
AMPHIBIAN TROPHIC ECOLOGY IN INCREASINGLY HUMAN-ALTERED WETLANDS

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Abstract.—Habitat destruction and alteration are among the major causes of worldwide amphibian declines. Resource limitation in altered environments can potentially affect trophic ecology of amphibians and contribute to decline. In this work, we analyzed changes in resource availability and use, and the population abundance of eight amphibian species from six wetlands that differ in type and degree of human disturbance. Food resource availability varied among sites and the occurrence of some arthropods was correlated with type of disturbance regime. Diet evenness, richness, and niche breadth were similar among sites or months. Nevertheless, diet composition showed significant variation among samples for all species. Diet composition changes among populations were correlated with resource availability in four species (*Lysapsus limellum*, *Dendropsophus nanus*, *Hypsiboas pulchellus* and *H. punctatus*), but not in the remaining species (*D. sanborni*, *H. raniceps*, *Scinax nasicus* and *S. squalirostris*). These results suggest that species that are able to adjust their diets according to prey availability may have an adaptive advantage in changing environments associated with anthropogenic disturbances. Given the increasing rate of alteration of wetlands by urbanization, agriculture, and livestock grazing, understanding trophic processes in these habitats is important for preserving the great biodiversity living in these habitats.

Key Words.—flood plain ponds; habitat alteration; Hylidae; prey availability; trophic plasticity

INTRODUCTION

Amphibian populations are experiencing serious declines around the world, driven principally by direct and indirect effects of habitat destruction and alteration (Alford and Richards 1999; Eskew et al. 2012). Amphibian communities from the large Neotropical wetlands are not exempt from the effects of fragmentation and habitat alteration (Peltzer et al. 2003). Sensitivity to habitat modification is species-specific, but for most species we lack information about how life-history characteristics and habitat use may affect population fluctuations and vulnerability to environmental changes (McKinney 2002; Green 2003; Ficetola and De Bernardi 2004). Although ecological mechanisms of population decline are not clear, habitat modification is known to affect amphibian abundance, richness, and assemblage composition (Jansen and Healey 2003; Smallbone et al. 2011; Eskew et al. 2012).

Habitat alteration can impact amphibian populations both directly and indirectly (Blaustein et al. 2010). Although destruction of breeding habitat may lead to extirpation (Vaira 2003), deterioration of freshwater systems by urban wastes (Ficetola et al. 2011) and river flow-regulation by dams negatively affects amphibian diversity and abundance by reducing area of riparian wetlands used for breeding (Eskew et al. 2012). Selective logging also deteriorates refuge and breeding

sites (Petranka et al. 1993; Lemckert 1999; Vaira 2002). Grazing and grassland burning for livestock alters plant communities and thereby potentially damages breeding, feeding, and refuge habitats and can reduce amphibian diversity (Vaira 2002; Jansen and Healey 2003; Cano and Leynaud 2010). Habitat modification affects amphibians indirectly by reducing energy reserves and energy allocated to growth and reproduction, and by affecting population dynamics and viability (Gray and Smith 2005; Brodeur et al. 2011). Brodeur et al. (2011) hypothesized that the body condition of frogs is reduced in human modified habitats because of decreased prey abundance, but the effect of human modifications on amphibian feeding ecology has not been well studied (Kovács and Török 1995).

Diets of amphibian vary seasonally and spatially in relation to the environment where they dwell (Maneyro and Da Rosa 2004; Menin et al. 2005; Falico et al. 2012b). Disturbance of ecosystems can affect not only amphibians but also their arthropod prey, affecting resource uptake (Trueba et al. 1999; Prinzing et al. 2007; Battles et al. 2013). Data on food resource availability are essential to understand frog trophic ecology (Hirai and Matsui 2001; Hirai 2002; López et al. 2009), and a relationship between diet composition and prey availability has been demonstrated (Maneyro and Da Rosa 2004; López et al. 2009). Prey availability is difficult to measure (Macale et al. 2008) and, therefore,



FIGURE 1. Study area in the alluvial valley of Paraná River (31° 40' S, 60° 40' W). Sites are at Sirgadero Island (S1, S2, S4, S5, S6) and the Natural Reserve of Universidad Nacional del Litoral (S3). Symbols: dotted zones, urbanized areas (Santa Fe City urban or suburban areas); white zones, high ground areas only inundated during extraordinary floods; gray zones, low lands flooded periodically or every few years; dark gray zones, permanent water bodies.

rarely included in anuran dietary studies (Toft 1980). Thus, the evaluation of resource availability is of central importance to understand the mechanisms through which habitat alteration affects amphibian trophic ecology.

When anthropogenic disturbance of habitat leads to variation in composition and abundance of resources, the ability to adjust diet to the more available resources may improve energy uptake and fitness, preventing population decline (Gray and Smith 2005; Williams et al. 2006; Falico et al. 2012b). Highly specialized species or those with specific and fixed trophic requirements would have greater difficulties coping with environmental alterations that lead to changes in prey availability (Anderson et al. 1999; Williams et al. 2006). The ability to adjust diet to resource availability has been referred to as trophic plasticity and is usually overlooked in trophic studies (DeWitt and Scheiner 2004; Guedes et al. 2009). Here we test the hypothesis that amphibians shift their diet across increasingly human-disturbed wetlands as a function of changes in trophic resource

availability. We predict that prey composition will shift along the anthropogenic habitat alteration gradient studied, and that trophic plasticity (i.e., the capability to shift diet in relation to prey availability) will differ among amphibian species.

