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Climate change may increase the suitable habitats for invasive freshwater cichlids in a Neotropical basin

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Although climate change may facilitate the spread of invasive alien species (IAS), research assessing this link remains limited. Recognizing suitable habitats where IAS have been introduced is crucial for biodiversity conservation and ecosystem management. Here, we integrated online, museum, and laboratory occurrence databases with local ecological knowledge (LEK) on IAS fishes from semi-structured interviews and georeferenced social network posts from traditional and recreational fishers to model the habitat-suitability of three voracious IAS Cichlids introduced in the Brazilian part of the Upper Paraguay River Basin (the Pantanal wetland and its tributaries). Our goal was to locate areas (regions, sub-basins, and reservoirs) most at risk from the spread of these IAS fishes in the basin. The findings reveal extensive suitable habitats for these IAS fishes throughout the study basin, currently covering half of the Pantanal wetland and up to 90% of the upstream sub-basins. Under future climate scenarios, these suitable habitats are projected to expand further, encompassing almost the entire Pantanal floodplain. These results highlight a potential IAS Cichlid range expansion in the Pantanal floodplains in the upcoming decades, correlating with common climate change forecasts. We also emphasize the value of integrating ecological niche models (ENMs) along with Citizen Science data to identify high-risk areas during early invasion stages, inform preventive strategies, and support conservation efforts to mitigate the impacts of IAS on native biodiversity.

Keywords Blue peacock bass, *Cichla piquiti*, Yellow peacock bass, *Cichla kelberi*, Nile Tilapia, *Oreochromis niloticus*, Instagram

Climate change and biological invasions pose significant threats to global biodiversity and ecosystem services[1–3]. Human activities have introduced over 37,000 invasive alien species (IAS) worldwide, contributing to 60% of documented global plant and animal extinctions[4,5]. In addition, IAS impact food security and human health through the spread of pests and diseases, often exacerbated by changes in climate patterns, resulting in an estimated global economic cost of USD 423 billion annually[6,7]. The specific role of climate change as a key driver of IAS proliferation is now widely recognized, as rising temperatures and changes in precipitation have altered ecosystems and created novel, suitable habitats for establishing, sustaining, and spreading IAS populations[8,9]. This pattern is expected to intensify, with important short-term impacts projected by 2050[10,11].

Freshwaters are among the most vulnerable ecosystems to climate change and IAS, given their limited extent, strong connectivity dependence, restricted species dispersal, and direct dependence on climate stability[12,13]. Furthermore, freshwater species face the highest extinction rates compared to their terrestrial and marine counterparts, with a quarter of freshwater fauna at significant risk of extinction[14,15]. In the Americas, particularly in Latin America, freshwater habitats face severe hydrological alterations, declining water quality, and ecosystem degradation, along with the impacts of IAS[16,17]. Fish species, the most commonly documented

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IAS in Latin American rivers, lakes, and wetlands, have rapidly spread through aquaculture, posing a major concern in freshwater ecosystems[18,19]. Several IAS fish species support profitable fisheries despite ecological risks, particularly in the Neotropical region[20]. However, in developing countries like Brazil, managing IAS fish is hindered by data gaps, socio-economic interests, and limited state intervention[21].

The Upper Paraguay River Basin (UPRB) is situated at South America's geodetic center and spans Brazil, Bolivia, and Paraguay. It encompasses the extensive Pantanal wetland, characterized by intricate floodplains nourished by upstream tributaries of the Paraguay River, supporting one of the richest freshwater fish faunas (≈ 300 spp.)[22,23]. The UPRB is particularly affected by numerous hydropower plants and reservoirs, with the development of more anthropogenic developments currently planned[24]. Over the past seventy years, the construction of dams has disrupted freshwater ecosystems by altering sediment flow and water chemistry composition, ultimately obstructing fish migration routes and altering fish assemblages[25]. Furthermore, hydroelectric reservoirs have provided favorable conditions for the proliferation of IAS fishes[26,27]. The ecological consequences associated with dam construction, including the proliferation of IAS in reservoirs, must be considered and understood[28].

Cichlids are the best example of potential IAS fish establishing themselves in the UPRB. Since 1982, the Blue Peacock Bass, *Cichla piquiti* Kullander & Ferreira 2006, a Cichlid introduced from the Araguaia-Tocantins basin, has been reported in the Brazilian stretch of the UPRB (hereinafter Br-UPRB)[29,30]. This species has progressively expanded its invasion range through the Pantanal wetland and some sub-basins like São Lourenço-Vermelho, Miranda, and Apa-Perdido[31]. Moreover, the finding the Yellow Peacock Bass, *Cichla kelberi* Kullander & Ferreira 2006, a second Araguaia-Tocantins Cichlid in lotic ecosystems in the basin, has raised concerns regarding these two IAS within the basin[30]. The Nile Tilapia, wich is another Cichlid with great invasive potential, has also been reported in the basin[32,33]. While *Oreochromis niloticus* Linnaeus 1758, is cataloged as an IAS in several tropical regions and considered highly detrimental to native fauna;, it has nevertheless been extensively cultured in local reservoirs of the Br-UPRB along Mato Grosso and Mato Grosso do Sul States recently[32,34,35]. Frequent escapes from fish farms have increased the presence of this IAS in river catches by local artisanal and recreational fishers (C.M-G Pers. Obs). While the short-term effects of IAS Cichlids proliferation are well documented, such as their role as aggressive predators and competitors that disrupt trophic webs, the long-term ecological impacts still remain uncertain[28,36–38].

In recent years, Ecological Niche Models (ENMs), a set of correlative techniques analysis known as has experienced a significant increase in popularity to identify the potential extent of IAS invasive ranges[4,39]. The rising implementation of this approach is partly due to the ability to integrate IAS occurrences with the recently available high-quality environmental data, also informing the magnitude of climate change impacts[8,40]. ENMs are based on the ecological niche concept, which posits that a species will have a greater preference for a location where the environmental conditions necessary for its survival are maximized[41]. In addition, ENMs have proven effective in evaluating fish species distribution, contributing to native conservation and non-native population control[42].

The ENMs assess the abiotic component (A) of the BAM framework (geographic distributions of species determined by: Biotic, Abiotic, and Mobility features) by analyzing the correlation between species occurrences and environmental variables[43,44]. While ENMs do not directly incorporate biotic interactions (B) or dispersal limitations (M), these models provide valuable insights into the ecological preferences constraining species distributions[41], i.e., the fundamental niche as the range of abiotic conditions where a species can potentially sustain viable populations[43]. On the other hand, the realized niche is further constrained by B and M[45]. These ENM techniques allow us to study past, present, and future species distributions, predicting the IAS invasion spread patterns by identifying the most suitable areas for the species in the early stages of invasion, thus allowing us to prioritize efforts in critical regions[46–49].

