Herpetological Conservation and Biology 16(2):259–270.
Submitted: 16 May 2020; Accepted 7 April 2021: Published: 31 August 2021.

Potential Effects of Dams in the Geographic Range Expansion of Hylid Frogs Associated with Aquatic Macrophytes

Pablo J. Torres[1], Juan M. Boeris[1], Juan A. Insaurralde[2], Diego Baldo[1], and Andrés E. Brunetti[1,3]

[1]*Laboratorio de Genética Evolutiva "Claudio Juan Bidau," Instituto de Biología Subtropical (IBS, UNaM-CONICET), Félix de Azara 1552, Posadas, 3300, Misiones, Argentina*
[2]*Instituto de Biología Subtropical (IBS, UNaM-CONICET), Bertoni 85, Puerto Iguazú, 3370, Misiones, Argentina*
[3]*Corresponding author: andresbrunetti@gmail.com*

Abstract.—**The Fluorescent Frog (*Boana punctata*) and the Uruguay Harlequin Frog (*Lysapsus limellum*) are two hylid species found in seasonal swamps and along large rivers in South America. Despite their wide distribution in the Amazon and Paraná River basins, they had never been recorded along the margins of the more than 340 km of the Paraná River in the provinces of Misiones, Itapúa, and Alto Paraná in Argentina and Paraguay. Comparisons of historical and recent satellite images and analyses of the Paraná River structure indicate that the lake formed after the construction of the Yacyretá Dam (140,000-160,000 ha), which has made novel lentic and semi-lentic environments in the tributary streams identified as large inlets, bays, and lagoons. These transformations favored permanent settlement of aquatic macrophytes, mainly Water Hyacinth (*Eichhornia crassipes*) and floating ferns (*Salvinia* sp.), which are the characteristic habitat of *L. limellum* and *B. punctata*. Because of these changes, we conducted surveys by boat and from shore to determine whether these frog species colonized the novel environments. We found *L. limellum* and *B. punctata* at several localities on the margins of Paraná River within the boundaries of the Yacyretá Lake. Because all observations of both species were at sites with abundant macrophytes, and because neither of them were found in field surveys we conducted before 2011 (i.e., when the Yacyretá Lake filled to maximum capacity), our results support the hypothesis that the new records are related to the artificial wetlands created after the construction of the Yacyretá Dam.**

Key Words.—amphibians; aquatic plants; *Boana punctata*; habitat loss riverine; *Lysapsus limellum*; Misiones; tree frogs; Yacyretá Dam

Introduction

Aquatic macrophytes are essential components of riverine ecosystems (Wetzel 2001) and provide habitat to a rich micro- and macroinvertebrate fauna (Collins and Williner 2006; Battauz et al. 2017). Because annual fluctuations of the hydrometric levels of large rivers displace extensive beds of macrophytes (Battauz et al. 2017), suppression of flood pulses by dam construction has profound effects on the distribution of this type of vegetation (Finer and Jenkins 2012). One of the main effects of reservoirs upstream of dams is the transformation of lotic ecosystems into lentic or semi-lentic environments that changes the biotic composition and the viability of populations of many riverine species (Bunn and Arthington 2002; Agostinho et al. 2008).

The Paraná River is the main river within del Plata Basin, the second largest in South America. It has an annual discharge of 500 million m^3, with peak flows of 65,000 m^3s-1, extensive fertile lands, and is one of the most important rivers in the world (Bonetto et al. 1989). Besides these natural characteristics, the Paraná River is the most intensively dammed river of South America, particularly in the Upper and High sections, which serve mainly to produce hydropower (Bonetto et al. 1989; Agostinho et al. 1994). The Yacyretá Dam is the second largest dam on the Paraná River and was constructed between Argentina and Paraguay (27°28′58.01″ S, 56°44′8.99″ W). In 2011, the reservoir of Yacyretá reached its maximum height (83 m above sea level), creating an artificial lake of 140,000-160,000 ha (Fulco 2011; Brites and Catullo 2016). When Yacyretá Lake filled, the water from the main reservoir inundated large sections of tributaries that drain into the river (Fontana and Iriarte 2016; Fulco 2011), creating inlets or bays. These inlets have spatial and seasonal characteristics such as shallow waters, increased nutrient input, protection from wind, and higher sedimentation rates that create favorable environments for the colonization and settlement of aquatic macrophytes (Thomaz et al. 1999). Although the effect of habitat modification on fish fauna was assessed in reservoirs from the Upper Paraná section (Benedicto-Cecilio et al. 1997; Agostinho et al. 1994, 2008), no research has examined the impact of habitat alteration as a consequence of dam construction in the Paraná River on amphibian diversity.

Several Neotropical hylid frogs (Anura: Hylidae: Hylinae) live near or by the margins of large rivers (particularly in floodplains and slow-flowing river channels), where they are strongly associated with aquatic macrophytes such as Water Hyacinth (*Eichhornia crassipes*), Horsetail Paspalum (*Paspalum repens*), and Floating Primrose-Willow (*Ludwigia peploides*; Hödl 1977; Manzano et al. 2004). Some of these frogs possess morphological adaptations for living in water, such as a paddle-like autopodium (species of the tribe Pseudini; Goldberg and Fabrezi 2008). The reproductive activities of the species living in these environments are tightly associated with aquatic macrophytes and vary in relation to the class and height of the vegetation used (Hödl 1977; Prado et al. 2005; Brunetti et al. 2014, 2015). For instance, males of the Uruguay Harlequin Frog (*Lysapsus limellum*) use plants that lie flat on the water surface like species of floating ferns (*Salvinia* sp.) and Water Cabbage (*Pistia stratiotes*; Hödl 1977). In contrast, the Fluorescent Frog (*Boana punctata*) uses plants with vertical structure like *E. crassipes*; males emit territorial calls at heights of approximately 40–70 cm or perform complex courtship behaviors at the water surface level (Brunetti et al. 2014).

Boana punctata and *L. limellum* are common hylid frogs with a wide distribution in South America. In Argentina, both species have a high degree of sympatry in the provinces of Chaco, Formosa, Corrientes, Entre Ríos, and Santa Fe along the Paraná and Paraguay Rivers (Vaira et al. 2012). Despite their common occurrence, they were never reported in the more than 340 km of Paraná River in the provinces of Misiones, likely because the river structure was characterized by a single and narrow channel (Peso et al. 2013), which lacked the suitable lentic habitat conditions for these species (Hödl 1977; Manzano et al. 2004). Here, we analyze the alterations on the shape and structure of the Paraná River generated by the construction of the Yacyretá upstream of the boundaries of the Yacyretá Lake aiming to (1) investigate the presence of *B. punctata* and *L. limellum*, (2) compare these presence/absence data with our amphibian surveys before 2011 (i.e., prior to the lake filling to maximum capacity), and (3) connect the presence of these hylid frogs to the altered structure of the Paraná River and the diversity and abundance of aquatic macrophytes. We predict that the novel lentic environments created by damming the river generated habitats that became occupied by amphibian species typical of these environments, which were not previously registered at this high section of the Paraná River.

