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Protected areas and compositional diversity of fish from Serranias Costeiras of the Ribeira de Iguape River basin, Southeast Brazil

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The Serranias Costeiras of the Ribeira de Iguape River basin comprise landscapes with steep slopes, where many streams are contained in protected areas. We evaluated the importance of these protected areas for stream fish diversity. We sampled the ichthyofauna during the dry season of 2010, 2018 and 2019 in 36 stream stretches. We used beta diversity measures and estimated species richness and dark diversity in streams from two types of protected areas (full protection, FP and sustainable use, SU) and outside (Out). The altitude-width and velocity gradient of the streams explained the species turnover. The PA type promoted the richness difference, with FP streams having less species richness than SU and outside. Streams from FP presented lower species richness and dark diversity. These results indicate that the few species in FPs are well protected. The FP streams contain a relevant proportion of the regional species pool and, therefore, are essential for conserving fish stream diversity in the study region. On the other hand, streams from SU or Out have higher species richness, but their fish fauna is more vulnerable. Due to longitudinal stream connectivity, we highlight the importance of rethinking the limits of protected areas.

Keywords: Beta diversity, Dark diversity, Stream connectivity, Species richness, Turnover.

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Os riachos das Serranias Costeiras da bacia do rio Ribeira de Iguape estão na região do estado de São Paulo com maior quantidade de áreas preservadas e com ictiofauna muito particular. Avaliamos a importância das áreas preservadas na diversidade da ictiofauna. Durante o período de seca de 2010, 2018 e 2019 coletamos a ictiofauna em 36 trechos de riachos em dois tipos de áreas protegidas (Proteção Integral, FP e Uso Sustentável, SU) e fora (Out). Utilizamos medidas de diversidade beta e estimamos a riqueza de espécies e a diversidade escura. A ictiofauna regional apresentou alta diversidade beta. O gradiente de largura e velocidade dos riachos e altitudinal explicou a substituição de espécies. A diferença de riqueza foi promovida pelo tipo de UC sendo que os riachos FP possuem menor riqueza de espécies que os SU e fora das UCs. Os riachos inseridos em FP contêm uma proporção relevante do pool regional de espécies e, portanto, são importantes para a conservação da diversidade de riachos na região de estudo. Por outro lado, os riachos que estão em SU ou Out possuem maior riqueza de espécies e sua fauna de peixes está mais vulnerável. Devido à conectividade longitudinal dos riachos ressaltamos a importância de repensar os limites das unidades de conservação.

Palavras-chave: Conectividade em riachos, Diversidade beta, Diversidade escura, Riqueza de espécies, Substituição.

INTRODUCTION

The Ribeira de Iguape River basin is the Southern limit of the Eastern coastal drainages (Langeani *et al*., 2009) and has well preserved extensive protected areas (PA) (Oyakawa *et al*., 2006). Oyakawa, Menezes (2011) provided a list of 97 species in this river basin, and we can add at least six species to this list (Cetra *et al*., 2020). Ancient crystalline rocks form the Serranias Costeiras with Serra do Mar and Paranapiacaba mountain ranges and hills in the upper Ribeira de Iguape River basin (Ross, 2002).

Protected areas (hereafter PA) alone are not enough to preserve nature but are the fundamental stones to build regional strategies. PA has two main functions: they must comprise a representative sample of the biodiversity of a given region and protect this biodiversity from processes that threaten its survival (Margules, Pressey, 2000). Full protection PAs have stricter constraints on extractive activities in Brazil, and biodiversity conservation is the principal objective. The sustainable use of PAs aims to reconcile nature conservation with sustainable extraction of natural resources conserving ecosystems and habitats and cultural values, and traditional natural resource management system. The sustainable use category represents the most numerous and extent PAs in Brazil (Vieira *et al*., 2019) and most of the PA downgrading, downsizing, and degazettement (PADDD) events were in sustainable use PAs (Bernard *et al*., 2014).

Since the 1970s, there have been discussions about the configurations of the areas with the potential to protect biodiversity, and aspects related to geometric basic principles and concepts to orient the shape of protected areas (Diamond, 1975) have been proposed to current days. Common sense is that connectivity is essential for healthy ecosystem management to conserve biodiversity in times of climatic changes in every biome and spatial scale (Hilty *et al*., 2020). Part of these discussions and proposals consider that well-connected ecosystems support diversified ecological functions and services (*i.e*., migration, hydrology, nutrient cycling, pollination, seed dispersal, food safety, climatic resilience, and resistance to diseases (Hilty *et al*., 2020). These studies are based mainly on studies of terrestrial plants and animals.

When discussing connectivity or the shape of PA, aquatic biodiversity conservation is rarely considered, especially for small fishes inhabiting streams (Castro, Polaz, 2020). Longitudinal connectivity allows the connection of habitats, species, communities, and ecological processes upstream and downstream. Frederico *et al.* (2018) showed that although all stream fish species in their study had at least part of their distribution in a PA, most of the large PAs do not correspond to areas with high direct conservation values organisms. They suggested that Systematic Conservation Planning (SCP) (Margules, Pressey, 2000) must explicitly include fishes and other organisms living in freshwaters to protect the Brazilian Amazon biodiversity completely. In that sense, Azevedo-Santos *et al.* (2019) suggested that new PA consider the aquatic environments covering whole hydrographic basins since these ecosystems provide essential environmental services. Furthermore, protected area planning based on freshwater systems can increase the benefit for freshwater biota seven times. If only aquatic connectivity is accounted for, the protected area can double biodiversity freshwater benefits for insignificant losses for terrestrial species (Leal *et al*., 2020).

