



## Co-occurrence patterns of fish species in two aquatic habitats of the Arauca River floodplain, Venezuela

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**Keywords:** Assembly rules, Co-occurrence networks, Fish community structure, Freshwater fish ecology, Seasonal environments.

**Abstract:** The study of co-occurrence patterns has been extensively applied to propose assembly rules for community organization. Recently, a new interest has grown in the effect of gradients on these patterns and to analyze them through new approximations such as co-occurrence networks, through which keystone species can be identified. Neotropical floodplains represent interesting systems to study such patterns, because of their spatial heterogeneity, temporal variability and their high fish species richness. With this in mind, our goal was to study the co-occurrence patterns of fish in a segment of the Arauca River's floodplain and the influence of the spatial and temporal variability on them. One stream and one floodplain lake were sampled with gill nets during 2014 – 2015 across a hydrological cycle and 5 matrices for each 5 sampled months in each water body were prepared to explore the co-occurrence patterns in each water body across months and 2 for the entire period, through a probabilistic pair-wise analysis of species co-occurrence that identified aggregated and segregated species pairs. With the observed co-occurrences  $\times$  water body  $\times$  month, the species weighted degrees and betweenness were calculated, and co-occurrence networks were constructed. The networks structures, in terms of the degrees of every species, were compared spatially and temporally through a generalized linear model. The stream showed the highest numbers of aggregated species pairs, and in general showed the most complex networks in terms of nodes, edges and degrees. The habitat type and the hydrological phases significantly influenced the structure of the fish co-occurrence networks. Two species, *Loricariichthys brunneus* and *Pygocentrus cariba* were identified as the core of the fish communities of the floodplain and as keystone species because they contribute to the connection of the networks by having a series of links with less frequent species.

**Nomenclature:** Eschmeyer et al. (2016).

### Introduction

Since MacArthur and Wilson's Theory of Islands Biogeography (1967), several assembly rules have been proposed to study the organization of communities. According to Keddy and Weiher (2004) the study of assembly rules has been approached through two paradigms: the island paradigm and the trait – environment paradigm. The first includes the study of mainlands, islands, immigration, dispersal and coexistence, and the second is based on pools, habitat filters and convergence. One of the first to propose assembly rules based on species coexistence was Diamond (1975). Even though some of his tenets were questioned by other authors (Connor and Simberloff 1979), one of them: “*Some pairs of species never coexist, either by themselves or as a part of a larger combination*”, has prompted an extensive research on species co-occurrence patterns within communities (Stone and Roberts 1992, Gotelli et al. 1997, Peres-Neto 2004, Horner-Devine et al. 2007). The main goal of these studies has been to detect if species exhibit nonrandom co-occurrence patterns and to try to explain the factors behind these patterns. However, as Weiher and Keddy (2004) pose, time has come to move on to other aspects such as how these assembly rules vary along gradients.

Co-occurrence patterns of species offer relevant information about the processes that shape the structuring of biotic communities. Initially, the approaches to study co-occurrence patterns focused on the patterns at the whole community level, through the contrasting of observed communities to null models (Gotelli and Graves 1996, Gotelli et al. 1997, Gotelli 2000, Gotelli and McCabe 2002), but recently the patterns at the species level have won more relevance (Veech 2006, 2014, Ulrich and Gotelli 2013), since it has been recognized that communities are not discrete spatial entities with compositions of species with little variation across localities (Veech 2014). Conversely, pair-wise analyses of entire presence-absence matrices may offer more insight into species distribution patterns and community organization. Likewise, this approach also offers a basis for the development of co-occurrence networks of biotic communities.

At the species level, these patterns reflect pair-wise associations, which can be either aggregated or segregated (Veech 2013, 2014). Aggregated patterns indicate that two species commonly occur together, whereas segregated ones indicate that two species tend to avoid each other or never coexist. The dominance of segregated patterns of co-occurrence in biotic communities has been attributed to the effect of biotic interactions such as predation or interspecific competition

(Diamond 1975, Connor and Simberloff 1979), while aggregated patterns have been explained as a consequence of similar environmental requirements of the species involved in them. In rivers, segregated patterns of co-occurrences of fish species have been explained as the result of segregation among predators and prey (Cecilio et al. 1997, Hoeinghaus et al. 2006). Nevertheless, this hypothesis has been questioned, and the alternative hypothesis of interspecific differences in habitat use has been proposed (Peres-Neto 2004).

