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The most important fishery resource in the Amazon, the migratory catfish *Brachyplatystoma vaillantii* (Siluriformes: Pimelodidae), is composed by an unique and genetically diverse population in the Solimões-Amazonas River System

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The migratory catfish *Brachyplatystoma vaillantii* is one of the most important fishery resources in the Amazon. Intense capture occurs associated to its life cycle. In order to know the genetic status, we sequenced the mitochondrial DNA control region from 150 individuals of *B. vaillantii*, collected in five fishing landing locations, covering the length of the Solimões-Amazonas River in Brazil. Genetic diversity parameters suggest there is no genetic differentiation between the five localities. Population's expansion indicated by R_2 and Fu's Fs tests was also confirmed by the high number of unique haplotypes found. The Analyses of molecular variance indicated that nearly all variability was contained within locations (99.86%), and estimates of gene flow among *B. vaillantii* were high (F_{ST} = 0.0014). These results suggest that *Brachyplatystoma vaillantii* forms a panmitic population along the Solimões-Amazonas River and, has greater genetic variability than other species of the *Brachyplatystoma* genus available so far. Although the influence of different tributaries on *B. vaillantii* migration patterns remains uncertain, a single population in the main channel should be consider in future policies for management of this resource. However, since the species' life cycle uses habitats in several countries, its management and conservation depend greatly of internationally joined efforts.

Keywords: Control region, Fishery resources, mtDNA, Piramutaba, Population genetics.

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O bagre migrador, *Brachyplatystoma vaillantii*, é um dos mais importantes recursos pesqueiros da Amazônia. Intensa captura ocorre associada ao seu ciclo de vida. Para conhecer seu status genético, sequenciamos a região de controle do DNA mitocondrial de 150 indivíduos, coletados em cinco locais de desembarque pesqueiro, abrangendo toda a extensão do rio Solimões-Amazonas no Brasil. Os parâmetros de diversidade genética sugerem que não existe diferenciação genética entre as cinco localidades amostradas. A expansão populacional indicada pelos testes R_2 e *Fs* de Fu, também foi confirmada pelo elevado número de haplótipos únicos encontrados. A análise de variância molecular indicou que quase toda a variabilidade estava contida nas localidades (99,86%), e as estimativas de fluxo gênico desta espécie eram altas (F_{ST} = 0,0014). Esses resultados sugerem que *Brachyplatystoma vaillantii* forma uma população panmítica ao longo do rio Solimões-Amazonas com maior variabilidade genética que outras espécies do gênero *Brachyplatystoma* disponíveis no momento. Embora a influência dos diferentes afluentes na migração de *B. vaillantii* permaneça incerta, em futuras políticas de gestão deste recurso deve-se considerá-lo como uma única população no canal principal. Entretanto, uma vez que seu ciclo de vida abrange habitats em vários países, seu manejo e conservação dependem muito de esforços internacionais em conjunto.

Palavras-chave: DNAmt, Genética populacional, Piramutaba, Recursos pesqueiros, Região controle.

INTRODUCTION

The Amazon Basin has features such as altitude, rainfall, temperature, forest cover and water chemistry that affect the diversity of local assemblages (Ríos-Villamizar *et al*., 2020). Aquatic organisms have not only adapted to these features, but also developed a variety of life cycles as a result (Reis *et al*., 2016). As a putative consequence of habitat diversity and life strategies, Amazonian ichthyofauna also became extremely diverse, with around 3000 described species (Dagosta, De Pinna, 2019). With the exception of the giant Osteoglossiform *Arapaima gigas*, the largest Amazonian fishes known belong to the Family Pimelodidae, of the Order Siluriformes (catfishes). In the Amazon the pimelodids, or goliath catfishes, mostly inhabit the main channels, and several species developed seasonal migratory behavior and use the entire length of the Amazon River System to complete their life cycle (Winemiller, 1995, 1989; Ruffino, Isaac, 2000; Klautau *et al*., 2016).

Brachyplatystoma vaillantii (Valenciennes, 1840) (*piramutaba* in Portuguese, *pirabutón* in Spanish, laulao catfish in English), an Amazonian pimelodid, is considered the most important freshwater fish exported from Brazil according to the annual capture records for the species (Frédou *et al*., 2010; Klautau *et al*., 2016). The life cycle of *B. vaillantii*, and other migratory pimelodid catfishes, as currently understood, was originally proposed based upon an analyses of several thousand individual samples obtained from rivers across the Amazon Basin (Barthem, Goulding, 1997). This hypothesis established a migratory pattern, where the headwater tributaries of the Solimões-Amazonas River, near the Andes, were considered the main spawning area. The mouth of the Amazon River, an estuarine area with high primary production, is the nursery area for young fish, while the main channel of the lower Solimões-Amazonas River forms the feeding habitat for juveniles and adults, due to a high biomass of prey fish (Barthem, Goulding, 1997, 2007). Currently, the greatest distances measured between spawning and nursery areas for *B. vaillantii* are 3,129 km in the Madeira River (Barthem *et al*., 2017), 4,754 km in Napo River and 4,847 in Marañon River (Maggia *et al*., 2017), determined by the presence of larvae and juveniles in those areas.

