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Between-year consistency of anuran assemblages in temporary ponds in a deforested area in Western Amazonia

Nathocley M. Venâncio¹, Albertina P. Lima², Moisés B. de Souza¹ & William E. Magnusson²

¹*Centro de Ciências Biológicas e da Natureza and Programa de Pós-Graduação em Ecologia e Manejo dos Recursos Naturais, Universidade Federal do Acre . BR 364, km 4, Distrito Industrial, CEP 69915-900. Rio Branco, Acre, Brazil*

²*Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, CP 2223, 69011-970, Manaus, Amazonas, Brazil*

Many studies have shown that forest fragments are depauperate in forest-dependent fauna, and that fragments are invaded by generalist or colonising species. However, rather than representing generalist species, the anurans that occur in disturbed areas around forest remnants may represent a specialist fauna with its own complex interactions rather than generalist species capable of colonising any water bodies available for reproduction. We studied anuran assemblages in 10 temporary ponds around a forest fragment in the State of Acre, Brazil, on the southern border of the Amazon forest, between October and June in 2008, 2009 and 2010. We recorded 24 species in 6 families. Assemblages in ponds were temporally stable, indicating strong deterministic control of assemblage composition. Although they contain fewer species than found in the original forest, these assemblages inhabiting novel ecosystems are highly structured and probably have complex interactions with their biotic and abiotic environments. They are worthy of further study.

Key words: anuran assemblages, ephemeral ponds, fidelity, temporal stability

INTRODUCTION

Many studies have shown that forest fragments are depauperate in forest-dependent fauna, and that fragments are invaded by generalist or colonising species (Laurance & Williamson, 2001), which are considered in some sense unnatural. However, defining species as generalist or colonising species based on short-term studies may result in a different classification than one based on a long-term landscape perspective. Most open areas were forested at some time in the past and vice versa. In general, open-area species are not generalists, and do not occur in forests. Tropical rainforest supports many more species of anurans than savannah areas, but the savannah anuran assemblages may be complex (Myers et al., 2000). In any case, there are no areas without human interference, and one of the imperatives for ecologists today is to learn to engage with novel ecosystems (Bridgewater et al., 2011; Hamer & McDonnell, 2008).

The southern border of the Amazon forest is known as the “deforestation arc” (Nepstad et al., 1999), because of the intense conversion of forest to pasture, agricultural land and urban areas (Fearnside, 2005). However, this region has unstable forest cover, and savannahs have advanced over the southern boundary of the Amazon forest repeatedly in the past (Latrubesse et al., 1997). Therefore, rather than representing generalist species, the anurans that occur in the more open edges around

forest remnants may represent an open-area specialist fauna with its own complex interactions rather than generalist species capable of colonising any water bodies available for reproduction (Hamer & McDonnell, 2008).

Conceptual models for the study of forest fragmentation have tended to different extremes in relation to habitat specialisation. Island-biogeography theory treats all species as though they were ecological equivalents (extreme generalists) and attributes differences in densities and distributions to factors that are random in relation to species characteristics (MacArthur & Wilson, 1967). At the other extreme, species are considered forest or non-forest specialists (e.g., Budowski, 1963). In fact, species may have different degrees of specialisation along many different niche dimensions, so that assemblage composition depends on adequacy of the locality for the individual species (Gleason, 1926), rather than a predictable super organism (Clements, 1936).

If open-area species that colonise deforested areas are extreme generalists, the assemblages they form are expected to be largely random and show little temporal stability (Hamer & McDonnell, 2008). That is, the assemblage composition in a pond in a given year should be no more similar to the assemblage composition in the same pond the following year than it is to neighbouring ponds (Hamer & McDonnell, 2008). In this paper, we show that anuran assemblages in temporary ponds in open areas and re-growth around a forest fragment

Correspondence: Albertina P. Lima (lima@inpa.gov.br)



Fig. 1. Chico Mendes Mendes Environmental Park in Rio Branco, Acre State, Brazil. The numbers indicate sampling ponds. Image obtained from Google Earth.

in the State of Acre, on the southern border of the Amazon forest, are temporally stable, indicating strong deterministic control of assemblage composition.