Networks theory has gained relevance in the study of biotic processes and the organization of biotic communities (Proulx et al. 2005). Networks have among their properties the community structure, that is reflected in different clusters that are formed among subsets of the vertices and that reflect the intensity of the interactions between the species that compose the network, which can be measured through the weights of their nodes (Girvan and Newman 2002). The network approach has been applied to study biotic organization at different levels, from gene and protein interactions, to metabolic pathways, mutualistic networks and food webs (Proulx et al. 2005). In freshwater systems, this approach has been used to study some food webs (Power and Dietrich 2002) and fish trophic networks (Winemiller 1990). On the other hand, co-occurrence networks are being analyzed to study the assembly processes of a variety of organisms, from microbes community structure among ecosystems (Williams et al. 2014) to bird mixed flocks in disturbance gradients (Mokross et al. 2014), to tree communities (Morueta-Holme et al. 2016), as well as to assess the impact of climate change on communities and biotic interactions (Araújo et al. 2011). These networks offer the opportunity to identify the species that are the core of communities in terms of holding numerous links with other less connected species (Morueta-Holme et al. 2016), and also their connectedness through measures of weighted degrees. In spite of this, co-occurrence networks of fish communities in freshwater ecosystems have barely been analyzed.

Undoubtedly, the assembly of fish communities has been intensely studied through different approaches that include the modeling of species abundances (Strange et al. 1992), the effect of environmental filters (Mouillot et al. 2007, Mouchet et al. 2013, Pease et al. 2015), trophic eco-morphology (Adlte and Winemiller 1996, Sampaio et al. 2013, Blasina et al. 2016), the elements of meta-community structure (Fernandes et al. 2013, Erős et al. 2016), among others. These studies have contributed to the understanding of the influence of environmental factors, landscape, the evolutionary history of the species and biotic interactions in the organization of communities. The patterns of coexistence of freshwater fish have been explored mainly with null models (Peres-Neto 2004, Arrington et al. 2005, Hoeinghaus et al. 2006) and at the community level. The results have been mixed, because some studies have given more weight to environmental factors and habitat requirements to explain non-random patterns of co-occurrence, whereas others have signaled the importance of biotic interactions to explain such patterns. On the other hand, it is worthy to mention Céréghino et al. (2005), who studied the co-occurrence patterns of small fishes in riv-

ers of Southern France and the influence of environmental variables through neural networks. They determined that the distribution of three fish species was influenced by their co-occurrence patterns as well as the slope, the elevation and the species richness.

However, neural models can be time-consuming to compute, and their results difficult to interpret, especially when analyzing data of Neotropical freshwater fish communities that are highly diverse at local and regional scales, such as those of our study. In this context, the study of co-occurrence networks represents a useful tool to explore the co-occurrence patterns of freshwater fish communities in the Neotropics, since it can help us identify in a simpler way those species that are involved in complex interactions and which are important for the functioning of ecosystems, such as keystone species (Jordán et al. 2008). Consequently, co-occurrence networks are relevant for conservation purposes. Likewise, they are easier to interpret in comparison with neural networks or other statistical analyses, which implies that they can be employed by a wider public such as people working in conservation, rather than just by scientific researchers. Another advantageous aspect of co-occurrence networks is that they are species-oriented, which can provide a different insight on the assembly of communities from other studies focused on species richness and abundances.

In tropical floodplains, the fish communities are under a constant reshuffle due to seasonal variations in water level across the hydrological cycle. These variations take form as pulses (Junk et al. 1989) that are gradual enough to enable the incidence of biotic interactions such as predation or interspecific competition, which influence the species occupation of available mesohabitats (Arrington et al. 2005). There are several factors that might influence the species occupancy of mesohabitats as well as the establishment of biotic interactions, such as the age of the patch and its structural complexity (Arrington and Winemiller 2006), or even if it is day or night (Arrington and Winemiller 2003). On the other hand, it has been suggested that the influence of biotic interactions depends on the degree of connectivity and the hydrological stability of the aquatic habitats (Hoeinghaus et al. 2006, Thorp et al. 2008) and also that these interactions have increased influence in the organization of fish communities during the hydrological seasons of low (Zaret and Rand 1971) and falling waters (Winemiller 1996).

Returning to Weiher and Keddy's (2004) view on the necessity to extend the study of co-occurrence patterns of species to the influence of gradients, tropical floodplains, with their high spatial heterogeneity and temporal variability, represent a suitable system to tackle that need. Floodplains are characterized by a high diversity of aquatic habitats such as streams, floodplain lakes, ephemeral ponds and backwaters, with their particular hydro-geomorphological features (Junk et al. 1989, Thorp et al. 2006). The differences among aquatic habitats influence the organization of their associated communities in different ways. One is regulating the magnitude of the effects of biotic interactions such as interspecific competition or predation (Thorp et al. 2008). Therefore, an effect of

these differences among habitat features on the co-occurrence patterns of species within their communities is expected.

Considering this theoretical frame, we expected to observe spatiotemporal variations in the co-occurrence patterns of fishes and their co-occurrence networks in our study area, located within a segment of the Arauca River floodplain in the Venezuelan lowlands of Apure. Thus, the first objective of the study was to explore the co-occurrence patterns of fish species in two water bodies: one stream, a lotic habitat, and a floodplain lake, a lentic habitat, across hydrological seasons. The second objective was to examine the structure of the co-occurrence networks within these water bodies. In tropical aquatic systems, predation and competition can be very intense during low waters due to less availability of food and refugia (Zaret and Rand 1971), on the contrary, during the months of high waters the flooded areas offer new resources for the fishes (Junk et al. 1989), therefore we predicted that 1) during the months of low waters the segregated pairs would be more frequent and inversely, during the month of high waters the aggregated pairs would be more frequent.