This migratory hypothesis for *B. vaillantii* has been reassessed by Hegg *et al*. (2015), who compared Strontium isotope signatures ($^{87}Sr/^{86}Sr$), and found that the juvenile *B. vaillantii* had strontium isotope signatures which belong to the Western Andean tributaries and the Amazon River main channel. Analyzes of the link between size classes distribution of larvae, juveniles and adults in the Amazon have also found evidence reassuring the migratory movements of several Amazonian goliath catfishes species, including *B. vaillantii*. The presence of mature adults in the Marañón and Napo rivers in Peru and Ecuador, respectively, also reinforces the evidence of spawning sites in the far Western Amazon (Barthem *et al*., 2017). In addition, the presence of *B. vaillantii* larvae in these two tributaries was also verified from DNA metabarcode analyzes (Maggia *et al*., 2017).

Although there is considerable evidence corroborating the existence of long migratory events for piramutaba, several details associated to it remain unclear. For instance, there is no information available concerning the number of times a single individual might complete a full migratory cycle, nor to what locations within the Basin the adults may move after spawning. The potential role of the different tributaries of the Amazon in segregating stocks or populations is also unknown (Araujo-Lima, Ruffino, 2003; Córdoba *et al*., 2011, 2000). In parallel to its migration pattern, or perhaps as a consequence of it, *B. vaillantii* is caught during the low water season in various Amazonian regions along the entire length of the Solimões-Amazonas River axis, under different fishing pressures. For instance, it is captured by the artisanal fishing fleet in Western Amazon, and predominantly by industrial fishing boats near the estuary at the mouth (Eastern) of the Amazon (Frédou *et al*., 2010; Klautau *et al*., 2016). Due to intense levels of fishing over several decades, *B. vaillantii* is currently considered to be overfished in the Amazon (Alonso, Pirker, 2005; Klautau *et al*., 2016). However, although the intense level of exploitation, little knowledge exists concerning how this species fully uses its habitat during their life cycle. Identification of the genetic structure of stocks and knowledge regarding the area covered by the species is of key importance for the implementation of effective strategies to manage and maintain this important natural resource (Ruffino *et al*., 2000). In this context, studies using DNA markers to estimate the genetic variability of species and populations can help identify and better manage fish stocks in the Amazon Basin. Some sequence-based mitochondrial DNA studies have been of key importance in elucidating various biological aspects of commercially important fishes in the Amazon as *Colossoma macropomum* (Cuvier, 1816) (Farias *et al*., 2010; Santos *et al*., 2018, 2007), *Zungaro zungaro* (Humboldt, 1821) (Boni *et al*., 2011), *Nannostomus eques* Steindachner, 1876 (Terencio *et al*., 2012), *Triportheus albus* Cope, 1872 (Cooke *et al*., 2012), *Cichla temensis* Humboldt, 1821 (Willis *et al*., 2015), *Prochilodus nigricans* Spix & Agassiz, 1829 (Machado *et al*., 2017), *Hypophthalmus marginatus* Valenciennes, 1840 (Santos *et al*., 2019), *Myloplus* spp. (Ota *et al*., 2020) including also migratory catfishes as *Pseudoplatystoma* spp. (García-Dávila *et al*., 2013), *Brachyplatystoma rousseauxii* (Castelnau, 1855) (Batista, Alves-Gomes, 2006; Batista, 2010), *Brachyplatystoma filamentosum* (Lichtenstein, 1819), *Brachyplatystoma capapretum* Lundberg & Akam, 2005 (Huergo *et al*., 2011), among others.

Accordingly, the current study aims to estimate the genetic variability of *B. vaillantii* in the Solimões-Amazonas River system (SARS) using mitochondrial DNA (mtDNA) control region sequences. Our main goal is to evaluate whether the species is composed of a single stock (genetically homogeneous), or if the fisheries industry exploit more than one stock (genetically differentiated), in the SARS.

MATERIAL AND METHODS

Sampling and data collection. Muscle tissues from 150 *Brachyplatystoma vaillantii* individuals were collected between 1999 and 2002 near fishing harbors or boat landing sites in 14 localities along the full length of the Solimões-Amazonas System in Brazil, in order to contemplate the main migratory area of piramutaba in the Brazilian Amazon. These 14 landing sites, were further grouped into five locations, which reflected geographical proximity and/or common commercial grounds as follow: Tabatinga (1 –Benjamin Constant and 2 – Tabatinga), Tefé (3 – Mucura Lake, 4 – Tefé, and 5 – Vila Nova), Manaus (6 – Manaus and 7 – Careiro da Várzea), Santarém (8 – Santarém and 9 – Tapará) and Estuary (10 – Almerim, 11 – Gurupá, 12 – Breves, 13 – Belém and 14 –Salvaterra). Each main location is represented by a different color in Fig. 1. All specimens were collected in accordance with Brazilian laws, using a collection license approved by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) via permit numbers 130 and 14278–1. Muscle tissue samples were preserved in 95% ethanol in the field, subsequently were conserved at -20 °C and deposited in the Genetic Resources Collection of the National Institute of Amazonian Research (CRG/INPA) (details described in **S1**).

