Amphibian species richness and diversity in a modified tropical environment of central Mexico

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Abstract: We analyzed the structure and taxonomic diversity of amphibian communities in a forest-fragmented landscape in central Mexico. Our study was undertaken in remnants of native tropical evergreen forest (TEF), shaded coffee plantations (SCP), and pastures (PAS) to assess richness, turnover, and taxonomic diversity of species among these environments. Our results show a decrease in the number of species from the native forest to the transformed environments. Similarity in species composition was higher between TEF and SCP, and between SCP and PAS. In TEF, we recorded a greater proportion of species of conservation concern at the national and global levels. Many of the species recorded in SCP and PAS may occur in TEF, but TEF holds species requiring conserved environments. Additional studies are needed at a local level to understand the effects of land-cover transformations and the interactions between native vegetation and its surrounding matrix to define appropriate management plans and conservation strategies for highly sensitive biological groups, such as the amphibians.

Key words: Amphibians, community, conservation, disturbance, diversity, frogs, Hidalgo, salamanders, toads, tropical landscapes.

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Introduction

Habitat loss and fragmentation are considered some of the greatest threats to biodiversity, especially in tropical regions (Laurance & Bierregaard 1997; Schelhas & Greenberg 1996). The effects of habitat loss and fragmentation can be studied in different ways depending on the spatial and temporal scales of analyses (Areendran et al. 2013; Haila 2002; Huey et al. 2009), as well as the biological groups under study (Dickman 1987). The effects of tropical forest loss and fragmentation can be analyzed based on different proportions of the remaining native vegetation, and the intensity of its modification to other land-cover uses (Fischer & Lindenmayer 2007). In this sense, the decrease in abundance and genetic variability of populations, and changes in species composition in communities are evidence of diversity loss. This has been studied in some biological groups namely birds,
mammals, amphibians, and reptiles (Laurance et al. 2002; Saunders et al. 1991). However, some insect species may increase in abundance when fragmentation of tropical environments is high and prolonged (Tocher et al. 1997).

Habitat fragmentation affects the biodiversity of a landscape, and species diversity in disturbed environments is lower than in conserved environments (Andrén 1994; Bhatt et al. 2015; Kerr & Degruise 2004). However, disturbed environments can generate high amounts of species turnover at the regional level, since they may favor presence of other species such as generalist or invasive species, as well as sustaining certain native species (Bellamy et al. 1996; Wanger et al. 2010). Thus, transformed or degraded environments could reduce native species richness within a landscape, for instance, due to habitat and microhabitat loss, reduction in food availability, higher competition levels, and higher predation risk when moving between native vegetation patches or due to invasive species (Amori & Luiselli 2013; Gardner et al. 2007; Nyelele et al. 2014). In a human dominated world, it is pressing to assess the effect of habitat alteration on the diversity of sensitive biological groups such as amphibian communities (Fischer & Lindenmayer 2007; Gardner et al. 2007).

Species composition in tropical amphibian communities is related to gradients of environmental variables at different spatial scales, such as elevation and vegetation cover (Crump 1971). Thus, the structure of an ecological community varies due to changes in these environmental variables (Gardner et al. 2007). In this sense, habitat fragmentation, which can also affect attributes of other variables synergistically, has been one of the main causes of changes in community composition and species loss (Clark et al. 1990), which is particularly relevant in a group with narrow range of ecological requirements, as in amphibians (Pineda & Halffter 2004).

In this study, we began with the premise that modified tropical environments such as coffee plantations and pastures might maintain a substantial richness of native tropical forest species due to the existence of surviving original floristic elements (Haila 2002). This might be particularly relevant in the case of amphibians, because ecological characteristics and life histories of many species make them highly sensitive to modified environments (Bitar et al. 2012), which also make them good candidates for evaluating effects of habitat alteration on richness and diversity at the local level.

Materials and methods

Study area

The study area included different sections of the municipality of Huehuetla (20° 23', 20° 41'N and 97° 59', 98° 11'W; Fig. 1), located in the eastern portion of Hidalgo state, Mexico. This municipality ranges in altitude from 200 to 1700 m asl (INEGI 2009). From a biogeographic point of view, the study area is located within subprovince of Sierra Otomí Tepehua between the Sierra Madre Oriental and the Gulf of Mexico (Morrone 2001). The climate is warm and humid, with an average annual temperature of 23.7 °C; the dry period occurs during spring and winter; the average annual precipitation is 2558 mm (INEGI 2009).