The use of geographic information systems (GIS) has been improving the interpretation of ENM outputs by considering biogeographical and ecological constraints, including dispersal barriers and habitat fragmentation (affecting M), the effect of IAS (affecting B), and climate change (affecting A)[50,51]. This integration is particularly valuable for getting closer to the actual species distribution ranges, especially in freshwater ecosystems that function as ecological networks or island-like habitats[42,52,53]. When ENMs are used to model the distribution of IAS, native range data is used to identify species' environmental tolerances[46,54]. In contrast, invaded range occurrences may reflect ongoing colonization processes, founder effects, or incomplete habitat exploration[46]. This approach helps to understand where invasive species might expand based on their known preferred ecological conditions, facilitating more reliable identification of suitable habitats in invaded regions, thus supporting invasion risk assessments and management actions in vulnerable ecosystems[55,56].

The Shared Socio-economic Pathways (SSPs): SSP1 1.9–2.6, SSP2 4.5, SSP3 7.0, and SSP5 8.5, consist of five narratives outlining potential changes in demographics, economics, technology, society, governance, and the environment over the ongoing century[57]. These pathways serve as a tool for comparing ENMs in scenarios of temperature increase, ranging from 1.5 °C in the near future (2040–2070), to 3.3 –5.7 °C in the distant future (2081–2100), assuming the greenhouse gas emissions and inequality scenarios persist[58]. Programs such as Citizen Science bride gaps between scientists and local ecological knowledge (LEK) of IAS, providing a cost-effective approach that engages community members in data collection and assessment of IAS impacts on fishing communities[59–61]. The Citizen Science data has been incipient, nevertheless, effectively implemented in some cases of ENMs and IAS management[62–64]. Estimating the potential distribution of the IAS fishes in the Br-UPRB is essential to support management actions, especially considering the predicted and ongoing climate change that threatens freshwater fish native species[23].

Using an ensemble of ENMs, we modeled the current and future (2050 - SSP2 4.5) suitable habitats for *O. niloticus*, *C. kelberi*, and *C. piquiti* across their native and introduced (Br-UPRB) ranges. The models integrated hydroclimatic and topographic predictors with IAS occurrences data from online, museum, and laboratory occurrence databases, supplemented by semi-structured interviews and georeferenced social network post, specifically, Instagram posts from traditional and recreational fishers. This study aimed to (i) identify the most suitable habitats for IAS Cichlids within Br-UPRB reservoirs and key regions, including wetland complexes in low-elevation areas (Pantanal), tributary sub-basins on the Brazilian plateau, and (ii) evaluate whether these suitable areas may expand under the 2050 - SSP2 4.5 climate scenario. Given the Nile and Araguaia-Tocantins basins' origin of the IAS Cichlids introduced in the Br-UPRB, we expect that climate change could expand the climatically suitable areas for these species. Specifically, we hypothesize that combining Pantanal wetland and reservoir conditions (e.g., stable water levels, reduced flow velocity, clear waters) and projected rising temperatures may increase favorable environments for these IAS to spread along the Br-UPRB. This hypothesis is supported by evidence that lentic ecosystems and reservoirs often facilitate the dispersal of Cichlid invasive species[65,66] and that rising temperatures may increase the range of neotropical IAS fishes[8].

Results

Selection of environmental variables and their contribution to ENMs

The climatic predictor variables for current and future environmental conditions were divided into two sets: (1) for Br-UPRB + Araguaia - Tocantins basins (for modeling the two *Cichla* spp. habitat suitability) and (2) for Br-UPRB + Nile basins (for modeling *O. niloticus* habitat suitability). We then added topographic predictors (elevation, flow, and slope), considering the Variance Inflation Factor (VIF) value < 5, to minimize multicollinearity and improve interpretability of the models (Tables S1-S6). In the ensemble of ENMs, precipitation seasonality was the most important single variable for both *Cichla* species in current and future 2050 - SSP2 4.5 scenarios. For *C. piquiti*, precipitation seasonality contributed 30.2% in current conditions and increased to 37.8% in future scenarios. For *C. kelberi*, precipitation and temperature seasonality accounted for 43.6% and 46.3% of variable importance in current and future scenarios, respectively. On the other hand, precipitation of the warmest quarter and mean temperature of the wettest quarter were the most important variables for *O. niloticus*, contributing 28.9% in current conditions and increasing substantially to 44.3% in the future 2050 - SSP2 4.5 scenarios (Figures S1-S11).

Calibration of the models, validation, and forecasting performance

The individual models selected to build the ENMs ensemble showed high reliability, with Sensitivity and Specificity consistently above 95%, supporting the predictive capacity to identify suitable habitats (Table 1). The evaluation of True Skill Statistic (TSS) and Area-Under-the-Curve (AUC) metrics also confirmed the good performance of the models selected, with a mean calibration AUC ≥ 0.98, validation AUC ≥ 0.93, calibration TSS ≥ 0.91, and validation TSS ≥ 0.78 for all IAS and climatic scenarios (Table 1 and Figure S14). MaxEnt and RF demonstrated the highest performance values among the individual algorithms across all species and scenarios. (Table S7). The findings of this study suggest that the models are appropriate for the projection of current and future (2050) changes in habitats available for the IAS Cichlids in the BR-UPRB.

IAS suitable habitats in the Br-UPRB

The ENMs ensemble confirm this high proportion of current suitable habitats for all IAS Cichlids in the Br-UPRB. Under current environmental conditions, IAS Cichlids in the Br-UPRB have access to approximately 29,483 km^2 of suitable lotic and lentic freshwater ecosystems, covering half of the basin (51.9%) (Table 2). *C. piquiti* is currently the IAS Cichlid introduced in the basin with the most suitable habitats available, and for its future expansion in the 2050 SSP2 4.5 scenario. Collectively, the IAS Cichlids may expand their suitable habitats over 12,713 km^2 in the future scenario modeled. These overlapped projections of *O. niloticus*, *C. piquiti*, and *C. kelberi* indicate that the habitats available for these IAS can cover two-thirds of the basin (74.3%) (Table 2).