Knowing how much a given PA represents the regional biodiversity is challenging by both the conceptual definition of biodiversity and the statistical methodology. Species diversity is only one of the biodiversity components, and species richness is only one component of species diversity. However, species richness is the most simple, intuitive, and frequently used measure to characterize biodiversity (Magurran, 2011). The gamma diversity is the species diversity present in all habitats in a region or hydrographic basin. It can be interpreted as the relationship between the species diversity found in a local habitat (alpha diversity) and the diversity between local habitats (beta diversity).

Beta diversity can be decomposed into turnover and the loss (or gain) of species leading to richness differences (Carvalho *et al*., 2012, 2013). Species turnover is the replacement of species by others resulting in a low proportion of shared species considering the identities of all species (Baselga, Orme, 2012). When losses or gains occur in an ordered manner, community pattern becomes nested (Atmar, Patterson 1993). Species nestedness results from differences in species richness when a more impoverished community is a subset of species from a richer community that ignores species identity (Baselga, Orme, 2012). Nestedness is low when beta diversity is high (Wright, Reeves, 1992). The species turnover pattern would require a larger number of PAs, and the nestedness pattern would permit the prioritization of just a small number of the richest sites (Baselga, 2010).

The relation among species coexisting in a community results from similarities in their habitat requirements and tolerances. However, the spatial limits of a community are not clear because species associations are difficult to predict. Hence, there are gradients rather than discrete communities at the regional level (Piqueras, Brando, 2016). Such compositional gradients can be due to turnover (Baselga, 2010). Regionally, beta diversity can be understood as a component of the gamma diversity, and the higher the turnover of species, the higher the regional richness (Tuomisto, 2010). The use of the compositional gradient aids to understanding the set of stream fishes from Serranias Costeiras of the Ribeira de Iguape River basin. This stream fish community is species-rich, with many endemic and threatened species (Oyakawa *et al*., 2006; Barrella *et al*., 2014) and high beta diversity (Cetra *et al*., 2020).

Legendre, De Cáceres (2013) proposed a method to estimate how many sites and species contribute to total beta diversity. Sites with a high local contribution to beta diversity (LCBD) have higher ecological uniqueness than the other sites sampled in a region. They can guide efforts to identify priority areas for conservation (Pozzobom *et al*., 2020). A regional monitoring program can use species with a relevant species contribution to beta diversity (SCBD) with a relatively high local abundance and site occupancy.

The set of all species capable of inhabiting a given place and regionally present is known as species pool (Pärtel *et al*., 2011). Therefore, the species pool concept must refer to species ecologically adapted to live in a particular habitat (Pärtel, 2014; Zobel, 2016). This concept differs from gamma diversity. In principle, species belonging to a specific pool can disperse and potentially inhabit all places of this region that meet their environmental needs (Carmona, Pärtel, 2021). This capability of regional species richness pool to colonize specific habitat types define the dark diversity (Lewis *et al*., 2017).

Regions with high observed species richness and low dark diversity have high completeness (Pärtel *et al*., 2013). These authors proposed the Community Completeness Index (CCI) based on the log-ratio between the observed richness and dark diversity. However, it is impossible to use CCI when this index is positively correlated with observed species richness (Fløjgaard *et al*., 2020). Relatively complete communities can act as an essential patch with a high-quality habitat in a source-sink dynamic. The completeness concerning the species pool can prove an informative biodiversity metric that helps sustain representative sites of regional biodiversity (Lewis *et al*., 2017).

This study aimed to evaluate the importance of the PAs in the stream fish species diversity from full protection, sustainable use and outside from Serranias Costeiras of the Ribeira de Iguape River basin. For this purpose, we analyse species composition suggesting species that contribute to the maintenance of beta diversity. Furthermore, we quantified local contribution and partitioned the total beta diversity. Finally, we estimated the species richness and dark diversity in stream stretches.