Laboratory analysis and DNA sequencing. The DNA extraction protocol used was SDS and phenol-chloroform (Sambrook *et al*., 1989), as described in Alves-Gomes *et al*. (1995), with minor adaptations. Total DNA concentration was diluted to between 10 and 20 ng/μL. This DNA extract underwent polymerase chain reaction (PCR) with buffer (1X), $MgCl_2$ (2 mM), Taq DNA polymerase (0.02U/μL), dNTPs (0.1 mM), and 0.25 μM of each primer. We designed the forward primer to amplify the control region: CytbPD- L (5′ CAC CTG AAT CGG AGG CAT GCC CGT 3′), and used the reverse primer DLR1-H (5` GGA TAC TTG CAT GTA TAA ATT GG 3`) (Huergo *et al*., 2011). Amplification was performed for 30 cycles, with the following temperature profile: the first five cycles were run for 1 min at 94 °C, 1 min at 53 °C and 1.5 min at 72 °C. In the remaining 25 cycles, the annealing temperature was 50 °C. PCR products were purified using a GFX kit (GE Healthcare), following the manufacturer's protocol. Primers FTTP-L (5` CCA AGC GCC GGT CTT GTA A 3`) (Huergo *et al*., 2011) and F-12R (5` GTC AGG ACC ATG CCT TTG TG 3`) (Sivasundar *et*

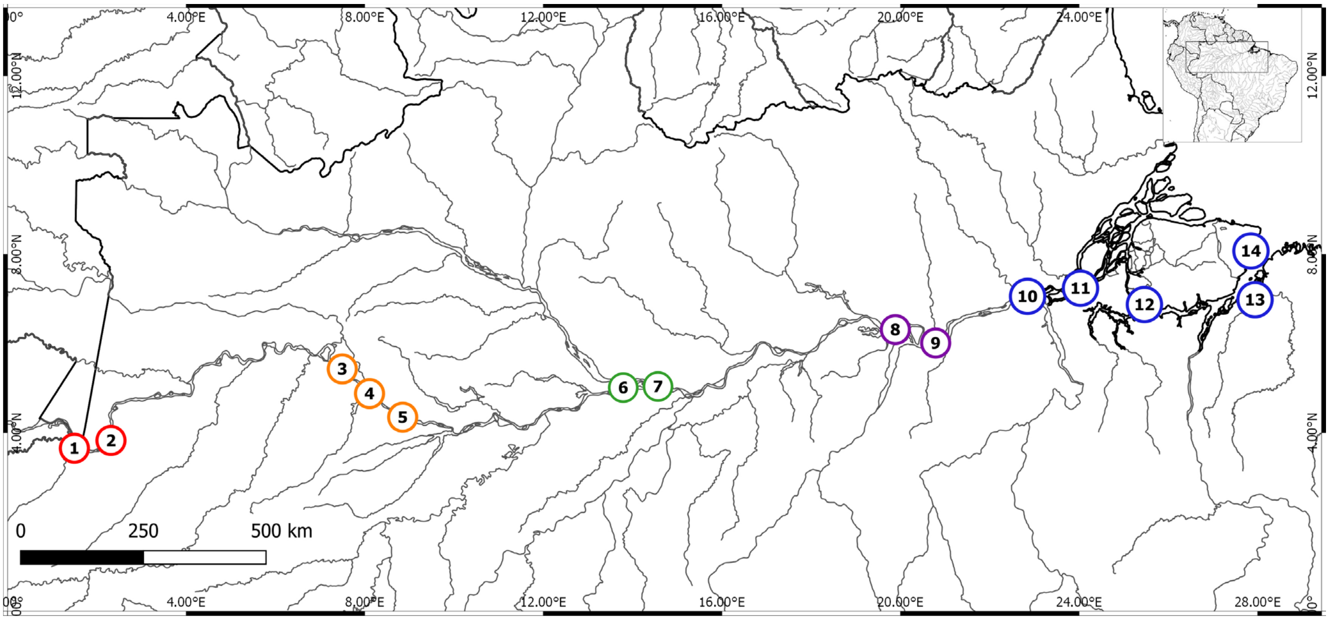

FIGURE 1 | Sampling sites for *Brachyplatystoma vaillantii* along the Solimões-Amazonas River axis. The localities were grouped in five fishing landing towns as follow: Red circles: Tabatinga (1 – Benjamin Constant, 2 – Tabatinga), Orange circles: Tefé (3 – Mucura Lake, 4 – Tefé, 5 – Vila Nova), Green circles: Manaus (6 – Manaus, 7 – Careiro da Várzea), Purple circles: Santarém (8 – Santarém, 9 – Tapará) and Blues circles: Estuary (10 – Almeirim, 11 – Gurupá, 12 – Breves, 13 – Belém, 14 – Salvaterra).

al., 2001) were used as internal primers for sequencing., cycle-sequencing using a DYEnamic ET dye terminator kit (GE Healthcare) under the manufacturers' protocols and submitted to capillary electrophoresis on a MegaBACE 1000 DNA sequencer (GE Healthcare).

