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Distribution modeling of *Psellogrammus kennedyi* (Eigenmann, 1903) and new records in the Lower Paranapanema River, Brazil

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Abstract

Understanding the potential distribution of non-native species can be an important tool in preventing biological invasions. We recorded for the first time *Psellogrammus kennedyi*, a small non-native characiform, in the Lower Paranapanema River, Brazil. According to environmental variables and prediction modeling, the species presents high potential distribution in the Upper Paraná river basin. The model used herein is an efficient tool to determine where non-native species may be able to establish. This approach can be used as a preventive measure, once the control and eradication measures are often ineffective and uneconomical.

Keywords

Characidae, dispersal, distribution, freshwater, invasion, Neotropical region, South America, Upper Paraná river basin

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Introduction

The Lower Paranapanema River, a major tributary of the Upper Paraná River system, shares many fish species which naturally occurs in the neighboring Paraguay–Lower Paraná River system (Jarduli et al. 2020). Several non-native species were introduced in the Upper Paraná basin due to the removal of the natural biogeographic barrier at Sete Quedas Falls due to the construction of the Itaipu Dam (Júlio Júnior et al. 2009; Ota et al. 2018). The introductions of these species have substantially modified the Paranapanema ichthyofauna, coupled with altered lentic conditions caused by impoundment, which suggests that the rivers' native fishes are increasingly threatened (Garcia et al. 2018a).

Recently, Jarduli et al. (2020) reviewed 90 independent studies. They compiled 225 fish species present in the Paranapanema river basin, and *Psellogrammus kennedyi* (Eigenmann, 1903) had not been previously recorded. *Psellogrammus* Eigenmann, 1908 is a monotypic genus, including only the lentic *Psellogrammus kennedyi*, which can grow to 5.9 cm long (Lima et al.

2003) and inhabits floodplains (Alves and Pompeu 2001). It was described from Campo Grande, Asuncion, Paraguay, in the Paraguay river basin (Reis et al. 2003), and its natural distribution is reportedly in the Lower Paraná–Paraguay system (Ota et al. 2018) and São Francisco river basin (Tondato et al. 2013; Fricke et al. 2021). However, the natural occurrence of *P. kennedyi* is reported to the stretch downstream of Sete Quedas Falls in the Lower Paraná River (Reis et al. 2020). The occurrence of *P. kennedyi* in the Upper Paraná river basin is a result of the elimination of this natural barrier after flooding by the Itaipu Dam; thus, this species is classified as non-native for this region (Graça and Pavanelli 2007; Júlio Júnior et al. 2009; Ota et al. 2018).

The large number of non-native fishes present in the Lower Paranapanema river basin (Garcia et al. 2018a; Jarduli et al. 2020) shows that this stretch of the river presents several optimal environmental conditions and resources for fish species in the system (Blackburn et al. 2011; Garcia et al. 2018b, 2019). Biological invasion is one of the main drivers of biodiversity loss and ecosystem damage. Invasive species are difficult to eradicate, and prevention is considered the best approach (Adelino et al. 2017). In this way, the knowledge of environmental conditions and species' distribution can be used as predictive tools for determining the establishment and invasive potential (Peterson 2003; Stohlgren et al. 2010).

Through occurrence records and environmental predictors of the native range of *P. kennedyi*, we used the species distribution models (SDM) (Franklin and Miller 2010) to generate a predictive model for the potential distribution of *P. kennedyi* in the Paraná river basin (Peterson 2003; Pereira et al. 2020). Models predicted high suitability for *P. kennedyi* in the Upper Paraná river basin. New records corroborate the prediction of the potential distribution in the Lower Paranapanema river basin, indicating that the basin presents the environmental conditions for this species to become well established. In addition, we discuss how the construction of dams and the biological aspects of *P. kennedyi* may have facilitated this invasive process.

