Importance of riparian remnants for frog species diversity in a highly fragmented rainforest

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Tropical forests undergo continuous transformation to other land uses, resulting in landscapes typified by forest fragments surrounded by anthropogenic habitats. Small forest fragments, specifically strip-shaped remnants flanking streams (referred to as riparian remnants), can be particularly important for the maintenance and conservation of biodiversity within highly fragmented forests. We compared frog species diversity between riparian remnants, other forest fragments and cattle pastures in a tropical landscape in Los Tuxtlas, Mexico. We found similar species richness in the three habitats studied and a similar assemblage structure between riparian remnants and forest fragments, although species composition differed by 50 per cent. Frog abundance was halved in riparian remnants compared with forest fragments, but was twice that found in pastures. Our results suggest that riparian remnants play an important role in maintaining a portion of frog species diversity in a highly fragmented forest, particularly during environmentally stressful (hot and dry) periods. In this regard, however, the role of riparian remnants is complementary, rather than substitutive, with respect to the function of other forest fragments within the fragmented forest.

Keywords: amphibians; biodiversity; conservation; habitat fragmentation; Mexico; tropical rainforest

1. INTRODUCTION

The continuing loss of forest can result in fragmentation and generate a landscape composed of forest remnants surrounded by transformed habitats. In the forest patches and transformed habitats that constitute a fragmented landscape, the effects of fragmentation on biodiversity can be observed in modifications to species number, abundance and species composition (Lindenmayer & Fisher 2006). The contribution of small forest fragment strips flanking streams (referred to as riparian remnants) for the maintenance, connection and conservation of species diversity could be significant within highly fragmented landscapes, particularly for amphibian fauna (de Lima & Gascon 1999; Becker et al. 2007). Many amphibian species depend on riparian habitats for various life-history functions (e.g. breeding, foraging; Semlitsch 1998) and high amphibian diversity in riparian areas can be attributed to cool moist conditions, high productivity and complex habitat (Olson et al. 2007). However, compared with undisturbed sites or large forest fragments, riparian remnants cannot provide sufficient habitat to maintain the abundance of some amphibian species, or preserve the microclimatic conditions necessary to support certain species (Marczak et al. 2010).

In Los Tuxtlas Biosphere Reserve, Mexico, approximately 90 per cent of the original rainforest cover has been transformed to cattle pastures (dominant land use), corn fields and other land uses (Guevara et al. 2004). Nowadays, few large forest fragments remain in the region and many small fragments, including riparian remnants, are dispersed across the entire reserve. In such a scenario, it is necessary to evaluate the importance of riparian remnants to anuran species diversity in order to recognize their value for biodiversity conservation. We therefore compare frog species diversity between riparian remnants, other forest fragments and cattle pastures, analyse differences in species composition between these three habitat types and identify the differences in frog assemblages related to each habitat.

2. MATERIAL AND METHODS

Fieldwork was carried out in the northern part of Los Tuxtlas Biosphere Reserve, Mexico (18°35′N, 95°5′W). The study area is situated at between 10 and 190 (m).a.s.l. Mean annual temperature during the study (June 2007 to April 2008) was 25°C; annual rainfall was 2.7 m, with the rainy season occurring between July 2007 and January 2008 (82% of total rainfall; source: UNAM meteorological station). The majority of vegetation was originally tropical evergreen rainforest, but the remaining rainforest (approx. 24% of the original coverage) is currently fragmented and surrounded by a matrix of cattle pastures and croplands (see Arroyo-Rodriguez et al. 2009). The study area includes three rivers (Balzapote, La Palma and Máquina), and along each river we selected three sites for sampling: one riparian remnant, one rainforest fragment (larger than riparian remnants and with an irregular form) and one pasture. Each of these nine sites (see electronic supplementary material, table S1, for details), separated by a distance greater than 500 m, was visited twice during June, August and November 2007 and April 2008 (total of eight visits). In each visit at night, three people collected anurans, during 1 h, from all possible microhabitats within a 900 m² transect (180 × 5 m) placed parallel to the river (thus sampling effort was the same per survey).