Materials and Methods

To test our hypothesis that environmental transformations related to the construction of the Yacyretá Dam favored the occupation of typically lentic amphibian species, we examined temporal and spatial variables, assessed macrophyte density, and conducted fieldwork studies to explore these novel environments as potential habitats for the establishment of *B. punctata* and *L. limellum*. For the temporal variable, we compiled a list of geo-referenced locality records for both species in the Paraná River Basin based on published literature (Brusquetti and Lavilla 2006; Weiler et al. 2013), available biodiversity databases (Global Biodiversity Information Facility. 2020. Available from https://doi.org/10.15468/dl.5ffqhq [Accessed 07 May 2020]), and information from the Herpetological Collection of the Laboratorio de Genética Evolutiva (LGE). Reports covered a wide span including the period before Yacyretá Dam creation in 1998 (about 1900–1998), the period from creation till the Yacyretá lake reached its maximum height in 2011, and the period from 2011 till present. We considered observations at sites surveyed by members of our laboratory before 2011 as pre-maximum height data. We located these on maps using satellite images from the years 1990, 2005 and 2020, and applied identifying water indices according to McFeeters et al. (1996) and two vegetation indices, Green Chlorophyll Index and Normalized Difference Vegetation Index (Ahamed et al. 2011; Hunt et al. 2011). We processed the satellite images with the Google Earth Engine platform using the Landsat 5 and 8 image collections (Gorelick et al. 2017).

We examined satellite images for 2019 (Google Earth Pro v.7.3.2.5776) to account for spatial variation and categorize the habitats likely having macrophytes along the shores of the High Section of the Paraná River for approximately 340 km in the province of Misiones, Argentina. Because aquatic macrophytes represent the characteristic habitat of *B. punctata* and *L. limellum*, we identified four habitats, small inlets, large inlets, bays, and lagoons, where this type of vegetation likely accumulates within the boundaries of the Yacyretá Lake, as follows. Inlets formed when lower parts of the tributaries draining into the Paraná River were flooded. In satellite images, they are distinguishable by a narrow channel, which connects the tributaries to the reservoir, and by a wetted width that is permanently inundated. We categorized these inlets as large when the length was ≥ 3 km, or small when it was ≥ 500 m and < 3 km (measured with Google Earth Pro v.7.3.2.5776; Fig. 3). Bays are similar to inlets but connect to the river by a wide mouth (i.e., width > 2 km length), and in most cases, not related to seasonal rains that flood tributaries (Fig. 3). Lagoons are flooded areas where the long axis parallels the flow direction of the river. In contrast to inlets and bays, lagoons connect to the river at more than one point (Fig. 3). In satellite images before 2011, we did not observe the four habitats defined above, which is consistent with the absence of a flooded valley at this section of the Paraná River before the Yacyretá Dam construction (Peso et al. 2013).

After satellite imagery analysis, we performed field surveys from September 2019 to 2020 at six localities and 12 sites: Posadas (Po1 and Po2), Candelaria (Ca1 and Ca2), San Ignacio (Si1, Si2, and Si3), Corpus Christi (CC1, CC2,

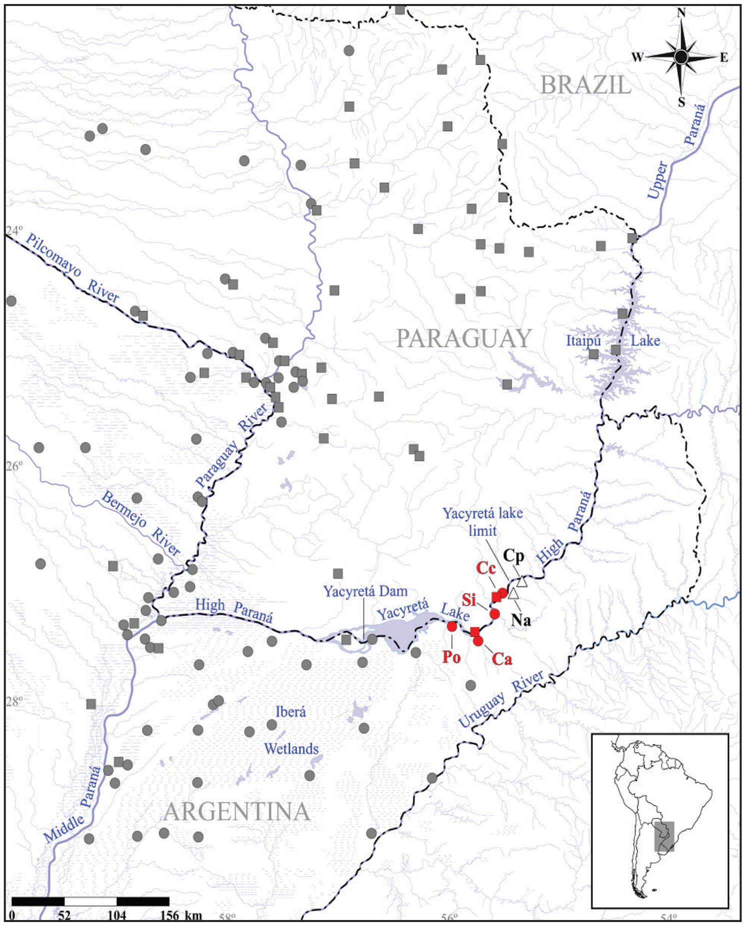


Figure 1. Historical records (grey) of the Fluorescent Frog (*Boana punctata*; squares) and the Uruguay Harlequin Frog (*Lysapsus limellum*; closed circles) in the Paraná River Basin adjacent to the Yacyretá Dam, in the Province of Misiones, Argentina. Contemporary observations (presence = red, white = absence) at sites sampled for this study along the margins of Paraná River in Misiones, Argentina. Site abbreviations are Po (Posadas), Ca (Candelaria), Si (San Ignacio), Cc (Corpus Christi), Ñacanguazú stream (Na), and Colonia Polana (Cp).

and CC3), Ñacanguazú stream (Na), and Colonia Polana (Cp; see Appendix Table 1 for the coordinates associated with each site). More than 130 river km separate the two most distant localities (Po and Cp). We described each site using our categories of inlet (small or large), bay, or lagoon, and classified the presence or absence of macrophytes: *E. crassipes*, *Salvinia* sp., *P. stratiotes*, and South American Spongeplant (*Limnobium spongia*). We analyzed macrophyte coverage at different sites with two methods; remote sensing using the Green Chlorophyll Index (Hunt et al. 2011), and direct observations in the field. For the second method, we categorized the presence of the most prominent macrophyte, *E. crassipes*, as abundant or few when the density was greater or lower than 50 m^2, respectively. We conducted field surveys in spring and summer, which coincided with the breeding season of both species in Argentina (Brunetti et al. 2014, 2015; Manzano et al. 2004). We listened for the characteristic vocalization emitted by each species (Brunetti et al. 2014; Garda et al. 2007) and visually searched different heights of the aquatic plants. Each survey lasted one day and was conducted during the afternoon (1500–1900) and after sunset (1900–2200). Groups of two to three researchers made observations from within the Paraná River using small watercraft (i.e., canoes, kayaks, and stand-up paddleboards) or walking along the shores. For voucher specimens, we euthanized frogs of both species with lidocaine, fixed them in formalin 10%, and preserved them in ethanol 70%. We deposited specimens in the Herpetological Collection of LGE, "Claudio J. Bidau", of the Instituto de Biología Subtropical (IBS-CONICET-UNaM), Posadas, Misiones, Argentina (Appendix Table 2).