Methods

Sampling was performed between April 2019 and June 2020 during a fish fauna monitoring project in the Paranapanema river basin (Project #11218/2018). Specimens were collected in the Rosana Reservoir at site 1 (22°32′06″S, 052°01′55″W) and in the Taquaruçu Reservoir at site 2 (22°39′12″S, 051°37′36″W), site 3 (22°38′48″S, 051°26′45″W), and site 4 (22°40′07″S, 051°24′10″W), both in the Lower Paranapanema River, which is the portion of the basin that begins after Salto Grande Falls (currently flooded by the Salto Grande Reservoir; Fig. 1). The samples were collected using standard ichthyological gear comprising sieve and seine nets of 2 mm mesh size. Fish were euthanized by overexposing to 1 g/ml clove oil, fixed with 10% formalin, and transferred to 70% alcohol. The Animal Ethics Committee authorized the field sampling (Comissão de Ética no uso de Animais, CEUA no. 24310.2017.78; collection license no. 16578). All specimens are deposited at the Museu de Zoologia da Universidade Estadual de Londrina (MZUEL). We confirmed identification based on the original description (Eigenmann and Kennedy 1903) and the description by Ota et al. (2018); we also consulted expert assistance. Measurements and counts were performed on 125 specimens following Fink and Weitzman (1974), using digital calipers, point-to-point, on the left side of the specimens whenever possible, and with a precision of 0.1 mm (SL = standard length).

Occurrence records of *P. kennedyi* were obtained from online databases of species in zoological collections by searching the Centro de Referência em Informação Ambiental (272 records) (SpeciesLink; CRIA 2021) and the Global Biodiversity Information Facility (126 records) (GBIF 2021). Only georeferenced records containing voucher specimens were considered valid for modeling purposes. For modeling the environmental niche in the native geographic range of *P. kennedyi* (Jiménez-Valverde et al. 2011), we used only native species occurrence data (261 records) (i.e., Paraguay basin) (Ota et al. 2018; Fricke et al. 2021) (Figs. 1, 3).

Bioclimatic variables are derived from the monthly temperature and rainfall values to generate more biologically meaningful variables. Temperature is responsible for altering the metabolism (e.g., enzymatic activity) of living organisms and precipitation for the seasonal variations of droughts and floods, synchronizing biological events of fish, such as migration, spawning, home range, and growth (Lopes et al. 2017; Ruaro et al. 2019). We used six bioclimatic variables related to the environmental tolerance of *P. kennedyi* to temperature and precipitation. Their respective codes were: BIO1 = annual mean temperature, BIO5 = maximum temperature of warmest month, BIO6 = minimum temperature of coldest month, BIO12 = annual precipitation, BIO13 = precipitation of wettest month, and BIO14 = precipitation of driest month. Bioclimatic variables were obtained from the WorldClim (http://www.worldclim.org/) v. 2.0 (Fick and Hijmans 2017). We used a principal component analysis (PCA) to remove redundancy among environmental variables to produce uncorrelated variables (Peterson et al. 2011). We chose to use the MaxEnt (maximum entropy; Phillips et al. 2006) model algorithm, as this method has a high capacity for predictive accuracy of modeling species–environment relationships using presence-only data (Franklin and Miller 2010).

We obtained an initial set of 100 models for the species, selected at random 75% of the occurrence localities at each run for training, and left the remaining 25% for testing models. The area under the ROC curve (AUC) was calculated to validate the quality of the final models generated (Phillips et al. 2006), as well as a true skill statistic (TSS) analysis which compares the number of correct forecasts, minus those attributable to random