MATERIALS AND METHODS

The study was undertaken in the Chico Mendes Environmental Park (Fig. 1) in Rio Branco city (10°02'11"S, 67°47'43"W). The park covers 57 ha, and has a mosaic of vegetation associations. About 50% is covered by selectively-logged forest, 40% by second-growth forest in various stages of recovery and 10% has open areas that have been deforested for decades.

We studied 10 temporary ponds: Two ponds were in open areas 40 and 60 m from the edge of the forest, the rest were in old-growth or regrowth forests, 0 to 10 m from more open grassy areas. The regrowth forest was less than 20 years old and growing in areas that previously had been pasture, but there are no detailed records of previous management. One pond was in old-growth forest that did not show evidence of having been clear cut in the past. The ponds have probably been forming for decades and, as they were more common in the regrowth forest, they are probably a result of previous land management that caused soil compaction. However, there are no records of ponds in the reserve before this study.

Climate in the area is highly seasonal, with most years having 3 or 4 months with less than 100 mm of rainfall (Duarte, 2006). There are no permanent water bodies in the park, and all the ponds dried during the dry season (July to November) each year. However, the hydroperiod varied between ponds, and we registered whether the

ponds contained water in each month of the study between August 2008 and October 2010.

Conductivity ($\mu\text{S}/\text{cm}$), temperature ($^{\circ}\text{C}$), acidity (pH) and dissolved oxygen concentration were measured with a multiparameter limnological probe (Hanna® Model HI 9829), at four equidistant points along the major axis of each pond. All limnological measurements were made on 25 April 2012 at the end of the rainy season. Temperature of the air and water were measured at the beginning and end of surveys on every night that surveys were undertaken.

Visual and auditory surveys for anurans were undertaken in a 10 m long section of bank of each pond weekly between October and June in 2008, 2009 and 2010. Each sampling unit was surveyed twice each week for 30 min, once during the day (0600–1000) and once at night (1900–2300). Individuals encountered were generally identified and released in the field, but voucher specimens of each species were photographed, collected (max. 2 individuals per pond) and deposited in the Herpetological Collection of the Federal University of Acre (CHUFAC).

Statistical analyses were based on the maximum number of individuals of each species vocalising in each month. Dissimilarities among ponds and years were quantified with the dissimilarity form of the Bray-Curtis index after transforming the frequencies of occurrence in each pond to proportions. Non-metric multidimensional scaling (NMDS) was used to reduce assemblage dimensionality and produce a smaller subset of linear descriptors of assemblage composition based on the compositional dissimilarity of assemblages between ponds. Analyses were carried out in the vegan

