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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Paper submitted February 20, 2007; revised manuscript accepted September 27, 2007.

Conservation Biology, Volume 22, No. 2, 362–374

DOI: 10.1111/j.1523-1739.2008.00883.x

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

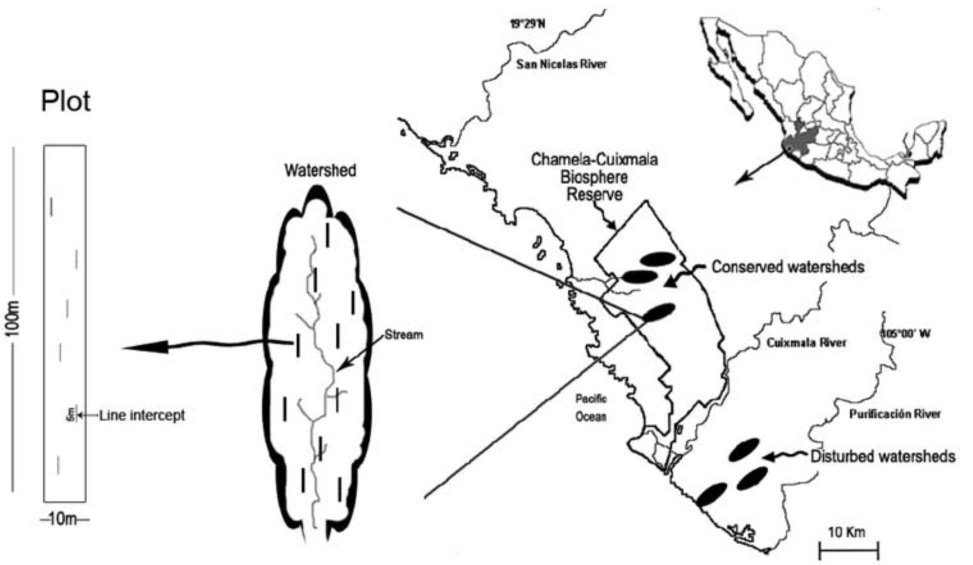

Figure 1. Site map and plot deployment scheme in a study of the effects of forest conversion on herpetofaunal assemblages. Gray section on inset of Mexico is Jalisco, and ovals are watersheds.

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*

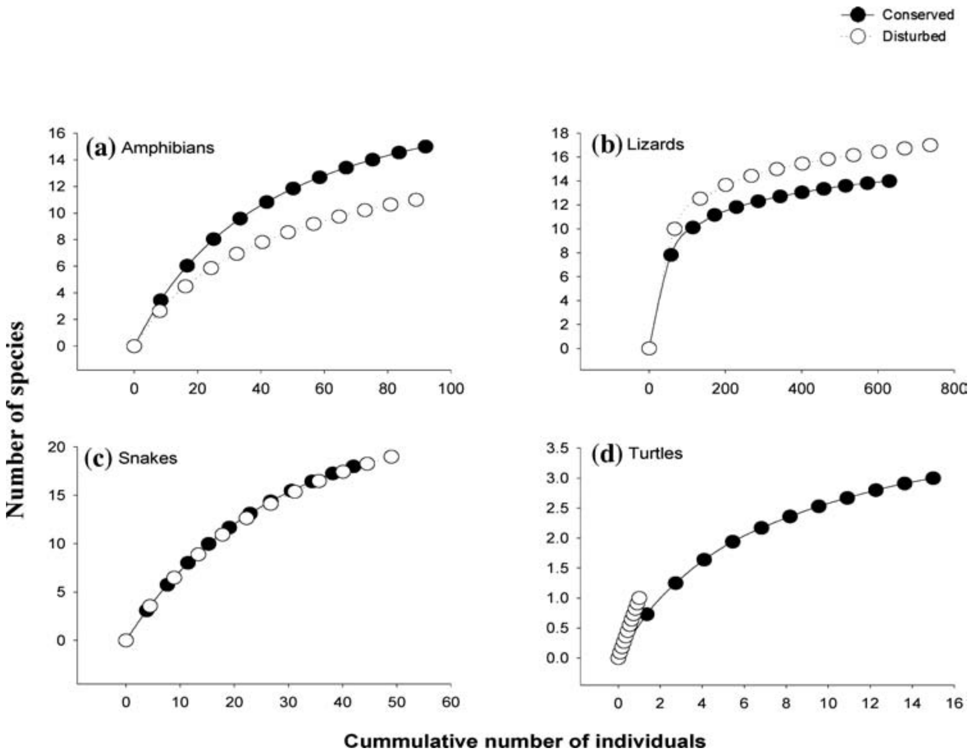

Figure 2. Species accumulation curves for (a) amphibians, (b) lizards, (c) snakes, and (d) turtles in conserved and disturbed forest at Chamela, Jalisco, Mexico.