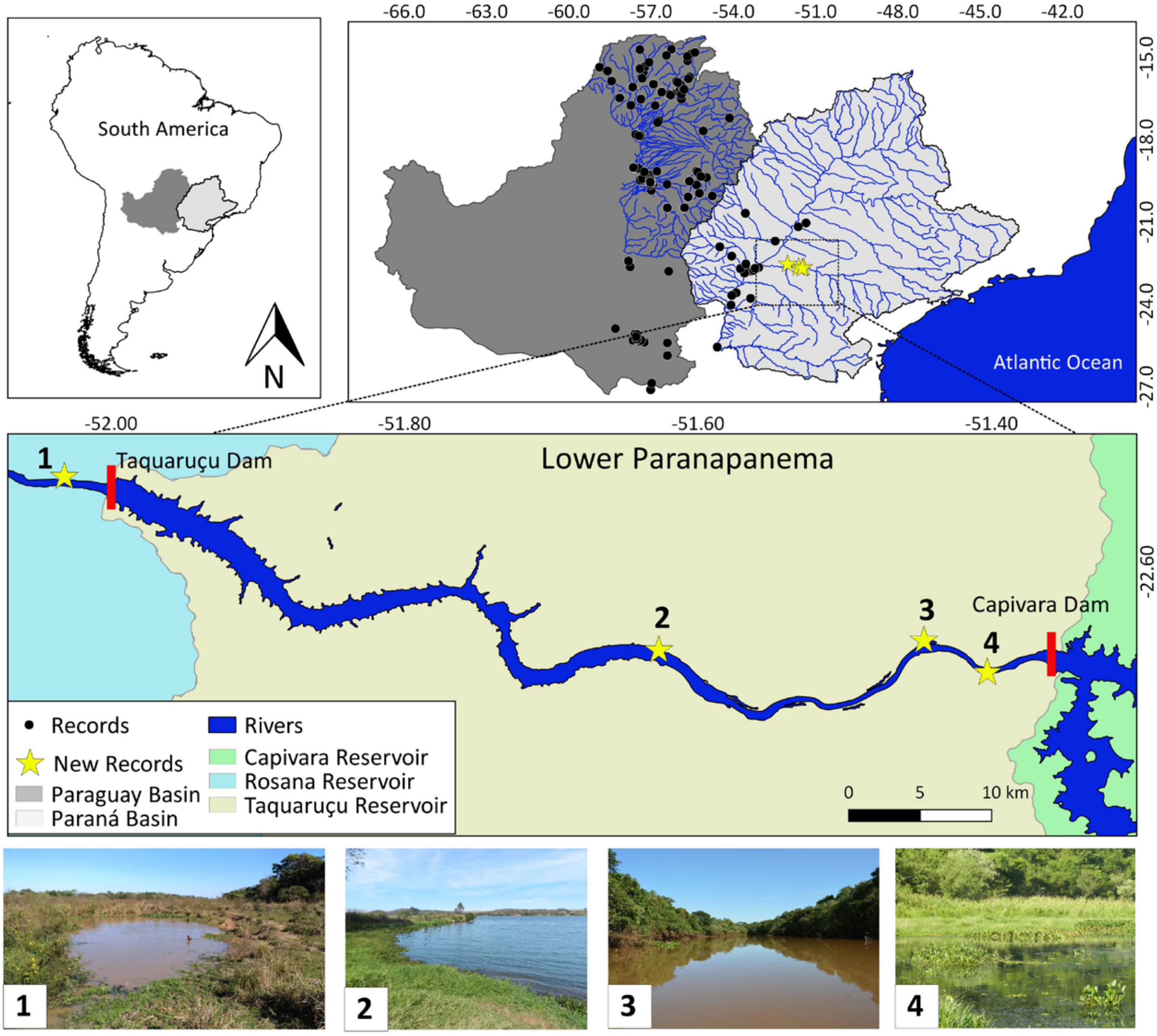

Figure 1. Distribution of *Psellogrammus kennedyi*. Yellow stars represent new records from the Paranapanema river basin. Black circles represent records from the Paraná and Paraguay river basins.

guessing, to that of a hypothetical set of perfect forecasts (Allouche et al. 2006). Models with AUC = 0.7 and TSS = 0.4 values were selected to construct the final model (Buisson et al. 2010). Maxent jackknife test of variable importance was used to evaluate the relative contribution of each predictor variable to construct the models (Yost et al. 2008). All analyses were conducted using the R software v. 3.6.3 (R Core Team 2020; R Studio Team 2020) dismo package (Hijmans et al. 2021).

Results

Psellogrammus kennedyi (Eigenmann 1903)

Figures 1–3; Tables 1, 2

New records. BRAZIL – **Paraná** • Paranapanema river basin, Taquaruçu Reservoir, Lupionópolis municipality; 22°39′12″S, 051°37′36″W; 12.IV.2019; Laboratório de Ecologia de Peixes e Invasões Biológicas LEPIB leg.; 1, sex undet., 33.9 mm SL, MZUEL 20869 • Porecatu municipality; 22°40′07″S, 051°24′10″W; 06.VI.2019; LEPIB leg.; 2, sex undet., 34.7 and 41.8 mm SL, MZUEL 20870 – **São Paulo** • Paranapanema river basin, Taquaruçu Reservoir, Narandiba municipality, near Anhumas River; 22°38′48″S, 051°26′45″W; 06.VI.2019; LEPIB leg.; 2, sex undet., 29.7 and 39.6 mm SL, MZUEL 20872 • Rosana Reservoir, Teodoro Sampaio municipality; 22°32′6″S, 052°01′55″W; 18.VI.2020; LEPIB leg.; marginal lagoon; 120, sex undet., 28.3–43.8 mm SL, MZUEL 20871.