Species	Scenario	Metric	Sensitivity %	Specificity %	Calibration	Validation
Oreochromis niloticus	Current	TSS	98.6	94.8	0.934	0.858
		AUC	98.6	94.8	0.994	0.951
	2050 - SSP2 4.5	TSS	98.6	94.8	0.934	0.858
		AUC	98.6	94.8	0.994	0.951
Cichla kelberi	Current	TSS	96.1	96.7	0.928	0.805
		AUC	96.1	96.7	0.986	0.934
	2050 - SSP2 4.5	TSS	95.7	97.1	0.928	0.873
		AUC	95.7	97.1	0.993	0.959
Cichla piquiti	Current	TSS	94.5	96.1	0.907	0.776
		AUC	94.5	96.1	0.984	0.939
	2050 - SSP2 4.5	TSS	96	94.6	0.907	0.812
		AUC	96	94.6	0.99	0.957

Table 1. Average performance of ecological niche models (ENMs) of IAS (Invasive alien Species) cichlids introduced in the Brazilian part of the upper Paraguay river basin (Br-UPRB) in current and future 2050 - SSP2 4.5 climate scenarios. Assessing the sensitivity and specificity of the models through calibration and validation metrics: area-under-the-curve (AUC) and true skill statistic (TSS).

IAS cichlids	Occ	Current		2050 - SSP2 4.5		%	%	IAS range change
		≈km²	% Br-UPRB	≈km²	% Br-UPRB	Loss	Gain	
Oreochromis niloticus	168	8,526	15	9,012	15.9	33.2	48.0	14.7
Cichla kelberi	130	2,536	4.5	6,943	12.2	9.7	66.4	56.7
Cichla piquiti	609	18,421	32.4	26,241	46.2	25.6	273.8	248.1
***IAS overlap**		29,483	51.9	42,196	74.3	12.6	65.3	52.7

Table 2. Current and future 2050 - SSP2 4.5 suitable areas in ≈ km² for IAS cichlids introduced in the study area (Br-UPRB), based on ENMs ensemble: generalized linear models (GLM), random forest (RF), and maximum entropy (MaxEnt). The occurrences (Occ), percentages (%) that these areas represent in freshwater ecosystems in the (Br-UPRB), and the suitable areas May show loss (%), May be gain (%), and the change ratio expected between these areas (% loss - % gain), i.e., IAS range Change. *The IAS overlap is the suitable area ≥ 1 IAS.

		Current			2050 SSP2 4.5		
		Overlap %	IAS %		Overlap %	IAS %	
1	Pantanal Wetland	58.10	*C. piquiti*	56.12	90.15	*C. piquiti*	87.52
-	Br-highlands (Plateau)	31.48	*O. niloticus*	21.42	41.79	*C. piquiti*	25.06
2	Jaurú-Sepotuba	15.69	*C. kelberi*	14.00	33.19	*C. kelberi*	31.80
3	Cuiabá	7.03	*C. piquiti*	4.08	10.00	*C. piquiti*	4.01
4	São Lourenço-Vermelho	25.13	*O. niloticus*	19.19	28.04	*O. niloticus*	25.98
5	Taquari-Coxim	15.56	*C. piquiti*	14.37	13.25	*C. piquiti*	11.13
6	Aquidauana-Negro	22.12	*O. niloticus*	19.05	76.44	*O. niloticus*	72.69
7	Miranda	78.79	*C. piquiti*	72.36	85.98	*C. piquiti*	80.15
8	Apa-Perdido	97.00	*O. niloticus*	89.96	93.52	*C. piquiti*	92.30

Table 3. Percentage of Pantanal wetland, Brazilian plateau, and tributary sub-basins (2–8) with suitable habitats for the IAS overlap (≥ 1 IAS), in current and future 2050 - SSP2 4.5 scenarios, based on ENMs ensemble: generalized linear models (GLM), random forest (RF), and maximum entropy (MaxEnt). IAS % with the most suitable habitat per each area is included.

According to the data, more than half of the Pantanal currently provides suitable habitats for IAS Cichlids (58.10%). At the same time, almost a third of the tributary sub-basins are suitable for these IAS (31.48%). However, future conditions predic that suitable areas for IAS Cichlids may increase to 90.15% of the available freshwater ecosystems in Pantanal and 41.79% of the tributary sub-basins (Table 3). These increases reflect shifts in the suitability of habitat, i.e., the areas that may no longer be suitable, those that may remain stable, and those that may become suitable for these IAS in the future (Table 2; Fig. 1).

By 2050, predicted climate change may influence the availability of suitable habitats for the three IAS differently. *O. niloticus* is predicted to maintain its suitable habitats relatively stable with moderate expansion in the future (IAS Range Change of 14.7%), showing the most conservative response among the three IAS (Table 2; Fig. 1a). On the other hand, *C. kelberi* exhibits a more pronounced rate of change (IAS Range Change of 56.7%), with suitable habitats expanding primarily around the sub-basin of introduction to the northwest of the basin (Jaurú-Sepotuba) and extending to the southeast of the Pantanal (Tables 2 and 3; Fig. 1b). Finally, *C. piquiti* might experience the highest rate of change (IAS Range Change of 248.1%), showing potential expansion from current optimal environments near the middle course of the Paraguay River (main river in Br-UPRB) to the whole flood plain and São Lourenço-Vermelho and sub-basins further south (Tables 2 and 3; Fig. 1c).

Consistent with the general basin-wide trend, the results reflect that the suitability of the habitats may increase in the Pantanal wetland (lowlands) and its tributary sub-basins in the Brazilian plateau (highlands). *O. niloticus* shows strong suitability in the southern Plateau sub-basins, particularly in Aquidauana-Negro and Apa-Perdido, coinciding with their initial introduction areas (Table 3). While *C. kelberi* could expand its presence in the Jaurú-Sepotuba sub-basin, where it was originally introduced. *C. piquiti* exhibits the most extensive suitable habitats in the Pantanal wetland, maintaining dominance in multiple sub-basins, including Miranda, and expanding significantly across the region in future modeled scenarios (Table 3). Although suitable habitats for *C. piquiti* are trending upwards, some sub-basins may experience a decrease in these habitats (e.g., Taquari-Coxim) or maintain limited suitable habitats (< 10% of the sub-basin, e.g., Cuiabá) compared to the remaining sub-basins. This pattern is explained by the expected turnover of suitable habitats, expressed by the Range Size Change (Table 2; Fig. 1c).

