provide a wide array of microhabitats favorable for the persistence of several herpetofaunal species. (2) Composition and dominance of species in riparian areas differ from those in the uplands; it is expected that some species are riparian-dependent, riparian-specialists, riparian-facultative or riparian independent. (3) The riparian environmental effects on assemblage structure is more pronounced in the dry than in the rainy season; it is expected that during the dry season, riparian areas function as refuges, where conditions are less limiting for several species. (4) The riparian environmental effects on assemblage structure is greater in the human disturbed than in the conserved areas if the upland is under greater degree of disturbance than the riparian sites.

METHODS

STUDY SITE.— The study was conducted at the Chamela Biosphere Reserve (MAB-UNESCO) and surrounding agricultural areas along the Pacific coast of Jalisco state (19º30'N, 105º03'W), México. Average annual rainfall is 788 mm, 80% of which falls in the rainy season (July – October), after a 7-8 month dry season; mean annual temperature is 24.6 °C (Lott 1993). Dominant vegetation is tropical dry forest with strips of semi-deciduous forest along riparian areas. Trees in the upland forest loss their leaves during the dry season. The upland forest presents a well-developed understory and canopy 4-15 m in height (Bullock 1986). Riparian forests remain green throughout the dry season (about 50% of trees keep the foliage), present 1.7 times higher litter production (Martínez-Yrízar & Sarukhán 1990) and present a more open understory and taller canopy than upland forests. More than 200 tree species have been recorded in the conserved forest (Lott 1993). This forest type exhibits higher tree and shrub diversity in riparian than in upland areas (Lott *et al.* 1987), and greater tree species turnover along riparian-upland gradients (Balvanera *et al.* 2002). The area outside the reserve is characterized by subsistence cultivation, selective extraction of trees for firewood, and conversion to pastures for cattle raising (Burgos & Maass 2004).

SAMPLING PROTOCOL.— The basic sampling unit was the watershed. We sampled 6 small independent watersheds (ca. 1 km^2 each), 3 of which were immersed in forest disturbed by agricultural activities and the other 3 in old-growth conserved forest. In each watershed there was a single seasonal stream. Details of site locations and description are given in Suazo- Ortuño *et al.* (2008). Each watershed had a minimum distance of 70 m upland perpendicular to streams before reaching a ridgeline and a minimum of 500 m of riparian and upslope area parallel to streams. In each watershed, the stream edge-upland length was divided into three distance categories from 0 – 60 m: stream edge 0 – 10 m (D1), 30 – 40 m (D2) or 50 – 60 m (D3).

We considered that D1 represented riparian conditions, D2 intermediate conditions and D3 upland conditions in the watersheds. Several site attributes differed significantly among distance categories both in conserved and disturbed forest (Table 1). Sampling plots (100 X 10 m) were established randomly, within each distance category, parallel to stream channel and watershed crest. We surveyed 359 plots in all 6 watersheds from November 2000 to November 2002; 264 plots were surveyed at D1, 217 at D2, and 178 at D3; 300 plots were surveyed during the dry season and 359 during the rainy season. Each plot was surveyed twice, once diurnally (0930–1600 h), and once nocturnally (2100–0400 h).

During each field reconnaissance period, a crew of 6 people surveyed the plots using time-constrained searches. Plots were surveyed visually by searching vegetation and ground surface for reptiles and anurans, including lifting cover objects (rocks, logs and debris). All encountered individuals were captured, identified to species, and released near where captured. To avoid counting the same individual more than once during the 2-year study period we clipped the toes of frogs and lizards and the ventral scales of snakes.

The sampling effort was measured in person-hours (ph). Over the 2-year study period, total search effort for each watershed was 330 ph, for a grand total of 1980 ph across the 6 watersheds. During each survey period, elapsed time between sampling the conserved and disturbed areas was no more than 72 h. Each watershed was sampled in two annual periods (dry season, November-June; rainy season, July-October) and in two different forest conditions (conserved and disturbed). Therefore, 4 combinations were considered: rainy season/conserved forest (RS/CF), dry season/conserved forest (DS/CF), rainy season/disturbed forest (RS/DF), and dry season/disturbed forest (DS/DF).

HABITAT ATTRIBUTES.— In conserved and disturbed forest we evaluated 22 site attributes associated with vegetation structure, ground cover and microclimatic features within each plot (100 x 10 m). Details of measured variables are in Suazo-Ortuño *et al.* (2008).

DATA ANALYSIS.— We calculated mean values per watershed for each distance category, forest condition, and season for each of the 22 site variables. For continuous data (e.g., air and soil temperature, tree height) we used Analysis of Variance (ANOVA) to test differences among distance categories per season and forest condition for continuous variables. Data on site variables were log transformed to meet homoscedasticity requirements when needed. To test for differences in proportional variables we used non-parametric Kruskal-Wallis tests.

Due to the unequal number of sampling plots per distance category, density data were adjusted, dividing the number of individuals by the number of plots in each distance category. Assemblage density was defined as number of individuals per (100 x10 m) plot and species richness as number of species obtained from a rarefied constant sample of individuals (specific to each assemblage). Species diversity, rarefied to a constant number of individuals was measured with the Shannon-Winner diversity index ($H' = - \sum p_i \ln p_i$, where p_i is the proportion of individuals of species i in the community). A mean value of assemblage density considering all surveying periods per season was obtained from 3 replicates (watersheds) for each distance category per forest condition. We summed up data from all plots corresponding to each distance category, forest condition, and season to obtain a single rarefied H´ and species richness value per watershed. Rarefied values were obtained using the routine provided by EcoSim (Gotelli & Entsminger 2001).

We used Repeated Measured Analysis of Variance (rANOVA) with Type III Sum of Squares (recommended for unbalanced sample designs) to test single and interactive effects of distance category, forest condition and season on each of the assemblages' structural traits. In these models, season was the repeated subject and distance category (3levels) and forest condition (2 levels) were factors with 3 replicates. All analyses were performed using the GLM routine of Data Desk 6.1 (1996).

Abundance (%) of the 6 most abundant species per assemblage was calculated per distance category, forest condition, and season. These species represented between 14.2% and 93.9% of total number of individuals per assemblage. To evaluate differences in assemblage structure and composition among distance categories, across forest conditions and seasons, we used principal component analysis (PCA). For each assemblage, a matrix of 12 columns (representing all combinations of distance category, forest condition, and season) by *n* rows (species) with number of individuals per cell was constructed. Numbers were transformed using a geometric scale to reduce heterogeneity among species abundance values as follows: 0 = 0; 1 = 1; 2 = 2; 3 = 3 to 4; 4 = 5 to 8; 5 = 9 to 16; 6 = 17 to 32; and 7 = more than 32.

RESULTS

HABITAT ATTRIBUTES.— In all four combinations of season and forest condition, D1 (0 – 10 m) presented a significantly greater number of forest canopy layers, tree height, and litter cover, as well as significantly lower canopy openness and air/soil temperature than other distance categories (Table 1). D2 (30 – 40 m) had significantly higher herb and grass cover, and greater canopy openness and temperature than other distance categories (Table

1). In general D3 (50 – 60 m) had lower tree height than the other distance categories (Table 1). Overall, in the rainy season, canopy openness (%, 1.5 m above ground) in conserved forest (19.01 ± 2.26) was 3.5 times lower than in disturbed forest (66.8 ± 2.5) (Table 1).

ASSEMBLAGE STRUCTURE.— Overall, we recorded a total of 1639 individuals representing 18 anuran, 18 lizard, and 23 snake species. Of these, 888 individuals (54.17 %) were registered in D1, 451 (27.51 %) in D2, and 300 (18.30 %) in D3. Lizards were the most abundant (83.0 %), followed by anurans (11.0 %) and snakes (5.6 %). As described below, assemblage density and diversity varied differentially among distance categories, forest condition and season.

FROGS.—During the rainy season in conserved forest, assemblage density was higher in D1 than in other distance categories ($F_{2,14} = 9.72$, $P = 0.002$). During the dry season, assemblage density significantly decreased ($F_{1,14} = 31.6$, $P < 0.0001$) and differences associated to distance category disappeared (Fig. 1a,b). Both, species richness ($F_{2,14} = 31.6$, $P < 0.0001$) and species diversity (H'; $F_{2,14} = 9.45$, $P < 0.0025$) showed significantly greater values in D1 but only in conserved forest during the rainy season; in disturbed forest, these community traits were higher at D2 (Fig. 1c-f).

Relative abundance of anuran species varied among distance categories. The frog species *Exerodonta smaragdina* was exclusively registered in conserved forest and presented higher abundance at D1 (riparian-facultative species); *Smilisca baudinii* was registered in both forest conditions, and in disturbed forest had greater relative abundance at D1. Both species decreased in abundance from D1 to D3 (Fig. 2ab). Other species showed greater relative abundance in D2, D3 or had similar relative abundance among distance categories (riparian-independent species) (Fig. 2). Four of the most abundant species (*E. smaragdina, S. baudinii, Pachymedusa dacnicolor, Lithobates forreri*) were not registered in uplands (D3). The two principal components of PCA explained 73.1% of the variation in species composition and abundance of anurans among all combinations of distance category x forest condition x season. During the rainy season in conserved forest, D1 clearly differentiated along the Axis-2 of the PCA from the other forest condition x season combinations (Fig. 3a). During the rainy season in disturbed forest, D1 differentiated along Axis-1 from D2 and D3. During the dry season in conserved forest there were not differences registered among distance categories (Fig. 3a).

LIZARDS.— In both seasons, density decreased from D1 to D3 ($F_{2,14} = 5.76$, $P = 0.015$). Independently of distance category, assemblage density was greater in the dry season ($F_{1,14} = 29.04$, $P < 0.001$) (Fig. 4a,b). Overall, D1 and D2 showed significantly greater species richness than D3 ($F_{2,14} = 14.22$, $P = 0.004$; Fig. 4c,d). Species richness was consistently greater in disturbed forest independently of distance category. A significant interaction between forest condition and season ($F_{2,14} = 14.36$, $P = 0.002$) indicated that species richness decreased in disturbed forest during the dry season independently of distance category (Fig. 4c,d). Distance category had an overall marginal significant effect on species diversity (H'; $F_{2,14} = 3.48$, $P = 0.059$), with a tendency of D1 and D2 to have greater diversity than D3 (Fig. 4e,f). Disturbed forest had greater species diversity than conserved forest independently of distance category and season ($F_{1,14} = 8.83$, $P = 0.010$).

Relative abundance of lizard species changed among distance categories. During the rainy season in conserved forest, 3 species had greater relative abundance in D1; *Ameiva* *undulata*, *Aspidoscelis lineatissima*, and *Phyllodactylus lanei* decreased from D1 to D3 (Fig. 5a). In the dry season, *A. lineatissima* showed the same trend (Fig. 5b). This was the most abundant lizard species at D1 in disturbed forest in both seasons (Fig. 5c, d) and was the only riparian-facultative species of all lizards. Other species maintained their relative abundance unchanged among distance categories, or had greater abundance in D2 and D3 in the different forest conditions and season (riparian-independent species) (Fig. 5).

The two principal components of PCA explained 90.4% of variation in lizard composition and abundance among all combinations of distance category x forest condition x season. Lizard assemblages of conserved and disturbed forests clearly differentiated along the Axis-2 of the PCA (Fig. 3b). Along Axis-1, D1 differentiated from D2 and D3 in conserved forest in both seasons. Such differentiation was not apparent for disturbed forest in any season (Fig. 3b).