We surveyed three vegetation types which are characterized by different levels of habitat alteration. One vegetation type was the tropical evergreen forest (TEF) in which about 25 % of the tree species are deciduous and canopy height is about 20 - 30 m. This plant community is physiognomically complex because it contains about five strata (Rzedowski 1978). The other two vegetation types were shade coffee plantations (SCP) and pasture (PAS). SCP contains characteristic trees of TEF, with heights reaching 30 m, which are used as shade for coffee plantations (Coffea arabica). PAS consists of totally open areas for bovine livestock and where only some genera of induced grasses occur, such as Paspalum sp. and Andropogon sp. (Rzedowski 1978).

Because amphibians are highly dependent on environmental and microhabitat humidity, we located streams and water bodies in the vegetation types we surveyed. TEF had streams within the forest, SCP had peripheral seasonal streams, and PAS had ponds.

Sampling of amphibian communities

We conducted a monthly sampling of amphibian communities from October 2009, February-November 2010, and February and May 2011. We sampled three sites each month representing one site of each vegetation type. The sampling method consisted on walking through paths, regardless of the boundaries among vegetation types. The transects were surveyed both in the daytime (10:00 - 14:00 h) and at night (19:00 - 23:00 h). We looked for amphibians in the different microhabitats based on their habits (i.e., arboreal, aquatic, or terrestrial species), including water bodies, under rocks, within crevices, and under wet logs (Casas-
Fig. 1. Location of sampling points by vegetation types (TEF = tropical evergreen forest, SCP = shade coffee plantation, PAS = pasture) in eastern Hidalgo, Mexico.

Andreu et al. (1991). Three observers surveyed all transects. We surveyed 24, 300 m transects separate by 20 m each by vegetation type. In total, our sampling effort was 288 person-hours per vegetation type. Because we estimated the relative abundance of each species by vegetation type, we avoided repeated sampling (transects) within the same area (Manzella & Péfaur 2000).

Whenever possible, individuals were identified directly in the field. Collected individuals were sacrificed in the lab by freezing and later fixed in 10 % formalin. We later identified these specimens using dichotomous keys (Duellman 2001; Ramírez-Bautista et al. 2009). Individuals were deposited in the Herpetological Collection of the Centro de Investigaciones Biológicas (CIB) at the Universidad Autónoma del Estado de Hidalgo.

Estimation of species richness

To estimate completeness of amphibian inventories in each vegetation type, we constructed species accumulation curves by using EstimateS Program V.7.50 (Colwell 2005). We used the nonparametric estimators ACE and Chao 1, both based on abundance data (Jiménez-Valverde & Hortal 2003). We also used the algorithms that assess species represented only by one (singletons) or two (doubletons) individuals in the sampling (Colwell & Coddington 1994). We performed a $\chi^2$ test to evaluate the frequency distribution of the data obtained by sampling in each environment (Zar 1997).

Estimation of species diversity

We used the method suggested by Jost (2006) to assess species diversity in each vegetation type. This method defines “true diversity” as the effective number of species (the measurement unit of species diversity in ecological communities; Moreno et al. 2011). For this analysis, we considered the order $q = 1$ that takes into account the proportional abundance of each species in communities (Jost 2006). The equation is represented as $^1D = \exp (H')$, where $^1D$ is the true diversity, and $\exp (H')$ is the exponential Shannon entropy index (Jost 2006).

Estimation of evenness

To assess the evenness of the species composition of the assemblages of amphibians in each vegetation type, we performed curves of Whittaker or rank-abundance curves (Feinsinger 2003; Magurran 1998), in which we considered the number of individuals recorded by species.
Estimation of taxonomic diversity