MATERIALS AND METHODS

Study area and site classification.—The Middle Paraná River floodplain is a complex system of islands with alluvial forests, wetlands, secondary rivers, streams, and lagoons that covers 20,000 km² of north-eastern Argentina (Drago et al. 2003). This diversity of landforms provides a large variety of terrestrial and aquatic habitats for amphibians. The Paraná River has flood pulses in which water elevations are approximately 2–3 m above mean levels with inter-annual variation in flood magnitude. During high water periods, the river connects with adjacent floodplain wetlands and a wide exchange of organisms and nutrients occurs (Iriondo et al. 2007). In this region, climate is damp and mesothermal. The warmer months are November to March, with a mean annual temperature of 18.4° C (Peretti 1996). Annual precipitation is about 1,000 mm and occurs mainly from October to April (Peretti 1996).

The banks of the Middle and Lower Paraná River sustain the largest human habitation of the country, with important harbors and industrial activities. In these regions, development of infrastructure, advancement of farming and ranching, and increasing contamination can be observed (Hamilton 1999; Lavilla 2002; López et al. 2005a). Human activities such as alteration of water courses, hydraulic works, construction of reservoirs, drainage and refilling of wetlands, inadequate management and overexploitation of resources, and destruction of vegetation in the basin are transforming wetlands adjacent to the Paraná River into a mosaic of environments with different degrees of modification and fragmentation (Bonetto 1994; Neiff 1999; Peltzer et al. 2003). Many of these habitat changes have local impacts, thus altered and pristine habitats exist in a matrix within relatively small areas. Given that amphibian assemblages respond mainly to microhabitat characteristics and processes (Richter-Boix et al. 2007), this wetland system allows us to test the effect of local habitat alterations on amphibian trophic ecology.

We sampled six sites with different types and degrees of anthropogenic alteration in the alluvial valley of Middle Paraná River near the city of Santa Fe (Santa Fe Province, Argentina). Five of the sites were on Sirgadero Island (S1, S2, S4, S5, S6), and one site was in the Natural Reserve of Universidad Nacional del Litoral (S3; Fig. 1). Sampling sites were in a unique environmental unit (Crevasse Splays and Levees of the Santa Fe and Coronda river channels; Marchetti et al. 2013) and were < 8 km apart. The close proximity of the

sites ensured similarity of climatic conditions and assemblage of species able to colonize the sampling sites.

To evaluate human impact on the study area, we defined six distinct categories of habitat alteration: (1) fire in marginal vegetation is associated with cattle grazing, but frequency and extent vary among sites independent of stocking density; (2) hydraulic alteration by construction of artificial channels, dams, fence slopes, and sand filling of swamps modifies flood pulses, draining of rainwater, connections between lotic and lentic habitats, water quality, and arthropod assemblages; (3) presence of livestock (i.e., cattle, horses, and pigs) in the extensively farmed wetlands de-vegetate the fixed routes between pens and grazing areas; (4) other vegetation alterations eliminate weeds adjacent to roads, houses and electrical lines, clear natural forest, remove straw for roof thatch, etc., and modify natural vegetation structure; (5) fragmentation impedes terrestrial animal dispersal and isolates ponds (e.g., the highway through a floodplain valley that connects Santa Fe City with Paraná City and the large sand filled areas for construction and other infrastructure); and (6) deposition and accumulation of construction debris and urban solid waste alter habitat structure and, as a result of the lack of control in waste composition, contaminate water bodies with a wide spectrum of chemicals. We scored the impact level in the aquatic buffer zone (about 60 m from pond shore; see Semlitsch and Bodie 2003) on a scale from 0 to 3 for each of the six alteration types; 0 = no alteration to 3 = maximum impact (modified from Peltzer et al. 2003). We did not classify sites with respect to the total amount of habitat alteration *a priori* because we lacked information about the relative impact that each alteration type could have on amphibians to weight its effect. We used the impact scores as different independent variables describing habitat alteration. To characterize variation from habitat alteration factors and avoid multicollinearity, we used a nonmetric multidimensional scaling analysis (NMDS; Faith et al. 1987). This method does not require linear relationships among variables and can often summarize more information in fewer axes than other techniques (Manly 1986). NMDS compiles information from a distance matrix in a predetermined number of axes (called dimensions) and uses an index called Stress to measure the extent to which derived distances differ from the original distances. As a distance measure we used Gower similarity coefficient (Gower 1971) because it considers combined absences (of alterations in our case) as informative (Moreno 2001). We expected that two sites lacking a particular type of alteration should be environmentally more similar because absence of alteration would indicate favorable conditions for amphibians and arthropods. This method allowed us to express the multiple habitat

alteration factors in two dimensions and use them in subsequent analysis as independent descriptors of habitat alteration. Analyses were performed in CANOCO statistical package (Version 5).

Sampling.—We sampled monthly at each of six sites from the end of spring to the beginning of autumn (November 2004 to April 2005), equaling 36 samples, when feeding activity was concentrated (López et al. 2011). We hand-captured eight species from the family Hylidae (*Dendropsophus nanus*: $n = 658$; *D. sanborni*: $n = 86$; *Hypsiboas pulchellus*: $n = 97$; *H. punctatus*: $n = 208$; *H. raniceps*: $n = 31$; *Lysapsus limellum*: $n = 581$; *Scinax nasicus*: $n = 77$; *S. squalirostris*: $n = 48$) that forage in riparian vegetation greatly affected by habitat alterations. We sampled all sites within a week during each month. We used a flashlight to search microhabitats where frogs forage (rooted and floating macrophytes growing up to 1 m of water depth, about 2 m offshore, and the periodically flooded zone beside water bodies, about 2 m onshore) through a transect approximately 500 m long and 4 m wide.

