The influence of the Rupununi portal on distribution of freshwater fish in the Rupununi district, Guyana

by

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ABSTRACT. - The Guiana Shield region in northern South America has a rich and diverse ichthyofauna with a high degree of endemism. The fauna of this region is shaped not only by the geology of the area but climatic events as well. The Rupununi district of southwestern Guyana is an area where seasonal rainfall floods a vast savanna. During the rainy season, this inundated savanna allows a connection between the Amazon and Essequibo Rivers that provides the potential for ichthyofaunal exchange. The connection is referred to as the Rupununi portal and this study investigates how this feature influences fish distributions and diversity between the drainages it links. In this study, fishes on either side of the portal were extensively sampled. Statistical comparisons of fish community structure from the two sides of the Rupununi portal were made using three common metrics: species richness, Shannon diversity and evenness. Significant community differences were found between the Essequibo and Amazon sides of the Rupununi portal. While the Rupununi portal serves as a conduit for some fish, it appears to be functioning as a barrier to dispersal for other species. Our study highlights the significance of the Rupununi portal in shaping fish distributions in this region.

RÉSUMÉ. - L'influence du portail du Rupununi sur la distribution des poissons dulçaquicoles dans le district du Rupununi, Guyana.

La région du bouclier guyanais, au nord de l'Amérique du Sud, possède une ichtyofaune riche et diverse, avec un haut taux d'endémisme. La faune de cette région n'a pas seulement été façonnée par la géologie de la zone mais aussi par les événements climatiques. Le district du Rupununi, dans le sud-ouest du Guyana, est une région où les précipitations saisonnières inondent une vaste savane. Durant la saison des pluies, cette savane inondée établit une connexion entre les fleuves Amazone et Essequibo, rendant l'échange d'ichtyofaune possible. Notre étude examine comment cette connexion appelée "Rupununi portal", ou portail du Rupununi, influence la distribution et la diversité des espèces entre bassins. Un important échantillonnage des poissons de part et d'autre du portail a été réalisé pour cette étude. Des comparaisons statistiques de la structure des communautés piscicoles de chaque bassin ont été faites en utilisant trois mesures classiques: la richesse spécifique, la diversité de Shannon et l'équitabilité. Des différences de communauté significatives ont été relevées entre l'Essequibo et l'Amazone. Alors que le portail du Rupununi sert de passage pour certaines espèces de poissons, il semble fonctionner en tant que barrière à la dispersion pour d'autres. Notre étude met en évidence l'importance du portail du Rupununi dans l'établissement de la distribution des poissons de cette région.

Key words. - Rupununi portal - Fish community – Ecology - Species richness - Shannon's diversity.

Fundamental to understanding processes that govern diversification of the Neotropical ichthyofauna is the geographical context that influences speciation and how the hydrological history of river drainage patterns, in conjunction, with geological history of the area affects dispersal, divergence and extinction of lineages. The Rupununi portal, in southern Guyana, is a unique biogeographic area providing a seasonal connection between two major South American river systems. The Rupununi portal seasonally connects the Amazon River (*via* the Takutu-Branco-Negro Rivers) and the Essequibo River (*via* the Rupununi River; Fig. 1). Both drainages have an incredibly diverse fish fauna (Reis *et al.*, 2003) and consistently are recognized as separate biogeographic provinces and areas of endemism (Géry, 1969; Weitzman and Weitzman, 1982; Lowe-McConnell, 1987; Hubert and Renno, 2006). This hydrological connection occurs from the inundation of the low-lying Rupununi savannas during the rainy season, allowing for faunal exchange between these two major drainages. Annual inundation of the Rupununi Savanna extends over 3,480km^2 with a hydroperiod of 49 days. The magnitude of the flood pulse varied over a nine-year study on floodplain inundation patterns in the Rupununi Savanna (Hamilton *et al.*, 2002). Consequently, variables associated with the seasonal cycle can have a major impact on the fish communities such as availability of food resources, rate of predation, habitat partitioning, reproduction and competition.

As with many of the Guiana Shield river systems, the Rupununi portal area shares a dynamic paleogeographic history (Lundberg, 1998). The North Rupununi savanna contains a rift valley, referred to as the Takutu graben located between the Pakaraima and Kanuku mountains. The Taku-

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tu graben is a sediment filled ENE-WSW trending rift that extends 280km long and 40km wide at the border of Brazil and Guyana, centred over the town of Lethem, Guyana (Hammond, 2005). A large endorheic lake, Lake Maracanata, filled the graben approximately 100 m deep during the early Cretaceous then by the Paleogene began transitioning to a fluvial system (Crawford *et al*., 1985). This fluvial system became the main stem of the proto-Berbice, which during the majority of the Cenozoic was a large northeast flowing river that drained most of the central Guiana Shield exiting into the Atlantic somewhere between present day towns of New Amsterdam, Guyana and Nickerie, Suriname (McConnell, 1959). A series of stream capture events by the Branco shifted the drainage patterns of the upper proto-Berbice, initially the Branco captured the Cotinga and Uraricoera then subsequently capturing the Takutu and Ireng Rivers during the Pleistocene (Crawford *et al*., 1985; Gibbs and Barron, 1993). The lower proto-Berbice shifted away from present day Berbice joining the Essequibo River as evidenced by the sharp elbow curve north of the confluence with the Rupununi River (Lujan and Armsbruster, 2011).

Currently, the North Rupununi savanna occupies the former Maracanata basin, thus creating a shallow divide between the east flowing Rupununi into the Essequibo and southwest flowing Takutu into the Branco and ultimately to the Amazon River. This divide is the current location of the Rupununi portal, the physical extent to which this divide floods is referred to as Lake Amuku. Although the Rupununi portal has been suggested to have played a strong role in structuring the flora and fauna of the region (Eigenmann, 1912; Lowe-McConnell, 1975; Hoogmoed, 1979; Turner *et al*., 2004), no study has thoroughly examined the fish communities of drainages that are linked. In order to accurately assess the role a biogeographic feature has on the local fauna, there must be solid comprehension of community structure (Ricklefs, 1987).

Studies of fish communities in the Neotropics are often hampered by taxonomic uncertainties and logistical difficulties of collecting repeated samples across multiple localities. Although important efforts were made by Planquette, Keith and Le Bail (1996, 2000) in the three-volume guide of freshwater fishes in French Guiana, few studies (Boujard, 1992; Mérigoux *et al*., 1998) have assessed fish communities in the Guiana Shield and only one study has characterized fish communities in Guyana (Lowe-McConnell, 1964). Rosemary Lowe-McConnell pioneered much of the research on the freshwater fish of the Rupununi district of Guyana. Over six years (1956-1962) she studied the fish fauna of the region, their ecology and the effects of the seasonal cycle on fish. She made several observations of fish movements at the onset of the wet and dry season; their migratory movements onto the savannas to spawn and the subsequent stranding of many fish in shallow ponds scattered throughout the savanna as the waters recede. These fish experience a physiological winter characterized by intense crowding, decreased food availability, desiccation, anoxic conditions and high rates of predation (Lowe-McConnell, 1964). Interestingly, these pond species were often observed in both Amazon and Essequibo drainages, while strictly riverine fishes were found only on the Amazon or Essequibo side. Therefore, the Rupununi portal may be a corridor of dispersal for some fish species and a barrier to dispersal for other species.