Because species richness does not necessarily reflect the evolutionary diversity of community members, we used the measures proposed by Warwick & Clarke (1995, 2001), in which, we calculated the average (Delta = \[ \Lambda' \]) and the variance (Lambda = \[ \Lambda \]; sensu Clarke & Warwick 1998) of amphibian taxonomic diversity in each vegetation type. This method is based on the premise that a community with high phylogenetic relationship among species (clustering) is less diverse (in a phylogenetic sense) than a community with a low phylogenetic relationship among species. The functions are represented as: \[ \Lambda' = \frac{2 \Sigma \Sigma \omega_{ij}^2}{[S - (S - 1)]} \] and \[ \Lambda = \frac{2 \Sigma \Sigma \omega_{ij}(\omega_{ij} - \Lambda')^2}{[S - (S - 1)]} \], where \[ \omega_{ij} \] is taxonomic distance between each pair of species \( i \) and \( j \), and \( S \) is the species number observed in the sampling (Warwick & Clarke 1995). A high value of \( \Lambda' \) reflects a low ratio among species and, therefore, it is presented as a high taxonomic diversity measure. Moreover, \( \Lambda' \) is a measure of no equity in the structure through taxonomic units. Therefore, a high value of \( \Lambda' \) indicates under- or overrepresentation of the taxa in the samples.

Furthermore, to detect differences in the taxonomic distinction of each environment, we compared the sampling (taxonomic list of species by vegetation type) and the regional pool of species with a random null model generated from 1000 random resampling (Clark & Warwick 1998). In this model, we used values of the mean and variance of the number of samples and species that plotted \( \Delta' \) and \( \Lambda' \) values with a confidence interval of 95% (Clark & Warwick 1998).

In the analysis of taxonomic diversity, we used the classification proposed by Wilson et al. (2013) when considering five taxonomic categories: species, genus, family, order, and class. A taxonomic diversity analysis was performed with the PRIMER 5 program (Clarke & Gorley 2001).

Estimation of beta diversity

We estimated the complementarity index to evaluate beta diversity among vegetation types, which refers to the degree of dissimilarity in composition of amphibian species between paired vegetation communities (Colwell & Coddington 1994). For this, we obtained the total species richness for pairs of combined plant communities using the formula: \[ S_{AB} = a + b - c \], where, \( a \) is the species number in site A, \( b \) is the species number in site B, and \( c \) is the number of species in common between sites A and B. The number of exclusive species to anywhere was estimated starting from: \[ U_{AB} = a + b - 2c \]. With these values, we calculated the complementarity of the sites A and B as: \( C_{AB} = U_{AB} / S_{AB} \). Thus, complementarity varied from zero when two sites were identical in species composition to one when species from both sites were completely different (Colwell & Coddington 1994).

Conservation status

We assigned a conservation risk category for each species base on the Mexican redlist (NOM-059-SEMARNAT-2010; SEMARNAT 2010) and the global redlist (IUCN Red List; IUCN 2014). Additionally, we used the Environmental Vulnerability Score (EVS; Wilson et al. 2013) that considers three risk categories: low (3 to 9 points), medium (10-13), and high (14-19). The score is the result of adding points assigned to the species features based on three criteria (i) extent of species geographic distribution, (ii) extent of ecological distribution (vegetation types used), and (iii) type of reproductive mode (see Wilson et al. 2013 for details).

Results

Species richness

In total, we found 18 amphibian species in the three vegetation types. We did not detect statistical differences among species averages in vegetation types (\( \chi^2 = 10.19 \), df = 22, \( P = 0.984 \)), but some difference might be present (if we compromise Type I error by reducing Type II error). The richest vegetation type was TEF with 12 species, followed by SCP with 11, and PAS with nine (Table 1). The completeness of the inventory was different among the three vegetation types. The SCP showed the highest survey completeness, followed by PAS, and ultimately the TEF according to values generated by estimators ACE and Chao 1 (Table 2). The true diversity values, showed that effective number of species among vegetation types was similar, where the value of TEF was of \( 1D_{TEF} = 7.3 \) effective species, followed by SCP with \( 1D_{SCP} = 7 \), and PAS with \( 1D_{PAS} = 5.4 \).

Amphibian evenness

The abundance and evenness of amphibian species show similar patterns among vegetation types, that is, all environments contain some numeri-
Table 1. List and abundance of 18 species of amphibians from Hidalgo state, Mexico, organized by vegetation type (TEF = tropical evergreen forest, SCP = shade coffee plantations, PAS = pasture), risk category by SEMARNAT (2010; P = extinction danger, Pr = special protection, Nc = not considered), Red list (IUCN, 2014; E = endangered, V = vulnerable, LC = Least concern, Nc = not considered), population trend (D = decreasing, I = increasing, S = stable, U = unknown), Environmental Vulnerability Score (EVS), and category of vulnerability (L = low, 3-9; M = medium, 10-13; H = high, 14-19) according to Wilson et al. (2013), and endemic to Mexico (E = endemic, Ne = not endemic, Nc = not considered). Species codes (capital letters) show the species in rank abundance plots (Fig. 2).