Data Analysis. The sequence data were checked and compiled in BIOEDIT 7.0.5 (Hall, 1999) and aligned using MUSCLE (Edgar, 2004). Sequences from each of the 14 localities were grouped into their five respective main areas in order to calculate the genetic parameters (see color code in Fig. 1). Genetic variability was estimated by the following parameters: number of haplotypes, number of single haplotypes, polymorphic sites, haplotype diversity (Nei, Tajima, 1981), nucleotide diversity (Nei, 1987) and average pairwise distance estimated via ARLEQUIN 3.5.2 (Excoffier, Lischer, 2010) and DnaSP 6 (Rozas *et al*., 2017).

Analyses were performed using DnaSP 6 (Rozas *et al*., 2017) to calculate the R_2 and Fu's F_S (Fu, 1997) statistics. These two statistics are considered to be among the most useful for detecting population expansion events in nonrecombining regions of the genome under a variety of different circumstances, especially when population sample sizes are large (Fu's Fs) or when sample sizes are small (R_2) (Ramos-Onsins, Rozas, 2002).

The relationships among haplotypes and their geographic distribution was assessed using statistical parsimony as implemented in TCS 1.21 (Clement *et al*., 2000), with a 95% connection limit.

To test for the presence of population structure, we estimated the number of clusters

(k) using Bayesian posterior probability in BAPS 6.0 (Cheng *et al*., 2013; Corander *et al*., 2013). A mixture model was applied to test for groups of individuals using four interactions of k ranging from one to ten. No prior information about sampling locations was provided. In order to verify possible lineages, a Maximum Likelihood (ML) tree was performed, under model HKY+I+G as evaluated in JModelTest 2 (Darriba *et al*., 2012), using RAXML-NG (Kozlov *et al*., 2019). The reliability of the ML tree was assessed by bootstrap analysis including 200 replications. The resulting best tree was visualized using FigTree v1.4.4 (Rambaut, 2018). Still using the hierarchical Bayesian clustering algorithm, we used FASTBAPS program (Tonkin-Hill *et al*., 2019) implemented in R 4.0.3 (R Core Team, 2019) with packages APE, GGPLOT2, GGTREE, MAPS and PHYTOOLS to infer genetic clusters for the data set.

The structure of genetic variation was quantified, in Arlequin 3.5.2, using analysis of molecular variance (AMOVA) with 10,000 permutations (Excoffier *et al*., 1992), considering haplotype frequency and sequence divergence. AMOVA produces estimates of covariance components and calculates φ_{ST} values that are analogues of Weir, Cockerham's F_{ST} estimator (Weir, Cockerham, 1984).

To estimate genetic exchange rates between localities, we used the program Migrate-N 4.4.3 (Beerli, Palczewski, 2010), under a bayesian inference coalescent model, and estimated effective population sizes and migration rates (migration/mutation). We used a one long chain, uniform prior distribution, 1,000,000 visited genealogies, 10,000 recorded genealogies with a burn-in of 100,000. In this analysis, the migration rates were only inferred between adjacent, hydrographically connected localities (forcing migration between non-adjacent groups to first occur through geographically intermediate localities).

RESULTS

For the 150 samples of *Brachyplatystoma vaillantii*, the mitochondrial DNA control region varied from 936 to 941 base pairs (bp). To align, one to six gaps in the sequences were added, representing insertion and exclusion events (indels), resulting in a final matrix with 942 bp. Within the final data matrix, 109 sites were variable, once indels

TABLE 1 | Summary of genetic parameters estimated from the *Brachyplatystoma vaillantii* mtDNA control region for five localities on the Solimões-Amazonas River. *N* = number of samples, *H* = number of haplotypes, *uH* = number of unique haplotypes, *S* = number of polymorphic sites, *ETA* = Total Number of Mutations sites, *HD* = haplotype diversity, π = nucleotide diversity, *k* = average number of nucleotide differences, * = p<0.02.

Localities	*N*	*H*	*uH*	*S*	*ETA*	*HD*	ϖ	*k*	R_2	Fu's *Fs*
Estuary	30	30	27	63	63	1.000±0.008	0.014±0.007	13.669±6.316	0.096	-20.12^{*}
Santarém	30	26	19	66	67	0.991±0.011	0.016±0.008	15.183±6.981	0.105	-8.59^{*}
Manaus	30	29	25	61	61	0.997±0.009	0.015±0.007	14.602±6.725	0.101	-15.81^{*}
Tefé	30	29	27	60	60	0.997±0.009	0.014±0.007	13.579±6.370	0.096	-16.52^{*}
Tabatinga	30	30	27	64	64	1.000±0.008	0.015±0.007	14.664±6.753	0.103	-19.17^{*}
All	150	134	125	109	111	0.997±0.001	0.015±0.008	14.399±6.487	0.059	-23.98^{*}

were considered a fifth character state and, among those, we observed indels at 10 sites.

Haplotype diversity (HD) at individual localities varied from 0.991 at Santarém to 1.000 at Estuary and Tabatinga. Nucleotide diversity ranged from 0.014 in Estuary and Tefé to 0.016 in Santarém. Results are summarized in Tab. 1.

The negative and significant Fs values ($P < 0.02$; Tab. 1) for the Fu test indicate that the species is undergoing population expansion at all sampled locations. The low R_2 obtained for the sampled locations corroborate the F_S values of the Fu statistical tests, suggesting that *B. vaillantii* has gone through a population expansion. Furthermore, since R_2 statistics is based on the difference between the number of singleton mutations and the average number of nucleotide differences, the high number of singletons seen in *B. vaillantii* were also taken as evidence of a population expansion.