Although Lowe-McConnell's work in the Rupununi on fish communities is insightful, the number of localities and sample sizes were low. Our study has the most extensive sampling effort to date, including four expeditions in the Rupununi district with collections from the Takutu and Rupununi River drainages. The aim of this study is to provide a thorough examination of the fish community at this seasonal connection and infer the potential role the portal may have on fish distributions of this region. Extensive baseline data of distribution and abundance of species richness is rare in Neotropical systems, particularly in the Guiana Shield. This baseline data has implications for assessment of biodiversity, diversification patterns, biogeography and conservation of the Guiana Shield ichthyofauna.

MATERIALS AND METHODS

Study site and sampling

The Rupununi portal area is located between the Western and Eastern Guiana Shield regions at the border between Brazil and Guyana (Fig. 1). Extensive sampling of similar areas in the Rupununi and Takutu River drainages was done during four expeditions to the region (2002, 2003, 2005 and 2007). Fishes were collected by a variety of methods including seine, gill net, cast net, hook and line and by hand. All collections were made during the dry season with collections made during the day and night. Localities included sites from the main river channel, tributaries, ponds, and borrow pits. Georeferencing data was recorded for each site using a handheld GPS. Individuals were sorted and identified using current taxonomic keys for the different groups and by having experts examine some taxa. Over 400 species and 55,156 specimens from over 100 localities were deposited at the Auburn University Museum (AUM) fish collection. In addition, duplicates are deposited at the University of Guyana Centre for the Study of Biodiversity, the Academy of Natural Sciences of Philadelphia (ANSP), and Southern Illinois University (SIU), but this analysis uses only AUM specimens.

Statistical evaluation

All sites were divided into their respective drainage area, 'Rupununi' or 'Takutu'. Sample-based species accumulation curves were generated for both drainages using EstimateS ver. 8.2 (Colwell, 2009) including 95% confidence intervals. Both curves reached an asymptote indicating sufficient sampling was done in order to assess fish community structure. Rarefaction was applied to the dataset in order to account for the variation in sample sizes among sites on estimates of species richness and diversity (Gotelli and Colwell, 2001). Data from each site were resampled 1,000 times without replacement to generate the rarefied estimates of species richness, diversity, and evenness (EcoSim, ver. 7.72, Gotelli and Entsminger, 2010). Species richness, Shannon diversity, and evenness were calculated for both Rupununi (n = 44) and Takutu (n = 45) sites. Differences between rarefied estimates of species richness, Shannon diversity, and evenness between fish assemblages in the Takutu and Rupununi drainages were assessed using Mann-Whitney U tests.

RESULTS

Collections to the Rupununi savannas resulted in 55,156 individuals of 433 species, 13 orders, and 41 families. The dominant orders in terms of species were Characiformes (44%) and Siluriformes (36%), with 192 and 155 species, respectively. Perciformes ranked third with 40 species (9.3%). Gymnotiformes was represented by 24 species, while Beloniformes, Clupeiformes, Cyprinodontiformes, Osteoglossiformes, Pleuronectiformes, Rajiformes, Synbranchiformes, and Tetradontiformes were represented by less than 10 species. Of the forty-one families represented, by more than one species, the dominant families were Characidae with 93 species (21.5%), Loricariidae with 46 (10.6%) species and Cichlidae with 33 species (7.6%). See table I for species list.

Species accumulation curves for the Rupununi and Takutu River drainages indicate that sampling for both drainages was sufficient to assess species richness and diversity (Fig. 2) (Colwell, 2009). A total of 343 species were collected from the Rupununi River with 89 species found only in the Rupununi, a total of 344 species were collected from the Takutu River with 90 species unique to the Takutu, and 254 species were shared between the two drainages (Fig. 3). The dominant orders in terms of species for shared species were Characiformes (48%), Siluriformes (31%) and Perciformes (9%) with 122, 79 and 25 species, respectively. Species only in the Rupununi predominantly included 36 species in Characiformes (40%) and 34 species in Siluriformes (38%). Species only in the Takutu predominantly included 42 species in Siluriformes (46%) and 35 species in the Characiformes (38%).