We standardized sampling effort by search time (the first two hours after sunset), duration, and transect area; thus, species abundances were comparable among samples (Heyer et al. 1994; Marsh and Pearman 1997). We sacrificed frogs *in situ* by immersing the animals in a buffered anesthetic solution of benzocaine (Heyer et al. 1994; European Commission 1997; Chen and Combs 1999). We did not perform stomach flushing because selected species were too small and fragile (Macale et al. 2008) and we needed to obtain the entire digestive tract including the intestine to avoid overestimating larger prey (Peltzer et al. 2000; López et al. 2007; Macale et al. 2008). This is especially important because the abundant prey (in guts of frogs and in the environment) were small (e.g., mites, collembolans). Within the studied assemblage, there were no threatened species (Vaira et al. 2012); population size and recruitment rate were large enough (López et al. 2011) to assume that our sampling exerted minimal effects even at the local population level. Collected animals have been used for other studies (López et al. 2007, 2009, 2011; Antoniazzi et al. 2013, 2014) and sampled populations have been monitored subsequently. We did not observe any sign of declining populations with the exception of those at the two most altered sites (S6 and S5) where habitat has been totally destroyed by a landfill.

Following the techniques described elsewhere (Hirai and Matsui 2001; López et al. 2009), we estimated prey availability by sweep-netting with an entomological net (handle length: 200 cm; hoop diameter: 40 cm; bag depth: 80 cm; mesh size: 0.1 mm) in microhabitats where amphibians were captured. We made sweep-net samples simultaneously with amphibian captures, always by the same person, walking at the same speed and

carried out in two 7-min zigzag transects (150m × 3 m), describing a 180° arc, parallel to the ground-water surface, striking the top of rooted and floating macrophytes canopy with net ring. We combined data from both transects for the analysis (López et al. 2009).

Environmental alteration, assemblage composition, and resource availability.—We used multivariate ordination techniques to analyze the relationships among amphibian and prey assemblage structure and environmental alterations. We used the matrix of species composition at the different sites as dependent variables and scores of NMDS as explanatory variables. From the matrix of prey taxa availability, we excluded those taxa that represented < 10% of the total abundance. To select the appropriate ordination method (unimodal or linear), we carried out a Detrended Canonical Correspondence Analysis (DCCA) to obtain the length of the gradient, an index that informs about the degree of species turnover among samples (Legendre and Gallagher 2001; Lepš and Šmilauer 2003). Following the suggestion of Lepš and Šmilauer (2003) that maximum gradient lengths < 4 indicate linearity, we selected the linear method of Redundancy Analysis (RDA; amphibian assemblage maximum gradient length = 0.919, prey assemblage maximum = 0.489). We evaluated significance of canonical axes with Monte Carlo tests (499 permutations). These analyses were performed in CANOCO statistical package (Version 5).

Trophic analysis.—To avoid underestimation of prey consumption, we included both stomach and intestine contents in diet analysis (Peltzer et al. 2000; López et al. 2007). We identified prey to the lowest possible taxon (generally Family). For each amphibian species, we estimated diet evenness (Pielou 1966), richness, niche breadth (Levins 1968), and mean number of prey per gut at each site and sampled month. We compared these parameters among sites and months using Kruskal-Wallis tests followed by multicomparison Dunn tests with GraphPad InStat software (Version 3.06; Table 3). We calculated niche breadths of species (Levins 1968) by summing the specimens from every site and month.

We evaluated the similarity of frog diets (relative abundance of prey items) and prey availability composition among months and sites using Pianka (1973) niche overlap index (O_{jk}). To determine whether measured overlap values differed from those expected by chance, we performed a randomization analysis with EcoSim software (Version 7). EcoSim performs Monte Carlo randomizations to create Pseudo-communities and then compares the patterns in these randomized communities with those in the observed data matrix. In this analysis, the values of the original matrix were randomized 1000 times. We assumed different resource states to be equally abundant in the environment

(equiprobable resource state). We used EcoSim randomization algorithm 3 (RA3) because it retains the niche breadth of each species (we did not find niche breadth variation among samples within a species; see results), but randomizes which particular resource states are used. It corresponds to a simple reshuffling of each row of the matrix (zero states reshuffled). We chose this option because we analyzed overlap among populations of each species, thus frogs of the same species should be able to eat every prey item foraged in other populations. Gotelli and Enstlinger (2004) recommended using RA3 when the goal is to retain the amount of specialization, but allow a species to potentially use other resource states. Winemiller and Pianka (1990) have shown that RA3 has good statistical properties for detecting non-random niche overlap patterns and found that RA3 was usually superior to RA4 for this purpose. Vignoli and Luiselli (2012) suggested that RA2 performed much better than RA3 at revealing community structure, but in our case RA3 successfully detected the diet structure of frogs in six out of eight species and in environmental prey availability; while RA2 detected diet structure in five frog species and food resources.