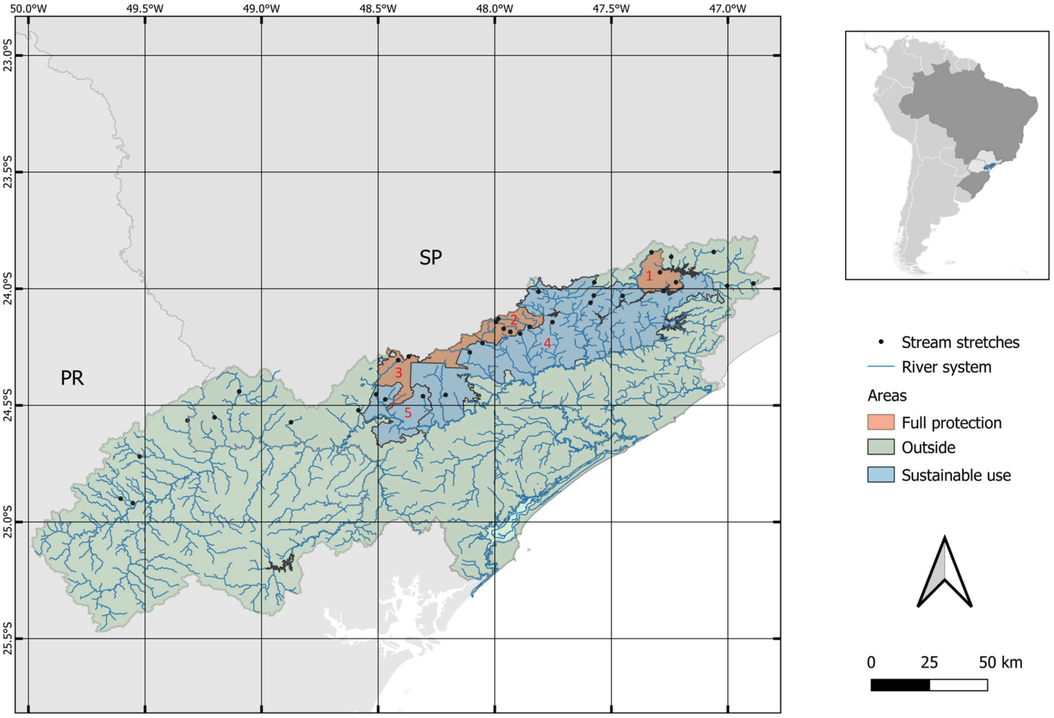
MATERIAL AND METHODS

Study area. The Ribeira de Iguape River basin covers approximately 27,000 km², comprising 13 municipalities from Paraná State and 23 from São Paulo State, which houses an estimated population of over 990,000 inhabitants (CBH-RB, 2016).

In the São Paulo State, the Water Resources Management Unit 11 (Unidade de Gerenciamento dos Recursos Hídricos – UGRHI 11) corresponds to the Ribeira de Iguape River basin and Southern Coastal drainages. The main rivers in the basin are the Ribeira de Iguape, Juquiá, São Lourenço, Jacupiranga, Pardo, Turvo, Una da Aldeia, Ponta Grossa, and Itarirí (CBH-RB, 2016). It presents one of the most comprehensive natural vegetation covers in the state of São Paulo, with 12,256 km^2 of native forest remaining, occupying approximately 72% of the area of UGRHI 11 (CBH-RB, 2016). The average precipitation in the UGRHI 11 is 1400 mm/year. UGRHI 11 has 44 protected areas, of which 17 are full protection, and 27 are sustainable (CBH-RB, 2016).

Fish sampling. Sampling occurred during the dry season (July to November) of 2010, 2018 and 2019, between 10h and 18h. In the dry season, the associations between fish assemblages and environmental structure are more evident (Pinto *et al*., 2006). Also, it is crucial to control the effect of temporal variation.

The fish assemblages were sampled in 36 70-m of streams sections in the Serranias Costeiras using electrofishing (LR-24 Electrofisher – Smith-Root) in the downstream-upstream direction with a single passage and without contention nets. These transects belong to full protection area (FP; Parque Estadual Jurupará, Parque Estadual Carlos Botelho, and Parque Estadual Intervales) (10 stream stretches), sustainable use (SU; Área de Proteção Ambiental da Serra do Mar and Área de Proteção Ambiental Quilombos do Médio Ribeira) (14 stream stretches) and to areas outside (Out; 12 stream stretches) (Fig. 1). The altitude of stream stretches (n = 36) ranged from 28 to 899 m, the width averaged 9.5 m (sd = 7.1 m), the depth averaged 33.4 cm (sd = 13.5 cm), the velocity



Datum - SIRGAS 2000
Rede de drenagem [shapefile]; 2015. [acesso em: 13 jan. 2020]
Disponível em: http://www.sigrb.com.br/index.php?id=5

FIGURE 1 | Protected Areas and stream stretches sampled in the rio Ribeira de Iguape basin. 1) Parque Estadual Jurupará (PEJU), 2) Parque Estadual Carlos Botelho (PECB), 3) Parque Estadual Intervales (PEI), 4) Área de Proteção Ambiental da Serra do Mar (APASM), and 5) Área de Proteção Ambiental Quilombos do Médio Ribeira (APAQMR).

averaged 0.29 $m.s^{-1}$ (sd = 0.16 $m.s^{-1}$), and the PHI ranged from 49 to 80 (Tab. **S1**). We used a physical habitat index (PHI) adapted from Barbour *et al.* (1999) to characterize the reaches. We evaluated the stream stretches with four habitat parameters: sediment deposition, channel flow status, vegetative protection, and riparian vegetative zone width (Tab. **S2**). The PHI range classification was: 0 to 18 (poor), 19 to 40 (marginal), 41 to 61 (suboptimal) and 62 to 80 (optimal).

Fish were anaesthetized with eugenol (clove oil) and fixed for at least 48h in 4% formalin. All specimens are stored in 70% ethanol in the collection of Laboratório de Ictiologia de Sorocaba (LISO), Universidade Federal de São Carlos, São Carlos (UFSCar). In addition, voucher specimens of all species were deposited in the ichthyological collection of Laboratório de Ictiologia do Departamento de Zoologia e Botânica, Universidade Estadual Paulista, São José do Rio Preto (DZSJRP 13618–13705 and 22983–23048) (Cetra *et al*., 2012, 2020).

Statistical analyses

Environmental data. A principal component analysis (PCA) was applied to reduce the dimensionality of the standardized (mean = 0, sd = 1) environmental data: altitude, width, depth, velocity, and PHI. Two components with an eigenvalue bigger than one were used to represent the environmental gradient (Kaiser-Guttman criterion). The PC1 represents the altitude-width and velocity gradient, and the PC2 represents the PHI-depth gradient. FP scores has minor PC1 and PC2 average values (Supplem. **S3**).