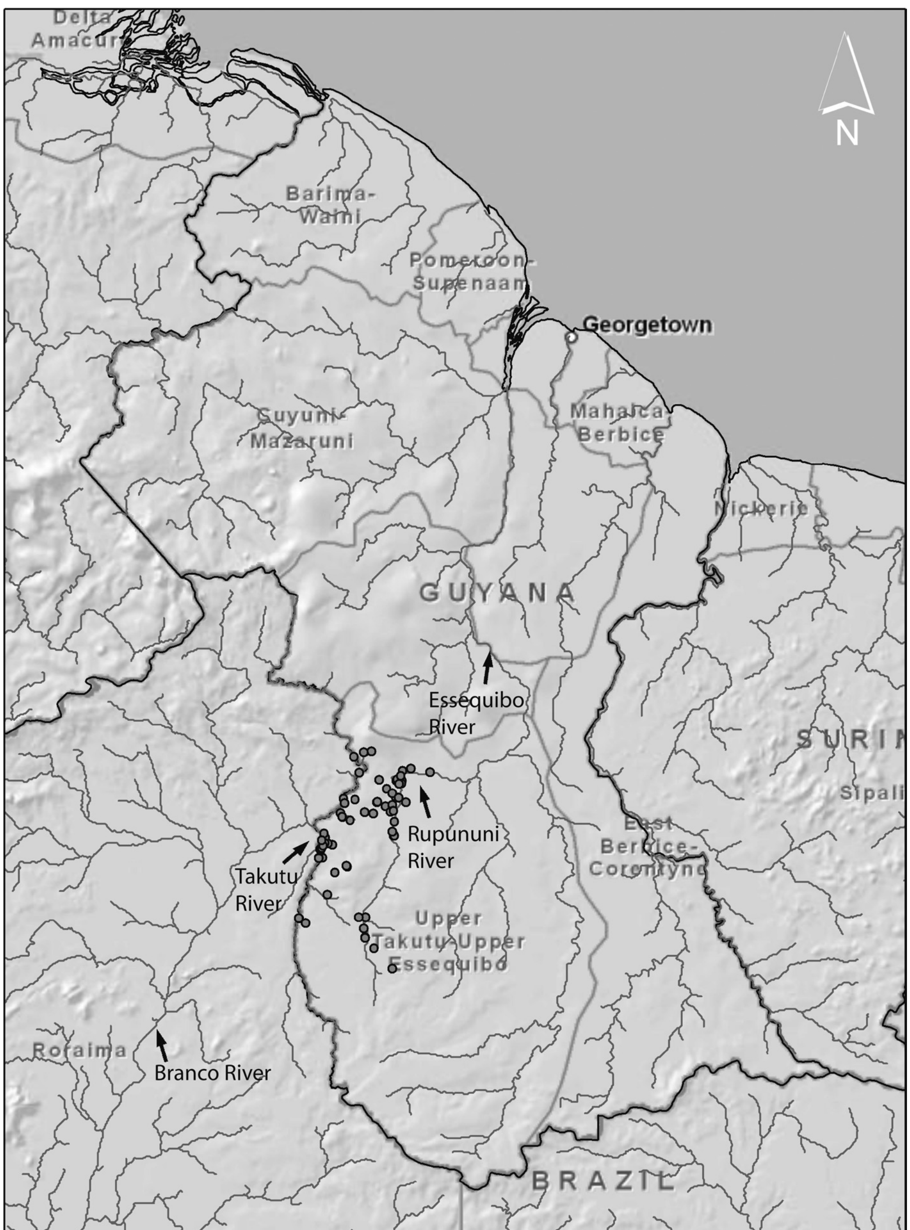

Figure 1. - Collection sites in the Rupununi and Takutu River drainages.

Table I. - Fishes of the Rupununi Savanna District, Guyana.

Taxa	Rupununi	Takutu	Both
Beloniformes			
Belonidae			
Potamorrhaphis guianensis	-	-	✓
Pseudotylosurus microps	-	-	✓
Characiformes			
Acestrorhynchidae			
Acestrorhynchus falcirostris	-	-	✓
Acestrorhynchus microlepis	-	-	✓
Acestrorhynchus minimus	-	-	✓
Acestrorhynchus falcatus	✓	-	-
Acestrorhynchus guianensis	-	✓	-
Anostomidae			
Anostomoides laticeps	✓	-	-
Anostomus ternetzi	-	-	✓
Hypomasticus megalepis	-	✓	-
Laemolyta proxima	-	-	✓
Laemolyta taeniata	✓	-	-
Leporellus vittatus	-	-	✓
Leporinus agassizii	-	-	✓
Leporinus desmotes	-	-	✓
Leporinus fasciatus	-	-	✓
Leporinus nigrotaeniatus	-	-	✓
Leporinus alternus	✓	-	-
Leporinus friderici	✓	-	-
Leporinus maculatus	✓	-	-
Leporinus sp.	✓	-	-
Leporinus cf. *agassizii*	-	✓	-
Leporinus granti	-	✓	-
Leporinus ortomaculatus	-	✓	-
Petulanos plicatus	✓	-	-
Petulanos cf. *spiloclistron*	-	✓	-
Pseudanos irinae	✓	-	-
Schizodon cf. *vittatus*	-	-	✓
Synaptolaemus cingulatus	-	✓	-
Characidae			
Acanthocharax microlepis	✓	-	-
Acestrocephalus sardina	-	✓	-
Aphyocharacidium melandetum	-	✓	-
Aphyocharax alburnus	-	-	✓
Aphyodite grammica	-	-	✓
Charax hemigrammus	✓	-	-
Astyanax bimaculatus	-	-	✓
Astyanax fasciatus	-	-	✓
Astyanax rupununi	-	-	✓
Astyanax clavitaeniatus	-	✓	-
Brittanichthys myersi	-	-	✓
Brycon falcatus	-	-	✓
Brycon pesu	-	✓	-
Bryconamericus hyphesson	-	-	✓
Bryconamericus sp.	-	-	✓
Bryconamericus sp. “deep body”	-	-	✓
Bryconops affinis	-	-	✓
Bryconops alburnoides	-	-	✓
Bryconops caudomaculatus	-	-	✓
Chalceus epakros	-	-	✓
Chalceus macrolepidotus	✓	-	-
Charax gibbosus	-	-	✓

Taxa	Rupununi	Takutu	Both
Creagrutus maxillaris	-	-	✓
Creagrutus melanzonus	-	-	✓
Creagrutus sp.	✓	-	-
Ctenobrycon spilurus	-	-	✓
Cynopotamus essequibensis	-	-	✓
Exodon paradoxus	-	-	✓
Galeocharax gulo	-	✓	-
Gephyrocharax sp.	✓	-	-
Hemigrammus analis	-	-	✓
Hemigrammus bellottii	-	-	✓
Hemigrammus cf. *schmardae*	-	-	✓
Hemigrammus cylindricus	-	-	✓
Hemigrammus iota	-	-	✓
Hemigrammus levis	-	-	✓
Hemigrammus microstomus	-	-	✓
Hemigrammus ocellifer	-	-	✓
Hemigrammus rodwayi	-	-	✓
Hemigrammus schmardae	-	-	✓
Hemigrammus stictus	-	-	✓
Hemigrammus unilineatus	-	-	✓
Hemigrammus gracilis	✓	-	-
Hemigrammus erythrozonus	-	✓	-
Hyphessobrycon bentosi	-	-	✓
Hyphessobrycon catableptus	-	-	✓
Hyphessobrycon gracilis	-	-	✓
Hyphessobrycon minor	-	-	✓
Hyphessobrycon sp.	-	-	✓
Iguanodectes spilurus	-	-	✓
Jupiaba atypindi	-	-	✓
Jupiaba pinnata	-	-	✓
Jupiaba polylepis	-	-	✓
Jupiaba scologaster	-	✓	-
Microschemobrycon callops	-	-	✓
Microschemobrycon casiquiare	-	-	✓
Microschemobrycon sp.	-	✓	-
Moenkhausia ceros	-	-	✓
Moenkhausia cf. *eigenmanni*	-	-	✓
Moenkhausia chrysargyrea	-	-	✓
Moenkhausia collettii	-	-	✓
Moenkhausia copei	-	-	✓
Moenkhausia dichroura	-	-	✓
Moenkhausia jamesi	-	-	✓
Moenkhausia lepidura “1”	-	-	✓
Moenkhausia lepidura “2”	-	-	✓
Moenkhausia oligolepis	-	-	✓
Moenkhausia sp. “ghost”	-	-	✓
Moenkhausia comma	✓	-	-
Moenkhausia sp.	✓	-	-
Moenkhausia lepidura “3”	-	✓	-
Moenkhausia megalops	-	✓	-
Moenkhausia sp. 1	-	✓	-
Odontostilbe gracilis	-	-	✓
Parapristella aubynei	-	-	✓
Phenacogaster microstictus	-	-	✓
Phenacogaster megalostictus	✓	-	-
Poptella brevispina	-	-	✓
Poptella compressa	-	-	✓

Table I. - Continued.