We identified 134 haplotypes in the control region sequences (details described in **S1**). Most haplotypes (125) were unique and there were only nine shared haplotypes among the different localities. Network's topology showed a random distribution of haplotypes across the five localities without association to geographic location (Fig. 2).

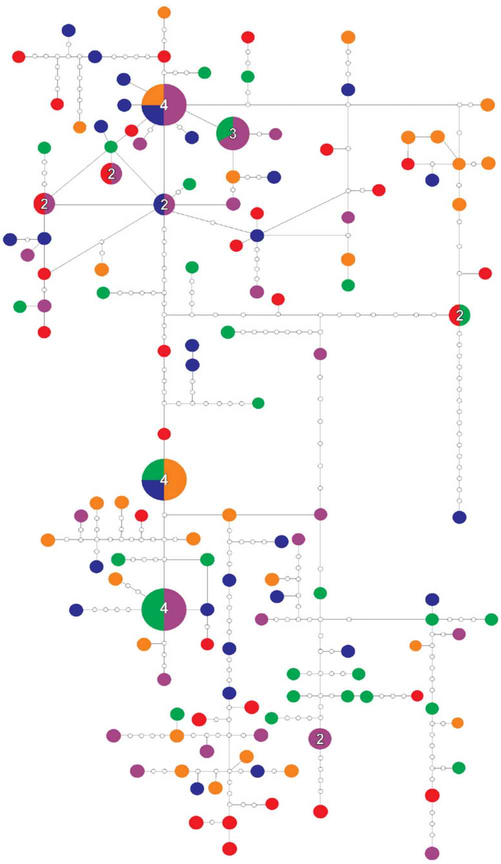

FIGURE 2 | Network of *Brachyplatystoma vaillantii* haplotypes. The number shown within a circle identifies the number of specimens sharing those haplotypes; circles without numbers represent unique haplotypes. White circles represent hypothetical intermediate haplotypes. Each locality is represented by the same colors in Fig. 1: red – Tabatinga, orange – Tefé, green – Manaus, purple – Santarém and blue – Estuary.

BAPS analysis defined three clusters (K = 3) distributed over the sampled localities (Fig. 3) showing no geographic segregation. The final ML tree recovered topology presenting weak support within clades (details described in **S2**). The hierarchical Bayesian clustering generated by FASTBAPS program also could not recover high bootstrap support (Fig. 4).

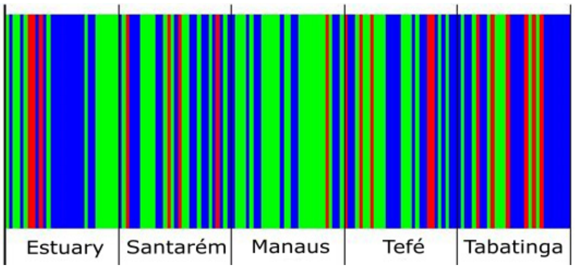

FIGURE 3 | Analysis of the BAPS 6.0 program showing three clusters (green, red, and blue) distributed between the five sampled locations of *Brachyplatystoma vaillantii*.

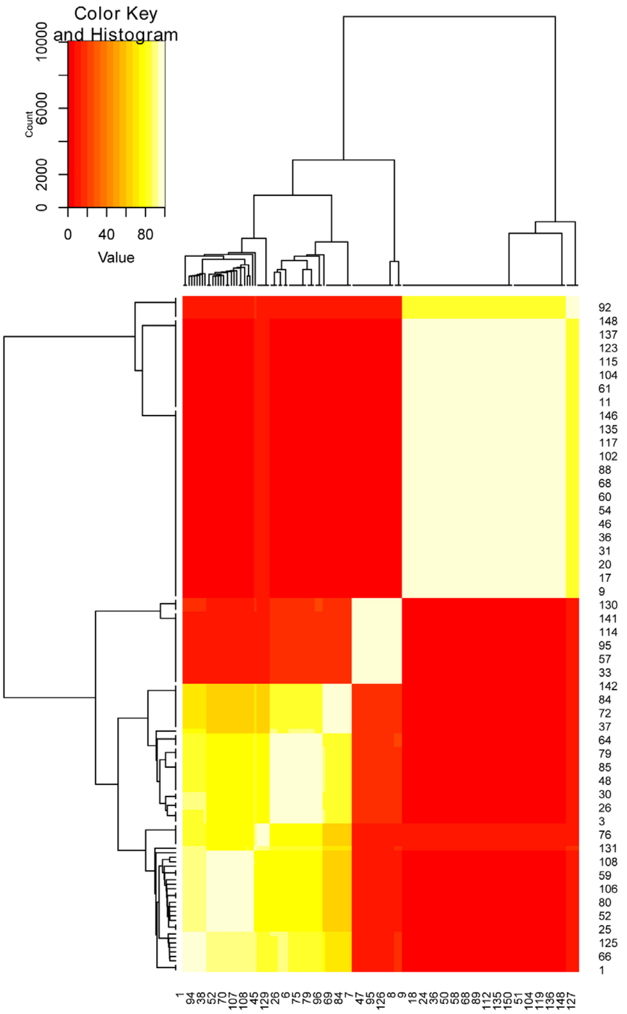

FIGURE 4 | Analysis of the FASTBAPS program. Numbers are individual sequence of *Brachyplatystoma vaillantii*. Colors ranging from red for the lowest probabilities and clear yellow for the highest probabilities support for bootstrap.