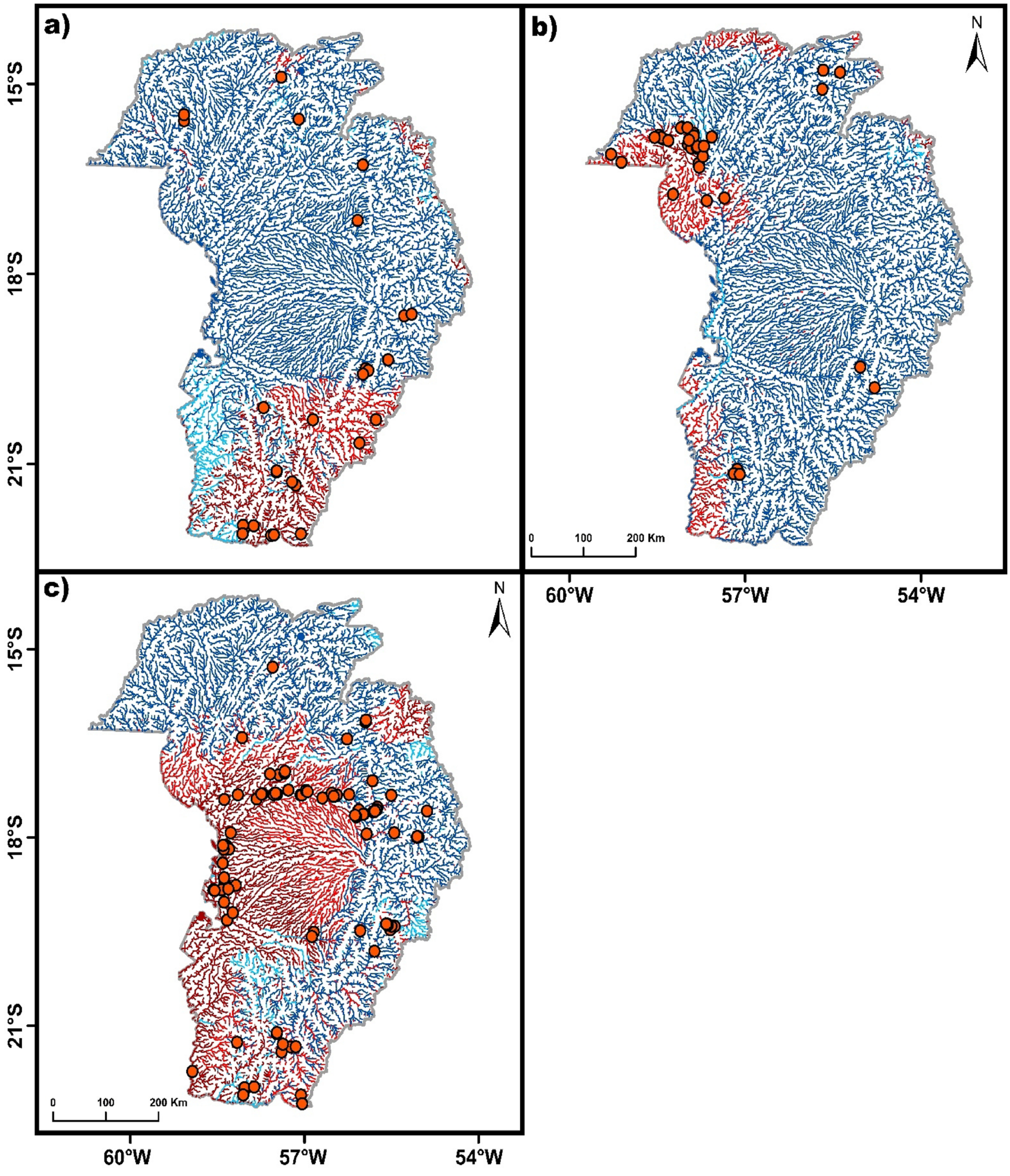

Fig. 1. Projected changes in habitat-suitability for: (**a**) *Oreochromis niloticus* (**b**) *Cichla piquiti*, and (**c**) *Cichla kelberi*, in the study area (Br-UPRB) between Current and Future 2050 - SSP2 4.5 scenarios, based on ENMs ensemble: Generalized Linear Models (GLM), Random Forest (RF), and Maximum Entropy (MaxEnt): Light blue: areas to be lost, Dark blue: areas to remain unsuitable, Light red: areas to may gain suitability, Dark red: areas to remain suitable, Orange dots: IAS Occurrences. The habitat-suitability maps were created using ArcGIS Pro 2.8: https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

IAS suitable habitats in Br-UPRB reservoirs

The IAS fish species introduced in the Br-UPRB currently exhibit limited suitable habitats in the basin's reservoirs (15.52% overall), with greater suitability available in large reservoirs. Small reservoirs (1–3 km²) show the lowest current suitability at 10.34%, while medium-sized reservoirs (3–13 km²) present moderate suitability at 18.18%, and large reservoirs (> 13 km²) demonstrate the highest current suitability at 28.57%. Nevertheless, according to our projections for 2050, the extent of suitable habitats for these species is expected to more than double within all three categories of these environments. Most notably, large reservoirs are projected to reach nearly 60% suitability (57.14%), representing a two-fold increase from current conditions. Overall, the total suitable habitat in reservoirs is projected to increase from 15.52% to 34.48%, indicating that more than one-third of all reservoirs in the Br-UPRB may become suitable for IAS establishment by 2050 (Table 4).

Discussion

The Pantanal wetland and its tributary sub-basins exhibit a large extension of suitable habitats that are optimal for the future proliferation of introduced IAS Cichlids, even under one of the most optimistic future climate scenarios (i.e., 2050 - SSP2 4.5)[67]. Conversely, there is a substantial loss of suitable habitats for native freshwater fish species in the Br-UPRB under climate change[23]. These opposing trends highlight a critical concern: while the expected environmental conditions may facilitate the thriving of IAS Cichlids, the native fish species may face a significant loss of diversity[15,23,68]. The potential proliferation of these introduced species assessed in our study may likely intensify the climate change challenges for native species, disrupt biological communities, alter ecosystem structure and function, and lead to important socio-economic consequences[35].