Taxa	Rupununi	Takutu	Both
Poptella longipinnis	-	-	✓
Brachychalcinus orbicularis	-	✓	-
Pristella maxillaris	-	-	✓
Roeboides affinis	-	-	✓
Tetragonopterus argenteus	-	-	✓
Tetragonopterus chalceus	✓	-	-
Triportheus brachipomus	-	-	✓
Triportheus cf. *venezuelensis*	✓	-	-
Triportheus albus	-	✓	-
Triportheus rotundatus	-	✓	-
Chilodontidae			
Caenotropus labyrinthicus	-	-	✓
Chilodus punctatus	-	-	✓
Crenuchidae			✓
Characidium hasemani	-	-	✓
Characidium pteroides	-	-	✓
Characidium steindachneri	-	-	✓
Characidium zebra	-	-	✓
Characidium sp.	-	✓	-
Crenuchidae sp.	-	✓	-
Elachocharax junki	-	-	✓
Elachocharax geryi	-	✓	-
Melanocharacidium dispilomma	-	-	✓
Melanocharacidium nigrum	-	-	✓
Melanocharacidium depressum	-	✓	-
Melanocharacidium pectorale	-	✓	-
Melanocharacidium sp.	-	✓	-
Microcharacidium eleotrioides	-	✓	-
Ctenoluciidae			
Boulengerella cuvieri	-	-	✓
Boulengerella lucius	-	-	✓
Curimatidae			
Curimata cyprinoides	-	-	✓
Curimata roseni	-	-	✓
Curimata sp.	✓	-	-
Curimatopsis crypticus	-	-	✓
Cyphocharax festivus	-	-	✓
Cyphocharax leucostictus	-	-	✓
Cyphocharax microcephalus	-	-	✓
Cyphocharax spilurus	-	-	✓
Cyphocharax sp.	✓	-	-
Psectrogaster ciliata	✓	-	-
Psectrogaster essequibensis	✓	-	-
Steindachnerina planiventris	-	-	✓
Cynodontidae			
Cynodon gibbus	✓	-	-
Hydrolycus armatus	-	-	✓
Roestes ogilveiei	✓	-	-
Erythrinidae			
Erythrinus erythrinus	-	-	✓
Hoplerythrinus unitaeniatus	-	-	✓
Hoplias malabaricus	-	-	✓
Hoplias sp.	-	-	✓
Hoplias aimara	✓	-	-
Gasteropelecidae			
Carnegiella strigata	-	-	✓

Taxa	Rupununi	Takutu	Both
Hemiodontidae			
Bivibranchia fowleri	-	✓	-
Hemiodus quadrimaculatus	✓	-	-
Hemiodus argenteus	-	-	✓
Hemiodus semitaeniatus	-	-	✓
Hemiodus sp.	-	-	✓
Hemiodus unimaculatus	-	-	✓
Hemiodus thayeria	✓	-	-
Lebiasinidae			
Copella nattereri	-	-	✓
Nannostomus eques	-	-	✓
Nannostomus harrisoni	-	-	✓
Nannostomus marginatus	-	-	✓
Nannostomus trifasciatus	-	-	✓
Nannostomus unifasciatus	-	-	✓
Nannostomus beckfordi	✓	-	-
Nannostomus minimus	✓	-	-
Pyrrhulina filamentosa	-	-	✓
Parodontidae			
Parodon bifasciatus	-	-	✓
Parodon nasus	-	✓	-
Prochilodontidae			
Prochilodus rubrotaeniatus	-	-	✓
Semaprochilodus insignis	-	✓	-
Serrasalmidae			
Catoprion mento	-	-	✓
Metynnis argenteus	-	-	✓
Metynnis luna	-	-	✓
Metynnis sp.	✓	-	-
Metynnis hypsauchen	-	✓	-
Metynnis lippincottianus	-	✓	-
Myleus pacu	-	-	✓
Myleus sp.	-	-	✓
Myleus setiger	✓	-	-
Myloplus rubripinnis	-	-	✓
Mylossoma aureum	-	✓	-
Prosomyleus rhomboidalis	✓	-	-
Pygocentrus nattereri	-	-	✓
Pygopristis denticulata	-	-	✓
Pristobrycon striolatus	-	-	✓
Serrasalmus eigenmanni	-	-	✓
Serrasalmus rhombeus	✓	-	-
Clupeiformes			
Engraulidae			
Amazonsprattus scintilla	-	✓	-
Anchovia surinamensis	✓	-	-
Anchoviella guianensis	-	-	✓
Anchoviella sp.	-	-	✓
Anchoviella sp. 1	✓	-	-
Anchoviella sp. 2	✓	-	-
Anchoviella sp. 3	✓	-	-
Jurengraulis juruensis	-	-	✓
Cyprinodontiformes			
Rivulidae			
Rivulus sp.	-	-	✓
Rivulus stagnatus	-	✓	-

Table I. - Continued.

Taxa	Rupununi	Takutu	Both
Gymnotiformes			
Apteronotidae			
Apteronotus albifrons	-	-	✓
Apteronotus sp.	-	-	✓
Platyurosternarchus macrostomus	-	-	✓
Sternarchorhynchus oxyrhynchus	-	✓	-
Gymnotidae			
Electrophorus electricus	-	✓	-
Gymnotus sp.	-	-	✓
Hypopomidae			
Brachyhypopomus brevirostris	-	-	✓
Brachyhypopomus sp.	-	-	✓
Brachyhypopomus pinnicaudatus	✓	-	-
Brachyhypopomus bullockii	✓	-	-
Brachyhypopomus sp. 2	✓	-	-
Hypopygus lepturus	-	-	✓
Microsternarchus sp.	✓	-	-
Steatogenys elegans	-	-	✓
Rhamphichthyidae			
Gymnorhamphichthys hypostomus	-	-	✓
Gymnorhamphichthys rondoni	-	-	✓
Gymnorhamphichthys rosamariae	-	-	✓
Gymnorhamphichthys sp. "fused saddles"	-	✓	-
Gymnorhamphichthys sp. "small saddle"	✓	-	-
Rhamphichthys marmoratus	-	-	✓
Rhamphichthys rostratus	✓	-	-
Sternopygidae			
Eigenmannia microstoma	-	-	✓
Eigenmannia virescens	-	-	✓
Rhabdolichops electrogrammus	-	✓	-
Myliobatiformes			
Potamotrygonidae			
Paratrygon aiereba	✓	-	-
Potamotrygon orbignyi	-	-	✓
Potamotrygon hystrix	-	✓	-
Osteoglossiformes			
Osteoglossidae			
Osteoglossum bicirrhosum	-	-	✓
Perciformes			
Cichlidae			
Acarichthys heckelii	-	-	✓
Acaronia nassa	-	-	✓
Acaronia sp.	-	✓	-
Aequidens tetramerus	-	-	✓
Aequidens potaroensis	-	✓	-
Apistogramma ortmanni	-	-	✓
Apistogramma rupununi	-	-	✓
Apistogramma steindachneri	-	-	✓
Apistogramma sp.	-	✓	-
Biotodoma cupido	-	-	✓
Chaetobranchopsis orbicularis	-	✓	-
Chaetobranchus flavescens	-	-	✓
Cichla ocellaris	-	-	✓
Cichlasoma bimaculatum	-	-	✓
Crenicichla alta	-	-	✓
Crenicichla lugubris	-	-	✓
Crenicichla reticulata	-	-	✓
Crenicichla saxatilis	-	-	✓
Crenicichla strigata	-	-	✓
Crenicichla wallacii	-	-	✓
Crenicichla acutirostris	✓	-	-
Geophagus sp.	-	-	✓
Geophagus sp. "takutu 2"	-	-	✓
Geophagus surinamensis	-	-	✓
Geophagus sp. "essequibo"	✓	-	-
Geophagus sp. "yupukari"	✓	-	-
Geophagus sp. "takutu"	-	✓	-
Guianacara sphenozona	-	-	✓
Guianacara dacrya	-	-	✓
Heros severus	✓	-	-
Mesonauta guyanae	-	-	✓
Satanoperca jurupari	-	-	✓
Satanoperca leucosticta	-	-	✓
Eleotridae			
Microphilypnus amazonicus	-	-	✓
Sciaenidae			
Pachypops fourcroi	-	-	✓
Pachypops sp.	✓	-	-
Pachypops trifilis	✓	-	-
Petilipinnis grunniens	-	-	✓
Plagioscion squamosissimus	✓	-	-
Plagiscion surinamensis	✓	-	-
Pleuronectiformes			
Achiridae			
Achirus achirus	-	✓	-
Hypoclinemus mentalis	-	-	✓
Apionichthys finis	-	-	✓
Siluriformes			
Aspredinidae			
Amaralia hypsiura	-	-	✓
Bunocephalus amaurus	-	-	✓
Bunocephalus sp.	-	-	✓
Bunocephalus verrucosus	✓	-	-
Hoplomyzon atrizona	-	✓	-
Xyliphius sp.	-	✓	-
Auchenipteridae			
Ageneiosus piperatus	✓	-	-
Auchenipterichthys coracoideus	✓	-	-
Auchenipterus demerarae	✓	-	-
Auchenipterus ambyiacus	-	✓	-
Centromochlus reticulatus	-	-	✓
Gelanoglanis sp.	-	✓	-
Glanidium leopardum	-	-	✓
Tatia intermeida	-	-	✓
Trachelyopterus galeatus	-	-	✓
Trachelyopterus sp.	-	✓	-
Trachycorystes trachycorystes	✓	-	-
Callichthyidae			
Corydoras bondi	-	-	✓
Corydoras melanistius	-	-	✓
Corydoras sipaliwini	-	-	✓
Corydoras blochi	-	✓	-