Identification. Body deep and compressed; greatest depth contained 2.1–2.5× and caudal peduncle depth 9.7–10.8× in standard length; head length 3.4–4.0×, predorsal distance 1.9–2.1×; snout length 3.5–4.0×, horizontal orbital diameter 2.3–2.8×, and least interorbital width 2.6–3.2× in head length. Mouth terminal; the inner row of premaxilla with 5 teeth, outer row with 3–5 teeth, dentary row with 8–11 teeth, and maxilla with 1 tooth. Lateral line irregular (incomplete or rarely complete); longitudinal series with 40–45 scales. Dorsal fin with 10 rays, pectoral fin with 12 or 13 rays, pelvic fin with 8 rays, anal fin with 39–46 rays, and caudal fin with 19 rays. Ground color whitish; with a diffuse, black humeral spot; with a dark-brown, rounded blotch on distal portion

Figure 2. *Psellogrammus kennedyi*. MZUEL 20872, 31.5 mm SL, Lower Paranapanema River, Upper Paraná basin, Paraná, Brazil. Scale bar = 1 cm.

of caudal peduncle and caudal-fin base. Fins hyaline (Graça and Pavanelli 2007; Ota et al. 2018). Other measurements are presented in Table 1.

Psellogrammus kennedyi is associated with marginal lagoons and macrophyte banks in the littoral zone of the reservoir in our new records. The model obtained for the present distribution of *P. kennedyi* in the Paraná basin (Fig. 2) performed well, with an average AUC value of 0.74 (± 0.02) and TSS 0.834 (± 0.064), the algorithm converged after 280 iterations. The model shows greater suitability for *P. kennedyi* in the Upper Paraná river basin areas, like the lower stretches of Paranaíba, Grande, Tietê, and Paranapanema rivers (Fig. 2). The mininum temperature of coldest month (BIO6) presented the greatest contribution to the model construction, followed by the precipitation of driest month (BIO14) and annual mean temperature (BIO1); tree variables combined sum up to a total of 95.6% of the contribution for the model construction (Table 2). The Jackknife analysis also shows the variable BIO1 as the one that presents a greater gain to the training of the model.

Discussion

Ecological niche modeling is an approach widely used to predict species distribution (Guisan and Zimmermann 2000; Franklin and Miller 2010). It has been an important tool in several research lines, such as biodiversity mapping, conservation planning, niche evolution, climate change impacts on species, and biological invasions (Peterson et al. 2008; Kriticos and Leriche 2010; Ruaro et al. 2019). Based on environmental predictors through niche modeling (Guisan and Thuiller 2005; Araújo and Guisan 2006; Pereira et al. 2020), we used data on the natural occurrence of *P. kennedyi* to understand the potential distribution and occurrence of the species outside its native range. New records of *P. kennedyi* in the Upper Paraná River in recent years are evidence of an expansion of the non-native distribution of this species (Fiori et al. 2016; Peláez et al. 2017; da Costa-Silva et al. 2018; Vicentin et al. 2019).

The suggested suitability model predicted that the Upper Paraná river basin has good to high potential for the increased distribution and establishment of *P.*

Table 1. Morphometric data of *Psellogrammus kennedyi* specimens collected in the Lower Paranapanema river basin, Brazil (N = 125). SD = standard deviation of averages.

Measurements	Range	Mean	SD
Standard length (mm)	28.3–43.8	36.1	—
Percents of standard length			
Body depth	11.2–19.3	15.3	2.9
Body width	2.8–5.0	3.9	0.8
Head length	7.0–10.9	9.0	1.4
Head depth	5.8–9.0	7.4	1.1
Predorsal length	14.6–21.1	17.9	2.3
Prepelvic length	10.9–17.8	14.4	2.4
Preanal length	16.3–23.6	20.0	2.6
Caudal peduncle depth	2.3–3.9	3.1	0.6
Dorsal-fin base length	3.7–5.6	4.7	0.7
Anal-fin base length	12.3–19.2	15.8	2.4
Pectoral-fin length	6.2–10.4	8.3	1.5
Pelvic-fin length	4.1–6.1	5.1	0.7
Dorsal-fin length	7.9–13.7	10.8	2.1
Anal-fin length	5.6–7.9	6.8	0.8
Caudal peduncle length	2.6–5.5	4.1	1.0
Dorsal-fin to adipose-fin distance	5.9–11.8	8.9	2.1
Eye to dorsal-fin origin	11.2–16.6	13.9	1.9
Dorsal origin to caudal origin	14.4–24.5	19.5	3.6
Percentages of head length			
Interorbital width	2.6–3.9	3.3	0.5
Snout length	2.9–3.9	3.4	0.4
Orbital diameter	2.7–3.7	3.2	0.4
Upper jaw length	2.0–2.8	2.4	0.3