The AMOVA results showed that most genetic variation is within sampled localities (99.86%) and no genetic differentiation was identified between the localities (F_{ST} = 0.0014). Estimates of population divergence with pairwise F_{ST} values revealed that all localities were not significantly divergent from each other (Tab. 2). A high gene flows levels between adjacent localities according to the migration rate values (M) obtained with Migrate-N program (Tab. 3).

DISCUSSION

Our study of *Brachyplatystoma vaillantii* genetic variability offers the most comprehensive genetic evaluation for a commercially important resource with a wide distribution across the Amazon Basin. Molecular data became a powerful tool for inferring populational structure, or the lack thereof. Using similar sample sizes, studies of different Neotropical fishes have be able to detect phylogeographic structure in species such as *Triportheus albus* (Cooke *et al*., 2012) and *Nannostomus eques* (Terencio *et al*., 2012). Further, it has been possible to detect genetic structuring in migratory and abundant freshwater fish species such as in the genus *Prochilodus* Agassiz, 1829 (Sivasundar *et al*., 2001) as well as in *Arapaima gigas* (Shinz, 1822) (Hrbek *et al*., 2005), a fish which also occurs over semi-continental geographic distances.

All estimated parameters associated with the *B. vaillantii* genetic diversity suggest that there is no genetic differentiation between the five localities sampled (Tab. 1).

TABLE 2 | Pairwise F_{ST} values between the *Brachyplatystoma vaillantii* individuals from the localities sampled.

Localities	Estuary	Santarém	Manaus	Tefé
Estuary	–			
Santarém	0.0000	–		
Manaus	0.0109	0.0000	–	
Tefé	0.0000	0.0000	0.0168	–
Tabatinga	0.0000	0.0000	0.0285	0.0016

TABLE 3 | Estimates of effective number immigrating individuals per generation for *Brachyplatystoma vaillantii*. Source population are in the row, recipient population in the columns. The signal “+” represents receiving localities. The signal “–” represents without comparison. Migration was defined between adjacent localities.

Localities	Estuary +	Santarém +	Manaus +	Tefé +	Tabatinga +
Estuary	–	123.3	–	–	–
Santarém	923.4	–	52.1	–	–
Manaus	–	955.9	–	935.7	–
Tefé	–	–	251.9	–	932.6
Tabatinga	–	–	–	76.2	–

The population's expansion indicated by the values of R_2 and Fu's Fs, can be also confirmed by observation of the number of unique haplotypes, which is either equal or close to the number of individuals collected. Although BAPS program analysis found three clusters, they have representatives from all five locations without geographic segregation. The generated ML tree did not have bootstrap support and presented a large amount of polytomies among analyzed individuals (**S2**). In the same way, the clades generated by the analysis performed in FASTBAPS program, presented low support values for bootstrap (Fig. 4). The three clusters are present in all the sampled locations along the Solimões-Amazonas River suggests high gene flow. The AMOVA results confirms this hypothesis showing 99.86% of genetic variation occurs within sampled localities, also indicating that specimens form a single genetic stock. Other studies of Amazonian fishes have found similar patterns and DNA polymorphism in mtDNA control region such as *Brachyplatystoma rousseauxii* (Batista, 2010; Batista, Alves-Gomes, 2006), *Serrasalmus rhombeus* (Linnaeus, 1766) (Hubert *et al*., 2007) and *Colossoma macropomum* (Santos *et al*., 2007).

In a similar study with *C. macropomum* (tambaqui), the mtDNA control region of 48 individuals collected in four locations in the Amazon Basin (Tabatinga, Parintins Oriximiná and Santarém), found 31 haplotypes, demonstrating high levels of genetic diversity for all locations sampled (Santos *et al*., 2007). This pattern can also be observed in another study (Santos *et al*., 2018) of the same species with larger sampling numbers along the Solimões/Amazonas River (Mexiana, Almeirim, Santarém, Manaus, Tefé and Tabatinga) including sequences of mtDNA control region and ATPase 6/8 concatenated gene. Likewise, there was very little clustering among the haplotypes found at most localities, resulting in haplotype diversity varying between 0.986 and 1,000. The haplotype network also showed numerous reticulations between the *Colossoma* Eigenmann & Kennedy, 1903 haplotypes implying a high degree of gene exchange. The data suggests that, as *C. macropomum* migrates over a much smaller geographic area than *B. vaillantii*, the relatively high rate of gene flow between locations also occurs in this species.

High genetic variability was also found in mtDNA control region of curimatã (*Prochilodus nigricans*) from the Solimões-Amazonas, Madeira, Purus and Juruá rivers (Machado *et al*., 2017). As in *B. vallantii*, *P. nigricans* in the Solimões-Amazonas System is genetically homogeneus and, albeit such high polymorphism have occurred mostly within populations, it was found that the upper Madeira and the Purus rivers may have restricted genetic flow.