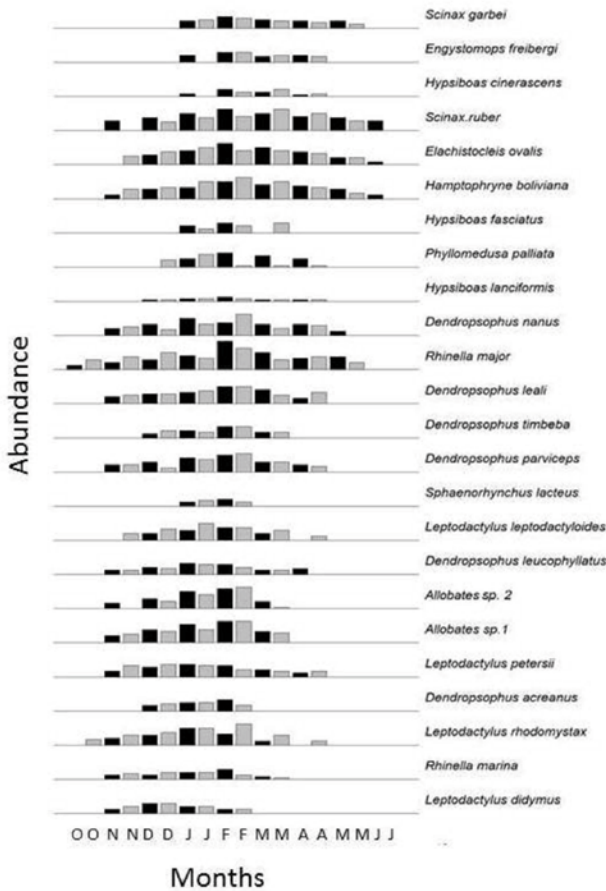


Fig. 2. Relative abundance of anuran species in ponds sampled in the 2008–2009 (grey bars) and 2009–2010 (black bars) reproductive seasons from October to June. The letters are: October (O), November (N), December (D), January (J), February (F), March (M), April (A), May (M) and June (J).

(Oksanen et al., 2007) and pgirmess packages of the R program (R Development Core Team, 2009). The capacity of the NMDS to capture assemblage patterns was assessed by the proportion of the variance in the original dissimilarity matrix explained by the distances in the NMDS configuration.

RESULTS

We recorded 24 species in 6 families: Aromobatidae (2 species), Bufonidae (2), Hylidae (13), Leiuperidae (1), Leptodactylidae (4) and Microhylidae (2). Species were found in one to six ponds (mean=2.79, $S=1.67$). All species were found in the same ponds in both reproductive seasons, except for *Elachistocleis ovalis*, which was recorded in six ponds in the first season, but only in three in the second. No species was found in a pond in the second reproductive season from which it had not been recorded in the first.

Some species started vocalising in October, but most had peaks of calling in January and February. However, the peak month of calling, and especially the length of the period in which individuals were present at ponds, differed among species. Calling periods were consistent within species between years (Fig. 2), and there was no

significant relationship between the mean hydroperiod of the ponds in which a species occurred and the mean duration of its presence at ponds ($r^2=0.006$, $p=0.83$).

Values of both NMDS axes were spatially autocorrelated at short distances (Moran's $I>0.45$, $p<0.046$). Assemblages showed tendencies to vary along both east-west and north-south directions across the reserve and the spatial coordinates of ponds were significant predictors of assemblage composition (Multivariate Multiple Regression, *Pillai Trace*=1.26, $F_{4,14}=5.98$, $p=0.005$). However, neither pond hydroperiod nor distance from forest edge was significantly spatially autocorrelated (Moran's I , $p>0.05$ at all distances).

Three ponds near the north-east corner of the reserve had similar assemblage compositions and were distinct from other ponds, with high values along NMDS axis 1 (Fig. 3). These ponds differed from the others because they had few species and were the only ponds with *P. palliata* (Fig. 4). The only pond in old-growth forest overlapped with several others in composition (Fig. 4).

Multivariate Multiple Regression detected no significant relationship between hydroperiod or distance from forest edge on the anuran assemblage composition represented by the NMDS axes (*Pillai Trace*=0.588, $F_{4,14}=1.46$, $p=0.267$). None of the water characteristics [pH ($p=0.313$), conductivity ($p=0.127$), dissolved oxygen ($p=0.246$)] could predict the composition of frog species summarised by the single NMDS axis.

As the spatial autocorrelation was only in the dependent variables, it does not affect the validity of inferential tests (Landeiro & Magnusson, 2011), and inclusion of the spatial coordinates in the analysis did not affect the conclusions in relation to hydroperiod and distance from border (*Pillai Trace*=0.05, $F_{4,10}=0.06$, $p=0.991$).