<table>
<thead>
<tr>
<th>Code</th>
<th>Species</th>
<th>TEF</th>
<th>SCP</th>
<th>PAS</th>
<th>SEMARNAT</th>
<th>IUCN</th>
<th>Population trend</th>
<th>EVS</th>
<th>Mexican endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Bolitoglossa platydactyla (Gray)</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>Pr</td>
<td>NT</td>
<td>D</td>
<td>H (15)</td>
<td>E</td>
</tr>
<tr>
<td>B</td>
<td>Chiropterotriton chondrostega (Taylor)</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>Pr</td>
<td>E</td>
<td>D</td>
<td>H (17)</td>
<td>E</td>
</tr>
<tr>
<td>C</td>
<td>Pseudoeurycea sp.</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>Nc</td>
<td>Nc</td>
<td>U</td>
<td>H (18)</td>
<td>Nc</td>
</tr>
<tr>
<td>D</td>
<td>Rhinella marina (Linnæus)</td>
<td>29</td>
<td>21</td>
<td>50</td>
<td>Nc</td>
<td>LC</td>
<td>I</td>
<td>L (3)</td>
<td>Ne</td>
</tr>
<tr>
<td>E</td>
<td>Incilius nebulifer (Girard)</td>
<td>17</td>
<td>39</td>
<td>30</td>
<td>Nc</td>
<td>LC</td>
<td>S</td>
<td>L (6)</td>
<td>Ne</td>
</tr>
<tr>
<td>F</td>
<td>Incilius valliceps (Wiegmann)</td>
<td>0</td>
<td>7</td>
<td>6</td>
<td>Nc</td>
<td>LC</td>
<td>S</td>
<td>L (6)</td>
<td>Ne</td>
</tr>
<tr>
<td>G</td>
<td>Craugastor decoratus (Taylor)</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>Pr</td>
<td>V</td>
<td>U</td>
<td>H (15)</td>
<td>E</td>
</tr>
<tr>
<td>H</td>
<td>Craugastor rhodopus (Cope)</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>Nc</td>
<td>V</td>
<td>D</td>
<td>H (14)</td>
<td>E</td>
</tr>
<tr>
<td>I</td>
<td>Eleutherodactylus longipes (Baird)</td>
<td>5</td>
<td>3</td>
<td>0</td>
<td>Nc</td>
<td>V</td>
<td>U</td>
<td>H (15)</td>
<td>E</td>
</tr>
<tr>
<td>J</td>
<td>Eleutherodactylus verrucipes (Cope)</td>
<td>3</td>
<td>15</td>
<td>0</td>
<td>Pr</td>
<td>V</td>
<td>S</td>
<td>H (16)</td>
<td>E</td>
</tr>
<tr>
<td>K</td>
<td>Ecnomiohyla miotympanum (Cope)</td>
<td>54</td>
<td>52</td>
<td>35</td>
<td>Nc</td>
<td>NT</td>
<td>D</td>
<td>L (9)</td>
<td>E</td>
</tr>
<tr>
<td>L</td>
<td>Smilisca baudinii (Duméril &amp; Bibron)</td>
<td>12</td>
<td>11</td>
<td>1</td>
<td>Nc</td>
<td>LC</td>
<td>S</td>
<td>L (3)</td>
<td>Ne</td>
</tr>
<tr>
<td>M</td>
<td>Trachycephalus typhonius (Linnaeus)</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>Nc</td>
<td>LC</td>
<td>S</td>
<td>L (4)</td>
<td>Ne</td>
</tr>
<tr>
<td>N</td>
<td>Leptodactylus melanonotus (Hallowell)</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>Nc</td>
<td>LC</td>
<td>S</td>
<td>L (6)</td>
<td>Ne</td>
</tr>
<tr>
<td>Ñ</td>
<td>Hypopachus variolosus (Cope)</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>Nc</td>
<td>LC</td>
<td>S</td>
<td>L (4)</td>
<td>Ne</td>
</tr>
<tr>
<td>O</td>
<td>Lithobates berlandieri (Baird)</td>
<td>11</td>
<td>20</td>
<td>26</td>
<td>Pr</td>
<td>LC</td>
<td>S</td>
<td>L (7)</td>
<td>Ne</td>
</tr>
<tr>
<td>P</td>
<td>Lithobates johni (Blair)</td>
<td>40</td>
<td>0</td>
<td>0</td>
<td>P</td>
<td>E</td>
<td>D</td>
<td>H (14)</td>
<td>E</td>
</tr>
<tr>
<td>Q</td>
<td>Lithobates spectabilis (Hillis &amp; Frost)</td>
<td>18</td>
<td>0</td>
<td>0</td>
<td>Nc</td>
<td>LC</td>
<td>D</td>
<td>M (12)</td>
<td>E</td>
</tr>
</tbody>
</table>