Results

Historical records of *B. punctata* and *L. limellum* in the Paraná Basin show that both species are tightly associated with the large rivers, Pilcomayo, Paraguay, and Paraná (Fig. 1). *Lysapsus limellum* occurs widely in the Iberá Wetlands in Argentina and nearby streams located west of the Paraguay River. *Boana punctata*

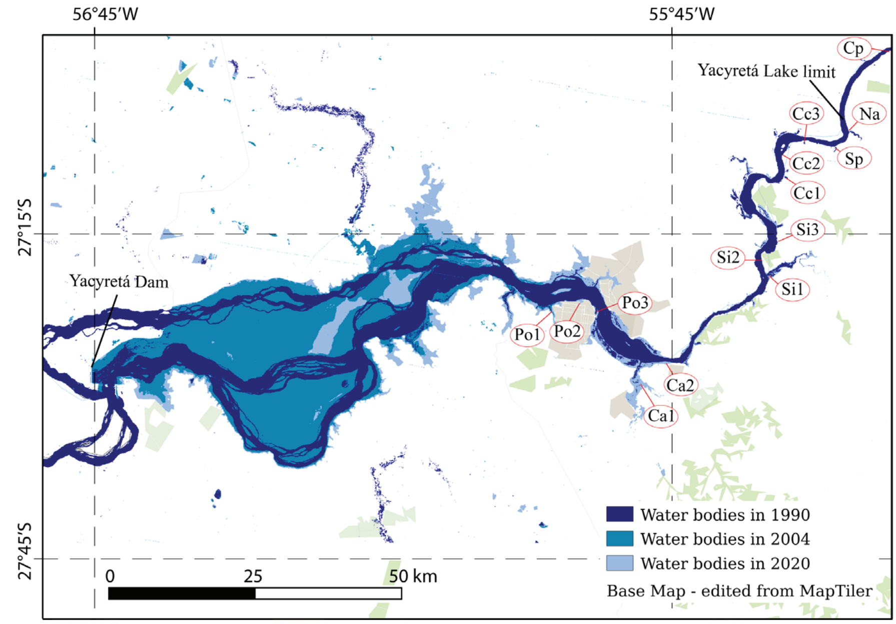


Figure 2. Map of the Paraná River calculated from the standard difference water index (McFeeters et al. 1996). Shades of blue indicate three critical time periods: 1990, before the opening of the Yacyretá Dam; 2004, after the opening of the dam and before the reservoir reached maximum capacity in 2011; 2019-2020, nine years after the maximum capacity reached. Five sites surveyed between 1998 and 2005 (Po1, Po2, Po3, Ca1, and Sp) were considered as pre-maximum height data for comparison. Three sites (Po1, Po2, and Ca1) were also surveyed between the years 2019-2020. Remaining sites surveyed between the years 2019-2020. Details of abbreviations for localities and sites in Table 1; geo-locations in Appendix Table 1.

occurs widely around different streams located between the Paraná and Paraguay Rivers. Along the Paraná River, both species occur downstream of the Yacyretá Dam in the Middle sections of the river, and in the High Section from the Paraguay River mouth to the Yacyretá Dam, and *B. punctata* also occur at the Paraná Upper Section in the Itaipú Lake. Neither of these species, however, was reported historically in the High Section of Paraná River along the 430 km section between Itaipú and Yacyretá Dams, including 340 km in the province of Misiones, Argentina (Fig. 1).

The Yacyretá Dam generated significant changes to the structure of the Paraná River at its High section (Fig. 1), which we clearly identified in maps by the formation of a reservoir of more than 140,000 ha and the permanent flooding of large islands (Fig. 2). When the reservoir reached its maximum capacity in 2011, the structure of the river changed significantly with bays and inlets along the shoreline, and permanent wetlands that did not exist before at this section of the river (Figs. 2, 3). Because the high interference with water impeded the estimation with remote sensing using the Green Chlorophyll Index (Appendix Figure), we determined that direct observations was the reliable method. We found that, regardless of categorization as inlet, bay, or lagoon, most of the margins of these areas were covered with high densities of macrophytes, of which *E. crassipes*, *Salvinia* sp., and *L. spongia* were the most recognizable (Fig. 3). In large inlets, like the one represented by Ca1 (Fig. 2), there were big, fixed islands of *E. crassipes* (Fig. 3). Also, on windy days, we commonly observed islands of *E. crassipes* moving downstream and within the bays (Fig. 3). In contrast, upstream of the limit of the Yacyretá Lake in Na and Cp (Fig. 1) we recorded no *E. crassipes*. Upstream of the influence of Yacyreta Lake, the Paraná River had the typical habitat composition of this section, comprised of a single water channel with rocky and sandy margins without inlets, bays, or lagoons, and without permanent macrophyte settlements (Fig. 3).

Surveys from the years 1998, 1999, and 2005 (i.e., prior to maximum reservoir elevation), along the margins of the Paraná River at the same or nearby coordinates as surveys we made post dam and reservoir filling, showed absence of *B. punctata* and *L. limellum* (Table 1). Aside from Po3, we found no *E. crassipes* in the study reach prior to reservoir inundation (Table 1); however, in 2019 and 2020 surveys, we observed *B. punctata* and *L. limellum* in three (Ca, Si, and Cc) and four localities (Po, Ca, Si, and Cc), respectively (Table 1; Figs. 1, 2). We observed *B. punctata* at Ca2, a bay, and Cc1, a small inlet (Table 1, Fig. 2). We also found *B. punctata* at Si1 in two small bays at the confluence of the Paraná River and the large inlet formed by the Yabebiry Stream (Table 1, Fig. 1). All of these sites had extensive mats of *E. crassipes* (> 50 m^2). Despite the high density of *E. crassipes* and the proximity to Ca1, we did not find *B. punctata* at Ca2, a subsite categorized as a large inlet. In contrast, within