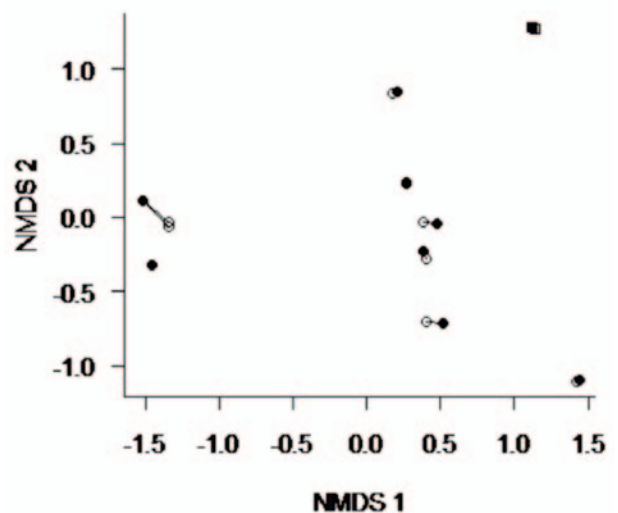


Fig. 3. Non-metric multidimensional scaling (NMDS) plot of ponds based on species composition. The pond in the forest is indicated by square symbols and other ponds by circles. Closed symbols represent species composition in the 2008–2009 reproductive season and open symbols the species composition in the 2009–2010 reproductive season. Lines connect points representing the same pond in different years.

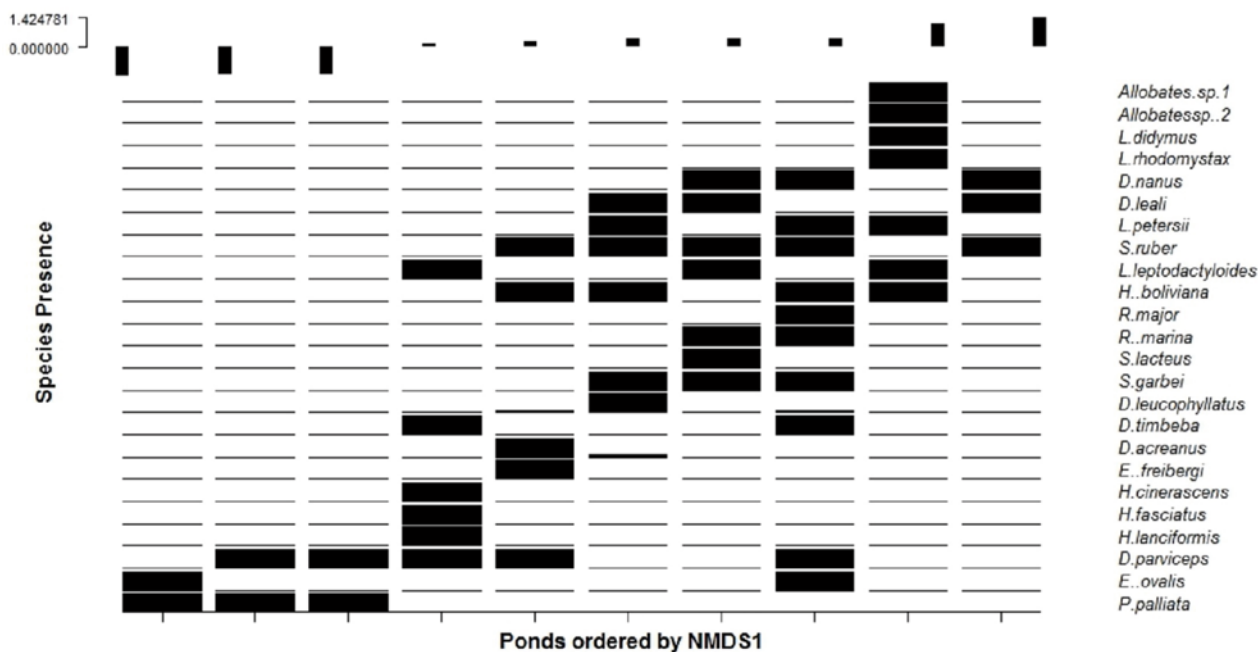


Fig. 4. Relative abundance of anuran species in a pond in the forest and ponds in disturbed areas in two reproductive seasons between 2008 and 2010. Ponds are ordered by their position along NMDS axis 1 in Fig. 3. Relative values of the NMDS axis are shown in the upper row of bars.