Finally, to study trophic plasticity among the amphibians, we evaluated the correlation between the variation of prey availability and the diet of the frog with a Mantel test (Mantel 1967) in the software XLSTAT (Version 7.5.3). Mantel test is a permutation method that calculates a Pearson correlation coefficient between two proximity matrices (similarity or dissimilarity) and gives a *P* value on the null hypothesis of lack of correlation. Euclidean distance dissimilarity matrixes (average linkage aggregation criteria) were built for diet of each anuran species between sites and months (samples), which were correlated to analogue matrixes built based on prey availability. Due to the seasonal patterns of occurrence of amphibian species of the assemblage (López et al. 2011), we did not collect every species in all samples (month/site). We built matrixes for each species including those samples for which at least one individual was captured. For each anuran species, we used only prey availability data of samples for which diet data were available. As in other works, the diet of frogs usually included a few dominant prey items and many rare taxa (López et al. 2005b; Falico et al. 2012b). Consequently, to prevent the inclusion of taxa with negligible weights in the analysis, we excluded prey items representing < 10% of relative abundance either in the diet or in trophic resource availability samples. For all statistical analysis we used an alpha level of 0.05.

RESULTS

Amphibian and prey assemblages.—NMDS successfully summarized the information of the six types

TABLE 1. Correlation coefficients between nonmetric multidimensional scaling (NMDS) analysis axes and semiquantitative variables of anthropogenic environmental alteration (AEA). Abbreviations of types of anthropogenic environmental alteration are Fire: burning of marginal vegetation; Hydraul.alter.: modification of natural hydrology in relation to flood pulse and draining of rainwater by construction of artificial channels or dams; Livestock: presence of cattle, horses, and pigs; Veg.alter.: vegetation alterations due to weed elimination or logging; Fragm.: habitat fragmentation by roads, dams or fence slopes; and Landfill: deposition and accumulation of construction debris and solid urban wastes.

AEA Types	NMDS1 (Livestock & Landfill)	NMDS2 (Damming)
Fire	0.9735	-0.1452
Hydraul.alter.	0.11	0.9272
Livestock	0.6981	-0.5112
Veg.alter.	0.9102	-0.1343
Fragm.	0.4046	0.8698
Landfill	0.7889	-0.1018

of alteration in two axes (stress value = 0.00043542). The first NMDS axis was related to livestock presence and landfill activities and summarizes information from four of the analyzed environmental alterations (named hereafter Livestock & Landfill). The second NMDS axis was related to modifications of natural hydrology of the water bodies and habitat fragmentation (named hereafter Damming; Table 1; Fig. 2). Sites were distributed along the gradient of environmental alterations defined by NMDS axes. Site S6 was the most disturbed habitat showing high scores for the axes named Damming and Livestock & Landfill. Site S5 was also highly disturbed and exhibited large values of Livestock & Landfill. Sites S2, S3 and S4 were moderately disturbed; S3 was associated with Damming; and S2 and S4 with Livestock & Landfill. Finally, S1 was the least altered site, with low values on both axes (Fig. 2).

Although most species occurred at every site, RDA showed that amphibian assemblage structure varied in association with the type of alteration (Monte Carlo test of significance of canonical axes: pseudo- $F = 2.5$, $P = 0.002$; Fig. 3a). *Dendropsophus nanus* and *Lysapsus limellum* were abundant in every site (their abundance ranging from 28% to 46% and 13% to 45% of all captures, respectively). *Dendropsophus* species showed their greatest abundances in the most altered sites, S5 and S6 (grouped at the top of the triplot). Site S3, associated with higher levels of damming, presented an assemblage composed largely of *D. nanus* and *Scinax* species. Abundance of frogs in the genus *Scinax* was

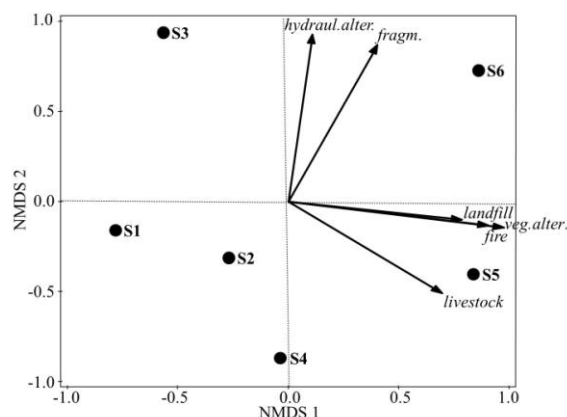


FIGURE 2. Plot of Nonmetric multidimensional scaling analysis (NMDS) based on Gower dissimilarity index of the environmental alterations. NMDS procedure computed configuration in 25 iterations, with stress value 0.00043542. Abbreviations: fire, burning of marginal vegetation; hydraul.alter., modification of natural hydrology in relation to flood pulse and draining of rainwater by construction of artificial channels or dams; livestock, presence of cattle, horses, and pigs; veg.alter., vegetation alterations due to weed elimination or logging; fragm., habitat fragmentation by roads, dams or fence slopes; landfill, deposition and accumulation of construction debris and solid urban wastes.

negatively related to Livestock and Landfill. Assemblages of sites S1, S2 and S4 (grouped at the bottom of triplot) were characterized by greater abundance of *Hypsiboas* species, which were related to lower alteration levels. In particular, *H. punctatus* and *H. raniceps* showed increased abundances in sites with low alteration impacts.

We identified 105 taxa (mainly at the level of Family) from the net-sampled prey. Most of the prey belonged to Insecta (90.74%) and Arachnida (9.05%). Prey composition changed along the habitat alteration gradient (Fig. 3b). RDA showed differentiation among sites according to environmental alteration (Monte Carlo test of significance of canonical axes: pseudo- $F = 2.4$; $P = 0.004$). The most altered sites showed greater abundances of Hemiptera, Orthoptera, Coleoptera and Acari. Some flying prey, such as Diptera and Hemiptera, had high relative abundances and were evenly distributed among the six sampled sites (Table 2). The most abundant arthropods available were two families of dipterans, Chironomidae and Culicidae. Chironomids exceeded 10% of available prey in all sites and were particularly abundant in S3. In contrast, culicids exceeded 10% of available prey in the three least altered sites. Muscidae (Diptera) were also abundant, but their abundance was more related to livestock presence and landfill. Formicidae were abundant in sites with alterations of natural hydraulic regime (Damming). Entognatha (springtails and related taxa principally in the family Sminthuridae) were abundant in S1, a site with slight alteration (Table 2).