The importance of climate seasonality in our ENMs is consistent with previous observations that seasonal temperature and precipitation patterns influence the potential spread of IAS fishes[69,70]. This antecedent could also be related to the fact that the colonization success of Cichlid species is greatly influenced by abiotic factors, their plasticity, and their high adaptive capacity[71,72]. Unexpected changes in the climatic patterns and seasonality (e.g., El Niño-Oscilación del Sur - ENSO, droughts, etc.), such as those projected for 2050, may influence the IAS Cichlids' establishment and spread in the study area[73–76]. Several authors also demonstrated that in a large regional-scale study, simple influences, such as altitude and basin area, seem enough to identify the distribution and suitable habitats for freshwater fish species[77,78]. In our case, precipitation and temperature seasonality were the main drivers of habitat suitability changes.

The contrasting habitat suitability patterns observed among introduced IAS Cichlids reflect their species-specific evolutionary histories, ecological requirements, physiological tolerances, and the establishment time in the basin[72]. *Cichla* spp. native to the adjacent Araguaia-Tocantins basin (contiguous to Br-UPRB) showed greater suitability in the Pantanal wetland, exhibiting preference for warm, shallow lentic or slow-flowing environments with complex structural habitats characteristic of floodplain ecosystems in both basins (native and introduced)[79]. Despite flowing into opposite mouths, the Amazon and Paraná rivers not only share similar environmental conditions but also share related freshwater fauna[80]. These antecedents could be related to the successful establishment of *Cichla* spp. in the Br-UPRB and other tropical ecoregions of the Americas, Africa, Southeast Asia, and the Pacific islands[81–83]. On the other hand, *O. niloticus* shows greater suitability in the southernmost tributary sub-basins of the Brazilian plateau, which provide more stable thermal conditions and diverse habitat heterogeneity that align with this species' broader environmental tolerance, opportunistic feeding behavior, and ability to thrive across a wide range of pH, conductivity, and turbidity conditions[84,85]. This invasion pattern has been documented in tropical and subtropical basins worldwide, including establishing the Nile Tilapia in the Pearl River system (China)[86], Lake Victoria (Central Africa)[87], various basins in Mozambique and Southern Africa[88,89], India[90,91], and several water bodies across the Americas[35], where these introductions have consistently resulted in substantial ecological and economic impacts[37,92,93].

Our results also support the growing evidence that climate change impacts on habitat suitability are species-specific, driven by habitat preferences, physiological variability, and thermal plasticity[45,51,94]. For instance, although *Cichla* spp. use habitats similarly; our ENMs show that the most suitable areas in the basin are exclusive to each species[81,83]. Specifically, 80% of the suitable habitats are occupied by a single species. This suggests that under climate change, IAS Cichlids in the Br-UPRB may not compete with each other for suitable habitats, but they could instead compete with native species[23]. In the case of *Cichla* spp., our projections of suitable areas for both species are consistent with their reported areas of introduction. While *C. piquiti* was introduced in the early 1980s to the Piquiri River and is well-established in the floodplain of the Paraguay River[28,29], *C. kelberi* was introduced most recently in the Padre Inácio and Caramujo rivers (northern of Br-UPRB) and has been expanding its invasion range toward the southern basin[30]. Climate change projections indicate that *C. piquiti*

Reservoirs type	%Current	% 2050 SSP2 4.5
Small reservoirs (1–3 km^2)	10.34	31.03
Medium-sized reservoirs (3 – 13 km^2)	18.18	31.82
Large reservoirs (> 13 km^2)	28.57	57.14
Total	**15.52**	**34.48**

Table 4. Percentage of the reservoirs in the study area (Br-UPRB) with predicted suitable habitats for the IAS overlap (≥ 1 IAS) in current and future 2050 - SSP2 4.5 scenarios, based on ENMs ensemble: generalized linear models (GLM), random forest (RF), and maximum entropy (MaxEnt).

may experience the most considerable expansion with an IAS Range Change of 248.1%, while *C. kelberi* shows a more moderate but still substantial rate of change at 56.7%. Both Cichlid species are very aggressive piscivores, and if these IAS establish viable populations in all suitable habitats along the basin where our models predicted, these species could drastically impact the native fish species populations[81,83].

The previous hypothesis that the invasion range of *C. piquiti* was restricted by the turbid waters, operating as an ecological barrier to its spread, has recently been refuted[29,95,96]. Our models' predictions include sub-basins and main rivers with turbid waters as suitable habitats for this species in the Br-UPRB, where the IAS has been fished regularly (12,961 kg in 2009, 994 kg in 2010, and 16,591 kg in 2018)[31,97]. The 2010 decline in catches could be related to cold fronts in July and August (4.6–9.2 °C) since this species prefers warmer waters (physiological optimum above 15 °C)[98,99]. Future climate scenarios with a temperature increase of at least 1.5 °C would likely favor the proliferation of this IAS. This is particularly concerning given that these IAS have already caused severe ecological damage in other ecosystems where they have been introduced, including the collapse of native fish assemblages in Brazilian reservoirs such as Três Marias, Sobradinho, and Itumbiara, the displacement of native piscivores in Colombian rivers and reservoirs, and the disruption of food webs in Venezuelan and Panamanian freshwater systems[81,99,100].

Despite *O. niloticus*'s well-documented history as an invasive competitor, it may show stability in its future habitat-suitability with an expected IAS Range Change of 4% [35,101]. However, considering the wide range and global occurrence availability, our results are limited by the number of records and the considerable geographical distance between the northernmost and southernmost occurrences of *O. niloticus* in the study basin. This limitation reflects the recent establishment of *O. niloticus* populations in the Br-UPRB and the concentrated sampling efforts in specific introduction areas rather than basin-wide and native surveys. This disjunct invasion pattern suggests the possibility of multiple events of introduction and diverse routes of spread within the study area. Given their recent economic importance in the basin, this potential IAS necessitates further research and urgent management actions[35].

Contrary to our expectations, reservoirs in the basin appear to offer limited habitats for introducing IAS Cichlids, with only 15.52% of reservoir habitats currently exhibiting suitability for these species, which is substantially below the 58.10% suitability observed in the Pantanal wetland (Tables 3 and 4). Nevertheless, our projections for 2050 show that the extent of suitable habitats for these species is expected to more than double within all reservoirs, with large reservoirs projected to reach 57.14% suitability and overall reservoir suitability increasing to 34.48%. This expected habitat suitability in large reservoirs, where there are usually more existing alien fish farms, and more in the planning stages[102,103]. The proliferation of IAS Cichlids in Br-UPRB reservoirs may also be determined by native species interaction, including predation, competition, and upstream ecosystems, as has been happening in other tropical reservoirs[26,99,104,105].