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

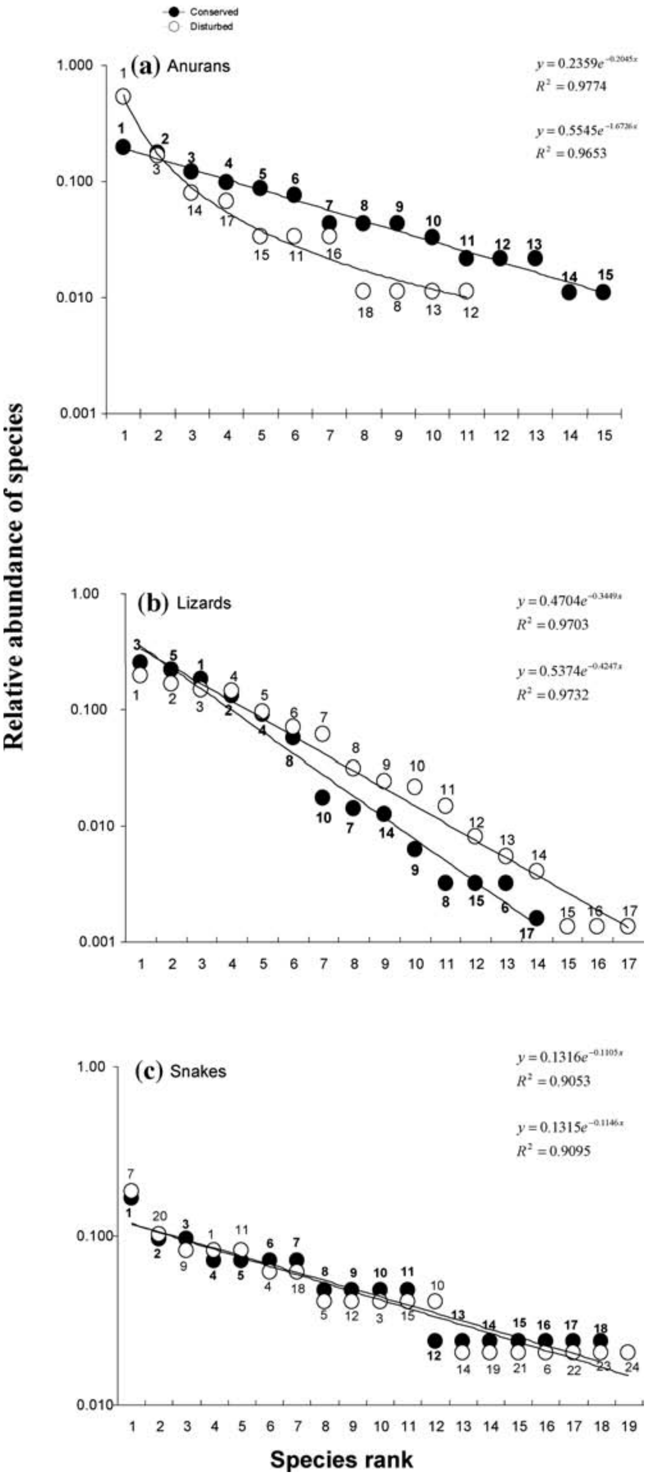

*Figure 3. Species-rank plots for anuran, lizard, and snake assemblages from conserved and disturbed forest at Chamela, Mexico. Species rank is ordered from the most to the least abundant species. Anurans: 1, Olma (*Ollotis marmorea*); 2, Crho (*Craugastor hobartsmithi*); 3, Smba (*Smilisca baudinii*); 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, Heho (*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*).*

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

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.