The number of species detected per pond was not related to hydroperiod or distance from border (multiple regression: $F_{2,7}=0.07$, $p=0.932$). However, the assemblage composition in individual ponds varied little between years in comparison to differences among ponds (Fig. 3). This suggests that there are strong forces structuring assemblages. If not, the assemblages in one pond in different years would be no more similar than assemblages in different ponds in the same year. Although the sample size limits the power of tests, most of the variation between ponds, and consistency between years is not attributable to hydroperiod, water characteristics or distance from the border of the forest.

DISCUSSION

There were distinct differences among ponds in anuran assemblages, but those differences were not attributable to edge effects or pond hydroperiod. As our focus was on anurans in disturbed areas around fragments, we surveyed only one forest interior pond. However, the assemblage in that pond was typical of the assemblages in forest ponds in the region (Souza, 2009). We had expected that the ponds on the forest border would accumulate species from the forest and open areas, and would also have more species than open areas because of the structural complexity of the vegetation. However, there was no relationship between the number of species and any of the variables we investigated.

Calling phenology varied among species and was highly consistent between years. However, the mean time that a species was present was unrelated to the mean hydroperiod of the ponds in which it occurred, so the limits to calling were not related to water availability, and may reflect other strategies, such as predator

saturation (Heyer et al., 1975; Magnusson & Hero, 1991) or lekking sites (Gerhardt, 1994).

The ponds in open areas around the Chico Mendes Environmental Park represent a novel ecosystem (*sensu* Bridgewater et al., 2011), but the assemblages are strongly structured, and that structure is consistent among years. It is unlikely that this results solely from philopatry by long-lived species. Small terrestrial anurans in Amazonia are generally annuals (Toft et al., 1982; Donnelly, 1989; Moreira & Lima, 1991; Amézquita et al., 2009) and individuals of even the largest terrestrial or arboreal Amazonian frog species rarely breed in more than one season (Galatti, 2002; Magnusson et al. 1999).

The two *Allobates* species are typically found in mature forest and the other 22 species, which are often found in naturally open areas, would generally be classified as colonising species in deforested areas. However, the central Brazilian savannas have dominated this area frequently in the past (Latrubesse et al., 1997). When forest was encroaching over savannah, the colonising species would have been considered stable elements of the fauna and the forest species as colonisers.

Many factors structure anuran assemblages, such as competition (Kopp & Eterovick, 2006; Wilbur, 1987), the reduction of water and wetland quality through adjacent land use (Houlahan & Findlay, 2003) and predation (Magnusson & Hero, 1991). However, these factors are usually associated with hydroperiod (Snodgrass et al., 2000) or connectivity to permanent water bodies (Becker et al., 2007). We do not have sufficient replicates to investigate all of these factors, but there are no permanent water bodies in the Chico Mendes Environmental Park, and assemblage structure in the ponds we studied was not related to hydroperiod. Edge effects have been reported for anurans (Hillers et al.,

2008; Tocher et al., 1997; Tsuji-Nishikido & Menin, 2011) but we detected no strong effects of edge effects on the assemblages we studied.

Hamer & McDonnell (2008) may be right in affirming that anthropogenic degradation of habitat in urban and urbanising landscapes is one of the greatest threats to amphibian diversity. However, whatever the factors structuring the anuran assemblages in the re-growth forests and open areas in the southern border of the Amazon forest, these novel ecosystems do not have simple anuran assemblages that are composed of generalist colonising species with random associations. The complex forest assemblages have been replaced by assemblages that are highly structured and that probably have complex interactions with their biotic and abiotic environments

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