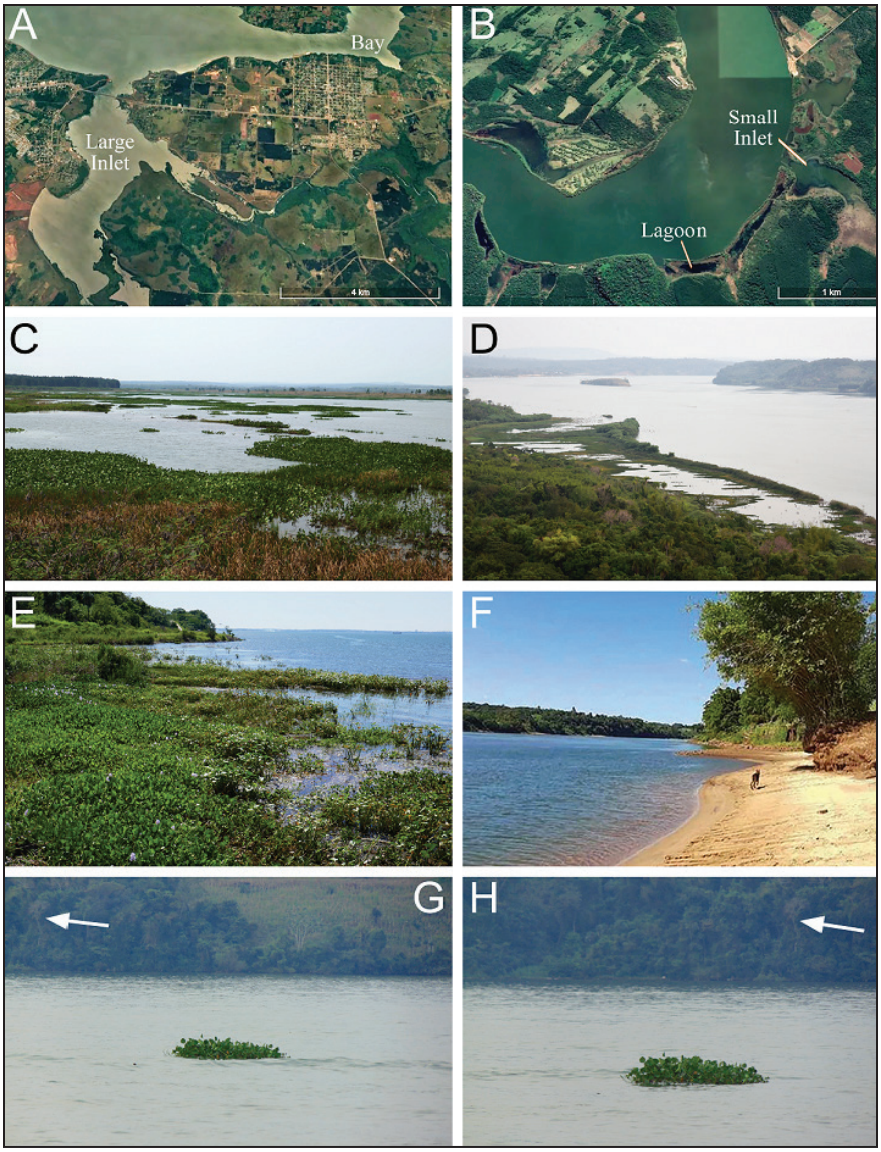


Figure 3. Novel environments created by the Yacyretá Lake on the High section of the Paraná River in the province of Misiones, Argentina (see text for further details). Satellite images from Candelaria (A) and Corpus Christi (B) depict small and large Paraná River at a Large Inlet in Candelaria (C), a lagoon in San Ignacio (D), a bay in Candelaria (E), and at a typical shore environment at the high section of the Paraná River upstream of the Yacyretá lake in Eldorado (F). Macrophyte raft moving by the main course of the Paraná River on the Yacyretá Lake (G, H; white arrow points to a reference tree). Abbreviations are W = width and L = length. (C-E photographed by Andrés E. Brunetti; F by Lourdes Rambo, and G, H by Pablo J. Torres).

the localities situated between Po and Cc (about 130 km; Fig. 2), we found *L. limellum* in all types of lentic habitats, with either high or low densities of *E. crassipes*, yet all sites had abundant flat floating macrophytes, such as *Salvinia* sp., *P. stratiotes*, and *L. spongia* (Table 1, Fig. 4). We did not detect *B. punctata* or *L. limellum* in Na and Cp, two localities situated at 8 and 24 km, respectively, from Cc3, which represents the upstream limit of the Yacyretá Lake (Fig. 1). Though Na and Cp resemble small inlets, they lack most of the characteristics found in similar environments within the Yacyretá Lake: very few macrophytes, no *E. crassipes*, and abundant vegetation characteristic of the Atlantic Forest at the margins.

We observed males of *L. limellum* vocalizing on floating macrophytes (Fig. 3) or, more frequently, semi-submerged in water during the afternoon and at night. In contrast, we observed male and female *B. punctata* on the roots at the water surface or at different heights above the water standing on the leaves or the petioles of *E. crassipes* (Fig. 4). We heard vocalizations of *B. punctata* soon after sunset (1900) and until the end of the surveys (2200), but in one of the surveys, we detected them only by visual encounters. We collected males and females of both species as vouchers.

Table 1. Association of the Fluorescent Frog (*Boana punctata*) and the Uruguay Harlequin Frog (*Lysapsus limellum*) with the presence of macrophytes (Water Hyacinth, *Eichhornia crassipes*, and floating ferns, *Salvinia* sp.) in the High Section of the Paraná River in the Province of Misiones, Argentina. Asterisks (*) depict sites surveyed prior to Yacyretá Lake filled to maximum capacity in 2011.

Locality	Site	Date	River structure	*Lysapsus limellum*	*Boana punctata*	*E. crassipes*	*Salvinia* sp.
Posadas (Po)	Po1	22 November 2019	Large Inlet	> 20	0	abundant	abundant
	Po1*	22 May 1998	Margin	0	0	absent	absent
	Po2	3 January 2020	Bay	> 20	0	abundant	few
	Po2*	17 October 1998	Margin	0	0	absent	absent
	Po3*	3 January 2005	Margin	0	0	absent	absent
Candelaria (Ca)	Ca1	10 October 2020 17 October /2020 28 October 2020	Large Inlet	> 50 > 50 > 50	0 0 0	abundant	few
	Ca1*	27 October 1999 3 January 2005	Stream tributary	0	0	absent	absent
	Ca2	24 November 2019 29 November 2109 31 January 2020	Bay	> 20 > 20 > 20	> 20 > 20 > 20	abundant	abundant
San Ignacio (Si)	Si1	7 December 2020	Bays at confluence of large inlet	> 50	> 20	abundant	abundant
	Si2	14 November 2019 6 September 2020	Lagoon	> 50 > 50	0	abundant	abundant
	Si3	9 October 2019	Bay	> 50	0	abundant	few
Corpus Christi (Cc)	Cc1	15 January 2020	Small Inlet, Lagoon	> 50	> 50	abundant	few
	Cc2	15 January 2020	Lagoon	> 50	0	abundant	few
	Cc3	15 January 2020	Small inlet, Lagoon	> 50	0	abundant	few
Santo Pipo stream	Sp1*	30 January 1998	Stream tributary	0	0	absent	absent
Ñacanguazú Stream (Na)	Na	4 January 2020	Small Inlet	0	0	absent	absent
Colonia Polana (Cp)	Cp	16 December 2019	Stream tributary	0	0	absent	absent

Discussion

We registered the first occurrences of *B. punctata* and *L. limellum* at several localities on the High Section of the Paraná River in the province of Misiones, Argentina. Our observations made pre- and post-dam are consistent with the hypothesis that three interlinked conditions were associated with the expansion: (1) the formation of new wetlands after the construction of the Yacyretá Dam (Meichtry de Zaburlín et al. 2013); (2) the strong association of both frog species with aquatic macrophytes (Hödl 1977); and (3) the role of macrophytes rafts as dispersal vectors for the frogs in riverine ecosystems worldwide (Schiesari et al. 2003; Bell et al. 2015; Guerrero et al. 2017), including the Paraná Basin (Achaval et al. 1979). *Boana punctata* and *L. limellum* usually occur in the floodplains of large rivers that are characterized by aquatic or marshy vegetation (Hödl 1977; Duellman 1978; Da Silva and Bates 2002; Garda et al. 2010). Despite their wide distribution in South America where they occur in different biogeographical regions like Amazonia, Cerrado, Pantanal, Chaco, and Atlantic Forest (Gallardo 1961; Duellman 1978; Brusquetti and Lavilla 2006;