SNAKES.— Snake density decreased from D1 to D3 in the rainy season in both forest conditions ($F_{2,14} = 2.67$, $P = 0.10$); this tendency disappeared in the dry season (Fig. 6 a,b). While snake density was similar between forest conditions in the rainy season, density was higher in disturbed than in conserved forest during the dry season ($F_{1,14} = 6.33$, $P = 0.025$). Snake species richness ($F_{2,14} = 14.22$, $P = 0.0004$) and species diversity (H' $F_{2,14} = 9.45$, $P = 0.0025$) significantly decreased from D1 to D3 for all cases. However, as indicated by a significant interaction between forest condition and season on species richness ($F_{1,14} = 14.37$, $P = 0.002$) and species diversity (H´$F_{1,14} = 29.45$, $P = 0.0001$) this change was more noticeable in the conserved forest for both seasons than in the disturbed forest in the dry season (Fig. 6c-f). Independently of distance category, both diversity parameters were greater in the rainy season than in the dry season in the conserved forest (species richness:

$F_{1,14} = 5.93$, $P < 0.029$; H′: $F_{1,14} = 6.03$, $P < 0.027$; Fig. 6c-f), whereas in disturbed forest these parameters showed no seasonal change.

Relative abundance of snake species changed among distance categories; *Leptodeira maculata* and *Oxybelis aeneus* were exclusively registered at D1 during the rainy season in conserved forest (Fig. 7a); whereas, *Dipsas gaigae*, *Manolepis putnami* and *O. aeneus* were exclusively recorded in D1 during the dry season in conserved forest (Fig. 7b); and *Imantodes gemmistratrus*, *Drymarchon melanurus*, *Hypsiglena torquata*, *L. maculata* and *Leptotyphlops humilis* were exclusively recorded at D1during the rainy season in disturbed forest; whereas under the same forest condition *Micrurus distans*, *Boa constrictor*, *L. maculata*, and *Leptophis diplotropis* were exclusively registered at D1during the dry season (Fig. 7c, d). Other species had similar relative abundance among distance categories or had greater abundance at D2 or D3 in all combinations of forest condition x season (riparian-independent species) (Fig. 7). In contrast, *M . ptunami*, *D. melanurus*, *H. torquata*, *L. maculata* and *L. humilis* were exclusively registered at D1 independently of forest condition and season (riparian-dependent species).

The two principal components of PCA explained 49.6% of variation in composition and abundance of snakes among all combinations of distance category x forest condition. A clear differentiation between conserved forest in the rainy season and disturbed forest in the dry season was observed along Axis-2 (Fig. 3c). D1 differentiated from D2 and D3 along Axis-1 during the rainy season in conserved forest and during the dry season in disturbed forest. D1 was similar to other distance categories in other forest condition x season combinations. During the dry season, the conserved forest showed the least differentiation among distance categories as compared to all other forest condition x season combinations (Fig. 3c).

DISCUSSION

Our results show an important environmental variation along the riparian-upland gradient. Generally, for both conserved and disturbed forests, riparian areas had lower understory solar radiation, lower temperature and greater soil and vegetation complexity. We found evidence that along this gradient, changes in anuran, lizard and snake assemblages were influenced by forest condition and season. Overall, riparian areas were an important habitat for several species and as a whole riparian habitats may play an important role in the conservation of herpetological assemblages in tropical deciduous forests.

FROGS.—Considering the physiological constrains of frogs, especially their vulnerability to direct solar radiation, high air temperature, and low environmental humidity (Duellman & Trueb 1994), we expected riparian areas to have greater abundance and diversity than upland areas, especially during the dry season in disturbed forest. This hypothesis was not supported by our results as anurans tended to disappear in the dry season for both forest conditions. Indeed, the markedly low number of frogs registered during the dry season suggests that in response to drought they reduce activity and remain dormant during this season.

Furthermore, contrary to our predictions, riparian habitats had equal or greater frog density and diversity (species richness and species diversity H’) in conserved than in disturbed forests during the rainy season. Riparian habitats showed more than a two-fold number of individuals and diversity than upland sites in conserved forest. Agricultural activities modified forest structure and the physical environment mainly at the middle of the riparian-upland gradient in disturbed forest (Table 1) and these changes may have resulted in higher frog diversity in such areas (distance category D2). At the onset of the rainy season, we observed that puddles formed in the bed of seasonal streams in conserved forest were readily used by most frog species for reproduction. In contrast, in disturbed forest puddles were formed during the rainy season on manmade dirt roads and fields, frequently found between stream edges and hill crests. Additionally, water availability in cattle drinking and irrigation devices in these intermediate sites may alter the association of frogs with natural riparian habitats. Perhaps, such purported higher puddle resource in the D2 areas in disturbed forest enables more species to reproduce. However, other factors besides availability of reproductive sites, such as higher food accessibility, may account for the higher frog abundance in riparian habitats in disturbed forest.

The PCA analyses indicated a rearrangement of species abundance and assemblage composition among distance categories depending on forest condition. Most abundant species in riparian habitats from conserved forest have an aquatic larval stage. In contrast, those species with higher abundance in uplands have small body size and a reproductive mode characterized by laying eggs on the ground (*Craugastor hobartsmithi*) or have medium/large body size (*Smilisca baudini*); *C. hobartsmithi* is restricted to environments with a relatively high humidity and low temperature (Suazo-Ortuño *et al.* 2008). Soil and air temperature in hill crests (D3) was lower during the rainy season in conserved forest than in other habitats (Table 1). Therefore, greater abundance of *C. hobartsmithi* at upland areas of conserved forest suggests that ground humidity and air temperature conditions allow use of such areas by disturbance-sensitive frogs (Suazo-Ortuño *et al.* 2008). This conclusion is strengthened by the fact that a greater number of abundant species was registered at upland habitat in conserved than in disturbed forest (Fig. 2).

Species of greater abundance in disturbed forest were large-sized frogs as discussed elsewhere (Suazo-Ortuño *et al.* 2008). Large anurans have proportionally lower rates of water loss than smaller species (Wells 2007). Therefore, large size is an important trait for anurans coping with a desiccating environment. The generalist toad *Incilus marmoreus* was the dominant anuran along the whole riparian–upland gradient. A number of morphological and physiological characteristics allow toads, like *I. marmoreus*, to tolerate dry conditions (Duellman *and* Trueb 1994). The markedly low number of frogs recorded during the dry season suggests that in our study area anurans drastically reduce activity during this season. Not surprisingly 50% of the few individuals registered during the dry season were toads (*I. marmoreus)*. Relative abundance of this species suggests that even in riparian areas, conditions at disturbed forest favor the prevalence of generalist anuran species, adapted to conditions associated with habitat disturbance.

The anuran assemblage found in riparian areas (D1) during the rainy season in conserved forest was clearly distinctive from those recorded at other distance categories, forest condition, or season. The ecological role of these habitats is evidenced by the higher abundance and diversity of anuran species that they support, and by the distinctive composition of the anuran assemblage, which complements that occurring in adjacent upland environments as has been discussed for other animal and plant groups (Sabo *et al.* 2005). This finding highlights the value of conserved riparian habitats for anurans in tropical dry forests.

LIZARDS AND SNAKES.—Reptiles are not as constrained by moisture requirements as anurans (Jellinek *et al.* 2004); therefore it is not surprising that unlike frogs, lizards and snakes remained active throughout the year. However, the shortage of resources associated to the dry season in tropical dry forests represents a survival challenge and some vertebrate species show reduced activity (e.g. anurans in our study area), whereas others (small mammals) may move from upland habitats to riparian habitats (Ceballos 1990). The last situation seems to be the case for lizards since regardless of forest condition they showed a preference to use the riparian areas, especially in the dry season. Foliage cover in riparian areas during the dry season provides terrestrial vertebrates with a mesic climatic environment when compared with more exposed conditions of the upland. Furthermore, higher productivity in riparian areas in the dry season allows sustained herbivory by invertebrates, which may in turn provide foraging opportunities for secondary consumers like lizards during a season when energy resources are markedly reduced.

As shown by the PCA analysis, assemblage structure and composition of lizards changed along the riparian–upland gradient, depending on forest condition and season. The hypothesis of higher food availability and less stressful conditions in riparian areas may explain the dominance of some species in such areas at one or both forest conditions and/or seasons. For example, *A. lineatissima* is a terrestrial insectivore species that has been observed in closed forest sites where temperatures are not higher than 33.2°C in the dry season and 30.5°C in the wet season (Navarro-García *et al.* 2008). These temperatures were more frequently registered for the case of the disturbed forest in the riparian (D1) than in the middle or upland areas (Table 1). Dominance patterns of several lizard species in uplands are more difficult to explain. For example, *Anolis nebulosus*, which increased in dominance towards the uplands, mainly in disturbed forest, is an arboreal insectivore lizard that lives in open habitats and forest edges (Ramirez-Bautista 2002); *Sceloporus utiformis*, dominant in uplands of conserved forest in both seasons is a terrestrial species that uses litter and herb cover for shelter and foraging (Suazo-Ortuño *et al.* 2008). This resource was not limited (> 90% of cover) along the riparian-upland gradient in conserved forest. Gienger *et al.* (2002) discuss that *S. utiformis* activity is greater in uplands than in riparian areas because uplands provide more thermal options and remain warmer latter in the day.

Snakes were more abundant and diverse in the riparian habitat in both forest conditions, particularly in the rainy season. These results may be in part explained by the fact that several snake species eat frogs and lizards and their higher abundance in riparian habitats may be related to greater prey availability. For example, anurans (preys) and snakes (predators) showed higher density in the riparian habitat during the rainy season, whereas lizards (preys) and snakes showed higher density in riparian areas of disturbed forest during the dry season. In all combinations of forest condition and season there was a high species turnover, and species dominance shifted among distance categories. The terrestrial snake-eater species *M. distans* was recorded in all distance categories in the conserved forest during the rainy season, whereas in disturbed forest during the dry season, this species was associated to riparian areas, suggesting that conditions like shade and leaf litter provide favorable conditions for search and capture of its prey. In contrast, *O. aeneus* occurred only at riparian areas in conserved forest in both seasons and had greater abundance at uplands in disturbed forest during the dry season. This snake is a lizard-eater species and the increase of lizards in the dry season, particularly in disturbed forest, may in part explain abundance changes for this species.

The importance of riparian areas for the conservation of herpetofauna in our study area varied with condition forest condition, season of the year and with the particular herpetological group assessed. Dry tropical forests in western Mexico seem to be inhospitable for anurans during the dry season when frogs were seldom recorded even in the riparian habitat, with its relatively benign conditions. During the rainy season frog activity was concentrated in the riparian habitat, but only in the conserved forest since water availability in the middle parts of the riparian-upland gradient in disturbed forest apparently releases frogs from riparian dependence. The riparian-upland gradient in conserved forest is partitioned by different species of frogs, with medium size species and an aquatic larval stage dominating the riparian environment and small species with direct development dominating the uplands. The presence of disturbance-sensitive frog species in the uplands in conserved forest suggests that this habitat presents relatively benign environmental conditions for anurans. In contrast, the riparian-upland gradient in disturbed forest was dominated by a single generalist species of toad with structural and physiological adaptations to cope with a relatively dry environment. Lizards and snakes presented affinity for the riparian environment in the conserved and disturbed forest for both seasons. Preference for the riparian habitat may be related to the availability of food resources throughout the year. This year-round prey availability may explain the fact that five snake and one lizard species are riparian-dependent and riparian-facultative, respectively. The higher herpetofaunal diversity registered in riparian areas highlights the ecological and conservation relevance of these habitats. Under the markedly strong seasonal dry conditions of the dry tropical forest, herpetofaunal assemblages may take advantage of favorable microclimates, surface water or other conditions and resources present in riparian areas. Additionally, the significant turnover in species pools between riparian and upland habitats show that riparian areas add to the diversity of the landscape mosaic and to the diversity of habitats and resources available to anuran and reptile assemblages. Thus, maintaining riparian habitats, even in modified agricultural landscapes, may help to maximize the conservation of the regional richness of herpetofaunal assemblages in tropical dry forests.