Table I. - Continued.

Taxa	Rupununi	Takutu	Both
Corydoras sp. “plain”	-	✓	-
Megalechis picta	✓	-	-
Megalechis thoracata	-	✓	-
Cetopsidae			
Cetopsidae sp. 1	-	-	✓
Cetopsidium soniae	-	✓	-
Cetopsidium roae	-	-	✓
Cetopsis cf. *montana/axelrodi*	-	✓	-
Denticetopsis macilenta	-	-	✓
Denticetopsis iwokrama	-	✓	-
Doradidae			
Acanthodoras cataphractus	✓	-	-
Acanthodoras spinosissimus	✓	-	-
Amblydoras affinis	-	-	✓
Doras carinatus	✓	-	-
Doras micropoeus	✓	-	-
Hassar sp.	-	-	✓
Hassar sp. 1	-	-	✓
Leptodoras hasemani	-	-	✓
Leptodoras linnelli	-	-	✓
Leptodoras praelongus	-	✓	-
Nemadoras leporhinus	-	-	✓
Nemadoras trimaculatus	-	-	✓
Nemadoras sp.	-	✓	-
Opsodoras sp.	✓	-	-
Opsodoras ternetzi	-	✓	-
Oxydoras niger	-	-	✓
Platydoras hancockii	-	-	✓
Rhinodoras armbrusteri	-	-	✓
Scorpiodoras affinis	-	-	✓
Trachydoras cf. *steindachneri*	-	-	✓
Trachydoras brevis	✓	-	-
Trachydoras pseudomicrostomus	-	✓	-
Heptapteridae			
Brachyrhamdia heteropleura	-	-	✓
Cetopsorhamdia insidiosa	-	✓	-
Chasmocranus cf. *tapanahoniensis*	✓	-	-
Chasmocranus longior	✓	-	-
Chasmocranus sp.	✓	-	-
Goeldiella eques	✓	-	-
Imparfinis hasemani	-	-	✓
Mastiglanis sp. “no spot”	-	-	✓
Mastiglanis sp. “spot”	-	-	✓
Phenacorhamdia sp. “slim”	✓	-	-
Phenacorhamdia sp. “short anal fin”	-	✓	-
Pimelodella cristata	-	-	✓
Pimelodella megalops	-	-	✓
Pimelodella sp. 2	✓	-	-
Pimelodella sp. “dark”	-	✓	-
Pimelodella sp. “ireng”	-	✓	-
Pimelodella sp.	-	✓	-
Rhamdella leptosoma	-	✓	-
Rhamdia quelen	-	-	✓
Rhamdia sp.	-	✓	-
Loricariidae			
Ancistrus circle E	-	-	✓
Ancistrus leucostictus	✓	-	-
Ancistrus sp.	✓	-	-
Ancistrus sp. 2	-	✓	-
Ancistrus nudiceps	-	✓	-
Farlowella acus	-	-	✓
Farlowella nattereri	-	-	✓
Farlowella reticulata	-	-	✓
Farlowella rugosa	-	-	✓
Harttia platystoma	✓	-	-
Hemiodontichthys acipenserinus	✓	-	-
Hypancistrus sp.	-	✓	-
Hypoptopoma guianense	-	-	✓
Hypoptopoma thoracatum	✓	-	-
Hypoptopoma sp.	-	✓	-
Hypostomus hemiurus	-	-	✓
Hypostomus macushi	-	-	✓
Hypostomus squalinus	-	-	✓
Hypostomus taphorni	-	-	✓
Lasiancistrus schomburgkii	-	-	✓
Limatulichthys griseus	-	-	✓
Lithoxus lithoides	-	-	✓
Loricaria cataphracta	-	-	✓
Loricaria sp.	-	-	✓
Loricaria sp. 1	-	✓	-
Loricariichthys brunneus	✓	-	-
Loricariichthys microdon	✓	-	-
Loricariichthys sp.	✓	-	-
Panaque sp.	-	✓	-
Parotocinclus britskii	-	-	✓
Peckoltia sabaji	-	-	✓
Peckoltia cavatica	✓	-	-
Peckoltia braueri	-	✓	-
Pseudacanthicus leopardus	-	-	✓
Pseudancistrus nigrescens	-	-	✓
Pseudancistrus megacephalus	✓	-	-
Pseudoloricaria laeviuscula	-	✓	-
Rhadinoloricaria macromystax	-	✓	-
Rineloricaria fallax	-	-	✓
Rineloricaria lanceolata	-	-	✓
Rineloricaria sp.	-	-	✓
Rineloricaria sp. 1	-	-	✓
Rineloricaria sp. 2	-	-	✓
Rineloricaria stewarti	✓	-	-
Spatuloricaria sp.	-	-	✓
Sturisoma monopelte	-	-	✓
Pimelodidae			
Hemisorubim platyrhynchos	-	-	✓
Hypophthalmus edentatus	✓	-	-
Megalonema platycephalum	-	-	✓
Pimelodus albofasciatus	-	-	✓
Pimelodus blochii	-	-	✓
Pimelodus ornatus	-	-	✓
Pimelodus sp.	-	-	✓
Pseudoplatystoma fasciatum	-	-	✓
Sorubim elongatus	-	-	✓
Sorubim lima	✓	-	-

Table I. - End.