Table 2. Observed amphibian species richness (Sobs), species predicted by the estimators ACE and Chao 1, and proportion of completeness according to such estimators by vegetation type (TEF = tropical evergreen forest, SCP = shade coffee plantation, PAS = pasture). We show average (Delta+) and variance (Lambda+) of taxonomic diversity by vegetation type.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Sobs</th>
<th>Species predicted ACE</th>
<th>% of completeness</th>
<th>Species predicted Chao 1</th>
<th>% completeness</th>
<th>Delta+</th>
<th>Lambda+</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEF</td>
<td>12</td>
<td>16</td>
<td>73</td>
<td>15</td>
<td>80</td>
<td>59.7</td>
<td>187.79</td>
</tr>
<tr>
<td>SCP</td>
<td>11</td>
<td>12</td>
<td>95</td>
<td>11</td>
<td>100</td>
<td>60.37</td>
<td>167.14</td>
</tr>
<tr>
<td>PAS</td>
<td>9</td>
<td>11</td>
<td>83</td>
<td>10</td>
<td>95</td>
<td>61.67</td>
<td>163.89</td>
</tr>
</tbody>
</table>
cally dominant and some rare species (Fig. 2). The rank-abundance curves showed that in TEF numerically dominant species were *Ecnomiohyla miotympanum*, *Lithobates johni*, and *Rhinella marina*; likewise, *E. miotympanum* and *Incilius nebulifer* were highly abundant in SCP; and *E. miotympanum* and *R. marina* displayed that pattern in PAS. Rare species were represented by the anurans *Hypopachus variolosus* and *Craugastor decoratus* (in PAS), and the salamander *Chirop terotriton chondrostega* (in TEF).

**Fig. 2.** Rank-abundance curves of amphibian species detected in the three studied vegetation types (TEF = tropical evergreen forest, SCP = shade coffee plantation, PAS = pasture). The letters in the figures represent codes assigned to species as in Table 1.

**Taxonomic diversity**

The taxonomic diversity values (Delta +) indicate that PAS had the highest value and was close to the value’s expected average, followed by of SCP and TEF (Table 2; Fig. 3A). Regarding the variation of taxonomic diversity (Lambda+), TEF showed higher value than SCP and PAS (Table 2; Fig. 3B).

**Beta diversity (β)**

According to the value of complementarity, we observed similar values among the three environments. However, the pair TEF-PAS showed the highest value (0.69), followed by SCP-PAS (0.57). The combination between TEF-SCP showed the lowest value of complementarity, reflecting low species turnover among vegetation types (0.47).

**Conservation status**

The amphibian community in the study area includes a total of six species (33.3 %) within a risk category at national level (SEMARNAT 2010). In the category of Endangered species is *L. johni*, and in Special Protection are *Bolitoglossa platydactyla*, *C. chondrostega*, *C. decoratus*, *Eleutherodactylus verrucipes*, and *L. berlandieri* (Table 1). TEF had the highest proportion of species of conservation concern at national level (41.66 %, five species), contrasting with PAS (22.22 %) and SCP (18.18 %).