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TABLE 1. *Descriptive statistics of habitat attributes for each distance category, forest condition and season.*

Variable	D1 Mean	D2 Mean	D3 Mean	F test/*U* test	*p*	
rainy season conserved forest						
Air Temperature (°C)	$31.0^{a} \pm 0.33$	$30.6^{a} \pm 0.44$	$28.2^{a} \pm 1.89$	F=1.82, $_{2,6}$ df	*0.24*	
Canopy layers (number)	$7.05^{a} \pm 0.40$	$7.02^{b} \pm 0.59$	$6.68^{b} \pm 0.21$	U= 5.95	0.05	*
Canopy openness (%)	$19.01^{a} \pm 2.26$	$19.4^{a} \pm 0.93$	$20.01^{a} \pm 2.24$	*U*=0.14	0.86	
Herbs (%)	$9.92^{a} \pm 4.17$	$16.44^{b} \pm 0.38$	$14.53^{a} \pm 0.48$	*U*=5.95	0.05	
Soil Temperature (°C)	$30.9^{a} \pm 0.31$	$30.6^{a} \pm 0.45$	$28.2^{a} \pm 1.89$	F=1.66, $_{2,6}$ df	*0.26*	
Trees height (m)	$10.42^{a} \pm 0.28$	$9.44^{b} \pm 0.38$	$9.26^{b} \pm 0.47$	F=7.61, $_{2,6}$ df	0.023	*
dry season conserved forest						
Air Temperature (°C)	$27.35^{a} \pm 1.90$	$29.93^{b} \pm 0.38$	$31.43^{b} \pm 0.77$	F=16.92, $_{2,6}$ df	0.003	*
Canopy openness (%)	$31.39^{a} \pm 0.94$	$38.56^{b} \pm 1.39$	$35.48^{c} \pm 0.8$	U=7.2	0.027	*
Lianas cover (%)	$0.58^{a} \pm 0.16$	$0.32^{b} \pm 0$	$1.12^{c} \pm 0.44$	U=6.48	0.039	*
Soil Temperature (°C)	$27.14^{a} \pm 1.76$	$31.45^{b} \pm 0.39$	$31.77^{b} \pm 0.51$	F=8.76, $_{2,6}$ df	0.017	*
Trees height (m)	$11.22^{a} \pm 0.55$	$9.53^{b} \pm 0.47$	$9.39^{b} \pm 0.36$	F=14, $_{2,6}$, df	0.005	*
rainy season disturbed forest						
Air Temperature (°C)	$31.9^{a} \pm 1.52$	$34.64^{a} \pm 0.27$	$33.47^{a} \pm 0.86$	F=1.83, $_{2,6}$ df	0.24	
Canopy openness (%)	$66.8^{a} \pm 2.59$	$70.46^{a} \pm 9.87$	$73.89^{a} \pm 3.04$	U=1.68	0.43	
Grasses cover (%)	$18.87^{a} \pm 5.07$	$40.08^{b} \pm 18.9$	$19.12^{a} \pm 4.8$	U=5.42	0.06	
Soil Temperature (°C)	$32.1^{a} \pm 1.47$	$34.64^{a} \pm 0.27$	$33.47^{a} \pm 0.86$	F=2.70, $_{2,6}$ df	0.14	
Trees height (m)	$6.54^{a} \pm 0.24$	$4.67^{b} \pm 1.16$	$4.56^{b} \pm 0.3$	F=7.39, $_{2,6}$ df	0.024	*
dry season disturbed forest						
Air Temperature (°C)	$32.38^{a} \pm 0.59$	$33.48^{a} \pm 0.92$	$32.68^{a} \pm 0.51$	F=3.25, $_{2,6}$ df	0.11	
Canopy layers (number)	$1.85^{c} \pm 0.12$	$1.5^{b} \pm 0.49$	$1.72^{a} \pm 0.58$	U=6.48	0.03	*
Canopy openness (%)	$44.62^{a} \pm 1.18$	$69.86^{b} \pm 12.9$	$63.58^{c} \pm 10.2$	U=7.22	0.027	*
Herbs (%)	$0.01^{a} \pm 0.02$	$0.22^{b} \pm 0.07$	0^{a}	U=6.72	0.035	*
Litter layer cover (%)	$58.34^{a} \pm 4.01$	$37.32^{b} \pm 16.9$	$43.74^{b} \pm 8.14$	U=6.48	0.03	*
Shrubs height (m)	$2.72^{a} \pm 0.32$	$1.64^{b} \pm 0.62$	$2.0^{a} \pm 0.74$	F=6.48, $_{2,6}$ df	0.03	*
Soil Temperature (°C)	$32.09^{a} \pm 0.35$	$36.76^{b} \pm 1.81$	$34.28^{b} \pm 0.7$	F=12.48, $_{2,6}$ df	0.007	*
Trees height (m)	$5.4^{a} \pm 0.64$	$4.12^{b} \pm 1.76$	$4.84^{a} \pm 0.86$	F=10.14, $_{2,6}$ df	0.01	*

*= significance

Figure legends

FIGURE 1. Density, species richness and species diversity of anurans at three distance categories, where D1 = 0 – 10 m; D2 = 30 – 40 m; and D3 = 50 – 60 m, forest condition (disturbed or preserved) and season (dry or rainy) at Chamela, Jalisco, México.

FIGURE 2. Percentage of abundance of the six most abundant anuran species at three distance categories, where D1 = 0 – 10 m; D2 = 30 – 40 m; and D3 = 50 – 60 m, forest condition (disturbed or preserved) and season (dry or rainy) at Chamela, Jalisco, México. RS-CF = rainy season-conserved forest, RS-DF = rainy season-disturbed forest.

FIGURE 3. Canonical correspondence analyses ordination of anuran (a), lizard (b), and snake (c) species recorded at three distance categories, where D1 = 0 – 10 m; D2 = 30 – 40 m; and D3 = 50 – 60 m, forest condition (disturbed or preserved) and season (dry or rainy) at Chamela, Jalisco, México.

FIGURE 4. Structural traits of lizards' assemblage at three distance categories, where D1 = 0 – 10 m; D2 = 30 – 40 m; and D3 = 50 – 60 m, forest condition (disturbed or preserved) and season (dry or rainy) at Chamela, Jalisco, México.

FIGURE 5. Percentage of abundance of the six most abundant lizard species at three distance categories, where D1 = 0 – 10 m; D2 = 30 – 40 m; and D3 = 50 – 60 m, forest condition (disturbed or preserved) and season (dry or rainy) at Chamela, Jalisco, México. RS-CF = rainy season-conserved forest, RS-DF =

rainy season-disturbed forest, DS-CF = dry season-conserved forest, DS-DF = dry season-disturbed forest.

FIGURE 6. Structural traits of snakes' assemblage at three distance categories, where D1 = 0 – 10 m; D2 = 30 – 40 m; and D3 = 50 – 60 m, forest condition (disturbed or preserved) and season (dry or rainy) at Chamela, Jalisco, México.

FIGURE 7. Percentage of abundance of the six most abundant snake species at three distance categories, where D1 = 0 – 10 m; D2 = 30 – 40 m; and D3 = 50 – 60 m, forest condition (disturbed or preserved) and season (dry or rainy) at Chamela, Jalisco, México. RS-CF = rainy season-conserved forest, RS-DF = rainy season-disturbed forest, DS-CF = dry season-conserved forest, DS-DF = dry season-disturbed forest.

FIGURE 1

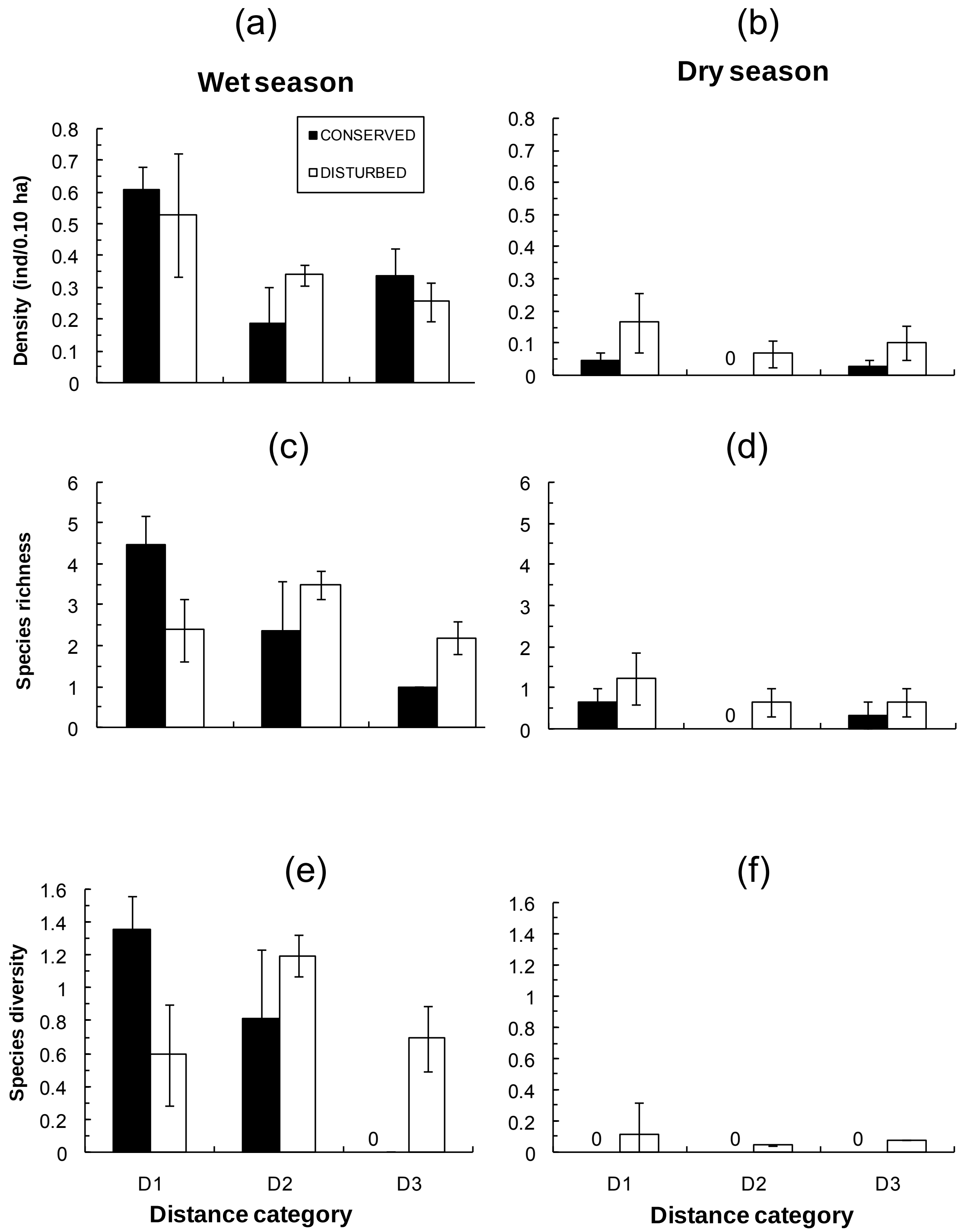

(a)
Wet season
(b)
Dry season
■ CONSERVED
□ DISTURBED
Density (ind/0.10 ha)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
(c)
(d)
Species richness
6
5
4
3
2
1
0
(e)
(f)
Species diversity
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
D1
D2
D3
Distance category