Taxa	Rupununi	Takutu	Both
Pseudopimelodidae			
Batrochoglanis villosus	-	-	✓
Microglanis poecilus	-	-	✓
Microglanis secundus	-	-	✓
Pseudopimelodus bufonius	-	-	✓
Pseudopimelodus sp.	✓	-	-
Trichomycteridae			
Acanthopoma sp. 2	✓	-	-
Acanthopoma sp.	-	✓	-
Haemomaster sp.	-	✓	-
Haemomaster venezuelae	-	✓	-
Henonemus punctatus	-	-	✓
Homodiaetus sp.	-	-	✓
Ituglanis sp.	-	✓	-
Ochmacanthus flabelliferus	-	-	✓
Ochmacanthus sp. 2	-	-	✓
Ochmacanthus sp.	-	✓	-
Paracanthopoma sp.	-	-	✓
Paracanthopoma sp. 1	-	✓	-
Paravandellia sp. 1	✓	-	-
Paravandellia sp.	-	✓	-
Pygidianops eigennmanni	-	✓	-
Sarcoglanis simplex	-	✓	-
Stegophilus sp.	-	✓	-
Trichomycterus sp.	-	-	✓
Typhlobelus sp.	-	✓	-
Vandellia beccarii	-	-	✓
Vandellia sanguinea	-	-	✓
Synbranchiformes			
Synbranchidae			
Synbranchus marmoratus	-	-	✓
Tetraodontiformes			
Tetraodontidae			
Colomesus psittacus	-	-	✓

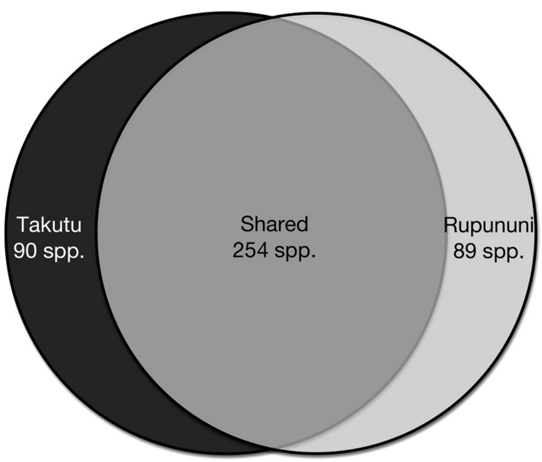

Figure 2. - Venn diagram of fish distributions in Rupununi and Takutu Rivers.

The dominant families in species shared between the two regions were Characidae (25%), Loricariidae (10%), and Cichlidae (7.5%) with 65, 26, and 23 species respectively. Species only in the Rupununi predominantly included Characidae (15%) with 13 species, Loricariidae (12%) with 11 species, and Anostomidae (9%) with 8 species. Species only in the Takutu predominantly included Characidae (17%) with 15 species, Trichomycteridae (12%) with 11 species, Loricariidae (10%) with 9 species and Crenuchidae (8%) and Heptapteridae (8%) representing 7 species each (Tab. II).

Several new species, cognate species (across the Rupununi portal), and endemic species were identified in this study. While there may be many more new species from these collections, listed here are Siluriformes recently identified as new species. Including, *Cetopsidium soniae*, *Gelanoglanis* sp. 1, *Gelanoglanis* sp. 2, *Hypostomus macushi*, *Hypancistrus* sp., *Panaque* sp., *Peckoltia cavatica*, *Peckoltia sabaji*,

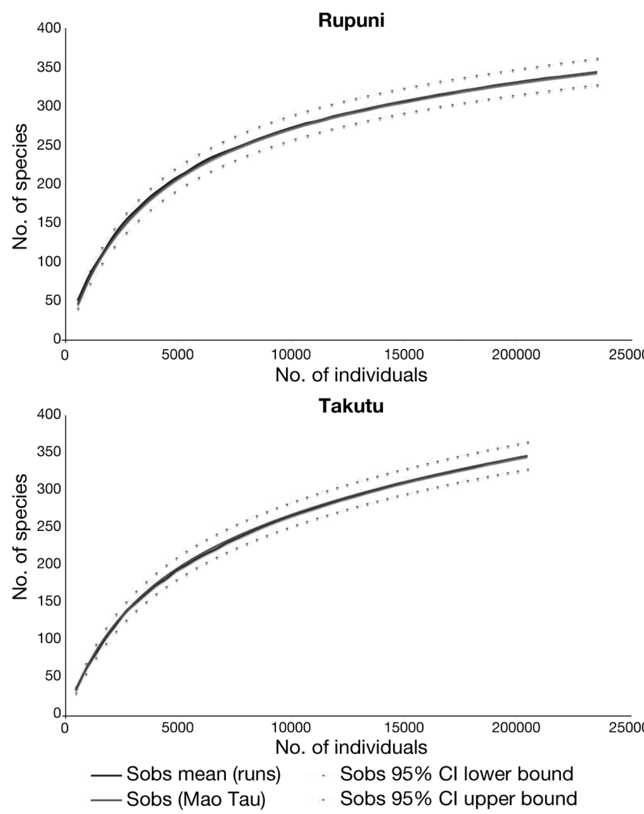

Figure 3. - Species accumulation curves for Rupununi and Takutu River drainages. Mao Tau is expected estimates at infinite number of randomizations. Dotted lines denote the upper and lower bound of 95% confidence intervals.

Typhlobelus sp., and *Rhinodoras armbrusteri*.

Cognate species are two or more geographically isolated forms that have diverged morphologically from their common ancestor. Cognate species-pairs found on either

Taxonomic level	Rupununi	Takutu	Shared	Overall
Dominant orders	Characiformes 40% (36) Siluriformes 38% (34) Perciformes 8% (8)	Siluriformes 46% (42) Characiformes 38% (35) Perciformes 6% (6)	Characiformes 48% (122) Siluriformes 31% (79) Perciformes 10% (26)	Characiformes 44% (192) Siluriformes 36% (155) Perciformes 9.3% (40)
Dominant families	Characidae 15% (13) Loricariidae 12% (11) Anostomidae 9% (8)	Characidae 17% (15) Trichomycteridae 12% (11) Loricariidae 10% (9)	Characidae 25% (65) Loricariidae 10% (26) Cichlidae 9% (13)	Characidae 22% (93) Loricariidae 11% (46) Cichlidae 7.6% (33)

Table II. - Dominant orders and families found in Rupununi, Takutu, shared and overall.