We compiled information on public datasets built from traditional scientific activity (field and laboratory occurrence records, online and museum databases), supplemented by data from Citizen Science (Structured interviews and Instagram posts). We highlight the recent use of fishers' local ecological knowledge (LEK) as a valuable alternative for gathering information on *Cichla* spp.[106]. Of all the occurrences documented in the study area through this research, 74.4% were contributed by Citizen Science Data. This approach is not always easy to implement, some fishers were reluctant to participate in interviews and share information on fishing locations, primarily due to their unfamiliarity with our research or apprehension regarding fishing regulations, including conservation areas and spawning season, regardless of the IAS status[37,107]. Despite the drawbacks, the simplicity of visually identifying the IAS Cichlids through the fishers and photographs has been another advantage of the methodology used[108]. However, there are challenges in visually identifying several unknown species with confidence (i.e., cryptic species). Using Citizen Data with the ENMs' capacity to predict the regions at risk of IAS invasion is a promising and cost-effective method to develop practical preventative actions and planning management in the basin[109,110].

Conclusion and recommendations

Previous research on IAS Cichlids introduced in the basin was based primarily on the fishing catch reports, focusing on a single species within a specific area or sub-basin[29–31]. Our study provides a comprehensive Spatio-temporal perspective on the IAS Cichlids' potential invasive areas, covering inter-regions and intra-basin levels. The model outputs shown here present a state-of-the-art estimation of suitable habitats for the three main fish species introduced in the Br-UPRB. It represents a second step in understanding the potential IAS impacts on Pantanal's native freshwater fish community, one of the most diverse in the Neotropical region (~ 300 species).

Mato Grosso state (northern half of Br-UPRB) restricts fishing, transport, and storage of introduced *Cichla* spp. through 2028 under State law 12.434[111]. This law, in addition to 16 other regulations protecting invasive Peacock bass (*Cichla* spp.) in Brazil, contributes to biodiversity loss, disrupts freshwater ecosystems, and generates social conflicts[37,112]. Considering the economic costs of biological invasions in the Neotropical basins[113] and the unintended consequences of valuing non-native freshwater species[37], we recommend the implementation of better control and management protocols in fish farm facilities and reservoirs to avoid the escapes of additional IAS fishes in suitable areas[114].

As suggested by other researchers, we recommend conducting field validation of habitat-suitability models for IAS[115]. This involves testing whether these models adequately predict observed data and, if accurate, using them to estimate the potential range of the invasive species[116]. Field reports conducted in 2021[31], after our field data collection (2018–2019), confirm the presence of *C. piquiti* in several habitats that were predicted as suitable in our models. We also believe that the constant update of the models with new data sources, through some automation processes by machine learning algorithms and artificial intelligence (AI), could produce dynamic and robust models that allow a better understanding of the invasion patterns and IAS ecology[117,118].

Among other actions, we also advocate for expanding the IAS impact studies to the Bolivian and Paraguayan share of the UPRB and increasing the sampling of *O. niloticus*, given its high-risk invasive potential. This would lead to developing joint monitoring and control plans with local fisher communities, government agencies, universities, research institutes, and recreational fishing tourism companies, e.g., by encouraging massive recreational and artisanal fishing and consumption, intending to reduce populations as a strategy to control the spread of IAS fish species[119]. We also promote a gradual change to the commercial production (fish farms) of native species and their repopulation into areas where they have been affected by the IAS Cichlids, safeguarding ecosystem services generated by native freshwater fishes[37]. The early detection of a potential IAS and the ability to map its invasion range are fundamental to effective management decisions[60].

Our study also demonstrates the advantage of integrating LEK with ENMs to enhance IAS detection[106,120]. This combined approach improves the identification of suitable habitats, enabling precise predictions of potential invadible areas[46]. Integrating Citizen Science Data with GIS methodologies is critical for early detection and control, as many IAS may not yet occupy all predicted suitable habitats[108,121,122]. The implementation of the methods used in this study allows the development of targeted management strategies that can effectively mitigate ecological costs during the crucial initial invasion stages[123]. Furthermore, the integration of real-time monitoring systems with predictive modeling provides decision-makers with the tools necessary to implement rapid response protocols, prioritize conservation efforts in high-risk areas, and allocate resources efficiently before IAS populations become established and irreversibly alter native freshwater ecosystems. This approach is particularly critical in biodiversity hotspots, where prevention costs are significantly lower than post-establishment control measures.

Materials and methods

Study area

The study is focused on the Br-UPRB, or Paraguay River, and its main upstream tributaries of the Pantanal wetland in the Brazilian part[101] (Fig. 2). This Ramsar site begins in the Brazilian plateau, covering an area of 361,666 km[276]. The basin experiences a tropical humid climate, averaging an annual temperature of 22.5 to 26.5 °C. Seasonal precipitation, mainly during the rainy period (October-March), contributes 70% of the total annual precipitation (800–1600 mm). These climatic dynamics impact substantial water level fluctuations of approximately 3.1 ± 0.9 m in the floodplain[76]. Over decades, the Br-UPRB has faced deforestation, ecosystem homogenization, habitat loss, fragmentation, biodiversity decline, and the introduction of IAS, all impacting regional wildlife persistence[24,101].

Mapping the hydroelectric reservoirs in the basin

To assess if the hydroelectric reservoir conditions are suitable for the IAS fishes introduced to the basin, we used the Brazilian Electric Energy Agency's (ANEEL) georeferenced database and Landsat 8 OLI- Operational Land Imager Collection-2 Level-2 (01/01/2018-06/01/2019) satellite imagery to confirm the presence of reservoirs[124–126]. We selected reservoirs with an area over 1 km^2 to match the environmental variables' spatial resolution, and the ANEEL classification of reservoir types was followed (Table 5; Fig. 2).

Species occurrence records

We collected data on IAS Cichlid occurrences (1989–2019) from museum specimens, field catches, and databases in native and study areas (Table S8). We acquired reliable occurrences of Blue Peacock Bass: *C. piquiti*, Yellow Peacock Bass: *C. kelberi*, and Tilapia: *O. niloticus* in the Br-UPRB. Record gaps were filled through Citizen Science data, obtaining information from interviews with local fishers and georeferenced photos of sport anglers obtained on the social network Instagram (Meta Platforms, Inc.)[111].