Spatial variables. We used distance-based Moran's eigenvector maps (db-MEM) analysis to provide spatial variables. These spatial variables are typically efficient in modelling spatial structures of community structure at multiple scales (Legendre, Legendre, 2012) covered by the geographical sampling area. The first spatial vectors show broad-scale variation, and subsequent spatial vectors show smaller scale variation (Borcard, Legendre, 2002). We used the first eigenvector (PCNM1) obtained from the principal coordinates in the subsequent analyses. The db-MEM spatial variables were obtained using the function "pcnm" from "vegan" package (Oksanen *et al*., 2019).

Beta diversity, species richness, and dark diversity. To elucidate the ecological processes underlying community structuring, we partitioned the total β diversity into their respective replacement (turnover) and richness difference components, *i.e.*, βtotal = βrepl + βrich (Carvalho *et al*., 2012). βtotal represents the total community taxonomic variation, reflecting both species replacement and loss/gain; βrepl reflects the replacement of some species by others from stream stretch to stream stretch; βrich denotes the beta diversity explained by species loss/gain (richness differences) alone. We generated three pairwise matrices according to the Jaccard index using the function "beta.multi" from the package "BAT" (Cardoso *et al*., 2021).

We estimated the stream stretches local (LCBD indices) and species (SCBD indices) contributions to beta diversity. These indices were derived from a beta diversity measure (BDTotal) independent of alpha and gamma diversity (Legendre, De Cáceres, 2013). We Hellinger-transformed the fish assemblage composition data for an appropriate assessment of beta diversity, *i.e.*, to standardize species composition data and avoid the influence of double-zeros. We used the function "beta.div" from the package "adespatial" (Dray *et al*., 2020) to calculate the SCBD and LCBD statistics.

We applied a nonmetric multidimensional scaling (nMDS) to obtain an ordination of species in two axes and to better represent the main dissimilarity relationships among the stream stretches by types of protected area and outside area. We used the Hellinger distance as a dissimilarity index with Euclidean property (Legendre, De Cáceres, 2013). We used "metaMDS" from "vegan" package (Oksanen *et al*., 2019).

We used the sample-size and coverage-based integration of rarefaction and extrapolation sampling curves of species richness with 95% confidence intervals based on a bootstrap method with 200 replications (Chao, Chiu, 2016) to compare species richness estimates ($\hat{S}_{700}$) among the three areas. The extrapolation extends up to a maximum doubled number of individuals ($\hat{S}_{\text{doub}}$). The interpolation and extrapolation were computed using the package "iNEXT" (Hsieh *et al*., 2020).

Finally, we calculated dark diversity using Beals smoothing (Lewis *et al*., 2017). Beals smoothing produces a probability of occurrence for a given species in each site based on the joint occurrence of this species with other species. We applied species-specific thresholds to translate such probabilities into species presences and absences in a particular stream stretch's dark diversity. For each species, the threshold is the lowest Beals smoothing value for those stream stretches in which the species occur. We estimate dark diversity based on species co-occurrences using the package "DarkDiv" (Carmona, Partel, 2020).

We tested if the three areas have similar species composition and beta diversity (βtotal, βrepl, and βrich) with a permutational multivariate analysis of covariance using distance matrix and PC1, PC2, and PCNM1 as covariates (Anderson, 2001). We applied a multivariate homogeneity of group dispersions to verify if these areas are homogeneously dispersed (Anderson, 2006). We used "betadisper" and "adonis2" functions from "vegan" package (Oksanen *et al*., 2019).

We applied a one-way analysis of covariance (ANCOVA) to compare stream stretches local contributions (LCBD) and dark diversity average of the three areas with PC1, PC2, and PCNM1 as covariates. All the above analyses were carried in the R environment (R Development Core Team, 2020) and RStudio Team (2020).

RESULTS

We sampled 3794 individuals representing 57 species, 40 genera, 13 families, and seven orders (Tab. 1). Approximately 33% of species (S = 19) occur in all areas. Sustainable use PAs and outside shared about 58% of the species (S = 33). The sustainable use PAs have the most exclusivity species richness (12) (Fig. 2).

The total beta diversity is exceptionally high (βtotal = 0.93, $s^2 = 0.18$) and was driven by species turnover (βrepl = 0.51, $s^2 = 0.10$) with less contribution from the richness difference (βrich = 0.42, $s^2 = 0.08$). Altitude-width and velocity gradient (PC1) explains βrich and βrepl diversity can be explained by the area type and marginally by the spatial variable (PCNM1) (Tab. 2).