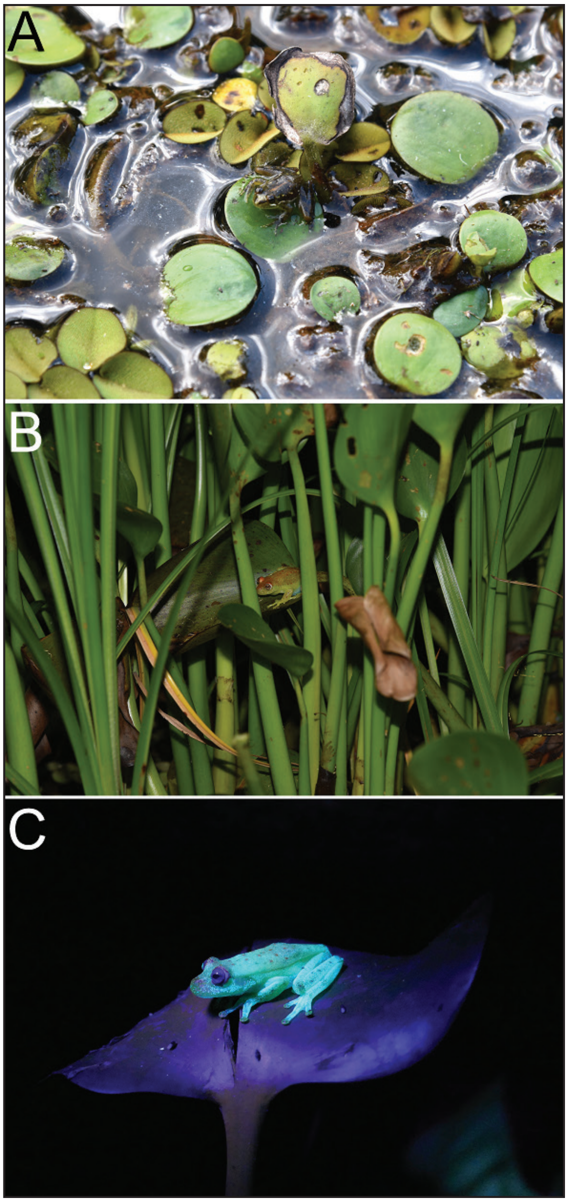


Figure 4. (A) Male individuals of the Uruguay Harlequin Frog (*Lysapsus limellum*) standing on leaves of floating ferns (*Salvinia* sp.). (B) Male of the Fluorescent Frog (*Boana punctata*) standing on leaves of Water Hyacinth (*Eichhornia crassipes*) under white light and (C) fluorescing under UV-light. Notice the use of flat macrophytes by *L. limellum* (A) and *B. punctata* (B, C), respectively. (A,B photographed by Andrés E. Brunetti; C by Pablo J. Torres and Andrés E. Brunetti).

Prado et al. 2005; Garda et al. 2010), these species had never been recorded along the almost 430 km at the High Section of the Paraná River between the Yacyretá and Itaipú Dams. Our observations at sites located in the biogeographical regions of Southern Cone Mesopotamian Savanna and Alto Paraná Atlantic Forest (sensu Olson et al. 2001), represent the first records for both species at this portion of the Paraná River. The nearest sites previously documenting *B. punctata* are downstream of Yacyretá Dam in the Apipé Island (Corrientes province), a straight-line distance of 130 km SW (Baldo et al. 2002), whereas upstream of this dam, previous records are about 250 km northeast (straight line) on the margins of the Itaipú Lake (Flavia Netto, pers. comm.). Prior records of *L. limellum* downstream of Paraná River also correspond to Apipé Island (Álvarez et al. 2002). For this species, an old record of two specimens in a temporary pond is more than 45 km West of the Paraná River in the province of Misiones, Argentina (Céspedez and Klein 2002).

Although limited research exists on the influence of dam construction on amphibians, studies suggest that habitat changes may favor the settlement of species that were not registered before (Stanescu et al. 2015). Conversely, dams may adversely impact populations that were common before flooding, particularly species that require intact stream habitat (Brandão and Araujo 2008; Naniwadekar and Vasudevan 2014; Stanescu et al. 2015). Given our results, we suggest that the creation of previously non-existent habitats like inlets, bays, and lagoons allowed colonization by *B. punctata* and *L. limellum*. These habitats offer protection from the wind and facilitate sedimentation, allowing permanent settlement of large areas of aquatic macrophytes that are suitable habitats for both species. In support of this inference, the upstream limit of the Yacyretá Lake, near the town of Corpus Christi (Cc), coincides with the upstream extent of large areas with permanent settlements of macrophytes and the new records of *B. punctata* and *L. limellum* on the Paraná River in Misiones.

Though *B. punctata* and *L. limellum* rely on floating vegetation along the margins of big rivers where they can camouflage during the day (Taboada et al. 2020), the two frog species differed markedly in the type and characteristics of the vegetation they use. While *B. punctata* uses the vertical structure of plants like *E. crassipes* and *P. repens* for their complex social interactions (Brunetti et al. 2014, 2015), and stand out over the red color of *E. crassipes* with their green-cyan fluorescence (Taboada et al. 2017; Fig. 4), *L. limellum* uses aquatic plants that lie flat over the water surface such as *Salvinia* sp. (Hödl 1977). The differing habitat-use of *B. punctata* and *L. limellum* may explain the distribution we documented of these species in the Paraná River under the influence of Yacyretá Dam. For instance, we only observed *B. punctata* in sites with a high density of *E. crassipes*, whereas we found *L. limellum* across a variety of densities of *E. crassipes* from low to high.

The distribution pattern of both frog species in the Yacyretá Lake may be explained by their potential forms of dispersal. In particular, the strong association between *B. punctata* and *Eichhornia* spp. suggests that when flood pulses or wind displace rafts of these macrophytes, they can serve as important dispersal vectors (Guerrero et al. 2017; Schiessari et al. 2003; Hödl 1977). Because there are old records of this species at the Itaipú Lake (upstream of all sites we surveyed), it is feasible that *B. punctata* may have dispersed into the surveyed wetlands via rafts, which can travel tens of km per day (Schiessari et al. 2003). This scenario could also explain why we observed *B. punctata* only in sites close to the river margins, like bays and lagoons, and not in large inlets where macrophytes occur > 3m from the mainstem Paraná River shore. Similar to *B. punctata*, *L. limellum* may also use macrophyte rafts for dispersal along the course of the large rivers, but unlike *B. punctata*, the observation of different populations of *L. limellum* at large inlets and at ponds disconnected from the river system indicate that this species can move longer distances in the water independently of macrophytes or the path of the river.