According to the IUCN criteria, 17 species (94 %) were evaluated, of which 11.8 % were considered Endangered (two species), 23.5 % Vulnerable (four species), 11.8 % Near Threatened (two species), and 52 % in the category of Least Concern (nine species; Table 1). TEF had more categories and a larger proportion of species of conservation concern (Endangered and Vulnerable) at global level (41.66 %, five species), whereas SCP had three Vulnerable species (27.27 %), and PAS, had only species considered of Least Concern and Near Threatened. According to the
IUCN, of the 18 recorded species, six have decreasing populations, eight are stable, one species is increasing, and three have unknown status (Table 1). TEF had the lowest proportion of species with stable populations (41.66 %, five species), whereas the other vegetation types had larger proportions (54.54 % in SCP and 66.66 % in PAS, both with six species). Conversely, TEF had the largest proportion of species with decreasing populations (33.35 %), compared with PAS (22.22 %) and SCP (18.18 %) (Table 1).

All recorded species were included within some level EVS. Nine species (50 %) were assigned to low EVS, one (5.6 %) to the medium, and eight (44.4 %) to the high. TEF had the largest number of species with high EVS (five species, 41.66 %), whereas SCP had a lower number (four, 36.36 %) and PAS the lowest (one, 11.12 %). Conversely, PAS had the highest number of species with low EVS (eight, 88.88 %), followed by SCP (seven, 63.3 %) and TEF (six, 50 %; Table 1).

Nine of the 18 recorded species are endemic to Mexico (50 %; Table 1). TEF had a larger proportion of endemic species (58.33 %, seven species), followed by SCP (36.36 %, four), and PAS (22.22 %, two; Table 1).

**Discussion**

Amphibian species richness was higher in TEF than in modified environments, such as SCP and PAS, although this seems to be non-significant statistically. Decrease in species richness has also been observed in other studies (Lips 1998; Wake 1991). We attribute this outcome to the ecological and physiological characteristics of many amphibians that, in general, make them dependent on conserved areas (Huey et al. 2009; Pineda et al. 2005).

Changes in the structure of forest landscapes might result in loss of microhabitats necessary for survival of certain species of amphibians with limited life history strategies (Lieberman 1986; Vitt & Caldwell 2001). We detected a decrease in species number and turnover with respect to modified environments. However, the abundance of some species was similar among the three environments, with species such as *E. miotympanum*, *R. marina*, and *I. nebulifer* having high abundances, which is probably attributed to their generalized habits, environments they occupy (i.e., tropical forest, pastures, etc.), and periods of activity for foraging or reproductive behavior.

Ecological pattern in which some species were broader in ecological and physiological characteristics, such as some numerically dominant toads and hylid frogs, was similar among the three environments. Daily & Ehrlich (1996) suggested that nocturnal species can move among preserved and matrix habitats due to the amelioration of abiotic conditions at night (i.e., low temperature, high humidity, and low UV radiation), which might promote exchange species among environments (Blaustein et al. 1994). In addition, specific ecological features, such as reproductive conditions, might favor establishment of populations of species that can use available microhabitats in each vegetation type such as small water bodies and crevices in logs and in the ground. For example, Haddad & Prado (2005) reported that open habitat species from the Cerrado region in Brazil tended to colonize areas of forest of the Atlantic region, as a consequence of having generalist reproductive modes and tolerance to sunstroke. In our study, generalist species such as *R. marina*, *I. nebulifer*, and *E. miotympanum*, use a high variety of microhabitats, which allow them to occur in all three vegetation types surveyed.

Contrary to observed species richness in each of the studied environments, PAS showed a higher value of taxonomic diversity when compared to SCP, and especially TEF. The PAS environment has a larger number of more distantly phylogenetically related species (different genera and families) than the others; however, this result might be influenced by differences in level of completeness of sampling in such communities. The higher values in taxonomic diversity of PAS and SCP coincide in turn with higher completeness in species inventory, unlike TEF (Table 2). This suggests that estimates of taxonomic diversity might be influenced by completeness of inventory. TEF had the lowest estimation in species inventory completeness, thus, a greater sampling effort in TEF should be invested, including all different types of microhabitats not surveyed in this study such as tree canopies, epiphytes (bromeliads), and deep crevices.

Species exclusive to any of the studied environments generate high levels of replacement or complementarity. In this study, the anurans *Leptodactylus melanototus* and *H. variolosus* and the salamanders *B. platydaictyla* and *C. chondrostega* were unique to one type of vegetation (Fig. 2), which might be due to microhabitats they occupy. For example, *C. chondrostega* is usually found only in areas of preserved vegetation, whereas *L. melanototus* deposit their eggs in
water-filled ditches in open environments around cattle pens (paddocks), which allows this species to occupy that environment (Urbina-Cardona et al. 2006).