To evaluate inventory completeness per habitat (thus validating comparisons) and for all habitats together, we used two non-parametric species-richness estimators: Mao–Taup and Bootstrap both performed using EstimateS 7.5 software (Colwell 2005). To compare species diversity between habitats, we used observed species richness and dominance–diversity graphs (Magurran 2004). We compared species richness and abundances between habitats and between rainy season (surveys from August and November) and dry season (June and April) using a G-test. To evaluate similarities in species composition and patterns of abundance between habitats, we used a Jaccard index, which uses presence–absence data, and a Bray–Curtis Index, which uses abundance data (Colwell 2005). To determine whether frog assemblages were habitat dependent, we grouped species according to two natural-history attributes: body size and reproductive mode, and examined the distribution of types using a 2 × 3 table and Q-test. Size was classified according to mean snout–vent length: small (less than 31 mm), medium (31–50 mm) and large (greater than 50 mm). Reproductive mode was classified by both oviposition site and the larvae development site, resulting in three modes: (i) eggs and larvae in water, (ii) eggs out of water and larvae in water, and (iii) eggs and larvae out of water.

3. RESULTS

Across all surveys, 18 anuran species of seven families were observed (electronic supplementary material,


Table 1. Observed and estimated anuran species richness and abundance in three habitats in Los Tuxtlas, Mexico.

<table>
<thead>
<tr>
<th>habitat</th>
<th>number of species observed</th>
<th>abundance</th>
<th>number of species estimated</th>
<th>completeness (% min–max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>riparian remnants</td>
<td>12</td>
<td>272</td>
<td>14</td>
<td>86</td>
</tr>
<tr>
<td>forest fragments</td>
<td>12</td>
<td>504</td>
<td>17</td>
<td>71–86</td>
</tr>
<tr>
<td>pastures</td>
<td>11</td>
<td>131</td>
<td>13</td>
<td>85–92</td>
</tr>
<tr>
<td>all habitats</td>
<td>18</td>
<td>907</td>
<td>23</td>
<td>78–90</td>
</tr>
</tbody>
</table>

*Including +95% of confidence interval.

Table S2). Twelve species were recorded both in riparian remnants (67% of the total) and in forest fragments, while 11 species were collected in cattle pastures. Species-richness estimators indicated that inventory completeness for habitat types was between 71 and 92 per cent, while for all habitats together, it was between 78 and 90 per cent (table 1). Total frog abundance was 907 individuals, with notable differences found between habitats ($\chi^2 = 233.58, p < 0.0001$): 272 individuals were recorded in riparian remnants, 504 in forest fragments and 131 in pastures. Abundance, recorded between seasons, was higher in remnants, 504 in forest fragments and 131 in pastures. Abundance between seasons in pastures remained practically unchanged.

In the dominance–diversity graphs (figure 1b), the slopes of the riparian remnant and forest fragment were similar, while the slope of the pasture was less steep. The same two species dominated in the riparian remnants and forest fragments, whereas three species were co-dominant in the pasture. The hierarchical order of the remaining species varied between habitats. Three singletons (species with just one individual) were recorded in the riparian remnants, five singletons were detected in forest fragments and just one singleton was found in the pasture.

Similarities of species composition between habitats (according to the Jaccard index) averaged 0.49. The lowest similarity value was between forest fragments and pastures (0.44), a higher similarity was found between riparian remnants and forest fragments (0.50), with a slightly higher value between riparian remnants and pastures (0.53). When similarity including abundance was calculated (Bray–Curtis index), the lowest value was again between forest fragments and pastures (0.18), the next highest value was between riparian remnants and pastures (0.40), while the greatest similarity was observed between riparian remnants and forest fragments (0.47).