For both *C. macropomum* and *P. nigricans* there are different scenarios of gene flow between the Solimões-Amazonas River and its tributaries. The genetic diversity of *B. vallantii* in the distinct tributaries is unknown so far, and this information is crucial for its conservation, since the species reproduction occurs in these areas.

Another example in the Amazon, the zebra shovelnose *Brachyplatystoma tigrinum* (Britski, 1981) is a commercially important catfish for the ornamental fish trade, especially in Peru. Although the species is listed among those fish whose export or capture from natural populations is prohibited, commercial pressure on this species continues to increase in this country. This is of concern since molecular data showed that this pimelodidae has a genetic variability much reduced in relation to *B. vaillantii* (Mori-Marin *et al*., 2012). The haplotype diversity is a clear example of this fact, since this index observed in *B. tigrinum* (0.527) is practically half of the value for *B. vaillantii* (0.997) and this value may, in the near future, compromise the recovery of genetic diversity in view of the continuous decrease in the population size of the species.

For the two pimelodid species commonly known as piraíba (*B. filamentosum* and *B. capapretum*), haplotype diversity (HD) values are also high (>0.95), and the nucleotide diversity (π) of *B. filamentosum* (0.0118) (Huergo *et al*., 2011) is closer to the value found in *B. vaillantii* (0.015) (details described in **S3**). However, the nucleotide diversity found for *B. capapretum* (0.0041) (Lira-Cordeiro, 2013) is only about between 1/3 and ¼ of that found in the previously mentioned species, respectively. Like in *B. vaillantii*, both piraíbas, also appear to have being overfished (Petrere *et al*., 2004), but unfortunately no study about their fisheries, up to date, has considered the piraíba as two distinct species (*B. filamentosum* and *B. capapretum*), and the current conservational status of each species remains unknown.

Another congener, the catfish known regionally as babão, *Brachyplatystoma platynemum* Boulenger, 1898, also has high levels of haplotype diversity, although two structured populations from the Amazon and Madeira rivers have been suggested (Ochoa *et al*., 2015). If we compare *B. platynemum* only in the main channel of the Solimões-Amazonas River with the data of *B. vaillantii* from our study, there is a single population in both species, but the haplotypes diversity of *B. vaillantii* (0.997) is slightly greater than *B. platynemum* (0.905). Influence of different tributaries on piramutaba genetic diversity composition remains unknow and this information is important to understand the real and complete its life cycle.

The genetic parameters and the DNA polymorphism analysis indicate that levels of genetic variability for *B. vaillantii* are high and homogeneous along the main channel of the SARS. This contrasts the data for dourada *B. rousseauxii*, which shows a significant decrease in genetic diversity towards the Western part of the Amazon (Batista, Alves-Gomes, 2006). A possible genetic segregation in *B. vaillantii* associated to the different tributaries or to a partial homing behavior, as already suggested for *B. rousseauxii* (Batista, Alves-Gomes, 2006), shall not be discarded until further data, collected in the headwaters of the Solimões system, be analyzed.

To evaluate gene flow levels between localities we initially considered a simple model of estimation of pairwise F_{ST}, which revealed absence of divergence. These results already indicate that *B. vaillantii* in the Solimões-Amazonas River behaves as a large and unique population. The hypothesis pattern is also confirmed by Migrate-N analysis results, which was similar to the pattern in the F_{ST} matrix, implying very high levels of gene exchange between localities. However, as this model essentially determine if a gene lineage is present in any given locality because of mutation *in situ* or immigration from another locality, in datasets with high genetic diversity, it can be difficult to distinguish which processes resulted in the observed patterns. Moreover, these estimates are based upon a single locus only, and only for estimates of female immigration. These facts likely contain unknown biases that can only be discovered with additional, multi-locus data.

Although we have information from a single locus, our data appear to be sufficiently robust pointing that *B. vaillantii* along the Solimões-Amazonas River is composed by one, large and panmitic population, with a genetically diverse and geographically homogeneous organization. In consequence, we suggest that, for all management purposes, that *B. vaillantii* should be considered as a single population along the main Amazon-Solimões River axis.

In general, the results for *B. vaillantii* are similar to those found in analyses of the control region from other Amazonian species, although its values are consistently higher. In fact, among the species of genus *Brachyplatystoma* so far tested, *B. vailantii* shows the highest genetic variability in the Solimões-Amazonas River (details described in **S4** and **S3**) (Batista, Alves-Gomes, 2006; Batista, 2010; Huergo *et al*., 2011; Mori-Marin *et al*., 2012; Lira-Cordeiro, 2013; Ochoa *et al*., 2015).