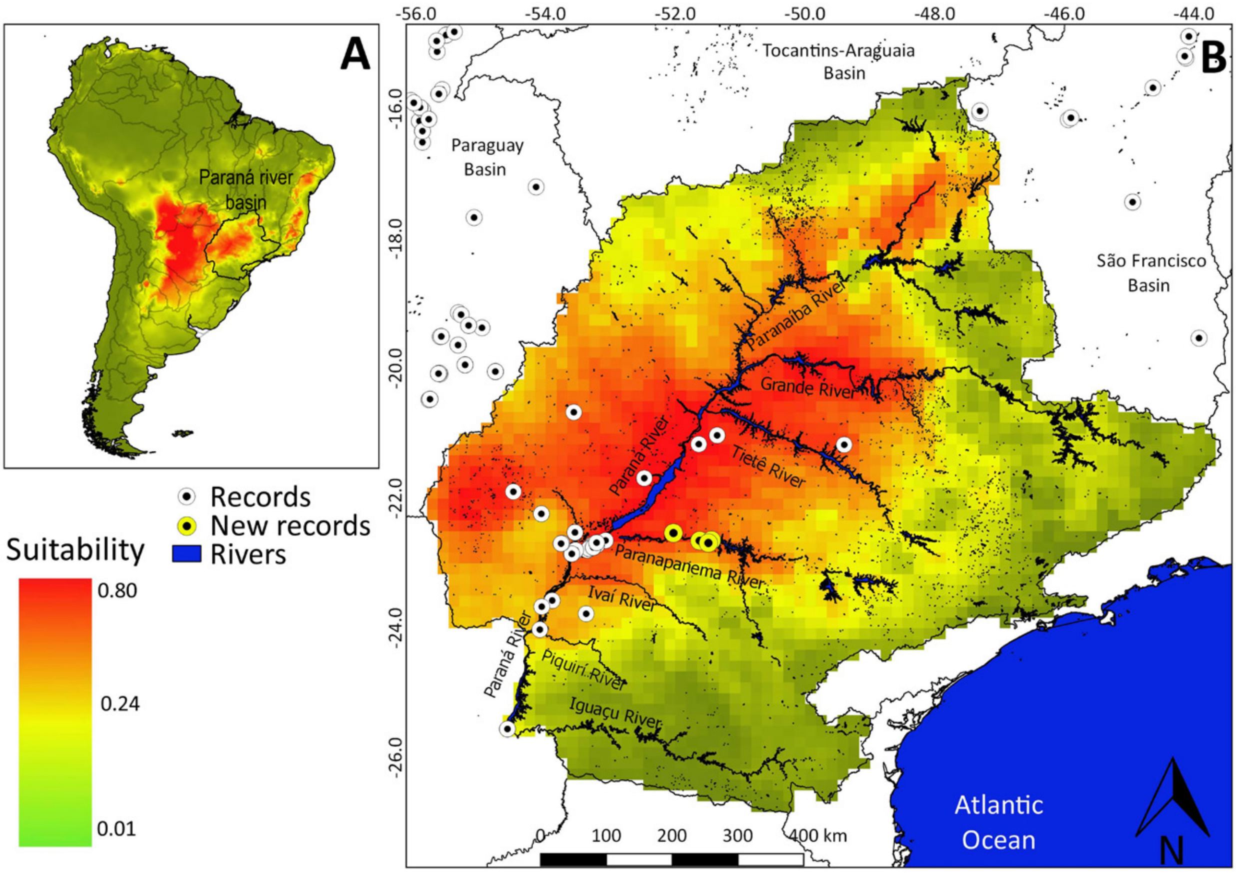

Figure 3. Suitability map for *Psellogrammus kennedyi*. **A.** South America. **B.** Paraná river basin.