Diversity measures	Rupununi (N = 45)	Takutu (N = 44)	Ustat	P-value
Mean richness	37.72	29.16	1283	0.015*
Mean Shannon's diversity	2.59	2.38	1244	0.035*
Mean evenness	0.73	0.72	1095	0.388

Table III. - Results from Mann-Whitney U tests comparing species diversity measures between the Rupununi and Takutu drainages.

side of the Rupununi portal (Takutu *vs*. Rupununi) consist of *Peckoltia cavatica* (Rupununi) and *Peckoltia braueri* (Takutu), *Auchenipterus ambyiacus* (Takutu) and *Auchenipterus demerarae* (Rupununi), *Curimata roseni* (Takutu) and *Curimata* sp. (Rupununi), *Acanthopoma* sp. (Rupununi) and *Acanthopoma* sp. 1(Takutu), *Brachioica* sp. (Rupununi) and *Brachioica* sp. 1(Takutu). It has also been suggested that *Geophagus abalios* are cognate species across the portal (H. López-Fernández, pers comm.). The following four species ranges are restricted to the Takutu-Branco drainage and considered endemic: *Peckoltia braueri*, *Hypancistrus* sp., *Typhlobelus* sp., and *Panaque* sp., while *Peckoltia cavatica* is endemic to the Rupununi River.

Rupununi River assemblages exhibited higher species richness and Shannon diversity than Takutu River assemblages, but evenness was not different between groups. A Mann-Whitney U test indicated that Species richness and Shannon diversity between the Rupununi and Takutu were significantly different (Tab. III). Evenness measures are strongly influenced by sample size (Kvalseth, 1991), therefore the lack of differences between the groups in evenness can be attributed to use of rarefaction, which accounts for disparity in sampling sizes.

DISCUSSION

The paleogeographic history of the Rupununi portal area suggests that vicariance, isolation, and faunal exchange with secondary contact have contributed to the origins of the fauna surrounding the portal. In conjunction with paleogeological events shifting river drainages between eastern and western Guiana shields is the recent development of the Rupununi portal. The seasonal connection at the Rupununi portal brings additional complexity to understanding the processes influencing diversification, because this allows for a reconnection of portions of the ancient proto-Berbice. Therefore, two processes at work influencing fish diversity and distribution are vicariance of the proto-Berbice break-up that was complete in the Pleistocene (or earlier) and/or recent dispersal *via* the Rupununi portal.

For species with ranges in the Takutu and Rupununi Rivers, a natural expectation is that this hydrological connection would allow aquatic species to freely disperse between the two drainages. Indeed, phylogeographic studies on *Potamorrhaphis*, *Cichla* and *Prochilodus* (Lovejoy and Araújo, 2000; Turner *et al*., 2004; Willis *et al*., 2007) all support the hypothesis of dispersal through the ephemeral aquatic connection at the Rupununi portal, in addition to historical biogeographical analysis of possible dispersal routes in South American Rivers that also suggest faunistic exchange via the Rupununi portal (Hubert and Renno, 2006). In this study, we found statistically significant differences in the fish assemblages of the rivers linked by the Rupununi portal, suggesting the portal is serving as a conduit for dispersal for some species and not for other species.

Measures of community structure like species richness, diversity, and evenness can reveal important information about structure, stability and function of species assemblages. Species richness is the number of species in an assemblage, diversity characterizes the number of species and their relative abundance, while evenness is the variation in the abundance of individuals per species within a community. These measures provide critical baseline data in assessing biodiversity and have strong conservation implications. Assessing the differences in fish community structure in the

Takutu and Rupununi Rivers enables us to infer the potential influence of the Rupununi portal on fish distributions. A Mann-Whitney U test revealed significant difference in species richness and diversity between the two drainages. Below we examine differences in community structure of the two drainages to further assess why these drainages differ in diversity and richness.

There is a consistent pattern across the groupings at a higher taxonomic level, where the dominant orders are Characiformes, Siluriformes, and Perciformes (Tab. III). The patterns are more structured as we examine the composition at lower taxonomic levels and smaller area. The species that are found in the Takutu but not the Rupununi are mainly characids, trichomycterids and loricariids. Characids and loricariids are the dominant families in the region, so it is not surprising that the list of endemic species should include them, but the diversity of the trichomycterids deserves explanation.

Trichomycterids are commonly thought of as parasitic fishes, although they are considered to have the widest trophic adaptations among catfish families (Schaefer *et al*., 2005). Some trophic modes include hematophagy (feeding on blood) in the candirus, lepidophagy (scales), mucophagy (mucus), necrophagy (carrion) and algivory (algae). Equally remarkable is the variation of ecological habitats and elevation occupied within this family (Arratia and Menu-Marque, 1984; Fernández and Schaefer, 2003). Those found in the Takutu but not in the Rupununi are primarily psammophilic species (sand-dwelling), an adaptation that has involved complex evolutionary specializations (Zuanon *et al*., 2006). The predominant substratum of the Takutu is sand and therefore could explain the prevalence of several species. In addition, the extensive network of tributaries with sandy bottoms and shores connected to the Takutu would allow for their increased presence. Conversely, the lack of psammophilic habitat in the Rupununi portal would pose as a barrier to dispersal and thus, the decreased numbers of species found in the Rupununi. Interestingly, the hematophagic species of *Vandellia* are psammophilic, but are found on both sides of the portal, and not found in the northeastern Guiana Shield outside of the Essequibo River. The two species *Vandellia* (*V. beccari* and *V. sanguinea*) could have ridden across the portal on a host and settled in the Rupununi as suggested by Zuanon and Sazima (2005) of dispersal in trichomycterids.

Anostomidae is considered to be highly diverse in the Guiana Shield (Sidlauskas and Vari, 2008), and anostomids were found to have many species present in the Rupununi but not in the Takutu. Their omnivorous diet and versatility in varying habitats could allow for their increased presence in the Rupununi drainage. Many of the anostomid species found in the Rupununi but not the Takutu are found in the Amazon basin, suggesting that the range of habitats we were able to sample in the Takutu may not be suitable for some species of anostomids to establish populations.

Several species found moving between the drainages were collected consistently at multiple sites. Many of these species, as Lowe-McConnell (1964) suggested, were found in savanna ponds as well as in the river system. Some species found in the ponds, like *Hoplias malabaricus, Pygocentrus nattereri*, *Cichla ocellaris* and *Acestrorhynchus microlepis*, have widespread distributions and are predatory fishes. This would enable them to endure conditions during the dry season in these ponds when competition for resources is high. Additionally, *Prochilodus rubrotaeniatus* is found throughout the drainages of the Guiana Shield and, not surprisingly, is among the species that occur on either side of the portal. This widespread detritivore makes long distance migrations, which would facilitate dispersal across the flooded savanna (Vari, 2004). Many of the species found between the two drainages are widely distributed, but there are also ones with smaller known ranges like *Hypostomus macushi* that were found on both sides of the portal.