FIGURE 2

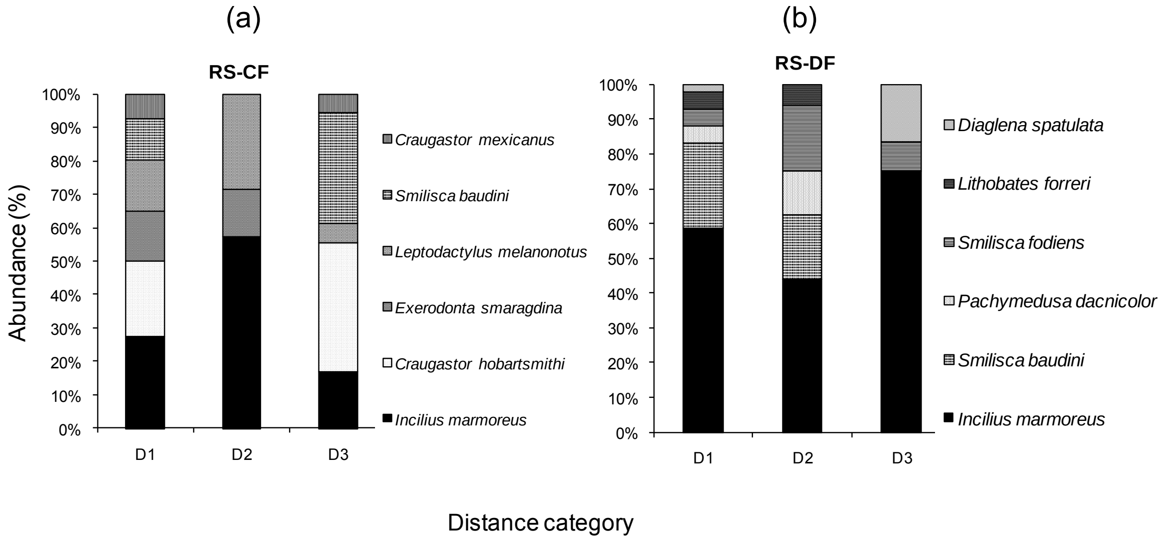

(a)
RS-CF
Abundance (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
D1
D2
D3
Craugastor mexicanus
Smilisca baudini
Leptodactylus melanonotus
Exerodonta smaragdina
Craugastor hobartsmithi
Incilius marmoreus
(b)
RS-DF
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
D1
D2
D3
Diaglena spatulata
Lithobates forreri
Smilisca fodiens
Pachymedusa dacnicolor
Smilisca baudini
Incilius marmoreus
Distance category

FIGURE 3

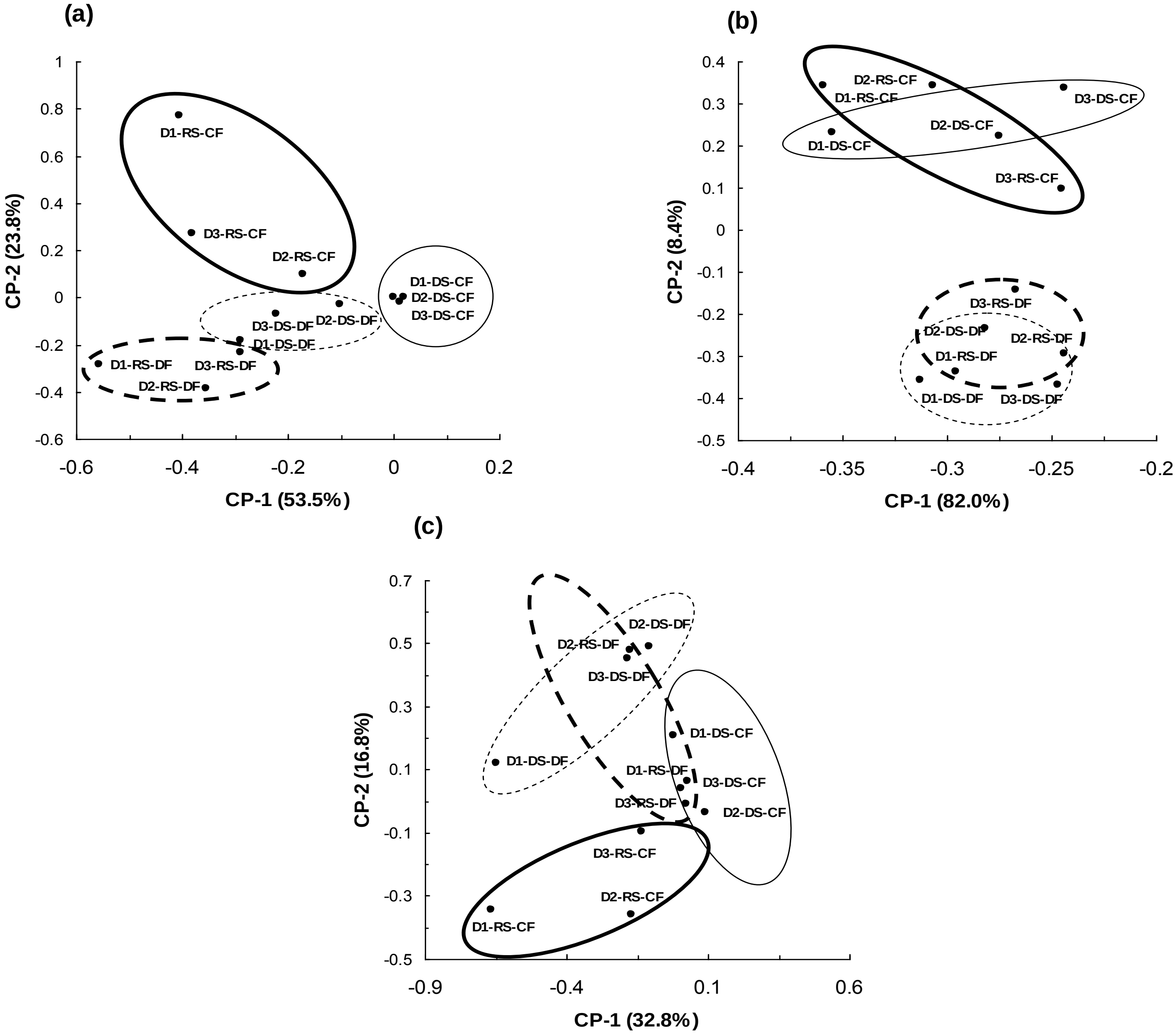
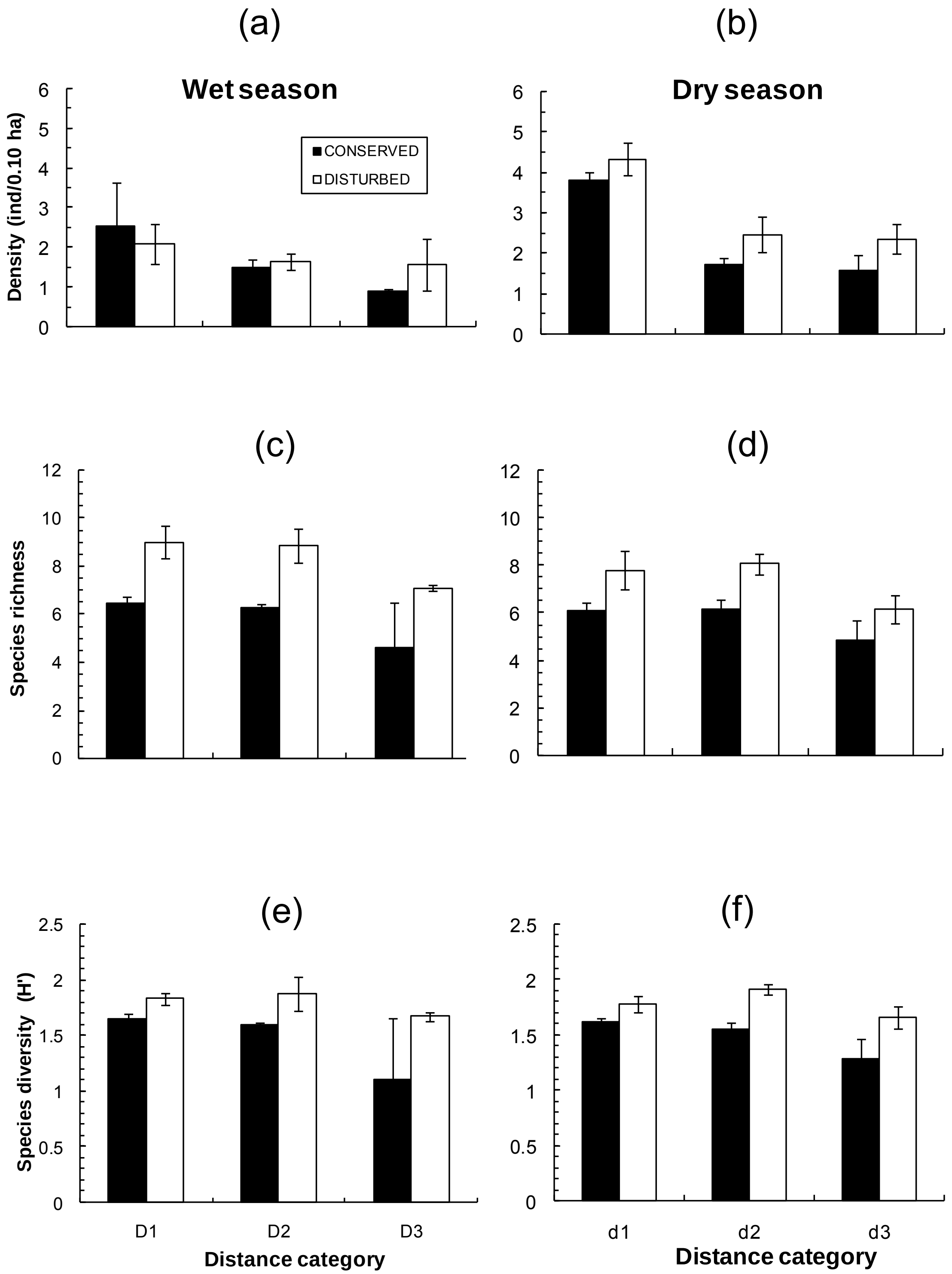

(a)
D1-RS-CF
D3-RS-CF
D2-RS-CF
D1-DS-CF
D2-DS-CF
D3-DS-CF
D3-DS-DF
D2-DS-DF
D1-DS-DF
D1-RS-DF
D3-RS-DF
D2-RS-DF
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.6
-0.4
-0.2
0
0.2
CP-2 (23.8%)
CP-1 (53.5%)
(b)
D2-RS-CF
D1-RS-CF
D3-DS-CF
D2-DS-CF
D1-DS-CF
D3-RS-CF
D3-RS-DF
D2-DS-DF
D2-RS-DF
D1-RS-DF
D1-DS-DF
D3-DS-DF
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.4
-0.35
-0.3
-0.25
-0.2
CP-2 (8.4%)
CP-1 (82.0%)
(c)
D2-DS-DF
D2-RS-DF
D3-DS-DF
D1-DS-CF
D1-DS-DF
D1-RS-DF
D3-DS-CF
D3-RS-DF
D2-DS-CF
D3-RS-CF
D2-RS-CF
D1-RS-CF
0.7
0.5
0.3
0.1
-0.1
-0.3
-0.5
-0.9
-0.4
0.1
0.6
CP-2 (16.8%)
CP-1 (32.8%)

FIGURE 4



(a)
(b)
Wet season
Dry season
■ CONSERVED
□ DISTURBED
Density (ind/0.10 ha)
0
1
2
3
4
5
6
(c)
(d)
Species richness
0
2
4
6
8
10
12
(e)
(f)
Species diversity (H')
0
0.5
1
1.5
2
2.5
D1
D2
D3
d1
d2
d3
Distance category
Distance category