All frog groups, according to the classification of the body size or reproductive mode, were represented in all habitats, but the proportion of individuals belonging to each group varied notably and was found to be habitat dependent (figure 2). From forest fragments to riparian remnants ($\chi^2 = 60.08, p < 0.005$) and from forest fragments to pastures ($\chi^2 = 245.02, p < 0.005$), the proportion of individuals belonging to reproductive mode III decreased, while the proportion of the other two groups increased. According to size trait, from forest fragments to riparian remnants ($\chi^2 = 136.35, p < 0.005$) and from forest fragments to pastures ($\chi^2 = 91.10, p < 0.005$), the large-species group decreased, while the medium- and small-species groups increased. From riparian remnants to pastures...
partitioned by season. Eighty-nine per cent of total species richness, and 86 per cent of total frog abundance, was recorded in riparian remnants and forest fragments together. In forest fragments and pastures together, 89 per cent of total species richness was also recorded, although abundance was lower (70%). This suggests that both riparian remnants and pastures can provide micro-environmental conditions suitable for the occurrence of certain species (at least at some stage of their life cycle). However, the quality of such conditions seems to differ, reflected in the greater abundance (twofold) found in riparian remnants compared with pastures, although it is also half the abundance recorded in forest fragments. In our study area, the most important environmental variables related to amphibian assemblages and species composition, at the local level, were canopy cover, understory density, leaf litter cover and temperature (Urbina-Cardona et al. 2006). Differences in these variables between study habitats may be related to the availability and quality of possible breeding sites, and therefore influence the species composition and abundance. These issues need to be assessed in future studies in the region. A significantly lower amphibian abundance in riparian remnants, compared with larger fragments or continuous forest, has been observed in several transformed landscapes (Marczak et al. 2010), suggesting that such a trend could be a generalized pattern for amphibians.

Both species turnover between seasons in riparian remnants and the greater abundance observed in the dry season suggest that this habitat has an important role in the temporal dynamics of frog assemblages, acting as a refuge in environmentally stressful periods. Migration between forest remnants and water bodies in fragmented landscapes is a common dynamic linked to the reproductive period in many amphibian species (Becker et al. 2007). Additionally, migration between matrix habitats and forest remnants containing streams could also be a strategy of some amphibian species to avoid periods of stress.

Maintenance of the same frog groups in riparian remnants, although in different proportions compared with forest fragments, suggests that riparian remnants maintain environmental conditions required for species with different natural-history traits, reflecting their importance in maintaining a portion of functional diversity within the landscape. From a conservation perspective, riparian remnants together with forest fragments may provide an adequate conservation strategy for certain amphibian species (Semlitsch & Bodie 2003). This must viewed from a landscape perspective, because amphibian species use multiple elements for different functions (Ficetola et al. 2009). Riparian remnants in the studied landscape could function as a refuge during periods of environmental stress, a reproduction site for a variety of species with different natural-history traits and as a habitat connector for many species.

We thank all who provided field assistance. Luis Canseco-Márquez helped with specimen identification. G. Halffter, J. Leon-Cortés, J. Galindo, A. Ramirez-Bautista and two anonymous reviewers provided valuable comments to

4. DISCUSSION

Our results suggest that riparian remnants play an important role in maintaining a portion of frog species diversity in highly fragmented tropical rainforests, mainly during stressful (hot and dry) seasons. However, the partial differences in species composition, and lower abundance and variation in assemblage proportions compared with forest fragments, suggest that the role of riparian remnants is complementary, rather than substitutive, to the function of other forest fragments in the study area.

The 18 frog species recorded in this study represent 53 per cent of historically recorded anuran species richness in the region (Ramírez-Bautista & Nieto-Montes de Oca 1997). The species richness observed in riparian remnants alone does not highlight the importance of this habitat to the frog species diversity within our study area. However, the perspective changes when species composition and abundance are examined, particularly when analyses are

\( \chi^2 = 19.43, \ p < 0.005 \), the large-species group increased slightly, while the small- and medium-species groups decreased.

Figure 2. (a) Body size and (b) reproductive modes (see §2 for categories) of frogs in three habitat types in a fragmented forest in Mexico. Numbers in bars indicate per cent of individuals that belong to each group. (a) Grey bars, large; black bars, medium; white bars, small. (b) Grey bars, i; black bars, ii; white bars, iii.

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