Twenty-one species (37%) contributed above the mean for abundance based on

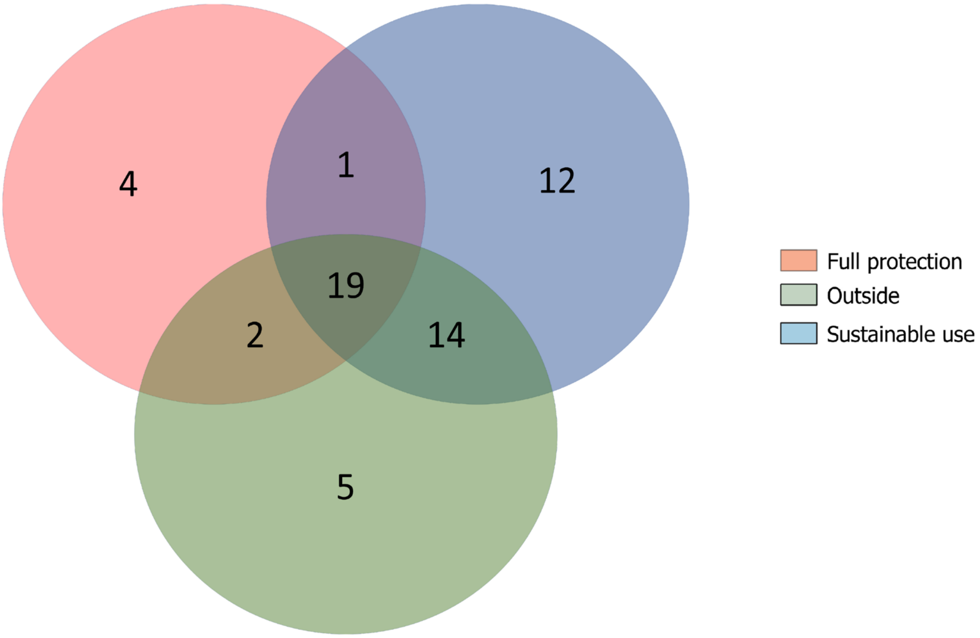


FIGURE 2 | Species richness shared and exclusive of the stream stretches from full protection, sustainable use, and outside areas.

SCBD (min = 0.0006, max = 0.076, mean = 0.017, sd = 0.018) (Tab. 1). *Isbrueckerichthys duseni*, *Characidium lauroi*, *C. pterostictum*, and *Harttia kronei* contributed around 25%. The SCBD was positively correlated with the number of streams stretches occupied by each species ($r = 0.76$, $p < 0.001$, $n = 57$) and with species abundance ($r = 0.80$, $p < 0.001$, $n = 57$). Two stream stretches from the full protection and one in the sustainable use have significant LCBD indices. Altitude-width and velocity gradient (PC1) explains LCBD (Tab. 3). The LCBD was negatively correlated with species richness ($r = -0.6$, $p < 0.001$, $n = 36$).

Fish species composition from full protection, sustainable use, and outside areas presented homogeneity among group dispersions (Pseudo-$F_{2,33} = 0.33$, $p = 0.72$) while having significantly different compositions, PC1 and spatial effects (Fig. 3; Tab. 4).

The sample-size-based rarefaction and extrapolation sampling curve (Fig. 4; Tab. **S4**) reveal that the curve from the full protection area has a significantly lower species richness. On the other hand, the curve of the sustainable use area lies above that of the outside area. However, the confidence intervals of the two latter areas overlap, implying that comparing two equally large samples is inconclusive regarding the test of significant difference in species richness between the two areas.

The species richness per stream stretch ranged from 2 to 20 species, and dark diversity ranged from 0 to 10 species. There was significant difference between the dark diversity of the areas with PHI-depth gradient effects (Tab. 5). Stream stretches from full protection area have lower average dark diversity ($D_{FP} = 2.7$, $sd = 1.5$) than sustainable use ($D_{SU} = 5.4$, $sd = 2.5$) or outside area ($D_{Out} = 4.4$, $sd = 2.6$).

TABLE 1 | List of captured species from Serranias Costeiras of the Ribeira de Iguape River basin. Protected Areas: Full protection (FP), sustainable use (SU), and outside (Out). Species contributions to beta diversity (SCBD).

Order/Family/Species	Code	FP	SU	Out	SCBD
CYPRINIFORMES					
Cobitidae					
Misgurnus anguillicaudatus (Cantor, 1842)	Mang	-	-	X	0.001
CHARACIFORMES					
Characidae					
Bryconamericus microcephalus (Miranda Ribeiro, 1908)	Bmic	-	X	X	0.014
Deuterodon iguape Eigenmann, 1907	Digu	X	X	-	0.023
Deuterodon janeiroensis (Eigenmann, 1908)	Djan	-	X	-	0.002
Deuterodon ribeirae (Eigenmann, 1911)	Drib	X	X	X	0.021
Hollandichthys multifasciatus (Eigenmann & Norris, 1900)	Hmul	-	X	-	0.001
Hyphessobrycon bifasciatus Ellis, 1911	Hbif	-	X	-	0.003
Hyphessobrycon reticulatus Ellis, 1911	Hret	-	-	X	0.004
Mimagoniates microlepis (Steindachner, 1877)	Mmic	-	X	X	0.010
Psalidodon anisitsi (Eigenmann, 1907)	Pani	-	-	X	0.002
Spintherobolus papilliferus Eigenmann, 1911	Spap	-	-	X	0.006
Crenuchidae					
Characidium lanei Travassos, 1967	Clan	X	X	X	0.017
Characidium lauroi Travassos, 1949	Clau	X	-	X	0.067
Characidium pterostictum Gomes, 1947	Cpte	X	X	X	0.060
Characidium schubarti Travassos, 1955	Csch	-	X	X	0.012
Erythrinidae					
Hoplias malabaricus (Bloch, 1794)	Hmal	X	-	-	0.001
GYMNOTIFORMES					
Gymnotidae					
Gymnotus pantherinus (Steindachner, 1908)	Gpan	X	X	X	0.038
Gymnotus sylvius Albert & Fernandes-Matioli, 1999	Gsyl	X	-	-	0.002
SILURIFORMES					
Callichthyidae					
Scleromystax barbatus (Quoy & Gaimard, 1824)	Sbar	-	X	X	0.009
Heptapteridae					
Acentronichthys leptos Eigenmann & Eigenmann, 1889	Alep	-	X	X	0.008
Chasmocranus lopezae Miranda Ribeiro, 1968	Clop	X	X	X	0.024
Pimelodella transitoria Miranda Ribeiro, 1907	Ptra	X	X	X	0.011
Rhamdia quelen (Quoy & Gaimard, 1824)	Rque	X	X	X	0.010
Rhamdioglanis transfasciatus Miranda Ribeiro, 1908	Rtra	X	X	X	0.023
Loricariidae					
Ancistrus multispinis (Regan, 1912)	Amul	-	X	X	0.011
Harttia kronei Miranda Ribeiro, 1908	Hkro	X	X	X	0.055
Hisonotus leucofrenatus (Miranda Ribeiro, 1908)	Hleu	-	X	X	0.003