Our study suggests a tight relationship between the environmental changes produced by the construction of Yacyretá Dam and the distribution of two hylid species that had not been previously observed along several kms at the High section of the Paraná River. The creation of novel lentic and semi-lentic habitats and the arrival of *B. punctata* and *L. limellum* are connected by the permanent establishment of aquatic macrophytes. We strongly believe the potential for dispersal of different plant and animal species into human-altered environments deserves the same concern and attention as dispersal within well-established natural environments. This belief is supported by the reconciliation ecology concept aiming to redesign and rethink anthropogenic habitats so that they are compatible with use by other species (Rosenzweig 2003). In particular, because wetlands are considered one of the most biological diverse ecosystems on earth (Keddy 2010), we recommend a reconciliation approach to manage the novel wetlands along the shores of the Yacyretá Lake. This approach would allow assessing these novel environments not just as isolated habitats, but in terms of a bigger wetland corridor that protects diversity and species interactions.

Acknowledgments.—We thank Flavia Netto for sharing information on occurrences of amphibians in the Itaipú Reservoir. We are grateful to Míriam C. Vera for her assistance in the field and to Hernán Maidana for loaning the stand-up paddle used during fieldwork. Lourdes Rambo provided the photograph of the Paraná River in Puerto Rico. We also thank Carolina Miño and Eduardo N. Brunetti for providing important suggestions that significantly improved the quality of the manuscript. All authors were supported by Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) PICT 2015-2381, 2018-03349. Collection permit was issued by Ministerio de Ecología y Recursos Naturales Renovables, Province of Misiones (Disp. 029, Exp. 9910-00049/18). We are grateful to the constant support of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

Literature Cited

Achaval, F., J.G. González, M. Meneghel, and A.R. Melgarejo. 1979. Lista comentada del material recogido en Costas Uruguayas, transportado por camalotes desde el Rio Paraná. Acta Zoológica Lilloana 35:195–200.

Agostinho, A.A., H.F. Júlio, Jr., and M. Petrere, Jr. 1994. Itaipu reservoir (Brazil): impacts of the impoundment on the fish fauna and fisheries. Pp. 171–184 *In* Rehabilitation of Freshwater Fisheries. Cowx, I.G. (Ed.) Osney Mead, London, UK.

Agostinho, A.A., F.M. Pelicice, and L.C. Gomes. 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Brazilian Journal of Biology 68:1119–1132.

Ahamed, T., L. Tian, Y. Zhang, and K.C. Ting. 2011. A review of remote sensing methods for biomass feedstock production. Biomass and Bioenergy 35: 2455–2469.

Álvarez, B.B., H.G. Aguirre, J.A. Céspedez, A.B. Hernando, and M.E. Tedesco. 2002. Atlas de Anfibios y Reptiles de las Provincias de Corrientes, Chaco y Formosa (Argentina) I (Anuros, Cecílidos, Saurios, Amphisbénidos y Serpientes). Universidad Nacional del Nordeste. Corrientes, Argentina.

Baldo, D., E. Krauczuk, and P. Suárez. 2002. *Hyla punctata rubrolineata,* Lutz, 1951 (Anura, Hylidae). Cuadernos de Herpetología 16:79–91.

Battauz, Y.S., S.B. José de Paggi, and J.C. Paggi. 2017. Macrophytes as dispersal vectors of zooplankton resting stages in a subtropical riverine floodplain. Aquatic Ecology 51:191–201.

Bell, R.C., R.C. Drewes, A. Channing, V. Gvoždík, J. Kielgast, S. Lötters, B.L. Stuart, and K. R. Zamudio. 2015. Overseas dispersal of Hyperolius reed frogs from Central Africa to the oceanic islands of São Tomé and Príncipe. Journal of Biogeography 42:65–75.

Benedito-Cecílio, E., A.A. Agostinho, H.F. Julio, Jr., and C.S. Pavanelli. 1997. Colonização ictiofaunística do reservatório de Itaipu e áreas adjacentes. Revista Brasileira de Zoología 14:1–14.

Bonetto, A.A., J.R. Wais, and H.P. Castello.1989. The increasing damming to the Paraná basin and its effects on lower reaches. Regulated Rivers: Research & Management 4:333–346.

Brandão, R.A., and A.F. Araújo. 2008. Changes in anuran species richness and abundance resulting from hydroelectric dam flooding in Central Brazil. Biotropica 40:263–266.

Brites, W.F., and M.R. Catullo. 2016. Represas y transformación socio-urbana. Un análisis comparativo de los proyectos hidroeléctricos de Salto Grande y Yacyretá. Cidades, Comunidades e Territórios 33:50–67. http://dx.doi.org/10.15847/citiescommunitiesterritories.dec2016.033.art04.

Brunetti, A.E., C. Taboada, and J. Faivovich. 2014. The reproductive biology of *Hypsiboas punctatus* (Anura: Hylidae): male territoriality and the possible role of different signals during female choice. Salamadra 50:215–224.

Brunetti, A.E., C. Taboada, and J. Faivovich. 2015. Extended vocal repertoire in *Hypsiboas punctatus* (Anura: Hylidae). Journal of Herpetology 49:46–52.

Brusquetti, F., and E.O. Lavilla. 2006. Lista comentada de los anfibios del Paraguay. Cuadernos de Herpetología 20:3–79.

Bunn, S.E., and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

Céspedez, J.A., and C. Klein. 2002. Citas puntuales de anuros para el norte de Argentina. Comunicações do Museu de Ciencia e Tecnologia da PUCRS, Serie Zoología 15:157–159.

Collins, P.A., F. Giri, and V. Williner. 2006. Population dynamics of *Trichodactylus borellianus* (Crustacea Decapoda Brachyura) and interactions with the aquatic vegetation of the Paraná River (South America, Argentina). Annales de Limnologie - International Journal of Limnology 42:19–25.

Da Silva, J.M.C., and J.M. Bates. 2002. Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. BioScience 52:225–234.

Duellman, W.E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publications of the University of Kansas, Museum of Natural History 65:1–352.

Finer, M. and C.N. Jenkins. 2012. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. PLoS ONE 7:1-9. https://doi.org/10.1371/journal.pone.0035126

Fontana, J.L., and D.E. Iriarte. 2016. Influencias de los embalses de Yacyretá sobre los ecosistemas costeros. Extensionismo, Innovación y Trasferencia Tecnológica - Claves para el Desarrollo 3:46–54.

Fulco, C.A. 2011. El paisaje costero como factor de integración. El proyecto hidroeléctrico Yacyretá y las trasformaciones del paisaje en las zonas urbanas-costeras de las ciudades involucradas, en el periodo 2005–2010. M.S. Tesis, Facultad de Arquitectura y Urbanismo. Universidad Nacional de La Plata, Buenos Aires, Argentina. 289 p.

Gallardo, J.M. 1961. On the species of Pseudidae (Amphibia, Anura). Bulletin of the Museum of Comparative Zoology 125:111–134.

Garda, A.A., G.C. Costa, F.G.R. França, and D.O. Mesquita. 2007. Ecology of *Lysapsus limellum* in the Brazilian Amazon river basin. Herpetological Journal 17:141–148.

Garda, A.A., S.D.J. Santana, and V. Avelar Sao-Pedro. 2010. Taxonomic characterization of Paradoxical frogs (Anura, Hylidae, Pseudae): geographic distribution, external morphology, and morphometry. Zootaxa 2666:1–28.