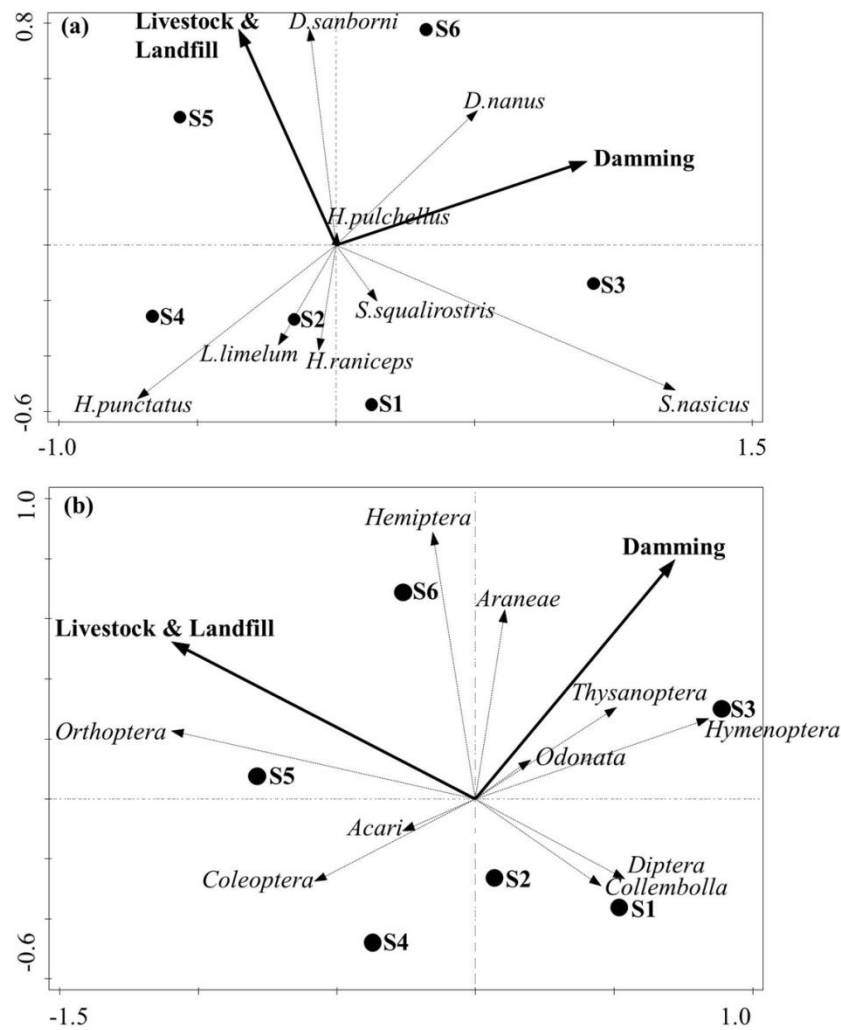


FIGURE 3. Redundancy analysis triplots using: (a) amphibian assemblage composition and habitat alteration gradient (centered and standardized by species; abundances $\ln(x+1)$ transformed and applying Hellinger standardization; eigenvalue axes 1 = 0.0859, 2 = 0.0473; species-environment pseudo-canonical correlations axes 1 = 0.6367, 2 = 0.5138; explanatory variables account for 13.3% of total variation; cumulative explained fitted variation axes 1 = 64.5%, 2 = 100%; Monte Carlo test of significance of canonical axes -499 unrestricted permutations-: pseudo- $F = 2.5$; $P = 0.002$); and (b) using more important arthropod orders of the trophic resources availability (items with more than 10% of relative abundance in any of the sites) and habitat alterations gradient (proportions of total abundance Arcsin transformed and applying Hellinger standardization; eigenvalues axes 1 = 0.0989, 2 = 0.0277; species-environment pseudo-canonical correlations axes 1 = 0.7299, 2 = 0.4924; explanatory variables account for 12.7% of total variation; cumulative explained fitted variation axes 1 = 78.11%, 2 = 100%; Monte Carlo test of significance of canonical axes -499 unrestricted permutations-: pseudo- $F = 2.4$; $P = 0.004$).

Trophic analysis.—Diet evenness, richness, and niche breadth did not vary significantly among sites or months (Table 3). There was seasonal variation in the number of prey consumed by *D. nanus* and *H. punctatus*, although no significant differences were found among any pair of months (Dunn test: $P > 0.05$ in all cases). For *L. limellum*, multicomparison Dunn tests showed significant differences in mean number of prey per gut between S4 and S1 (ranks mean difference = 15.5; $P < 0.05$) and between S4 and S6 (ranks mean difference = 16.35; $P < 0.05$). Niche breadth by species was: *D.*

nanus = 10.16, *D. sanborni* = 6.19, *H. pulchellus* = 25, *H. punctatus* = 38.58, *H. raniceps* = 4.87, *L. limellum* = 10.53, *S. nasicus* = 7.07 and *S. squalirostris* = 9.64.