FIGURE 5

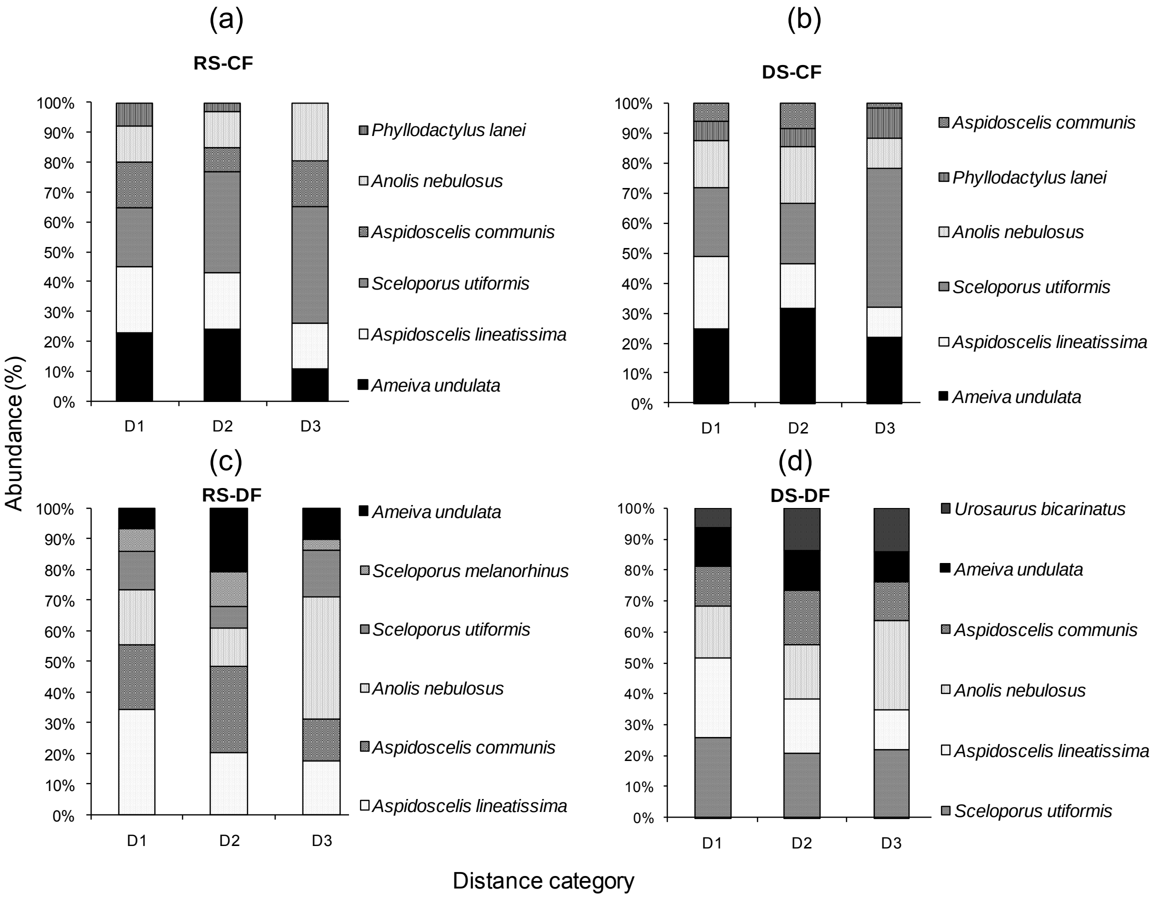

(a)
RS-CF
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
D1
D2
D3
Phyllodactylus lanei
Anolis nebulosus
Aspidoscelis communis
Sceloporus utiformis
Aspidoscelis lineatissima
Ameiva undulata
(b)
DS-CF
Aspidoscelis communis
Phyllodactylus lanei
Anolis nebulosus
Sceloporus utiformis
Aspidoscelis lineatissima
Ameiva undulata
Abundance (%)
(c)
RS-DF
Ameiva undulata
Sceloporus melanorhinus
Sceloporus utiformis
Anolis nebulosus
Aspidoscelis communis
Aspidoscelis lineatissima
(d)
DS-DF
Urosaurus bicarinatus
Ameiva undulata
Aspidoscelis communis
Anolis nebulosus
Aspidoscelis lineatissima
Sceloporus utiformis
Distance category

FIGURE 6

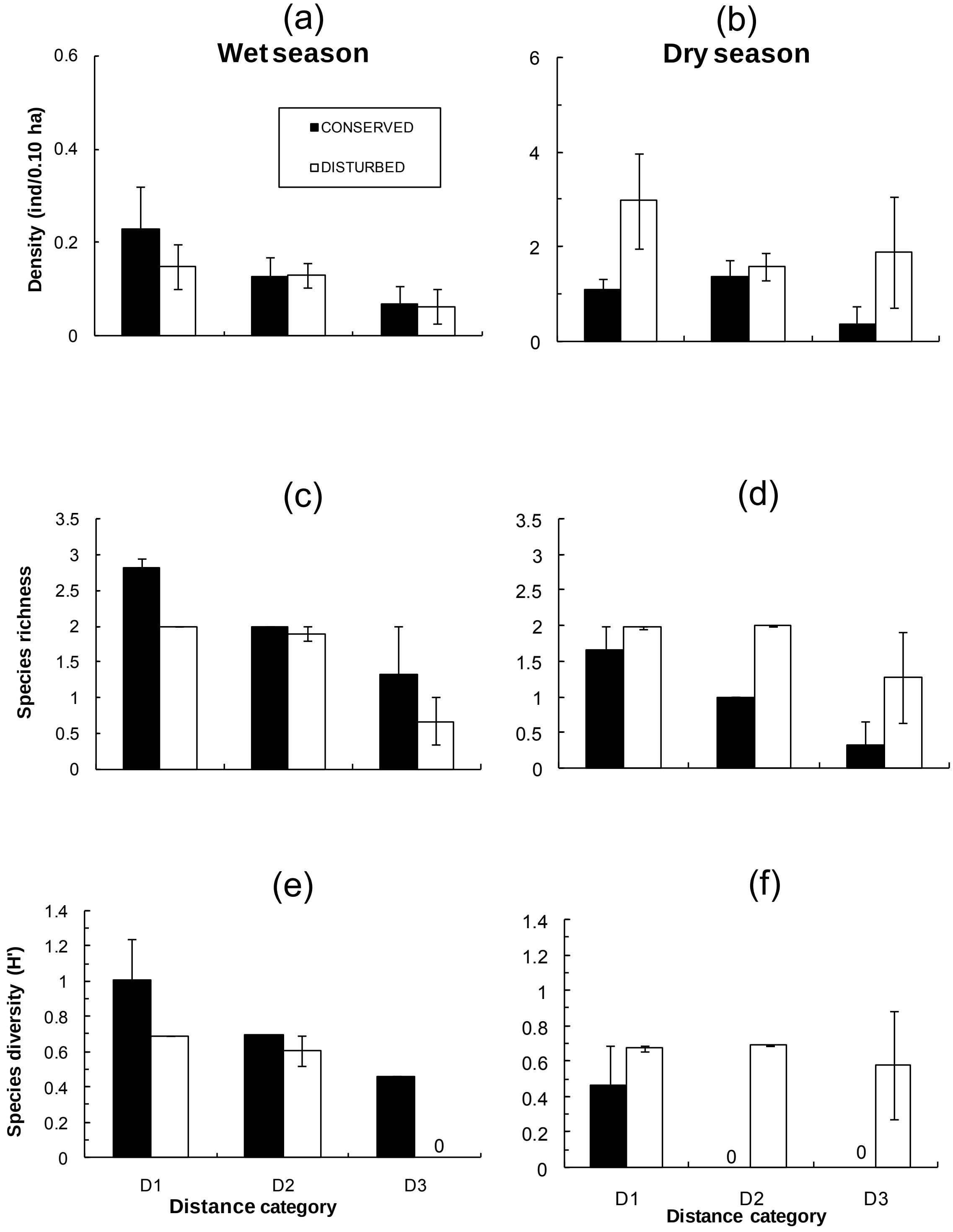
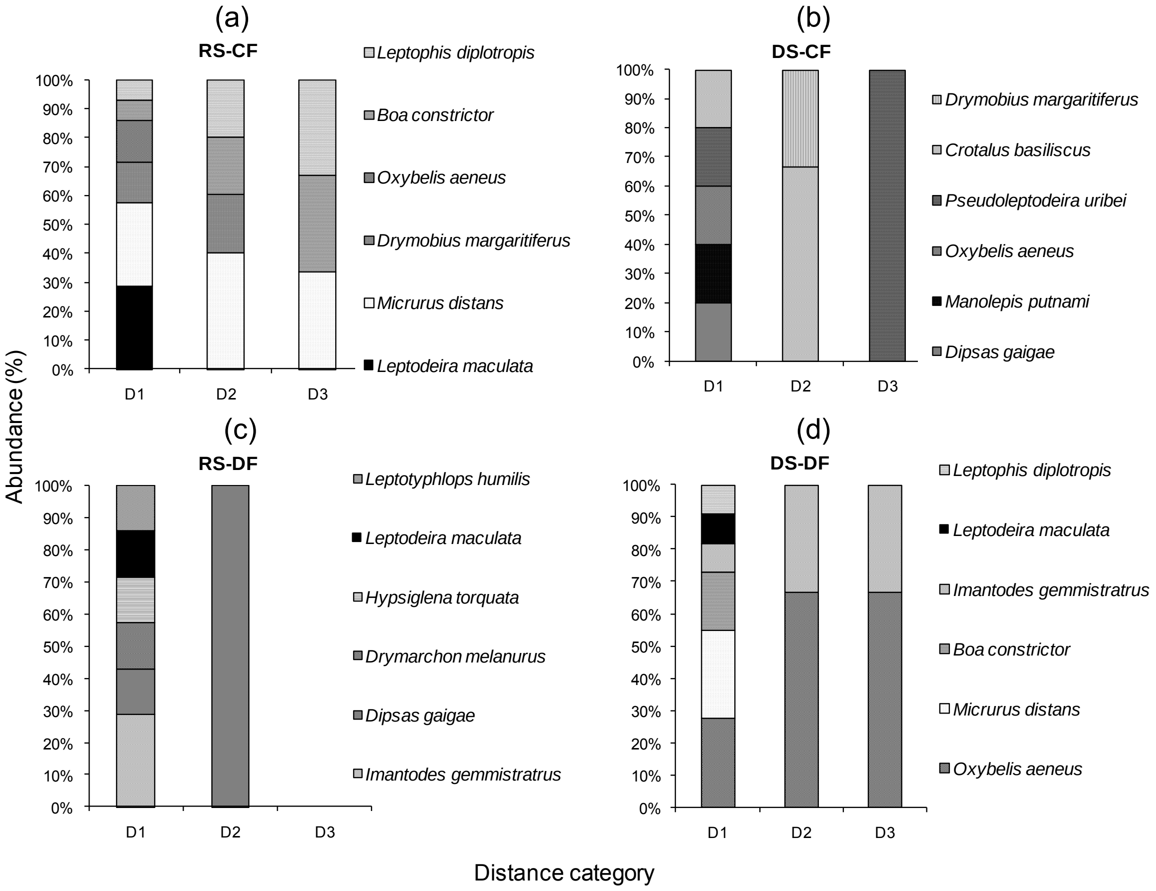

(a)
Wet season
(b)
Dry season
(c)
(d)
(e)
(f)
Density (ind/0.10 ha)
Species richness
Species diversity (H')
■CONSERVED
□DISTURBED
0
0.2
0.4
0.6
2
4
6
0.5
1
1.5
2.5
3
3.5
0.8
1.2
1.4
D1
D2
D3
Distance category

FIGURE 7


(a)
RS-CF
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
D1
D2
D3
▨ Leptophis diplotropis
▨ Boa constrictor
▨ Oxybelis aeneus
▨ Drymobius margaritiferus
☐ Micrurus distans
■ Leptodeira maculata
(b)
DS-CF
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
D1
D2
D3
▨ Drymobius margaritiferus
▨ Crotalus basiliscus
▨ Pseudoleptodeira uribei
▨ Oxybelis aeneus
■ Manolepis putnami
▨ Dipsas gaigae
Abundance (%)
(c)
RS-DF
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
D1
D2
D3
▨ Leptotyphlops humilis
■ Leptodeira maculata
▨ Hypsiglena torquata
▨ Drymarchon melanurus
▨ Dipsas gaigae
▨ Imantodes gemmistratrus
(d)
DS-DF
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
D1
D2
D3
▨ Leptophis diplotropis
■ Leptodeira maculata
▨ Imantodes gemmistratrus
▨ Boa constrictor
☐ Micrurus distans
▨ Oxybelis aeneus
Distance category

CAPÍTULO IV

Diet of the Mexican marbled toad (*Bufo marmoreus*) in conserved and disturbed tropical dry forest

DIET OF THE MEXICAN MARBLED TOAD (*BUFO MARMOREUS*) IN CONSERVED AND DISTURBED TROPICAL DRY FOREST

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Abstract—We collected data on diet of the marbled toad (*Bufo marmoreus*) on conserved and disturbed areas of tropical dry forest on the coast of Jalisco, Mexico, during 2000 and 2001. Although the diet of *B. marmoreus* consisted of 19 prey taxa, the moderately low dietary diversity measure (H′ = 1.51) reflected the dominance in the diet of only 3 groups of prey: ants, beetles, and termites. Toads in the conserved area consumed greater proportions of ants (36.7% by volume), whereas toads in disturbed forest consumed greater proportions of beetles (53.1% by volume). Diet diversity was significantly lower in the disturbed area. However, abundance, size, and weight of toads was similar in both areas, suggesting that prey availability was not affected by disturbance.