Goldberg, J., and M. Fabrezi. 2008. Development and variation of the anuran webbed feet (Amphibia, Anura). Zoological Journal of the Linnean Society 152:39–58.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Guerrero, E.L., F.L. Agnolin, P. Grilli, F.A. Suazo Lara, E. Boné, A.B. Tenorio, M. Derguy, S. Lucero, N. R. Chimento Ortíz, J.A. Milat, et al. 2017. Inventario de la fauna transportada por balsas de vegetación flotante en el Sistema fluvial del Río de La Plata. Revista del Museo Argentino Ciencias Naturales 19:177–183.

Hödl, W. 1977. Call differences and calling site segregation in anuran species from central Amazonian floating meadows. Oecología 28:351–363.

Hunt, E.R., C.S.T. Daughtry, J.U.H. Eitel, and S. D. Long. 2011. Remote sensing leaf chlorophyll content using a visible band index. Agronomy Journal 103:1090–1099.

Keddy, P.A. 2010. Wetland Ecology: Principles and Conservation. Cambridge University Press, Cambridge, UK.

Manzano, A.S., D. Baldo, and M. Barg. 2004. Anfibios del litoral fluvial Argentino. Insugeo, Miscelánea 12:271–290.

McFeeters, S.K. 1996. The use of the Normalized Difference Water Index (NDWI) in the delineation of open water features. International Journal of Remote Sensing 17:1425–1432.

Meichtry de Zaburlín, N., J.G. Peso, and P. Araya. 2013. Humedales del Embalse de Yacyretá y ambientes asociados. Pp.113–122 *In* Inventario de los Humedales de Argentina. Sistemas de Paisajes de Humedales del Corredor Fluvial Paraná-Paraguay. 1st Edition. Benzaquén, L., D.L. Blanco, R.F. Bó, P. Kandus, G.F. Lingua, P. Minotti, R.S. Quintana, S. Sverlij and L. Vidal (Eds.). Secretaria de Ambiente y Desarrollo Sustentable de la Nación, Buenos Aires,

Argentina.
Naniwadekar, R., and K. Vasudevan. 2014. Impact of dams on riparian frog communities in the southern Western Ghats, India. Diversity 6:567–578.
Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'Amico, I. Itoua, H.E Strand, J.C. Morrison, et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51:933–938.
Peso, J.G., N. Meichtry de Zaburlin, and P. Araya.2013. Humedales del Alto Paraná en fisiografía rocosa. Pp.129–136 *In* Inventario de los Humedales de Argentina. Sistemas de Paisajes de Humedales del Corredor Fluvial Paraná-Paraguay. 1st Edition. Benzaquén, L., D.L. Blanco, R.F. Bó, P. Kandus, G.F. Lingua, P. Minotti, R.S. Quintana, S. Sverlij and L. Vidal (Eds.). Secretaria de Ambiente y Desarrollo Sustentable de la Nación, Buenos Aires, Argentina.
Prado, C., M. Uetanabaro, and C. Haddad. 2005. Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. Amphibia-Reptilia 26:211–221.
Rosenzweig, M.L. 2003. Reconciliation ecology and the future of species diversity. Oryx 37:194–205.
Schiesari, L., J. Zuanon, C. Azevedo-Ramos, M. Garcia, M. Gordo, M. Messias, and M.E. Monteiro Vieira. 2003. Macrophyte rafts as dispersal vectors for fishes and amphibians in the Lower Solimes River, central Amazon. Journal of Tropical Ecology 19:333–336.
Stănescu, F., E. Buhaciuc, P. Székely, D. Székely, L. Rozylowicz, and D. Cogălniceanu. 2015. The impact of dam construction on amphibians and reptiles. Study case–Iron Gates I. Analele Științifice ale Universității "Alexandru Ioan Cuza" din Iași, s. Biologie Animal 15:19–24.
Taboada, C., A.E. Brunetti, F.N. Pedron, F. Carnevale Neto, D.A. Estrin, S.E. Bari, L.B. Chemes, N.P. Lopes, M.G. Lagorio, and J. Faivovich. 2017. Naturally occurring fluorescence in frogs. Proceedings of the National Academy of Sciences of the United States of America 114:3672–3677.
Taboada, C., A.E. Brunetti, M.L. Lyra, R.R. Fitak, A.F. Soverna, S.R. Ron, M.G. Lagorio, C.F. Haddad, N.P. Lopes, S. Johnsen, et al. 2020. Multiple origins of green coloration in frogs mediated by a novel biliverdin-binding serpin. Proceedings of the National Academy of Sciences of the United States of America 117:18574–18581.
Thomaz, S.M., L.M. Bini, M.C. Souza, K.K. Kita, and A.F.M. Camargo. 1999. Aquatic macrophytes of Itaipu Reservoir, Brazil: survey of species and ecological considerations. Brazilian Archives of Biology and Technology *42:15–22.*
Vaira, M., M. Akmentins, M. Attademo, D. Baldo, D.A. Barraso, S. Barrionuevo, N.G. Basso, B.L. Blotto, S. Cairo, R. Cajade, et al. 2012. Categorización del estado de conservación de los anfibios de la República Argentina. Cuadernos de Herpetología 26:131–159.
Weiler, A., K. Nuñez, K. Airaldi, E. Lavilla, S. Peris, and D. Baldo. 2013. Anfibios del Paraguay. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Asunción, Universidad de Salamanca. San Lorenzo, Paraguay.
Wetzel, R.G. 2001. Limnology Lake and Reservoir Ecosystems. Academic Press, San Diego, California, USA.

Pablo Javier Torres obtained his Bachelor's degree in Biological Sciences at the Universidad de la Patagonia San Juan Bosco, Chubut, Argentina, in 2014. He has experience in marine pollution studies that include the Southern Right Whale (*Euabalaena australis)* and the edible snail *Buccinanops globulosus*. Pablo studied the Pantanal Cat (*Leopardus braccatus*) in Bolivia and the Charco Frog (*Dendropsophus carnifex)* in Ecuador. Since 2015, he has been a Technician of Biological Collections at the Institute of Subtropical Biology (Misiones, Argentina). His research interests are focused on herpetology. (Photographed by Laura Rodrigues).

Juan Martín Boeris graduated as a Geneticist from the National University of Misiones, Argentina. He has authored and co-authored scientific articles in cytogenetics and in other biological topics, mostly in anurans amphibians. Juan has participated in several technical reports on fauna and vegetation surveys and is currently working as a Field Technician at the Institute of Subtropical Biology (Misiones, Argentina). (Photographed by Alberto Taffarel).

Juan Ariel Insaurralde has a Ph.D. in Geography and specializes in Remote Sensors and Geographic Information Systems (GIS) analyses. He has experience in remote sensing of spatial coverage and thematic mapping as well as in spatial analysis of biophysical variables. (Photographed by Juan A. Insaurralde).

Diego Baldo is a researcher of the Institute of Subtropical Biology (CONICET-UNaM), Curator of Herpetology (LGE), and Professor of Evolutionary Genetics at the National University of Misiones, Argentina. His research is focused on taxonomy, systematic, and the evolution of amphibians. (Photographed by Diana Szekely).