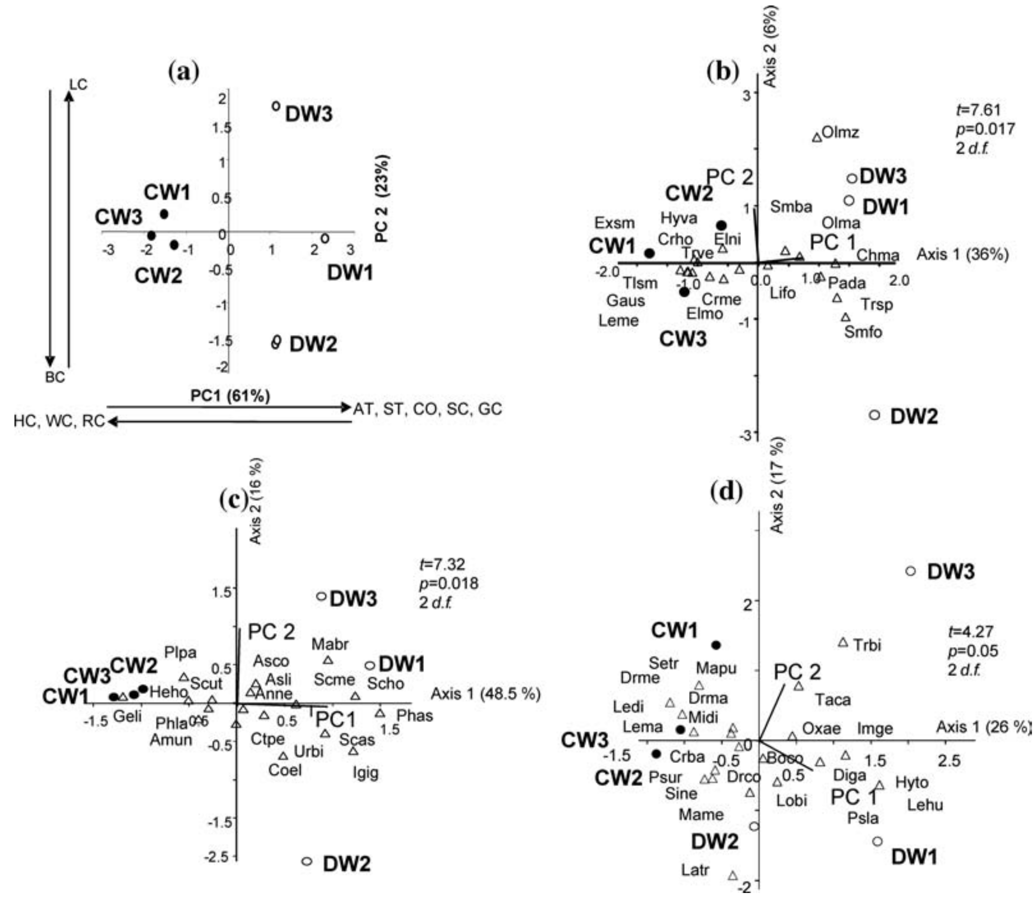

*Figure 4. Ordination of anuran, lizard, and snake species recorded in conserved (CW1–CW3, black dots) and disturbed forest sites (DW1–DW3, open dots): (a) principal component analysis of watersheds by habitat variables (arrows indicate significant correlations [*p < 0.05*] of PC 2 with different habitat 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.

Acknowledgments

We thank M. Quintero, D. García, A. Estrada, and K. Novas for their assistance in the field. The manuscript was improved by comments by L. López-Hoffman and A. Quijada-Mascareñas. I.S.O. was supported by a CONACYT scholarship and J.A.D. by a Consejo de Investigación Científica, Universidad Michoacana de San Nicolás de Hidalgo grant.

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.

Literature Cited

Alvarado-Díaz, J., A. Estrada-Virgen, D. García-Parra, and I. Suazo-Ortuño. 2003. *Rhinoclemmys rubida*. Diet. Herpetological Review **34:**363.

Araujo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography **33:**1712–1728.

Bell, K. E., and M. A. Donnelly. 2006. Influence of forest fragmentation on community structure of frogs and lizards in Northeastern Costa Rica. Conservation Biology **20:**1750–1760.

Brook, B. W., N. S. Sodhi, and P. K. L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature **35:**103–114.

Brown, G. W. 2001. The influence of habitat disturbance on reptiles in a Box-Ironbark eucalypt forest of south-eastern Australia. Biodiversity and Conservation **10:**161–176.

Ceballos, G., and A. García. 1995. Conserving Neotropical biodiversity: the role of dry forests in Western Mexico. Conservation Biology **6:**1349–1356.

Colwell, R. K. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application. University of Connecticut, Storrs. Available from http://purl.oclc.org/estimates (accessed November 2006).

Conroy, S. 1999. Lizard assemblage response to a forest ecotone in Northeastern Australia: a synecological aproach. Journal of Herpetology **33:**409–419.

Cosson, J. F., J. M. Pons, and D. Masson. 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. Journal of Tropical Ecology **15:**515–534.

Crawley, M. J. 1993. GLIM for ecologist. Blackwell, Oxford, United Kingdom.

Daily, C. G., P. R. Ehrlich, and G. A. Sanchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications **11:**1–13.