Resumen—Registramos información sobre la dieta del sapo marmóreo (*Bufo marmoreus*) en áreas conservadas y perturbadas del bosque tropical seco en la costa de Jalisco, México, durante el 2000 y 2001. Aunque la dieta de *B. marmoreus* consistió de 19 taxa de presas, el moderadamente bajo valor de diversidad (H′ = 1.51) reflejó la dominancia en la dieta de solamente 3 grupos de presas: hormigas, escarabajos y termitas. Los sapos en el área conservada consumieron mayor proporción de hormigas (36.7% en volumen), mientras que en el área perturbada consumieron mayor proporción de escarabajos (53.1% en volumen). La diversidad de la dieta fue significativamente menor en el área perturbada. Sin embargo, la abundancia, tamaño y peso de los sapos fue similar en ambas áreas, sugiriendo que la disponibilidad de las presas no fue afectada por la perturbación.

Amphibians occupy many diverse habitats across the globe; however, they are sensitive to a number of natural and anthropogenic factors. Amphibian declines have numerous potential and complex causes, including habitat modification (e.g., Delis et al., 1996; Anderson et al., 1999; Lynn and Lindle, 2002). Toads of the genus *Bufo* have been regarded either as indiscriminate predators feeding on a wide variety of arthropods (Zug and Zug, 1979) or as highly selective feeders relying mainly on ants and coleopterans (Flowers and Graves, 1995; Hirai and Matusi, 2002). Because forest disturbance has been reported to affect the structure of arthropod communities (e.g., Greenberg and Thomas, 1995; Heliölä et al., 2001), knowledge of food habits might be important for understanding the influence of habitat disturbance on anuran populations.

The Neotropical marbled toad *Bufo marmoreus* is endemic to Mexico, where it inhabits the tropical dry forest in coastal areas of the states of Colima, Guerrero, Oaxaca, Jalisco, and Veracruz (Smith and Smith, 1976). The tropical dry forest is considered one of the most threatened tropical habitats (Primack, 1998), and in Mexico, it has been reduced to about 70% of its original area (Dirzo and Trejo, 2001). Because there are limited data available on the biology of the marbled toad (Ramírez-Bautista, 1994), we report on the food habits of this species. We specifically evaluate diet differences in toads inhabiting conserved and disturbed areas of tropical dry forest on the coast of Jalisco.

Our study was conducted in the coastal region of the state of Jalisco, Mexico. Vegetation type in the area is tropical dry forest. Toads were collected in an area of conserved forest in the Estación de Biología Chamela, a reserve approximately 3 km from the coast, and in an area of modified forest adjacent to the reserve. Mean annual temperature is 24.9°C, with an average annual rainfall of 748 mm, 80% of which falls from July through October after a 7 to 8 mo dry season (November to June) (Bullock, 1986; Lott et al., 1987). During the dry season, most of the trees lost their leaves. The conserved forest featured lush undergrowth during the rainy season and the canopy was about 15 m. The disturbed area consisted of a matrix of cattle pastures with almost no canopy, patches of secondary forest with moderate undergrowth and sparse to moderate canopy, and patches of primary forest. In the study area, *B. marmoreus* is active mainly during the rainy season. Therefore, field activities were conducted during this season (August to October) of 2000 and 2001. Three small watersheds within the reserve constituted the conserved area, and 3 small watersheds outside the reserve constituted the disturbed area. Nearest collecting sites between conserved and disturbed areas were ca. 15 km apart. Elapsed time of collecting between conserved and disturbed areas was no longer than 72 h, and the search was conducted at each area after sunset (between 2000 and 0400 h) in thirty 100-m × 10-m transects randomly established. Search effort was the same for both areas (120 person hours).

Stomach contents were extracted by stomach flushing (Legler and Sullivan, 1979) within 15 min after capture. After this procedure, toads were measured (snout-vent length: SVL), weighed, and released at the capture site. Food items were preserved in 70% ethanol and were classified as follows: lepidopterans were classified either as plume moths (Alucitidae) or ''other Lepidoptera,'' opiliones were classified either as Laniatores (suborder) or ''other opilones,'' and all other prey were classified to order, except for ants, which were classified to family (Formicidae). Prey were counted and measured volumetrically by using the fluid displacement method of Milstead (1957). Calculations were made of the relative abundance by numbers (%N), relative abundance by volume (%V), and the relative number of stomachs the food item occurred in (%F) for each taxon. From these data, we calculated the index of relative importance: IRI = (%N + %V) (%F) (Pinkas et al., 1971). Values of IRI (range = 0 to 20,000) indicate the relative importance of food items. Unidentified materials (digested items that could not be identified) and material considered to be ingested accidentally (parts of plants, sand, and stones) were not considered in the analyses.

To test for the variation in diet between toads of conserved and disturbed areas, we compared frequency of occurrence and volume of main prey items (>15% by volume) by Mann-Whitney *U*-tests. Dietary diversity and overlap were estimated using the index of relative importance. We calculated the Shannon-Wiener Index (H′) to estimate diet diversity (see Krebs, 1999). The diversity index increases with an increase in the number of dietary items, so low values represent dietary specialists and high values represent dietary generalists. Differences between dietary H′ values of toads of conserved and disturbed areas were compared using Hutcheson's *t*-test (see Magurran, 1988). As a descriptive measure of dietary concordance among toads of conserved and disturbed areas, we used Schoener's (1970) percent overlap index. This estimate makes no assumption about overall food availability in the habitat. An alpha level of 0.05 was used in all statistical tests. Means are reported ±1 *SE*.

We examined the stomach contents of 36 *B. marmoreus* individuals. Of the 36 individuals, 18 were collected in the conserved area (SVL = 55.3 ± 3.8 mm, range = 27 to 83 mm; weight = 17.8 ± 3.2 g, range = 2 to 45 g) and 18 in the disturbed area (SVL = 49.3 ± 3.0 mm, range = 29 to 83 mm; weight = 11.7 ± 2.6 g, range = 1.8 to 45 g). There was no significant difference in size between toads of conserved and disturbed areas. Therefore, possible differences in the diet of toads between areas due to body size were not analyzed.

Stomach contents for the entire sample of toads consisted of 19 types of terrestrial arthropods (Table 1). However, a few groups composed the greatest portion of the diet. Ants

TABLE 1—Stomach contents of *Bufo marmoreus* in conserved and disturbed tropical dry forest. The top line in each entry is presented as follows: percent in numbers / percent in volume (mm^3) / percent of frequency of occurrence. The number in the second line of each entry corresponds to the index of relative importance (IRI).

Food item	Conserved forest (n = 18)	Disturbed forest (n = 18)	Pooled (n = 36)
Acari	1.94 / 0.94 / 22.22 64.12	—	0.58 / 0.21 / 11.11 8.85
Araneae	0.24 / 0.13 / 5.55 2.09	2.92 / 1.53 / 22.22 99.10	2.12 / 1.22 / 13.88 46.47
Opiliones	—	0.10 / 0.00 / 5.55 0.60	0.07 / 0.00 / 2.77 0.21
Opiliones (Laniatores)	0.24 / 0.47 / 5.55 4.0	0.31 / 1.25 / 11.11 17.43	0.29 / 1.08 / 8.33 11.50
Coleoptera	2.42 / 5.46 / 50.0 394.74	23.11 / 53.14 / 77.77 5931.71	16.89 / 42.71 / 75.0 4470.98
Collembolla	0.72 / 0.02 / 16.66 4.05	—	0.219 / 0.01 / 5.55 0.610
Diptera	0.48 / 0.02 / 11.11 5.68	0.10 / .03 / 5.55 0.77	0.21 / 0.03 / 8.32 1.12
Hemiptera	0.24 / 0.04 / 5.55 1.37	—	0.80 / 2.931 / 8.33 0.35
Homoptera	0.24 / 0.12 / 5.55 2.05	1.35 / 0.08 / 1.11 8.03	1.02 / 0.09 / 8.33 5.84
Hymenoptera (Formicidae)	27.67 / 36.66 / 83.33 5361	18.30 / 28.88 / 72.2 3408.5	21.14 / 30.79 / 88.8 4616.2
Isoptera	64.56 / 30.04 / 38.89 3677.6	52.40 / 11.04 / 22.22 1409.9	56.10 / 15.36 / 36.11 2580.9
Lepidoptera	0.48 / 16.25 / 11.11 185.9	—	0.07 / 3.11 / 2.77 8.8
Lepidoptera (Alucitidae)	0.24 / 1.20 / 5.55 8.0	—	0.07 / 0.27 / 2.77 0.9
Neuroptera	0.24 / 7.73 / 5.55 44.3	0.20 / 0.24 / 5.55 5.0	0.21 / 1.93 / 8.33 17.9
Orthoptera	0.24 / 0.96 / 5.55 6.6	0.10 / 0.00 / 5.55 0.6	0.14 / 0.22 / 5.55 2.0

(Formicidae) were the most frequently consumed, followed by termites (Isoptera) and beetles (Coleoptera). Volumetrically and numerically, ants dominated, followed by termites and beetles. Ants presented the highest IRI values, followed by beetles and termites (Table 1). The rest of the items presented IRI values well below the former groups of prey (range = 0.20 to 46) (Table 1). Ants, beetles, and termites constituted 88.9% by volume and 91.2% by number of the diet. Dietary diversity measure (H′) for the entire sample was 1.51.

There was some diet variation in toads of conserved and disturbed areas. Although 5 prey items (Acari, Collembolla, Hemiptera, Lepidoptera, Alucitidae) were absent in the diet of toads from the disturbed area, 3 groups (Formicidae, Coleoptera, Isopoda) composed the highest proportion of the diet in both areas (Table 1). Whereas ants were the most important item in the conserved area (36.7% by volume), beetles were the dominant item in the disturbed area (53.1% by volume). Using frequency of occurrence values, we detected no significant difference in the importance of ants, termites, and beetles in the diet of toads from disturbed and conserved areas. However, there was a significant difference in volume of beetles (Mann-Whitney *U*-test: $U = 17.0$, $P = 0.001$) between conserved and disturbed areas. Because we did not quantify potential availability of food resources, we cannot speculate whether this difference was a result of selective foraging, or might simply reflect the relative availability of various prey groups. The diversity index was significantly different for conserved (H′ = 1.54) and disturbed (H′ =

0.97) areas ($t = 35.07$, $df = 34$, $P < 0.05$). Dietary overlap between both types of areas was 48.2%.