Overlap among samples (month/site) was modest to low for the diet of eight species and prey availability (Table 4). Except for *H. pulchellus* and *S. nasicus*, observed overlap was higher than expected by chance (Table 4). For species except *D. nanus*, diet overlap among samples was lower than available prey overlap among samples (Table 4).

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TABLE 2. Relative abundance (percentages) of food resource taxa at six study sites, showing values for invertebrate groups that exceed 5%. Mites were identified at Subclass level, Acari.

Class, Order, Family	S1	S2	S3	S4	S5	S6
Entognatha						
Entomobryomorpha	4.86	1.37	5.99	3.15	2.52	11.73
Entomobryidae	4.86	1.37	5.99	3.15	2.52	11.73
Poduromorpha	-	-	0.3	-	-	-
Symphyleona	16.44	6.86	0.63	4.4	4.53	0.38
Sminthuridae	16.44	6.86	0.63	4.4	4.53	0.38
Insecta						
Blattaria	0.02	0.31	0.02	0.27	0.28	0.11
Coleoptera	1.93	5.42	1.49	10	11.59	3.22
Coleoptera larvae	0.16	0.49	0.08	0.80	7.48	0.09
Dermaptera	0.004	-	-	-	-	-
Diptera	44.12	43.09	50.91	43.75	32.44	34.17
Chironomidae	11.00	12.71	29.31	12.19	10.89	11.09
Chloropidae	1.90	0.45	0.47	1.23	1.48	6.45
Culicidae	14.94	11.05	13.78	5.96	7.87	6.90
Dolichopodidae	3.69	5.75	0.63	4.88	3.51	2.13
Muscidae	9.29	8.75	2.49	14.52	5.40	4.20
Hemiptera	13.35	17.74	13.24	11.99	12.81	24.89
Cercopidae	2.60	1.72	3.05	1.08	1.94	10.92
Cicadellidae	6.98	8.23	1.47	4.40	5.00	8.81
Hymenoptera	2.65	2.69	11.42	3.91	2	2.34
Formicidae	1.80	1.47	10.92	3.33	1.61	1.69
Lepidoptera	0.07	0.26	0.85	0.19	0.1	0.34
Mantodea	0.01	0.17	0.03	0.01	0.07	-
Neuroptera	0.02	0.01	0.27	-	-	0.02
Odonata	3.32	2.85	1.26	0.87	1.19	2.97
Orthoptera	1.45	8.69	0.71	3.89	13.24	8.89
Tettigonidae	0.98	5.29	0.34	1.96	11.94	5.22
Thysanoptera	5.54	0.51	4.16	0.88	5.71	2.67
Phlaeotripidae	4.40	0.25	2.70	0.43	5.07	2.05
Trichoptera	0.13	0.23	0.08	0.13	-	0.05
Indeterminate larvae	0.51	0.2	0.29	1.59	0.99	0.07
Arachnida						
Acari	3.41	6.30	2.14	10.51	6.82	4.34
Araneae	1.99	2.81	6.21	4.34	3.22	3.74
Malacostraca						
Isopoda	-	-	-	0.08	-	-
Gastropoda						
Pulmonata	0.18	0.51	-	0.04	2.49	0.07

There was significant co-variation between diet and prey availability for *D. nanus*, *H. pulchellus*, *H. punctatus*, and *L. limellum* (Table 4). Thus, samples (site/months) with greater similarity in environmental prey composition also were the samples with greater diet similarity for these four species. The co-variation between diet and prey availability was non-significant for the remaining species.

DISCUSSION

Feeding plasticity contributes to the adaptive evolution of populations exposed to new or altered

environments (Guedes et al. 2009). Herein, the response to spatial-temporal changes in trophic resources differed among analyzed anuran species. Responses were not phylogenetically structured, as closely related species (e.g. *Dendropsophus nanus* and *D. sanborni*; Faivovich et al. 2005) significantly differed in their feeding plasticity. Indeed, species considered to be more plastic belonged to three different genera (*Dendropsophus*; *Hypsiboas* and *Lysapsus*), two of which had members considered to be among the less plastic group of species (*Dendropsophus* and *Hypsiboas*).

Although most species occurred at every studied site, species relative abundances varied in association with

TABLE 3. Comparison of evenness (E), richness (R), niche breadth (Nb) and mean number of prey per gut (n) for diet of amphibians among study sites and sampled months with outcomes (*H*) of Kruskal-Wallis tests. An asterisk (*) indicates statistical significance at $P < 0.05$.