Our study also suggests that the portal served as a barrier of dispersal for one-fourth of the species unique to the Rupununi and Takutu drainages. Although this may be an artifact of collecting for some species (for example, *Roestes ogilviei* was only collected in the Rupununi, but it is known from the Amazon basin), the savanna is clearly a barrier for other species. For example, *Cichla temensis* is restricted to the Amazon side of the portal. This could be explained by habitat preference of this species, typically blackwater systems (Willis *et al*., 2007). Loricariids like *Peckoltia cavatica*, *Ancistrus leucostictus* and *Pseudancistrus megacephalus* are restricted to the Essequibo side of the portal. All three species are found in swift flow among gravel, cobble and boulders. They are often found clustered together and therefore may not disperse long distances or the inundated savannas may not provide suitable habitat for these species. The possibility of competition for niche occupancy cannot be ruled out and therefore confine them to smaller ranges.

Despite the extensive sampling in the Rupununi and Takutu over four expeditions, species accumulation curves reveal slight differences. The Takutu curve has just barely reached an asymptote, whereas the Rupununi curve has, suggesting that increased sampling in the Takutu would likely demonstrate increased species richness compared to that of the Rupununi. The Takutu and Rupununi were part of the proto-Berbice until the Amazon captured the Takutu about 2 MYA, and likely had similar faunas. The Amazon had more species than the proto-Berbice, so capture of the Takutu by the Amazon likely enriched the Takutu over the Rupununi. The Rupununi Portal has also likely enriched the fauna of the Essequibo over that of other eastern Guiana Shield rivers. The enrichment of the Takutu can especially be seen in the increased presence of trichomycterids that are found there as well as the rest of the Amazon, but not in the Rupununi.

The ecology of fishes seems to play a role in the overall pattern of distributions; however, very little is known about the specific ecologies of many of these species. There is evidence that the ecologies of fishes affect dispersal through the Casiquiare River, which drains part of the Upper Orinoco into the Upper Negro and ultimately into the Amazon River. Examination of this connection revealed that the Casiquiare River serves as a zoogeographical filter, functioning as a corridor for some species and barrier for others (Winemiller *et al.*, 2008). Distribution of fishes was based on an environmental gradient found along the Casiquiare River defined by shifts in water chemistry, habitat, and food resources. Additionally, further evidence from species specialized to rheophilic habitat, *Pseudancistrus brevispinis*, supported utilization of different mechanisms for dispersal influencing their distribution patterns in the Guiana Shield (Cardoso and Montoya-Burgos, 2009). Dispersal and diversification in *Pseudancistrus brevispinis* among adjacent basins is suggested to have occurred when marine waters receded followed by allopatric divergence during the marine incursions. Therefore, sea level fluctuations are suggested to have played a role in diversification and distribution of the Neotropical fish fauna.

Some of these factors could be driving the differences in fish assemblages across the Rupununi portal. Firstly, there are compositional differences in the drainages linked by the Rupununi portal. The Rupununi River has a larger floodplain surrounded by savanna and gallery forests, whereas the Takutu River is primarily surrounded by savanna. Steep banks are characteristic of the Takutu along many stretches of the river, which is due to tilting of basement layer of the Shield and a result of stream capture by the Branco (Gibbs and Barron, 1993). Water chemistry differences can also contribute to the differences. The Takutu River transitions between blackwater (starting at the Ireng) to whitewater as it flows into the Branco. Blackwater systems, dark in appearance due to the leaching of tannins from decaying leaves, tend to have low pH, low conductivity, and low dissolved oxygen (Val and Almeida-Val, 1995). This could pose physiological constraints on aquatic organisms. Low pH alone influences ionic balance, in addition to other physiological processes in fishes such as osmotic balance, oxygen affinity for haemoglobin and digestion (Wilson *et al.*, 1999; Matsuo and Val, 2002). Therefore, blackwater fishes are adapted to the specific environmental physicochemical characteristic of their environment (Val and Almeida-Val, 1995). The Rupununi River is a clearwater to whitewater system. There is moderate pH and dissolved oxygen concentrations in these systems, but also in whitewater portions there is sediment load when the waters levels are high, giving it a muddy appearance. In addition to the water chemistry within the drainages, waters throughout the vegetation of the inundated savanna during the rains affect differences in water chemistry (Carter, 1934; Sarmiento, 1984). Therefore, species adapted to specific characteristics of water type could find movement into another water type as a barrier to dispersal. In our study, water chemistry could explain the absence of widespread taxa that prefer whitewater (like *Leporinus friderici* and *Roestes ogliviei*) from the Takutu.

In order to survive and persist, organisms are driven to adapt, thereby developing characteristics for differing environmental conditions, acquisition of food resources and reproduction. These ongoing processes are evident in the tremendous specializations found in much of the Neotropical ichthyofauna. For instance, species that bury themselves in the sand (*Potamotrygon*, *Gymnorhamphicthys*, *Sarcoglanis* and *Vandellia*), species hidden in cavities of lateritic boulders (*Rhinodoras* and *Parotocinclus*), species associated with floating vegetation (*Apistogramma*), ones able to move over floating vegetation (*Hoplias* and *Hoplerythrinus*), and many found on submerged woody debris (many loricariids). Many of the specializations reveal the ecology of fishes have an important role in distributional patterns. Additionally, the ecology allows us to have a better understanding of the effect a biogeographic feature has on taxa (Bermingham and Martin, 1998). Closer examination of the ecologies of species at the portal could provide more insight to specific diversifying processes driven by the Rupununi portal. Further, recent population genetics and phylogeographic studies have provided important new insights to biogeographical distributions of Neotropical fish across the Casiquiare River connection as well as the Rupununi portal (Lovejoy and Araújo, 2000; Sivasundar *et al.*, 2001; Turner *et al.*, 2004; Moyer *et al.*, 2005; Willis *et al.*, 2007) further revealing the intimate relationship of South America's geological history and evolution of the Neotropical fish fauna. Willis *et al.* (2010) points out that what is lacking in these biogeographical studies is an examination of these biogeographically important features of fishes across differing ecological requirements. Currently, we are attempting to fill this gap with a population genetics study of fishes with varying ecologies across the Rupununi portal in an attempt to determine how diverse ecologies affect gene flow. Assessing the genetics of species across the portal could reveal unsuspected diversity as found in *Pseudancistrus brevispinis*, where population genetics revealed six distinct lineages within the Guianas region (Cardoso and Montoya-Burgos, 2009).

This study has provided the most extensive assessment of the fish distributions in the Rupununi district, Guyana, while also resolving the composition of the fish fauna across the Rupununi portal. The fish community structure reveals the intrinsic role of the Rupununi portal on aquatic taxa likely influencing diversifying processes, as in cognate species. The highly structured fish fauna across the portal reveals a fauna that is constantly adapting to changes imposed by a fluctuating system of seasonal floods. The significance of the Rupununi portal on fish distributions has strong implications for conservation of this vital watershed for supporting flora and fauna.

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