Although the diet of *B. marmoreus* consisted of 19 prey taxa, the moderately low dietary diversity measure ($H' = 1.51$) reflects the dominance in the diet of only 3 groups of food items. In general, toads of the genus *Bufo* have been regarded as indiscriminate predators because they consume a wide variety of arthropods, as well as unpalatable prey (Zug and Zug, 1979). However, several studies have indicated that bufonids are selective feeders. According to the review by Clarke (1974) on diet information of *Bufo*, ants and beetles were the most frequent food items in 26 of 29 cases. Studies that are more recent have reported similar results, with bufonids feeding mainly on ants or beetles (e.g., Toft, 1981; Sweet, 1992; Flowers and Graves, 1995; Hirai and Matusi, 2002; Isacch and Berg, 2002), including, in some cases, also termites (e.g., Strüssmann et al., 1984). Our results with *B. marmoreus* agree with these previous studies, because ants and beetles were among the 3 most important food groups taken by this species. In general, ants and various beetle groups (e.g., carabids and harpalids) are unpalatable to many predators because they contain formic acids and quinones, respectively. Clarke (1974) suggested that food habits that exploited prey unpalatable for other predators accounted for the worldwide success of *Bufo*, by reducing food-related competition with other insectivorous predators. The same explanation might account for the wide distribution of *B. marmoreus* in Mexico. The striking similarity in food profiles of bufonids, dominated by ants and beetles, reported by authors in a variety of environments strongly suggests that they are selective feeders. The importance of termites in the diet of *B. marmoreus* suggests that this species is also an opportunistic feeder, because termites have been reported to be active and available throughout the year in tropical habitats with a marked seasonality (Teixeira-Filho et al., 2003).

The conclusion by Toft (1980, 1981) that toads are active foragers was supported by our data. According to Toft (1981) and Donnelly (1991), there might be a correlation between an active foraging strategy and the occurrence of prey that is difficult to digest in the diet (e.g., chitinous or noxious prey). This is characteristic of the ants and beetles that contributed significantly to the diet composition of *B. marmoreus* in our study. Termites, considered a relatively sedentary prey, with clumped distribution, are also an important prey in the diet of active foragers (Teixeira-Filho et al., 2003).

Although diet diversity was lower in the disturbed area, abundance, size, and weight of toads were similar in conserved and disturbed areas, suggesting that prey availability was not significantly limited by disturbance. According to the optimal foraging theory (reviewed by Begon et al., 1986), a wider feeding niche would be expected if prey were less abundant and available. Therefore, the narrower feeding niche of *B. marmoreus* in the disturbed area further suggests that prey availability was not negatively affected by disturbance. Whereas habitat modification is detrimental to many species of anurans, it might benefit others. Several species of *Bufo* have been reported to respond positively to habitat modification (e.g., Duellman, 1999; Mazerolle, 2003). Forest disturbance frequently results in an increase in temperature and decrease in relative humidity, imposing physiological constrains on amphibians. A number of structural and physiological features (reviewed by Duellman and Trueb, 1994) allow toads (*Bufo*) to be remarkably tolerant of dry conditions. Therefore, the tolerance to drier conditions might be the critical feature that enables *B. marmoreus* to survive the negative effects of disturbance, and to be active and forage efficiently under the environmental conditions of the modified forest.

We thank the Estación de Biología de Chamela and the director R. Ayala for making all facilities available during this study. We thank S. García, A. Estrada, D. García, M. Quintero, and K. Jaimes for their collaboration in the field. We are grateful to J. Benitez-Malvido for her constructive comments on the manuscript. Funding for this project was provided by the Consejo de Investigación Científica, UMSNH (project 5.5).

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CAPÍTULO V

Discusión General y aplicaciones al diseño de estrategias de conservación

El disturbio antrópico en su manifestación más visible origina cambios en la estructura original del hábitat. Estos cambios resultan de diferentes fuentes, que van desde el aprovechamiento forestal de bajo impacto hasta la fragmentación y la pérdida total del hábitat. Cualquiera que sea el agente causal del cambio, la modificación del hábitat puede repercutir en la organización y composición de especies de las comunidades bióticas (Czech y Krausman 1997; Wilcove et al. 1998; Lynam y Billick 1999; Sala et al. 2000; Escamilla et al. 2000; Daily et al. 2003; Lindenmayer et al. 2003; Hill y Hamer 2004; Driscoll y Weir 2005; Ashton et al. 2006).

La importancia de la modificación del hábitat para las especies de anfibios y reptiles ha sido analizada principalmente en las regiones templadas, en mucho menor grado en las regiones tropicales húmedas y prácticamente no se ha analizado en los trópicos secos (Gardner et al. 2007). Aunque el conocimiento generado en estos estudios puede ayudar a establecer estrategias de conservación, las comunidades animales y vegetales presentes en diferentes regiones poseen atributos particulares que demandan estudios específicos para su conservación. Adicionalmente, si consideramos el acelerado proceso de transformación a mosaicos agrícolas y ganaderos que enfrentan los bosques tropicales caducifolios (BTC), el estudio de las comunidades animales y su respuesta a la perturbación humana se vuelve más apremiante.

El tema de esta tesis ha sido el de los efectos de las actividades agrícolas y ganaderas que, de manera generalizada, se realizan en los BTC de México sobre la organización de las comunidades herpetofaunísticas. Como se expuso en el capítulo I, existe suficiente evidencia empírica para considerar que los anfibios y reptiles presentan la mayor proporción de taxa en riesgo en relación al resto de las especies de vertebrados (Shine 1991, Nilson et al. 1999; Houlaham et al. 2000; Gibbons et al. 2000; Gascon et al. 2007; Roelants et al. 2007). De igual manera los bosques tropicales caducifolios constituyen uno de los ecosistemas más alterados y en proceso de desaparición (Trejo-Vazquez y Dirzo 2000; Trejo-Vazquez 2005). En México los bosques tropicales secos están siendo deforestados a una tasa anual del 2% y únicamente el 27% del bosque original permanece intacto (Trejo-Vazquez y Dirzo 2000; Trejo-Vazquez 2005; García 2006). Los estudios incluidos en esta tesis aportan información clave y novedosa acerca de los factores que afectan la organización y distribución de la herpetofauna una vez que el BTC es transformado por las actividades agrícolas y ganaderas. En esta capítulo se discuten cuales son las aportaciones más novedosas de la tesis desarrollada al conocimiento de la herpetofauna.

1. Hábitats exitosos para la herpetofauna en paisajes modificados por las actividades agrícolas y ganaderas

Los bosques tropicales caducifolios han sido extensamente transformados y reemplazados por áreas urbanas y tierras dedicadas a la agricultura y la ganadería a una tasa significativamente más alta que los bosques tropicales húmedos (Murphy y Lugo 1986). La región de Chamela, Jalisco, no es la excepción y sin contar el BTC de la Reserva de la Biósfera Chamela-Cuixmala y sus áreas cercanas, este ecosistema se encuentra fuertemente fragmentado por las actividades turísticas y por la conversión del bosque para actividades agrícolas y ganaderas; fragmentación que tenderá a aumentar conforme se incremente la demanda de estas actividades (Sánchez-Azofeifa et al. 2009). Los resultados del capítulo II sugieren que en esta región, la transformación del BTC a mosaicos agrícolas y ganaderos resulta en cambios importantes en la estructura y composición de la herpetofauna, aunque la respuesta de los ensambles a la modificación del hábitat difiere dentro y entre los grupos taxonómicos.

Los ensamblajes de anuros y tortugas disminuyen en diversidad, las serpientes tienen una respuesta neutra, mientras que las lagartijas se benefician. Para muchos anfibios este nuevo paisaje representa un reto, pues son especies altamente vulnerables a la radiación solar y tienen un rango estrecho de tolerancia a los cambios de humedad y temperatura (Duellman y Trueb 1994). Los atributos del hábitat medidos durante este estudio, mostraron que la mayoría de las variables estructurales del hábitat (con excepción de la apertura del dosel y cobertura de herbáceas) y las condiciones ambientales (con excepción de la temperatura), disminuyen una vez que ocurre la transformación del bosque. Estos cambios pueden modificar las condiciones ambientales del hábitat, afectando negativamente la supervivencia de muchas especies y favoreciendo a las especies generalistas, tal y como se ilustra de manera hipotética en la figura 1.

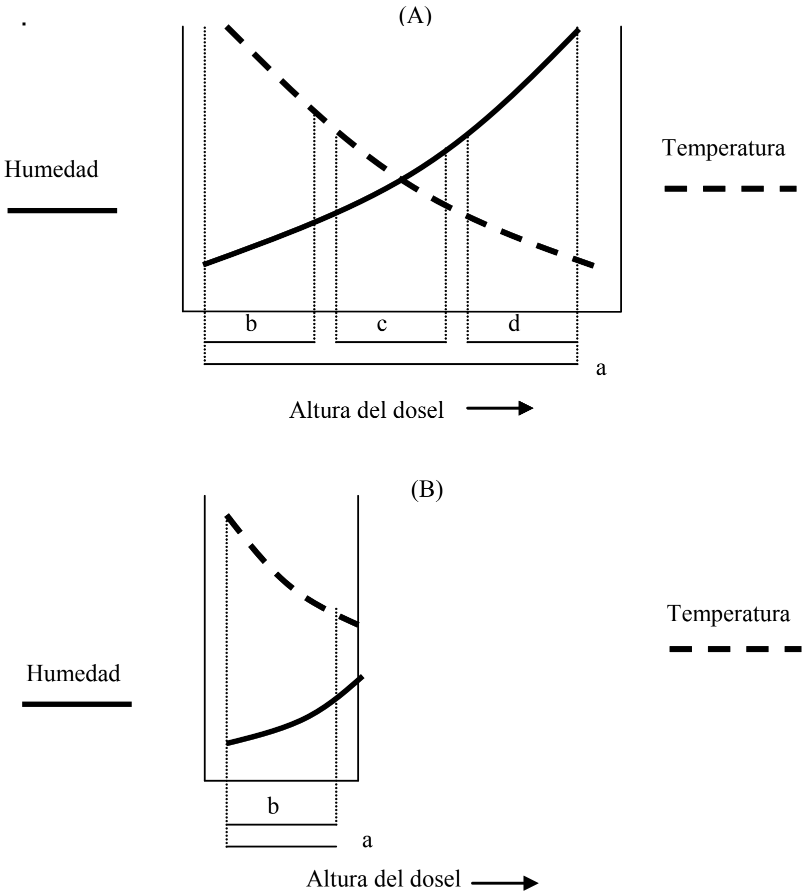

Fig. 1. Efecto de la conversión del bosque sobre la amplitud de las condiciones ambientales. En (A) existe una especie generalista (a) que se distribuye en todo el ámbito de humedad y temperatura y tres especies con un ámbito estrecho (b, c y d). En (B) después de un disturbio la amplitud de las condiciones se modifica y sólo permanecen la especie generalista y la especie adaptada a las nuevas condiciones resultantes (a,b).

Las lagartijas, al igual que las serpientes, no se encuentran restringidas por requerimientos de humedad como los anuros (Jellinek et al. 2004), por lo tanto no es sorprendente que la heterogeneidad ambiental (i.e. pastizales-campos de cultivo-parches de bosque en diferentes estadios sucesionales) producto de la conversión del BTC provea hábitats exitosos para varias de las especies de lagartijas (e.g. incremento en la disponibilidad de alimento y micrositios para la termorregulación); condiciones fuertemente relacionadas con la sobrevivencia y el éxito reproductivo de las lagartijas. Las tortugas terrestres, por su parte resultaron ser muy sensibles a la modificación del BTC, quizá sus hábitos alimenticios expliquen este comportamiento, ya que se ha reportado que son especies frugívoras de árboles característicos de los BTC maduros (Alvarado et al. 2003).

Los resultados del capítulo III sugieren que en los BTC con periodos largos de estiaje, los hábitats provistos por las zonas riparias son esenciales para varias especies de anfibios y reptiles, y éstos juegan un papel importante en la conservación de los ensambles herptofauníticos. La importancia de estos hábitats varía con la condición del bosque, la estación del año y el ensamble estudiado. Así, para los anfibios, las zonas riparias son esenciales en los bosques conservados, mientras que en los mosaicos agrícolas la creación de charcas y reservorios artificiales de agua por las actividades humanas, parecen que liberan a las especies de su asociación con el hábitat ripario. Tal efecto permite una mayor diversidad de especies en las partes intermedias entre el arroyo y las crestas de los lomeríos (gradiente arroyo-laderas) aunque, al igual que en los sitios conservados, la mayor abundancia de anfibios se observa en las zonas riparias. La época de secas representa un reto para la sobrevivencia de muchas especies dada la reducción de una gran cantidad de recursos asociada con este periodo, por lo que los reptiles que permanecen activos durante todo el año muestran preferencia por las zonas riparias, en particular, durante los periodos de estiaje.