The semi-structured interviews with local fishers were done following the Rapid Assessment Protocol (RAP) developed for detecting IAS fish species in Brazilian lakes[108]. We conducted 257 interviews with experienced local fishers between 2018 and 2019, covering most of the study area (Main rivers and sub-basins). To ensure accuracy, cross-validation of interviews involved presenting images of common fish species absent in the basin and avoiding false-positive occurrence records (model of the interview in Table S9 and Figure S10). Each validated interview was transformed into an occurrence of IAS only if the fisher could specify the nearest water body section where the species was found.

Beyond interviews, an Instagram IAS georeferenced photo analysis was conducted in the study area. Original posts, official accounts, and fishing-related hashtags were cataloged. We communicated with photographers and fishers to confirm the location details. Out of 326 potential IAS records, only 80 were validated through direct messages, ensuring precise georeferencing. IAS occurrences within 1 km of the next water body were relocated to align with gridded environmental variables[127]. Records that did not meet this criterion or duplicated within the same 1 km^2 cell were eliminated, retaining only the most recent occurrence.

Environmental variables and climate scenarios

To model the current and future suitable habitats for IAS Cichlid species, we selected topographic and bioclimatic variables relevant to climate change and IAS modeling in 30 arc-seconds of resolution (≈ 1km[2]. For current conditions, we used the database of freshwater-specific environmental variables for biodiversity analysis[127]. For the future climatic scenario, we employed WorldClim bioclimatic variables from CMIP6 (Coupled Model Intercomparison Project) simulations representing 2050 conditions (average for 2041–2060) in the Shared Socio-economic Pathways SSP2 4.5, a mid-term scenario[58]. The SSP2 4.5 scenario foresees a moderate path for climate action, aligning with countries' emissions commitments[67]. This outlook estimates a global temperature rise of 2.1–3.5 °C from 1950, with a population of 9.6 billion. The radiative forcing in the SSP2 4.5 scenario peaks

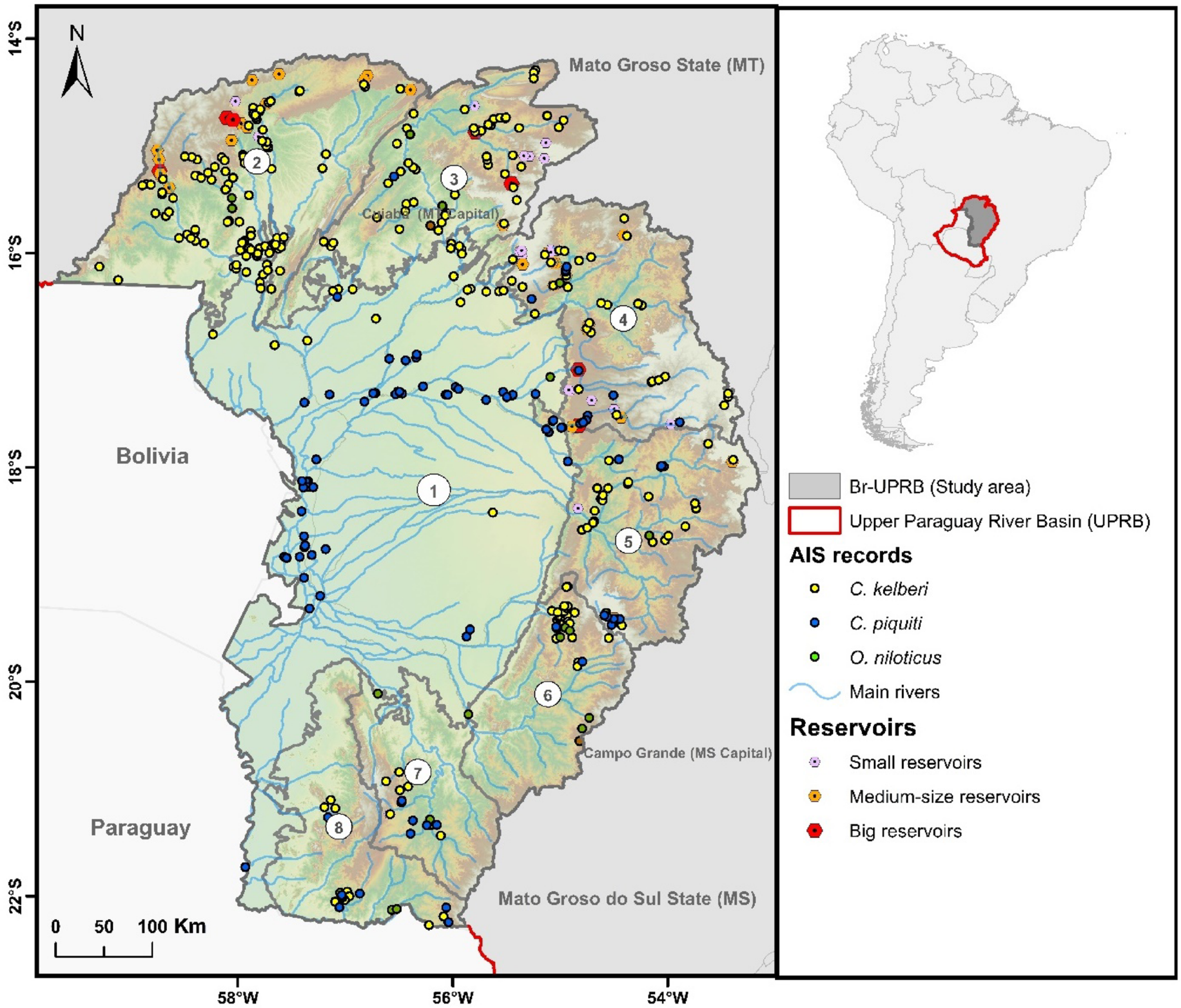

Fig. 2. Study area - Brazilian part of the Upper Paraguay River Basin (Br-UPRB). (**1**) Pantanal wetland and the main tributary sub-basins in the Brazilian plateau (**2**–**8**). (**2**) Jaurú-Sepotuba, (**3**) Cuiabá, (**4**) São Lourenço-Vermelho, (**5**) Taquari-Coxim, (**6**) Aquidauana-Negro, (**7**) Miranda, and (**8**) Apa-Perdido. The location of reservoirs and Introduced Alien Species (IAS) occurrences are included. The map was created using ArcGIS Pro 2.8: https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Reservoirs type	# of reservoirs	Area
Small reservoirs	20	1–3 km^2
Medium-sized reservoirs	29	3 – 13 km^2
Large reservoirs	6	> 13 km^2

Table 5. Identified reservoirs in the Brazilian part of the Upper Paraguay River Basin (Br-UPRB) to June 2019. Small reservoirs, medium-sized reservoirs, and large reservoirs.

at 4.5 Wm^{-2} by 2050, then decreases if priority is given to international cooperation for environmental aims; nevertheless, inequalities persist[58].