Table 2. Estimates of average contribution and permutation importance of the environmental variables used in the MaxEnt modeling algorithm for *Psellogrammus kennedyi*.

Variable	Code	Percentage contribution	Permutation importance
Min. temperature of coldest month	BIO6	62.2	35.5
Precipitation of driest month	BIO14	23.0	13.6
Annual mean temperature	BIO1	10.4	45.9
Precipitation of wettest month	BIO13	2.3	0.8
Max. temperature of warmest month	BIO5	1.2	1.5
Annual precipitation	BIO12	0.9	2.6

Threshold kappa: 0.58524682
Sensitivity: 0.58944197

kennedyi (> 0.50) (i.e., between 15°S and 24°S in Brazil). Our model identified that some environmental variables, such as variations in temperature and the annual mean precipitation, explain the current range of *P. kennedyi*. We found that the minimum temperature of the coldest month, precipitation of the driest month, and annual mean temperature are important climatic contributors in predicting suitable areas for *P. kennedyi*. This species is favored in regions where climate is less variable, like in the Paraguay basin (native region), and also in nearby areas at similar latitudes such as the Upper Paraná river basin (non-native region), where the average annual temperatures vary between 22.5 °C and 26.5 °C and the average annual precipitation in the basin is 1,396 mm, ranging from 800 to 1,600 mm (Gonçalves et al. 2011).

The presence of *P. kennedyi* in the Upper Paraná region is due to the Canal da Piracema, a fish transposition system that connects the region downstream Itaipu Dam to the region upstream (Júlio Júnior et al. 2009; Ota et al. 2018). After the flooding of the reservoir behind the Itaipu Dam, the loss of the Sete Quedas Falls allowed for hydrologic connectivity between the Lower and Upper Paraná River. Many fishes of the lower region of the Paraná River were able to colonize the upper stretches (Vitule et al. 2012), including the Paranapanema River (Garcia et al. 2018a). The damming of stretches of the Lower Paranapanema River for hydroelectric power seems to have favored the establishment of *P. kennedyi* in reservoirs, as reported by Garcia et al. (2018b) for other non-native fish species in the Paranapanema River. Artificial reservoirs are globally known to be hotspots for invaders (Johnson et al. 2008). The colonization of reservoirs by small species is well-documented in the literature, and species that habitually associate with macrophytes in the littoral zone are favored (Casatti et al. 2003; Pelicice and Agostinho 2009; Agostinho et al. 2016). Fiori et al. (2016) found that *P. kennedyi* has physiological adaptations that allow it to obtain the maximum energy from food, even if of low nutritional value, or that this species can compensate for low-nutrition foods by increasing consumption. Thus, *P. kennedyi* has great food plasticity allowing diet changes according to the environment, thus favoring its dispersion and invasion.

Species with generalist reproductive and trophic niche strategies are more likely to have invasion success (Agostinho et al. 2007, 2016; Garcia et al. 2018a, 2018b, 2019). Galvão et al. (2016) observed that *P. kennedyi* might be sexually mature throughout the year, with both females and males with three stages of gonadal maturation. Thus, *P. kennedyi* has asynchronous development of oocytes and mature males throughout the year. This allows males to always reproduce, making the release of sperm possible in the most favorable conditions. This reproductive strategy can assist in the colonization of new areas, where different niches in temporal and spatial scales are occupied with different size classes (de Carvalho et al. 2009; Agostinho et al. 2016; Araújo et al. 2019). In addition, *P. kennedyi* has a laterally depressed body, and its body is taller than several small characiforms which have a fusiform body. This allows *P. kennedyi* to establish in lentic environments such as marginal zones of reservoirs and marginal lagoons (Breda et al. 2005).

Biological invasions are a serious threat to the Upper Paraná and Paranapanema river basins (Langeani et al. 2007; Júlio Júnior et al. 2009; Pelicice and Agostinho 2009; Garcia et al. 2018a), and understanding the biology, ecology, and potential distribution of non-native species can serve as a basis for preventive measures (Simberloff 2003; Broennimann and Guisan 2008). Our results indicate that distribution modeling should be used to understand potential dispersion, establishment, and invasion of non-native species. This knowledge should be used preventively, since control and eradication measures are often ineffective and with high costs.

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