Brachyplatystoma rousseauxii and *B. vaillantii* are believed to have similar life cycles, and the fishing efforts over both resources have evolved taking into account their migration routes and seasonality. The geographic extent of the routes used by these two species includes the whole Solimões-Amazonas River and their headwater tributaries. Basically, these two species use the entire Amazon from the estuary next to the Atlantic Ocean to the headwater's streams near the Andes in order to complete their life cycle (Barthem, Goulding, 1997). However, some studies and local reports suggest that there are migratory differences between *B. rousseauxii* and *B. vaillantii*. The former do not form large schools; they are found near the surface or mid-water year-round along the SARS and their frequency increases during the dry season (Telles *et al*., 2011; Carvajal-Vallejos *et al*., 2014; Barthem *et al*., 2017). On the other hand, *B. vaillantii* is a river-bottom swimmer, but can explore the entire water column in search of prey, probably preferring preys that inhabits the range of 5–10 m of depth (Barthem, Petrere Jr, 1995; Barthem, Goulding, 1997). *Brachyplatystoma vaillantii* tends to migrate in large schools, but they are found in large numbers mainly during the low water season (July to December) (Chaves *et al*., 2003; Barthem, Goulding, 2007; Leite *et al*., 2007; Maggia *et al*., 2017; De Pinna, 2019).

It is well established that *B. rousseauxii*'s maximum length (192 cm) is larger than that of *B. vaillantii* (105 cm) (Barthem, Goulding, 1997). On the other hand, *B. vaillantii* reaches the first sexual maturation at an earlier age (2 years) than *B. rousseauxii* (3 years) (Alonso, Pirker, 2005). Differences in genetic diversity between *B. rousseauxii* ($\pi = 0.0079$, Haplotype diverstity = 0.933 S (Polymorphic sites) = 54) and *B. vaillantii* ($\pi = 0.0150$, Haplotype diverstity = 0.997 S = 133) may be reflecting peculiarities inherent to each species, and are very probably associated with subtle differences in their life cycles. Based on coalescence theory Batista *et al*. (2004) estimated the evolutionary age, using Watterson's population genetics estimate, suggesting a relative age of approximately 242,600 and 335,200 years for *B. rousseauxii* and *B. vaillantii*, respectively. If the mutation rates were equal for both species, this difference in evolutionary age could represent more time for *B. vaillantii* to accumulate mutations, resulting, consequently, in higher levels of genetic variability reflected in nucleotide and haplotype diversity. Nevertheless, other factors may also be involved in different genetic variability of these species, such as the time of sexual maturation, the number of offspring produced per life span, and potentially different intrinsic mutational rates.

Despite being overfished, *B. vaillantii* is still genetically more diverse than any other commercially important species within the genus *Brachyplatystoma* studied so far: dourada (*B. rousseauxii*), piraíba (*B. filamentosum*), filhote capapreta (*B. capapretum*), babão (*B. platynemum*) and dourada zebra (*B. tigrinum*). Such situation suggests that either the *B. vaillantii* possesses an intrinsic mechanism, such as, for example, a mutation rate that is faster than that of other conspecific species or, alternatively, the other species are even more highly overfished and their stock are even more depleted genetically than *B. vaillantii*. Such a scenario requires serious consideration by those tasked with effective long-term fish-stock management in the Amazon, especially considering that these migratory resources overpass political borders and require joined efforts and policies from the Amazonian countries.

The intense exploitation of *B. vaillantii* in the estuary, performed mainly by industrial fleet, should also be considered a critical issue that needs to be addressed urgently. The industrial fleet mostly catches small (20–30 cm) and medium-sized (30–50 cm) specimens. In an attempt to minimize this impact, exclusion areas for the industrial fleet were implemented, but there are no studies or guarantees demonstrating that those defined areas actually correspond to habitats naturally occupied by the species (Barthem *et al*., 2015).

As with several other migratory species in the Amazon, the current situation of *B. vaillantii* stock requires a multidisciplinary approach and a complex case evaluation. The several challenging issues to be considered include, but are not limited to: the increasing demand for fish on the national and international market; the increasing capture effort of the fishing fleet, as well as their numerical growth in the Amazon, without any compensatory policies to increase the stocks; the lack of control over the size and amount of fish captured; a lack of detailed information about the life cycle of the resource; the absence of fishery statistics in the entire Amazon; the uncontrolled land use and forest clearing in several basins and sub-basins in the Amazon resulting in habitat deterioration, especially those areas of spawning; the construction of large dams for electricity generation in key rivers, which threatens migration routes and access to spawning habitats and; the fact that these fish do not recognize political borders and require coordinated international planning and action (Klautau *et al*., 2016; Forsberg *et al*., 2017; Silva-Júnior *et al*., 2017).

In summary, the sustainability of these fish resources/population and the economical chain they support, especially across international borders, continue to depend on accurate population assessments, including their genetic parameters, and detailed knowledge of their behavior and ecology (Pelicice *et al*., 2015; Barthem *et al*., 2017).

Any discussion of a fishery resource management must include, especially in the Amazon, at least two contexts: the complex commercial and social interactions associated with the fishing activity itself, and the ecological interconnections that characterize the species under consideration. For a migratory fish such as *B. vaillantii*, both fishing activity and the ecology of the species are subject to changes from one region to another, since the fish only spawn in the headwaters of the Amazon River's affluents, but grow up in the mouth of the Amazon River. Thus, in order to construct a series of policies that will provide full and effective management and conservation of this resource, a well-coordinated series of actions among the countries involved is mandatory.

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AUTHOR'S CONTRIBUTION

Kyara Martins Formiga: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

All specimens were collected in accordance with Brazilian laws, using a collection license approved by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) via permit numbers 130 and 14278–1.

COMPETING INTERESTS

The authors declare no competing interests.

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