➡

TABLE 1 | (Continued)

Order/Family/Species	Code	FT	SU	Out	SCBD
Hypostomus ancistroides (Ihering, 1911)	Hanc	X	-	-	0.006
Hypostomus interruptus (Miranda Ribeiro, 1918)	Hint	-	X	X	0.023
Isbrueckerichthys alipionis (Gosline, 1947)	Iali	X	-	-	0.003
Isbrueckerichthys duseni (Miranda Ribeiro, 1907)	Idus	X	X	X	0.076
Isbrueckerichthys epakmos Pereira & Oyakawa, 2003	Iepa	X	X	X	0.041
Kronichthys lacerta (Nichols, 1919)	Klac	X	X	X	0.044
Kronichthys subteres Miranda Ribeiro, 1908	Ksub	X	X	X	0.020
Lampiella gibbosa (Miranda Ribeiro, 1908)	Lgib	X	X	X	0.020
Neoplecostomus paranensis Langeani, 1990	Npar	X	X	X	0.035
Neoplecostomus ribeirensis Langeani, 1990	Nrib	X	X	X	0.014
Neoplecostomus cf. *yapo* Zawadzki, Pavanelli & Langeani, 2008	Nyap	-	X	-	0.002
Parotocinclus maculicauda (Steindachner, 1877)	Pmac	-	X	X	0.012
Pseudotothyris obtusa (Miranda Ribeiro, 1911)	Pobt	-	-	X	0.007
Rineloricaria kronei (Miranda Ribeiro, 1911)	Rkro	-	X	X	0.016
Rineloricaria lima (Kner, 1853)	Rlim	-	X	X	0.019
Schizolecis guentheri (Miranda Ribeiro, 1918)	Sgue	-	X	-	0.006
Pseudopimelodidae					
Microglanis cottoides (Boulenger, 1891)	Mcot	-	X	-	0.002
Trichomycteridae					
Cambeva davisi (Haseman, 1911)	Cdav	X	-	X	0.044
Cambeva tupinamba (Wosiacki & Oyakawa, 2005)	Ctup	-	X	X	0.008
Homodiaetus graciosa Koch, 2002	Hgra	-	X	-	0.001
Ituglanis proops (Miranda Ribeiro, 1908)	Ipro	-	X	-	0.005
Microcambeva ribeirae Costa, Lima & Bizerril, 2004	Mrib	-	X	-	0.004
Trichomycterus alternatus (Eigenmann 1917)	Talt	X	X	X	0.036
Trichomycterus lauryi Donin, Ferrer & Carvalho, 2020	Tlau	-	X	X	0.013
SYNBRANCHIFORMES					
Synbranchidae					
Synbranchus aff. *marmoratus* Bloch, 1795	Smar	-	X	-	0.003
CICHLIFORMES					
Cichlidae					
Crenicichla iguapina Kullander & Lucena, 2006	Cigu	-	X	-	0.003
Geophagus iporangensis Haseman, 1911	Gipo	X	X	X	0.019
CYPRINODONTIFORMES					
Poeciliidae					
Phalloceros harpagos Lucinda, 2008	Phar	-	X	X	0.034
Phalloceros reisi Lucinda, 2008	Prei	X	X	X	0.045
Poecilia vivipara Bloch & Schneider, 1801	Pviv	-	X	-	0.002

TABLE 2 | Beta diversity PERMANOVA table. Beta diversity (βdiv): Beta total (βtotal), beta replacement (βrepl), and beta richness difference (βrich). Source: Area type (Area), environmental principal components (PC1 and PC2), spatial variable (PCNM1). Degrees of freedom (Df), sums of square (SS), R square (R^2), F statistics (F), and p-value (P). *Significative effect.