La cobertura del follaje de la vegetación de las zonas riparias durante la época de secas provee a los vertebrados de un ambiente con condiciones mésicas comparado con las condiciones más secas de áreas más abiertas de las laderas adyacentes. Adicionalmente la productividad de las zonas riparias durante el estiaje permite el mantenimiento de una comunidad de invertebrados que a su vez proveen oportunidades de alimento para consumidores secundarios como las lagartijas durante una estación cuando los recursos energéticos son marcadamente reducidos. La abundancia de lagartijas en estas zonas quizá sea también la explicación de la mayor abundancia y diversidad de serpientes registradas en esta zona, ya que un número importante de especies de serpientes se alimenta de lagartijas.

La importancia de los hábitats resultado de la conversión del bosque para el ensamble herpetofaunístico es diferencial dependiendo de los grupos taxonómicos. Estos hábitats son favorables para un grupo grande de lagartijas y serpientes, mientras que son desfavorables para varias especies de anfibios y tortugas. En general los hábitats riparios juegan un papel importante en el mantenimiento de la diversidad herpetofaunística en los paisajes transformados.

2. Efecto de la conversión del bosque tropical caducifolio sobre la riqueza, composición y abundancia de la herpetofauna

Existe evidencia de que en general la abundancia y la diversidad de especies, así como los grupos funcionales de anfibios y reptiles, se reducen bajo el efecto de la fragmentación y de las actividades agropecuarias (Laurance et al. 2002; Pineda y Halfter 2004; Reynoso-Rosales et al. 2005; Urbina-Cardona 2006). Los resultados obtenidos en este estudio (Capítulos II y III) sugieren que una vez que el BTC es convertido a mosaicos agrícolas, ocurren cambios a nivel de la estructura de los ensambles de anfibios y reptiles, además de que las especies que presentan ciertos atributos se ven más favorecidas. Los anfibios en general mostraron un declive en la diversidad de especies en los sitios con perturbación antrópica, aunque también se observó un efecto neutral, más que negativo en la abundancia total de anfibios. Esto debido a que la abundancia de *Ollotis marmorea*, *Smilisca fodiens* y *Pachymedusa dacnicolor* incrementó notablemente en el bosque perturbado, lo que explica porque la abundancia de los anuros no difiere entre los bosques conservados y perturbados aunque la riqueza y diversidad de especies decline en la condición de disturbio. La mayor abundancia de estas especies en el bosque perturbado, puede ser explicada por sus características anatómicas y fisiológicas que las vuelven exitosas en estos ambientes: poseen un tamaño del cuerpo relativamente grande, depredan sobre una gran cantidad de presas y presentan fase larvaria de nado libre con huevos puestos en charcas. Las lagartijas aumentaron su riqueza y abundancia en los sitios perturbados, sin embargo, la dominancia y composición de las especies en general fueron similares entre las dos condiciones del bosque. La estructura y composición del ensamble de serpientes fue similar entre los sitios conservados y perturbados, lo que sugiere que las serpientes en general son flexibles en su respuesta a la conversión del bosque tropical a mosaicos agrícolas y ganaderos. En relación a los grupos funcionales de especies, tanto los anfibios como reptiles generalistas en la dieta, modos reproductivos o con mayor tolerancia fisiológica fueron las especies más dominantes en los sitios perturbados.

La estructura de la comunidad de anfibios y reptiles también mostró cambios en relación con la distancia al arroyo y éstos estuvieron influenciados por la condición del bosque y la estación. En particular, para los anfibios, en la época de lluvias las zonas riparias del bosque conservado son esenciales para mantener una mayor densidad y riqueza/diversidad de especies, mientras que en las áreas transformadas por las actividades agrícolas, la riqueza/diversidad de especies fue mayor en las partes intermedias, quizá debido a que la formación de charcas y cuerpos de agua artificiales durante la época de lluvias producto de las actividades humanas alteran la asociación de la comunidad de anfibios con las zonas riparias. La comunidad de lagartijas y serpientes en general presentaron una mayor abundancia y diversidad de especies en las zonas riparias en ambas condiciones del bosque y estación del año, lo que pone de manifiesto la importancia de mantener los hábitats riparios en los paisajes modificados.

3. Vulnerabilidad de los anfibios y reptiles especialistas de bosque maduro a la conversión del bosque tropical caducifolio

Los resultados indican que por lo menos 7 de las 60 especies registradas pueden considerarse especialistas de bosques maduros y ser vulnerables a la extinción local dentro de los paisajes agrícola-ganaderos. De las 10 especies de anfibios sensibles al disturbio, siete se encontraron exclusivamente en el bosque conservado a diferencia de las 2 especies de lagartijas y 8 especies de serpientes sensibles al disturbio pero que también se registraron en el bosque perturbado. Estos resultados muestran que el ensamble de anfibios está constituido por una mayor cantidad de especialistas de bosques maduros y que su permanencia local puede estar comprometida si desaparecen estos bosques en los paisajes transformados.

En el capítulo III se muestra que un número importante de especies se encuentran distribuidas a lo largo de todo el gradiente ripario-laderas en los bosques conservados (por ejemplo *C. hobartsmithi* especialista de bosques maduros). Este hecho sugiere que las condiciones de humedad y temperatura del aire que ocurren en las laderas cubiertas por vegetación, amplía el rango microespacial utilizado por las especies. Por ello la pérdida de estas condiciones de ladera en los sitios perturbados puede reducir el ámbito hogareño de las especies con la consecuente reducción poblacional y extinción local.

4.- Historias de vida y cambios estructurales del hábitat

Los anfibios de cuerpo pequeño presentan proporcionalmente una mayor área superficial con respecto al volumen del cuerpo, y por lo tanto sufren mayores tasas de evaporación de agua que las especies más grandes (Duellman y Trueb 1994). Esto quizá ocasione que los anfibios pequeños sean intolerantes a las condiciones de desecación que ocurren en las áreas perturbadas y explica porque las especies sensibles al disturbio fueron las más pequeñas. Por otro lado, las especies que depositan los huevos en tierra en lugares húmedos y presentan desarrollo larvario directo (Hödl 1990) fueron sensibles a la perturbación, por lo que las condiciones microclimáticas asociadas con la remoción del dosel y la reducción de la humedad retenida en la capa de hojarasca son condiciones críticas que restringen la persistencia de especies de anfibios de tamaño pequeño en los bosques perturbados. Por otro lado, las especies tolerantes al disturbio fueron aquellas de tamaño grande y con desarrollo larvario acuático. Así mismo, en el capítulo IV se muestra que *Incilius marmoreus=Bufo marmoreus* presenta plasticidad alimentaria, pues además de que consume una amplia variedad de presas incluyendo hormigas, termitas y escarabajos, puede cambiar de presas dependiendo de la disponibilidad de las mismas. Esta capacidad de forrajeo ayuda a explicar porque los bufonidos son dominantes en los bosques perturbados. En el caso de los reptiles y debido a que éstos no están restringidos por la humedad como los anfibios, atributos como la plasticidad en la dieta y en la termorregulación, les permite explotar con mayor eficiencia los nuevos microambientes una vez que la conversión del bosque se lleva a cabo.

5. Elementos del paisaje modificado que favorecen una estructura de la comunidad de anfibios y reptiles similar a la encontrada antes del disturbio

Los resultados de este trabajo indican que las zonas agrícola-ganaderas presentan significativamente más apertura del dosel, menor cobertura de hojarasca, menor humedad y mayor temperatura del aire y del suelo que los bosques conservados y que las zonas riparias tanto en las áreas conservadas como perturbadas (capítulos II y lll), condiciones que influyen directamente sobre la tolerancia fisiológica de los anfibios. Por lo que la permanencia de parches de bosque maduro y de vegetación riparia que garanticen condiciones estructurales del hábitat adecuadas para las especies sensibles son esenciales en los sitios transformados por las actividades agrícolas y ganaderas. Por ejemplo, en el caso de las tortugas terrestres (*Rhinoclemys*) cuya sensibilidad al disturbio quedó claramente demostrada, sus hábitos frugívoros obligan a la permanencia de árboles frutales dentro de estos parches. Así mismo, y dado que el ámbito hogareño de muchas especies, principalmente los anfibios, se distribuye desde las zonas riparias hasta las laderas adyacentes, es importante asegurar condiciones de ladera con suficiente cobertura de dosel (arriba del 70%) que provean las condiciones ambientales adecuadas para estas especies.

6. Implicaciones para la conservación y manejo

Con la información obtenida en este estudio y los fundamentos teóricos en los que se sostiene dicha información, es posible vislumbrar algunas estrategias que pueden aplicarse en la dinámica de uso de suelo para mantener y asegurar la diversidad herpetofaunística en los bosques tropicales secos:

1) *Desarrollar estrategias de conservación a escala regional.* Los resultados de este estudio muestran que la conversión del bosque tropical caducifolio a mosaicos agrícolas y ganaderos deberá llevarse a cabo bajo la base de un ordenamiento regional de tal manera que se asegure la permanencia de parches de bosque maduro, bosques en diferentes estadios de regeneración, entremezclados con campos agrícolas y ganaderos, unidos por una red de vegetación que permita la interconexión entre los diferentes elementos del paisaje.

2.- *Promover el establecimiento y la permanencia de bosques secundarios en diferentes estadios de regeneración.* Se ha observado que después de 30 a 40 años, algunos bosques secundarios mantienen una biomasa y riqueza de especies similar a los bosques maduros (Chadzdon et al. 2008). Los bosques secundarios son quizá los bosques del futuro (Azofeifa et al. 2005), por lo que asegurar su permanencia en los paisajes agrícola-ganaderos es fundamental en las estrategias de conservación de la vida silvestre.

3.- *Mantener una red de vegetación riparia.* En muchos trabajos incluyendo éste, se ha demostrado que los corredores de vegetación riparia son fundamentales para muchas especies, principalmente las especies sensibles a la desecación y las que permanecen activas durante la época de estiaje, por lo que mantener una red riparia con coberturas de dosel superiores al 70%, en todos los arroyos y cauces de agua de los paisajes transformados puede ayudar a mitigar el efecto de la conversión del bosque sobre las especies con mayor grado de vulnerabilidad a la fragmentación del hábitat.

4.- *Mantener una matriz con una elevada conectividad entre los fragmentos de bosque maduro, los fragmentos de bosques secundarios y las zonas riparias*. Debido a que muchas especies de anfibios y reptiles que habitan los bosques tropicales secos presentan comportamiento filopátrico (ISO observación personal, Blaustin et al. 1994) es necesario reducir en lo posible el aislamiento entre los fragmentos de bosque maduro, bosques secundarios y vegetación riparia de tal manera que se garantice una adecuada movilidad de las especies.

5.- *Enriquecer con especies nativas tanto maderables como frutales los bosques secundarios,* de tal manera que se promueva la permanencia de estos bosques más allá de los 30 años (Harvey et al. 2008), se evite la extinción local de especies y se garanticen recursos esenciales para los anfibios y reptiles especialistas de bosques maduros (e.g. tortugas del género *Rhinoclemmys* cuyos hábitos frugívoros las vuelven vulnerables en los estadios suscesionales tempranos).

Por último es necesario destacar que muchas especies de anfibios y reptiles son vulnerables a la extinción y si se continúa con la tasa de reducción y transformación de los bosques tropicales caducifolios continuarán ocurriendo cambios importantes en la composición y estructura de los ensambles herpetofaunísticos, pudiendo llegar a causar la extinción local o regional de las especies de anfibios, tortugas y lagartijas. Por ello, el bosque tropical caducifolio, como hábitat para la herpetofauna, así como las especies sensibles al disturbio deberán ser cuidadosamente monitoreados e incorporados a ordenamientos territoriales. Esto garantizaría los requerimientos para el mantenimiento del hábitat y de las especies, pues la batalla actual en contra de la extinción se ganará o perderá en los paisajes modificados.

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