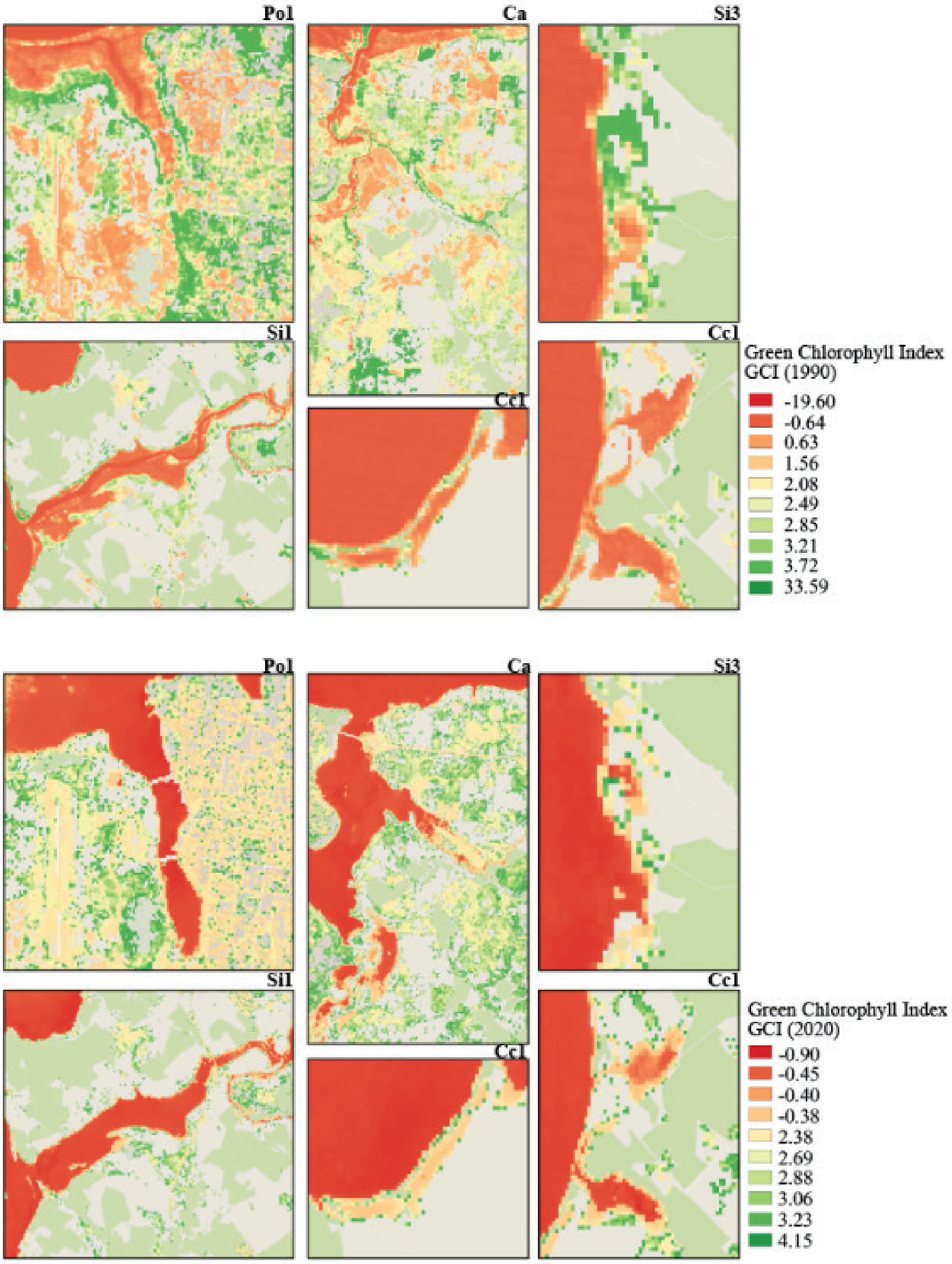
Andrés E. Brunetti currently serves as a Researcher at the Institute of Subtropical Biology (CONICET-UNaM), Misiones, Argentina. He received his Ph.D. in Biology at the University of Buenos Aires, Argentina. His research aims to investigate the molecular and metabolic bases of symbiosis between bacteria and amphibians. His research interests include diverse topics of amphibian biology like morphology, chemical secretions, behavior, and evolution. (Photographed by Laura Andrade).

Appendix Table 1. Location of fieldwork conducted in this study. Asterisks (*) indicate surveys prior to Yacyretá Lake filling to maximum capacity in 2011.

Locality Name	Site	Coordinates	Pre-dam
Posadas (Po)	Po1	27°22'08.9"S 55°57'47.0"W	
	Po1	27°22'00.0"S 55°58'52.0"W	*
	Po2	27°21'06.8"S 55°54'23.8"W	
	Po2	27°21'06.0"S 55°54'37.0"W	*
	Po3	27°21'57.0"S 55°53'00.0"W	*
Candelaria (Ca)	Ca1	27°28'58.8"S 55°47'51.3"W	
	Ca1	27°27'00.0"S 55°48'36.0"W	*
	Ca2	27°27'05.8"S 55°45'33.6"W	
San Ignacio (Si)	Si1	27°18'54.4"S 55°34'30.3"W	
	Si2	27°17'19.0"S 55°35'41.2"W	
	Si3	27°15'55.0"S 55°34'01.8"W	
Corpus Christi (Cc)	Cc1	27°09'42.0"S 55°33'07.3"W	
	Cc2	27°07'44.2"S 55°33'33.9"W	
	Cc3	27°06'34.0"S 55°31'17.1"W	
Santo Pipo stream	Sp1	27°07'10.0"S 55°27'56.0"W	*
Ñacanguazú Stream (Na)	Ns	27°05'39.9"S 55°26'11.9"W	
Colonia Polana (Cp)	Cp	26°58'04.3"S 55°20'00.3"W	

Appendix Table 2. Catalog numbers of voucher specimens housed in the Herpetological Collection of LGE, "Claudio J. Bidau," of the Instituto de Biología Subtropical (IBS-CONICET-UNaM), Posadas, Misiones, Argentina.

Species	Vouchers
Boana punctata Flourescent Frog	**Candelaria (Ca)**: LGE 22656, 22675–80, 22993–23000. **San Ignacio (Si)**: LGE 23277–23284. **Corpus Christi (Cc)**: LGE 22772–3, 22781–5.
Lysapsus limellum Uruguay Harlequin Frog	**Posadas (Po)**: LGE 22653. **Candelaria (Ca)**: LGE 20088, 22489, 22666–8, 22988–90. **San Ignacio (Si)**: LGE 22484–6, 22650, 23262, 23268–76. **Corpus Christi (Cc)**: LGE 22774–5, 22778–80, 22786, 23020–2, 23025–35.



Appendix Figure. Green Chlorophyll Indices (GCI) estimated for some sites surveyed in this study (abbreviations as in Appendix Table 1) in 1990 (upper panel, before Yacyretá Dam construction) and 2020 (lower panel, after the Lake reached maximum capacity). The processing of the satellite images was performed on the Google Earth Engine platform with the Landsat 5 and 8 image collections.