Species	Variable		E	R	Nb	n
<i>Dendropsophus nanus</i>	sites	<i>H</i>	2.031	5.686	5.596	2.883
		<i>P</i>	0.845	0.338	0.348	0.718
	months	<i>H</i>	9.128	8.682	4.05	14.19
		<i>P</i>	0.104	0.122	0.542	0.014*
<i>Dendropsophus sanborni</i>	sites	<i>H</i>	5.241	8.671	4.635	5.29
		<i>P</i>	0.387	0.123	0.462	0.382
	months	<i>H</i>	5.693	9.327	9.351	6.184
		<i>P</i>	0.337	0.097	0.095	0.289
<i>Hypsiboas pulchellus</i>	sites	<i>H</i>	0.894	6.609	5.911	4.58
		<i>P</i>	0.925	0.158	0.206	0.333
	months	<i>H</i>	5.084	9.044	9.27	2.387
		<i>P</i>	0.279	0.06	0.055	0.665
<i>Hypsiboas punctatus</i>	sites	<i>H</i>	3.218	8.148	5.558	4.181
		<i>P</i>	0.522	0.086	0.235	0.382
	months	<i>H</i>	7.446	1.254	1.696	9.845
		<i>P</i>	0.114	0.869	0.791	0.043*
<i>Hypsiboas raniceps</i>	sites	<i>H</i>	6.737	2.032	1.735	6.67
		<i>P</i>	0.241	0.804	0.884	0.245
	months	<i>H</i>	2.235	6.051	6.881	7.201
		<i>P</i>	0.816	0.301	0.23	0.206
<i>Scinax nasicus</i>	sites	<i>H</i>	3.101	5.578	3.881	3.467
		<i>P</i>	0.541	0.233	0.432	0.483
	months	<i>H</i>	6.253	3.892	8.272	5.1
		<i>P</i>	0.282	0.565	0.142	0.404
<i>Scinax squaleirostris</i>	sites	<i>H</i>	7.209	3.86	5.094	2.393
		<i>P</i>	0.206	0.57	0.405	0.793
	months	<i>H</i>	5.474	0.644	1.494	5.488
		<i>P</i>	0.361	0.986	0.914	0.359
<i>Lysapsus limellum</i>	sites	<i>H</i>	12.48	12.72	6.939	15.245
		<i>P</i>	0.29	0.26	0.225	0.009*
	months	<i>H</i>	6.604	6.162	9.306	3.502
		<i>P</i>	0.252	0.291	0.097	0.623

type of alteration. *Dendropsophus* species seem to be less affected by analyzed alterations. *Lysapsus limellum*, although abundant at every site, was more common in the less altered environments. *Scinax* species were less abundant in environments heavily affected by livestock and landfill, while *Hypsiboas* species were associated with a low degree of habitat alteration. Differences in amphibian assemblages among sites could not solely be attributed to trophic resource dissimilarities, despite the expectation that changes in prey availability due to local habitat characteristics certainly contribute to structure amphibian assemblages.

Shifts in prey composition.—As predicted, prey composition changed with habitat alteration of wetlands. The structure of arthropod assemblages changes across

habitat disturbance gradients (Basset et al. 2008), although these changes do not necessarily imply an overall reduction of diversity (Battles et al. 2013). Non-flying arthropods such as spiders and ants could be negatively affected by floods when nests and subterranean refuges are inundated (Prinzing et al. 2007). Thus, dam construction can favor the occurrence of more terrestrial taxa. Dragonflies also may be favored by the fragmentation of large permanent lakes into smaller semipermanent ponds because of reduced fish predation on eggs and aquatic larvae (Welborn et al. 1996). Xerothermophilic coleopterans, orthopterans, and mites may have been favored by riparian vegetation alterations produced by livestock and landfill (Lambeets et al. 2009). Collembolans are sensitive to changes in leaf litter humidity, plant cover, fire, and other habitat

TABLE 4. Diet overlap and trophic plasticity of eight hylid frog species. Pianka's (1973) niche overlap index (O_{jk}) depicts similarity of relative abundance of prey among samples (months and sites). Statistical significance (P) of measured overlap values among samples (O_{jk} obs) indicates difference from what would be expected by chance (O_{jk} exp). Prey with < 10% relative abundance were excluded from the analysis. For trophic plasticity, Mantel tests indicate the Pearson correlation coefficients (r) of dissimilarity matrices (Euclidean distance, average linkage aggregation criteria) of the diet of frogs and environmental prey composition. The genus *Dendropsophus* abbreviated *Dendro.*

Diet overlap and plasticity	<i>Dendro. nanus</i>	<i>Dendro. sanborni</i>	<i>Hypsiboas pulchellus</i>	<i>Hypsiboas punctatus</i>	<i>Hypsiboas raniceps</i>	<i>Scinax nasicus</i>	<i>Scinax squalirostris</i>	<i>Lysapsus limellum</i>	prey
O_{jk} obs	0.484	0.422	0.166	0.296	0.279	0.184	0.321	0.346	0.465
O_{jk} exp	0.239	0.165	0.145	0.16	0.176	0.189	0.146	0.196	0.292
$P(\text{obs} \leq \text{exp})$	1	1	0.877	1	0.999	0.473	1	1	1
$P(\text{obs} \geq \text{exp})$	< 0.001	< 0.001	0.123	< 0.001	0.001	0.527	< 0.001	< 0.001	< 0.001
r	0.293	-0.060	0.309	0.229	0.279	-0.249	0.195	0.164	
P	0.023	0.299	0.021	0.047	0.074	0.051	0.158	0.008	

perturbations (Trueba et al. 1999). Their abundance (mainly Sminthurids) in the study area decreased with increasing site perturbation (cattle overgrazing, fire, and bulldozing). The alteration in riparian areas can lead to significant changes in aquatic and semi-aquatic hemipterans composition even though species richness may not be affected and some families may increase their abundance under intermediate habitat disturbances (Dias-Silva et al. 2010; Bianchi et al. 2014).

The dispersal ability of flying insects (e.g. dipterans and hemipterans) and their capacity to recolonize sites after the periodical floods (Montalto and Paggi 2006) might explain their abundance in all sampled sites, compared to small non-flying insects (e.g. mites and springtails). Particularly, chironomids are among the most diverse and abundant insects of the Paraná River wetlands (Montalto and Paggi 2006; Zilli and Paggi 2013). The diversity of species with different life histories within nonbiting midges, hoppers, and froghoppers, allows the presence of assemblages with different species of these insects and maintain their abundance throughout the environmental gradient of wetlands (Zilli and Paggi 2013).