βdiv	Source	Df	SS	R^2	F	P
βtotal	Area	2	1.24	0.08	1.60	0.010*
	PC1	1	0.63	0.04	1.63	0.010*
	PC2	1	0.45	0.03	1.16	0.214
	PCNM1	1	0.67	0.04	1.73	0.010*
	Residual	30	11.67	0.76		
βrepl	Area	2	0.85	0.15	2.75	0.005*
	PC1	1	-0.05	-0.01	-0.30	0.905
	PC2	1	0.19	0.03	1.22	0.448
	PCNM1	1	0.34	0.06	2.20	0.089
	Residual	30	4.62	0.80		
βrich	Area	2	0.05	0.01	0.22	0.945
	PC1	1	0.36	0.09	3.39	0.035*
	PC2	1	0.11	0.02	0.99	0.408
	PCNM1	1	0.10	0.02	0.95	0.373
	Residual	30	3.21	0.76		

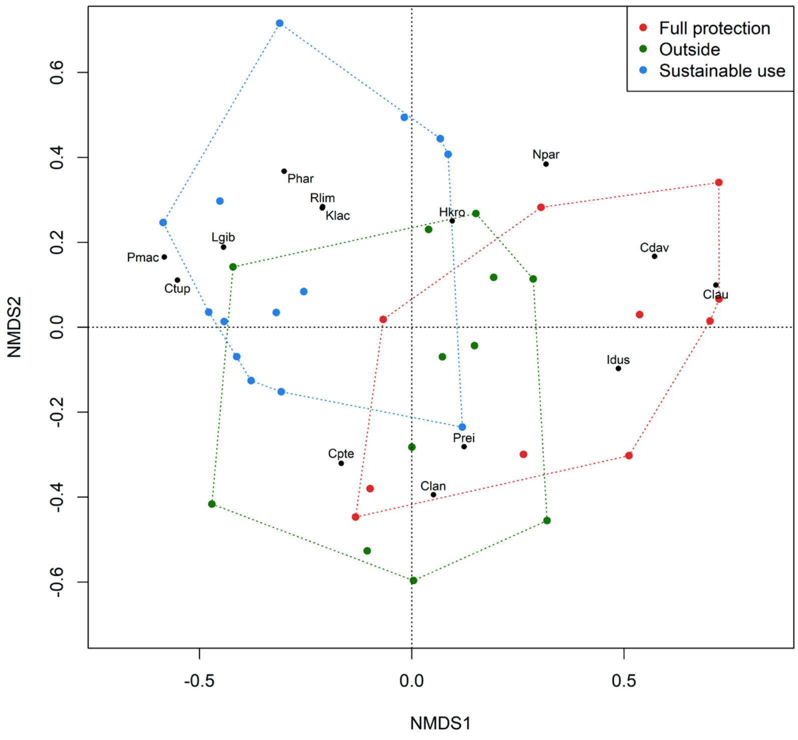


FIGURE 3 | NMDS biplot of the fish abundance data (Hellinger- transformed and Euclidean distance matrix). Stress = 0.20. The 30% most frequent species with 50% best axis fit were added using weighted averages. Species identification with code is in Tab. 1.

TABLE 3 | LCBD ANOVA table. Source: Area type (Area), environmental principal components (PC1 and PC2), spatial variable (PCNM1). Degrees of freedom (Df), sums of square (SS), mean squares (MS), F statistics (F), and p-value (P). *Significative effect.

Source	Df	SS	MS	F	P
Area	2	0.00005	0.000027	1.25	0.302
PC1	1	0.00012	0.000118	5.51	0.026*
PC2	1	0.00006	0.000006	0.27	0.604
PCNM1	1	0.00002	0.000002	0.11	0.738
Residuals	30	0.00064	0.000021		

TABLE 4 | Fish species composition PERMANOVA table. Source: Area type (Area), environmental principal components (PC1 and PC2), spatial variable (PCNM1). Degrees of freedom (Df), sums of square (SS), R square (R^2), F statistics (F), and p-value (P). *Significative effect.

Source	Df	SS	R2	F	P
Area	2	2.00	0.07	1.56	0.025*
PC1	1	1.44	0.05	2.23	0.015*
PC2	1	0.75	0.03	1.17	0.269
PCNM1	1	1.47	0.05	2.29	0.005*
Residual	30	19.28	0.72		

TABLE 5 | Dark diversity ANOVA table. Source: Area type (Area), environmental principal components (PC1 and PC2), spatial variable (PCNM1). Degrees of freedom (Df), sums of square (SS), mean squares (MS), F statistics (F), and p-value (P). *Significative effect.

Source	Df	SS	MS	F	P
Area	2	41.41	20.70	4.70	0.017*
PC1	1	9.07	9.07	2.06	0.162
PC2	1	33.29	33.29	7.56	0.010*
PCNM1	1	1.68	1.68	0.38	0.541
Residuals	30	132.18	4.41		