Duellman, W. E., and L. Trueb. 1994. Biology of amphibians. Johns Hopkins University Press, Baltimore, Maryland.

Flores, V. O., and P. Gerez. 1994. Biodiversidad y conservación en México: vertebrados, vegetación y uso del suelo. Universidad Nacional Autónoma de México (U.N.A.M.), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), México.

Gotelli, N. J., and G. L. Entsminger. 2001. EcoSim: null models software for ecology. Acquired Intelligence and Kesey-Bear, Burlington, Vermont.

Heck, K. L., G. van-Belle, and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology **56:**1459–1461.

Heliölä, J., M. Koivula, and J. Niemelä. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest–clearcut ecotone. Conservation Biology **15:**370–377.

Hill, J. K., and K. C. Hamer. 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. Journal of Applied Ecology **41:**744–754.

Hödl, W. 1990. Reproductive diversity in Amazonian lowland frogs. Fortschitte der Zoologie **38:**41–60.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75:**3–35.

Jellinek, S., D. A. Driscoll, and J. B. Kirkpatrick. 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. Austral Ecology **29:**294–304.

Krebs, C. J. 1999. Ecological methodology. Addison-Welsey Educational Publishers, Menlo Park, California.

Lenski, R. E. 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. Ecological Entomology **7:**385–390.

Lips, K. R., P. A. Burrowes, J. R. Mendelson, and G. Parra-Olea. 2005. Amphibian declines in Latin America: widespread population declines, extinctions, and impacts. Biotropica **37:**163–165.

Lott, E. J. 1993. Annotated checklist of the vascular flora of the Chamela Bay Region, Jalisco, Mexico. Occasional Papers of the California Academy of Sciences **148**.

Lunney, D., A. L. Curtin, D. Fisher, D. Ayers, and C. R. Dickman. 1997. Ecological attributes of the threatened fauna of New South Wales. Pacific Conservation Biology **3:**13–26.

McDiarmid, R. W., and M. S. Foster. 1987. Cocoon formation in another hylid frog *Smilisca baudini*. Journal of Herpetology **21:**352–355.

McGarigal, K., and S. A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications **12:**335–345.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science, Malden, Massachusetts.

Nagy, K. A. 1982. Field studies of water relations. Pages 483–501 in C. Gans, and F. H. Pough, editors. Biology of the reptilia. Academic Press, New York.

Parker, W. S. 1994. Demography of the fence lizard, *Sceloporus undulatus*, in northern Mississippi. Copeia **994:**136–152.

Pineda, E., and G. Halffter. 2004. Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico. Biological Conservation **117:**499–508.

Primack, R. B. 1998. Essentials of conservation biology. Sinauer Associates, Sunderland, Massachusetts.

Reed, R. N., and R. Shine. 2002. Lying in wait for extinction: ecological correlates of conservation status among Australian elapid snakes. Conservation Biology **16:**451–461.

Rodríguez-Robles, J. A. 2002. Feeding ecology of North American gopher snakes (*Pituophis catenifer*, Colubridae). Biological Journal of the Linnean Society **77**:165–183.

Sanders, H. 1968. Marine benthic diversity: a comparative study. The American Naturalist **102:**243–282.

Soberón, J., and J. Llorente. 1993. The use of species accumulation functions for the prediction of species richness. Conservation Biology **7:**480–488.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry and statistical tables. W. H. Freeman, New York.

Suazo-Ortuño, I., J. Alvarado-Díaz, E. Raya-Lemus, and M. Martínez-Ramos. 2007. Diet of the marbled toad (*Bufo marmoreus*) in conserved and disturbed tropical dry forest. The Southwestern Naturalist **2:**305–309.

Tocher, M. D., C. Gascon, and B. L. Zimmerman. 1997. Fragmentation effects on a central Amazonian frog community: a 10-year study. Pages 124–137, in W. F. Laurance and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Trejo, I., and R. Dirzo. 2000. Deforestation of seasonally dry tropical forest-a national and local analysis in México. Biological Conservation **2:**133–142.

Trenham, P. C., and H. B. Shaffer. 2004. Amphibian upland habitat use and its consequences for population viability. Ecological Applications **15:**1158–1168.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology **33:**200–209.

Urbina-Cardona, J. N., M. Olivares-Pérez, and V. H. Reynoso. 2006. Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, México. Biological Conservation **132:**61–75.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science **277:**494–499.

Whitfield, S. M., and M. A. Donnelly. 2006. Ontogenetic and seasonal variation in the diets of a Costa Rican leaf-litter herpetofauna. Journal of Tropical Ecology **22:**409–417.