Differences in diet composition and trophic plasticity.—The few studies that analyzed the direct effect of habitat alteration on trophic niche dimension of amphibians have found some degree of diet change among habitats with different degrees of fragmentation, hydroperiod, and vegetation composition (Kovács and Török 1995; Falico et al. 2012b). In the studied species, we found a greater diet similarity among populations inhabiting environments with similar habitat alterations, independent of site location, reinforcing the idea that human disturbance of habitat affects amphibian trophic niche dimension, and that each disturbance conveys a different impact on biota. Moreover, the general absence of variation of diet diversity and mean number of prey per gut indicates that diet change among

populations is driven principally by a turnover in taxonomic composition of prey taxa. According to other studies (Menin et al. 2005; López et al. 2007; Falico et al. 2012b), taxonomic identity of principal prey items changes among populations, probably as a result of local prey availability, while the number (and their ecomorphological characteristics) of primary versus accessory prey remains relatively stable.

It has been proposed that the decrease or absence of some prey resources may negatively affect amphibians or cause the decline of entire populations (Blaustein and Wake 1995), but generalist species should be less susceptible to fluctuations in any particular food type than species that forage in a more specialized way (Williams et al. 2006). In our study, species such as *D. nanus*, *D. sanborni*, *H. punctatus*, and *H. pulchellus*, and to a lesser degree *S. nasicus* and *S. squalirostris*, that feed on superabundant prey, such as chironomids, should be less vulnerable to perturbations in the riparian environment occurring in the floodplain. In the same way, species feeding on ants could be favored in sites with damming alterations. In spite of the abundance of ants in dammed sites, studied frogs fed only secondarily on this resource (but see Peltzer and Lajmanovich 2000). This is probably associated with physiological restrictions on the consumption of formic acid in ants (Zug and Zug 1979).

Most authors have described the studied species as generalist feeders (Basso 1990; Duré and Kehr 2001; Menin et al. 2005; Macale et al. 2008; Falico et al. 2012a) and, in a few cases, as specialist or intermediate feeders (between generalist and specialist; Basso 1990; Peltzer and Lajmanovich 2000, 2001; Maneyro and Da Rosa 2004; Macale et al. 2008). Foraging designations have differed among authors. For example, *D. sanborni* has been characterized as a specialist (Macale et al. 2008), intermediate (Basso 1990), and generalist forager (Menin et al. 2005). *Dendropsophus nanus* has similarly been identified as a specialist (Basso 1990; Macale et al.

2008), intermediate (Peltzer and Lajmanovich 2000), and generalist (Menin et al. 2005). The lack of prey availability data in these studies may have lead to misleading classifications of the foraging patterns of frogs (López et al. 2009). On the one hand, our results support the classification of *D. nanus*, *H. pulchellus*, *H. punctatus* and *Lysapsus limellum* as generalist feeders, capable of adjusting their diet to prey shifts and having greater niche breadth. Generalist foragers typically have highly flexible diet breadth that depends on the relative value and availability of different food types (Stephens and Krebs 1986) and may opportunistically prey upon momentarily abundant resources (Falico et al. 2012a). This may explain differences in niche breadth reported among authors (Duré and Kehr 2001; Menin et al. 2005; Macale et al. 2008; Falico et al. 2012a; and this study). On the other hand, *D. sanborni*, *H. raniceps*, *S. nasicus*, and *S. squalirostris* could be classified as intermediate feeders (Basso 1990; Peltzer and Lajmanovich 2001). They may have a wide niche breadth (e.g., *S. nasicus*: Peltzer and Lajmanovich 1999), but also display less trophic flexibility, thereby increasing their susceptibility to fluctuations in food resources.

The association between prey selection and seasonal or geographical changes in prey availability has been analyzed for few amphibian species (Measey 1998; Maneyro and Da Rosa 2004; Peltzer et al. 2010). The higher trophic plasticity observed in *L. limellum*, *D. nanus*, *H. pulchellus*, and *H. punctatus* can be considered an adaptive advantage in changing environments (DeWitt and Scheiner 2004). In this way, the ability to follow spatiotemporal variations in prey availability, by shifting diet composition, would allow these species to improve resource acquisition. However, most of species (with the exception of *P. limellum* and *H. raniceps*) showed a tendency to feed on superabundant prey like chironomids, which would reduce to some extent the detrimental effects of resource changes. In contrast, *H. raniceps* exhibited low trophic plasticity and fed mostly on larger and less abundant prey, which suggests a higher susceptibility to variation in trophic resources. This observation is consistent with the reduced abundance of this species observed in the most altered environments.

Conclusions.—The assessment of amphibian trophic plasticity can identify species highly vulnerable to habitat alterations which are associated with trophic resource modification and can predict which species might be favored inside the increasingly human disturbed environmental matrix. Changes in resource availability and use due to habitat modification are sensitive ecological indicators that could anticipate future population declines and changes in community composition (Dempster and Pollard 1981; Yang et al. 2008). This information should be valuable for future

studies and wetland conservation programs. Determining the effects of habitat alteration on amphibian populations requires an understanding of ecological relationships that exceed the analysis of species patterns of occurrence and their relationship to abiotic factors (Smallbone et al. 2011). To maintain ecological structure of wetland landscapes, it is particularly important to preserve vegetation structure and hydrological regime (Tilton 1995). For example, preventing use of fire as a management strategy for livestock grazing would undoubtedly help to protect amphibians and their prey habitats, preserving in turn the natural interactions and dynamics of populations. As the use of riparian environments or large rivers for agricultural or industrial purposes increases (Lavilla 2002), understanding the ecological process affected by habitat alteration represents an important initial task to preserve the great biodiversity of floodplain habitats.

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