To reduce the uncertainty associated with a single global climate model, we used an ensemble (unweighted mean) of CMCC-ESM2 (Centro Euro-Mediterraneo sui Cambiamenti Climatici Earth System Model version 2) and HadGEM3-GC31-LL (Hadley Centre Global Environment Model version 3, Global Coupled configuration 3.1, Low-Resolution) projections[128,129]. This approach provides more robust predictions and better represents the potential future scenarios[130,131]. Additionally, it improves accuracy by capturing different climate sensitivities and regional patterns[132].

We divided the climatic and topographic predictor variables into two sets: (1) for Br-UPRB + Araguaia - Tocantins basins (for modeling the two *Cichla* spp. habitat suitability) and (2) for Br-UPRB + Nile basins (for modeling *O. niloticus* habitat suitability). We utilized the variance inflation factor (VIF) to address multicollinearity, selecting the bioclimatic variables with VIF values < 5 (Tables S1-S4)[133]. Additionally, we included elevation, slope, and flow accumulation in models, considering their impact on IAS fish habitat selection and dispersal[134]. These climatic data, used in various ENMs, are considered standard for modeling freshwater species distributions[77,135].

Modeling assessment and ensemble forecasting approach

Using Ecological Niche Models (ENMs), we identifed the suitable habitats for the selected IAS Cichlid species in their native range (calibration area) and introduced region (Br-UPRB) under present and future climatic conditions (Figures S11-S13)[120,136]. We modeled the geographic range (native + UPRB areas) to capture each IAS's filled environmental niche breadth, avoiding underestimating potential suitable habitats when modeling only invaded ranges[46,136]. IAS Cichlid occurrences and environmental variables were linked using three ENM algorithms: Generalized Linear Models (GLM), Random Forest (RF), and Maximum Entropy (MaxEnt)[137]. These three algorithms' ensemble forecast (EF) enhances individual projections for IAS with limited occurrence points in undersampled regions[46,138]. Unlike maximizing the projected range, this EF approach relies on overlapping regions of employed ENMs, which is favorable for dealing with uncertainty and species with changing niche tolerances[137,139]. Models were fitted using the ensemble platform for species distribution modeling "Biomod2" in the R environment[140].

The three selected algorithms use different input data: GLM uses presence-absence data, while RF and MaxEnt use presence-background data[141]. Pseudo-absence data were generated randomly from the background outside the occurrence points, with 1,000 pseudo-absence points generated per run. To prevent model bias during training, occurrence and pseudo-absence points were weighted equally (50% total weight for presences, 50% for pseudo-absences) using the bootstrap technique[142]. We used stepwise feature selection with quadratic terms based on the Akaike Information Criterion (AIC) for GLM. RF was applied with 1,000 trees and the default node size. MaxEnt was conducted with 1,000 maximum iterations and a 10^{-5} convergence threshold[143]. Species occurrences were randomly divided into 80% for model calibration and 20% for testing the models[140]. We assessed model performance through random cross-validation, measuring sensitivity (accuracy in identifying occurrences), specificity (accuracy in identifying background points), AUC (area-under-the-curve), and TSS (True Skill Statistic). Only individual algorithms with AUC > 0.7 and TSS > 0.5 were selected for each ensemble model.

A minimum of 100 ensemble models were constructed per species per climatic scenario by merging algorithms ("mergedAlgo" parameter), combining in each EF predictions from three algorithms selected: RF, GLM, and MaxEnt, using "EMmean" (probability mean averaging) and "EMca" (committee averaging) parameters. Only EFs with TSS > 0.7 were selected for final modeling, which may reduce the number of models contributing to the final predictions depending on individual ensemble performance.

IAS binary presence maps

We converted ENMs' continuous frequencies into binary projections, transforming probability values (0-100) into binary (1: Predicted suitable habitat / 0: Predicted unsuitable habitat). Applying the TSS > 0.7 threshold, we selected values (70–100) as suitable habitats (conservative predictions)[139]. This scenario reasonably forecasts the IAS potential range with few occurrences, as in our study, which is widely used in invasion ecology 46. Suitable / Unsuitable values were extracted for each sub-basin and reservoir, analyzing IAS habitat-suitability patterns in the study area.

Analysis of climate change scenarios

We utilized the R package " BIOMOD_RangeSize" for a climate scenario analysis of our IAS overlap[140]. Comparing binary projections (current vs. 2050 SSP2 4.5), we assessed changes in four habitat types:

(a) Areas that may no longer be suitable: predicted to be lost.
(b) Areas that may remain unsuitable: predicted to remain stable.
(c) Areas that may gain suitability: predicted to be gained.
(d) Areas that may remain suitable: predicted to remain stable.

Model outputs have a 0.926 km^2 resolution (pixel size at equator latitude). Nevertheless, the study area's size and distance from the equator alter potential suitable habitat values, presenting results in ($\approx km^2$) rather than exact values (Supplementary Material 1, Tables S10-S11).

Data availability

The occurrence data of the introduced Cichlid species studied in its native distribution area were obtained from available biodiversity databases and georeferenced research papers (Supplementary Material), and the occurrence data in its introduced range are available in the Figshare repository: https://doi.org/10.6084/m9.figshare.26961754. The climatic and topographic data used are available at https://www.earthenv.org/streams and https://www.worldclim.org/data/bioclim.html. Additionally, upon request, the corresponding author could provide the high-resolution rasters generated in this study.

Code availability

The script codes generated in this study have been deposited in the following Figshare repository: https://doi.org/10.6084/m9.figshare.26961754.

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Author contributions
CM-G and JMFP conceived, designed, and approved the study. LAdFM and YRS provided the data collection in the field. TS-S contributed to the development of the models and/or revisions. CM-G carried out the analysis and wrote the first draft of the manuscript. All authors contributed to subsequent versions and the interpretation of the data and results. All authors approved the final version of the manuscript.

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Declarations

Competing interests
The authors declare no competing interests.

Ethics declarations
This study included the participation of local fishing communities of artisanal and recreational fishers and was approved by the Federal University of Mato Grosso's ethical research committee (register: 3.511.327). All the interviews were performed following relevant guidelines and regulations, protecting the identity of the interviewed fishers. Additionally, we confirmed that all interviewed fishers signed informed consent.

Additional information
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