Sites with different levels of modification intensity from TEF to coffee plantations and pastures can be good places to assess species loss and develop conservation strategies (Wanger et al. 2010). As has been observed in various studies, open areas are hostile environments for most small ectothermic organisms such as amphibians, primarily because of high risks from predation and dehydration (Rothermel & Semlitsch 2002). SCP and PAS were dominated by generalist species that may also occur in areas of native vegetation and often exploit several microhabitats, as in the case of many small reptilian species (Mesquita et al. 2006; Vitt et al. 2007). In our study, generalist species used all vegetation types and a variety of microhabitats. In TEF we found these species under rocks, logs, and leaf litter; within bark, ground and tree crevices, in body waters, and other microhabitats. In the SCP these species occurred under leaf litter, rocks, and logs; in PAS they occurred under rocks, in body waters, and within ground crevices.

Although the change in the structure of forest landscapes can reduce species richness in remnants of original forest (Vitt & Caldwell 2001), this process can also promote diversity at regional level due to turnover in species composition related to presence of microhabitats for generalist and invasive species (Pearman 1997). However, low levels of disturbance can increase regional diversity (beta diversity), whereas higher levels, often of anthropic origin, promote reduction. Those disturbances might favor species that benefit from processes of disruption, but generally they are less important in terms of conservation than those that disappear. The disturbances tend to favor the presence of generalist species that occupy a wide range of environment and microhabitat types (Blaustein et al. 1994). For instance, in all three vegetation types surveyed the anuran species R. marina, E. miotympanum, and I. nebulifer were abundant, have stable or increasing populations (IUCN 2014), and have low EVS, contrasting with the salamander species B. platydactyla and C. chondrostega, and the anuran C. decoratus, which only occurred in one vegetation type, have decreasing populations, and high EVS.

The exchange of amphibian species among TEF, SCP, and PAS with differences in their community structure might be due, in part, to two mechanisms discussed by Brown et al. (2001): (i) that the regional pool of species (in this case amphibians in tropical environments) provides a high potential for colonization since the existence of this pool implies that the local environments are open to species exchanges, and (ii) that the regional pool contains species able to use existing resources (generalist and exotic species), a capacity that depends on their ecological necessities and environmental tolerances that allow species to persist there (Wiens & Donoghue 2004).

The high number of amphibian species in any risk category stresses the need to preserve areas of native forest to sustain their populations. In a context of a human dominated world many species also tolerate disturbed areas with some level of native vegetation cover, such as SCP. In our study, we found individuals of species at risk in SCP (Table 1). Our results are relevant at local level and for the time frame of study. Evaluation of ecological communities, species abundances, and ecological features (e.g., reproductive modes, edge effect) need to be evaluated in longer time spans (several years) to better assess the impact of landscape change (from native vegetation to coffee plantations and pastures) on amphibian species richness, population structure, and species turnover (Gairola et al. 2015; Pineda et al. 2005).

Conclusions

The effect of disturbance on amphibian communities is suggested by the decreased number of species found in disturbed environments compared to numbers found in conserved environments; in addition to the occurrence of a higher proportion of species of conservation concern and high EVS in TEF, in contrast with SCP and PAS where generalist species are dominant. This study shows a decrease in amphibian species richness in transformed environments containing SCP and PAS. Still, the complexity of preserved forest and its species richness might influence taxonomic diversity in modified environments. We found that the highest taxonomic diversity was exhibited in pasture paddocks when compared to other communities.

In terms of conservation, species that occur in TEF that we found in high numbers in SCP and PAS might suggest that they are highly tolerant to environmental pressure in such transformed environments. However, the assumption that transformed environments retain or maintain a similar richness to conserved environments...
requires some caution, since only a few species were abundant in transformed environments. Most of the species cannot live in such environments because they fail to contain specific ecological conditions. Therefore, in future studies we suggest to assess the availability of microhabitat types and the temperature and humidity ranges in which amphibian species occur.

The analysis of the structure and turnover of communities in tropical, temperate, and arid environments, in relation to changes in land use, is a way to assess the effects of disturbance and, as a result, generate management plans and promote conservation in forest remnants and in the modified areas.

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