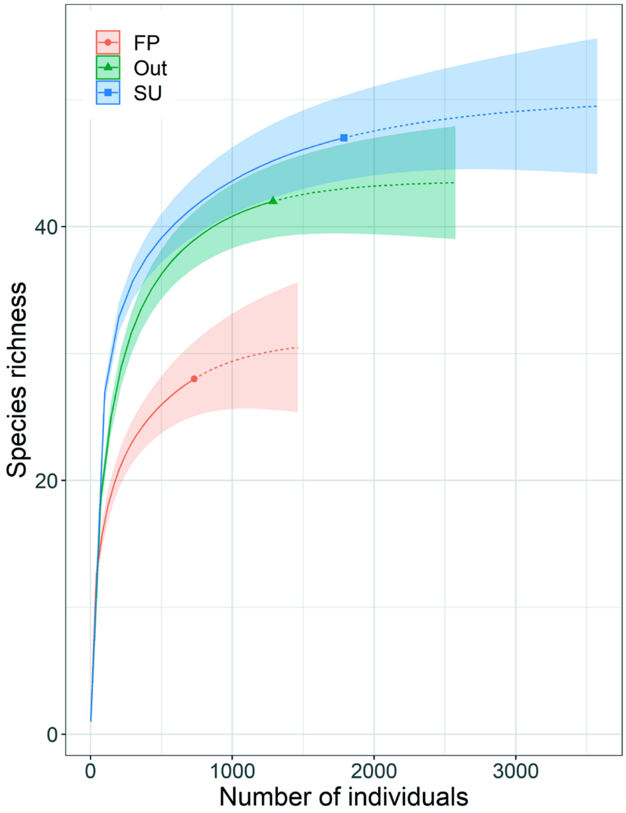


FIGURE 4 | Sample-size-based species richness rarefaction interpolation (solid line) and extrapolation (dotted line) sampling curves of full protection (FP), sustainable use (SU), and outside (Out) with confidence intervals.

DISCUSSION

The stream fish community from Serranias Costeiras of the Ribeira de Iguape River basin presented high beta diversity. The environmental heterogeneity that explained the species replacement was the gradient of streams morphological characteristics such as width, velocity, and altitudinal. The difference in species richness was promoted by area type, with streams inserted in full protection areas having less species richness than those found in sustainable use and outside areas. Most of the frequent species contributed to the compositional diversity. The streams in the full protection area have low dark diversity and contributed significantly to the beta diversity having lower species richness.

The streams that showed the highest species richness estimates are in sustainable use or outside areas. These areas have, on average, greater dark diversity, which can be an indicator of the vulnerability of a large portion of the species pool of fishes estimated for the Serranias Costeiras streams of the Ribeira de Iguape River basin. On the other hand, electrofishing is efficient in catching fish from streams, but every sampling methodology has limitations. Still, the failure to use other fishing gear may have led to the non-detection of the species in larger environments, which may have caused the highest values in dark diversity in SU and outside streams.

Isbrueckerichthys duseni, *Characidium lauroi*, *C. pterostictum*, and *Harttia kronei* are small species that live near the bottom of streams. *Characidium* feeds on small insects carried by the continuous flow of the river (Aranha *et al*., 2000). Loricariids have an inferior suckermouth adapted to attach to the substrate and relatively long intestines that characterize them as bottom scrapers (Buck, Sazima, 1995). Hence, among the species that contribute to the maintenance of high beta diversity, there are two distinct groups regarding the use of food resources that are entirely dependent on their surroundings.

We found a positive correlation of SCBD index with occurrence and abundance of species. Species with high occupancy in all sites and high total abundance in the data contribute to beta diversity, albeit they are not replaced, a factor that would usually generate beta diversity (Heino, Grönroos, 2017; Silva *et al*., 2018). Isolated streams located in high altitudes have low species richness (Súarez *et al*., 2011) and high uniqueness (LCBD) as streams from the full protection area. This pattern is expected in assemblages structured by dispersion limitation (Carrara *et al*., 2012) as stream fish assemblage of isolated headwater streams (Borges *et al*., 2020). In this sense, sustainable use stream stretches have a better hydrological connection with higher species richness and exclusivity.

We used a measure of completeness independent from the observed richness, however, with the same ecological meaning: the lower the dark diversity, the more complete the assemblage. Completeness, together with uniqueness (LCBD), can indicate conservation priorities given that complete and unique communities are expected to have high levels of functional stability that generate ecosystem services (Lewis *et al*., 2017). Furthermore, these high completeness communities can act as an essential source for other connected communities and function as a refuge for many species independent of shifts in the environmental condition (Lewis *et al*., 2017).

The FP stream stretches harboured the lowest observed and estimated species richness. Of the four species captured exclusively in these streams, only *Isbrueckerichthys alipionis* is endemic. On the other hand, the uniqueness of these stream stretches contributed to significant LCBD. The lower dark diversity in these streams indicates that we captured the species with the potential to occupy these environments meaning that FP contains a relevant proportion of the regional species pool and therefore is essential for conservation stream fish diversity in the study region. The streams of these PAs are at high altitudes, shallow with fast velocity and have high PHI values. We remember that PAs were designed from a "terrestrial biodiversity perspective", in this sense, with our results, full protection PAs have only a minimal role in fish diversity conservation.

The SU stream stretches deserve much attention aiming at stream fish conservation strategies. They harbour the most outstanding richness of exclusive species, have one stream with a high local contribution to beta diversity and the highest estimated species richness as in outside areas. The low value of dark diversity may be due to the morphological characteristics of the streams, with deeper water with reduced velocity, making it challenging to capture some species. On the other hand, environmental changes can lead to the absence of species with the potential to occupy these environments meaning that SU streams do not contain a relevant proportion of the regional species pool. Therefore, these stream stretches are essential for the study region's conservation of fish diversity. We highlight that a sustainable use PA has the function of conserving biodiversity while maintaining the economic activities of local inhabitants (Brasil, 2000).

Therefore, mechanisms considering stream conservation with economic development must be encouraged and kept, as in APA Quilombos do Médio Ribeira with several socio-environmental initiatives such as the Programa Vale do Ribeira (Pasinato, 2012). We also call attention to the need to amplify the PA sustainable use encompassing those outside due to their essential role in longitudinal connection in river and stream systems.

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COMPETING INTERESTS

The authors declare no competing interests.

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