Bearing in mind that the floodplain lake went through a pronounced reduction of water volume and therefore of habitat availability during low waters due to its desiccation during this hydrological phase, and that biotic interactions tend to be more important in more constant habitats in terms of their hydrological regime (Thorp et al. 2008), we predicted that 2) the number of significantly associated pairs would be higher in the stream in comparison to the floodplain lake due to a higher variation in the water level of the later, and finally 3) the co-occurrence networks would be simpler in terms of number of nodes and links in the floodplain lake for the reasons previously stated for prediction number two. With this research, we also wanted to provide information about the keystone species of the fish communities of the floodplain of Caño La Piedra that might be relevant for their management and conservation.

## Materials and methods

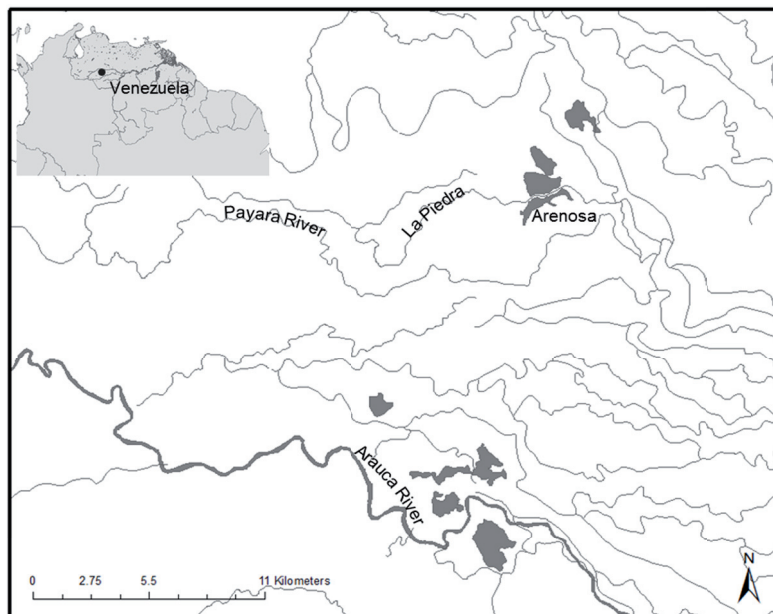
### *Study area*

The study was carried out in a segment of the Arauca River floodplain. This segment is drained by Caño La Piedra, a secondary tributary of the Arauca, in the lowlands of Venezuela known as llanos de Apure. The samplings were taken within the private cattle ranch Hato Santa Luisa, approximately 19 km south from San Fernando de Apure. The area has an annual average precipitation of 1475 mm. The monthly precipitation patterns are reflected in the fluctuations of the water level across hydrological seasons. The low waters season takes place from December to March, with an average precipitation of 5.94 mm. The rising waters season occurs from April to June. The high water season takes place from late June to September, with an average precipitation of 289.5 mm. During this season, the highest water depths in Caño La Piedra are registered, usually in August. Finally, the falling waters spans from September to November.

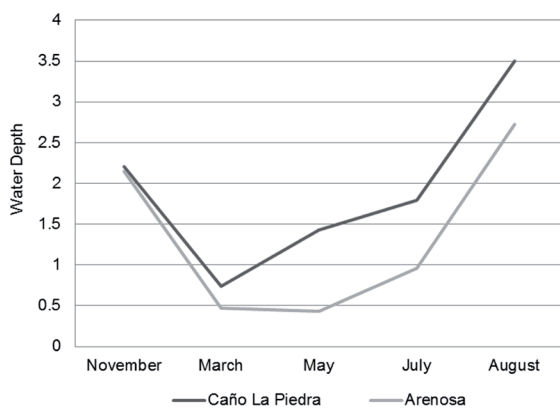
Within the segment of Caño La Piedra, there are different habitats that include the channel of this stream, as well as floodplain lakes and smaller ponds. Even though the channel suffers obvious variations in the water level, it maintains an important volume of flowing water throughout the hydrological cycle. The samplings were taken from a segment of 15 km of the channel of Caño La Piedra and the floodplain lake Arenosa with 128 hectares (Fig. 1). Arenosa is connected to Caño La Piedra during high waters and becomes isolated during low waters.

### *Sampling protocols*

Samplings were carried out during November of 2014, March, May, July and August of 2015. During March and May, Caño La Piedra showed the lowest water depths and



**Figure 1.** The segment of the Arauca River floodplain drained by the stream Caño La Piedra and the floodplain lake Arenosa, and its relative position within Venezuela and the lowlands of Apure.



**Figure 2.** Average water depth per sampled month in the stream Caño La Piedra and the floodplain lake Arenosa.

during August the highest depths. Even though normally the beginning of rising waters took place in May, due to an atypical extension of the dry season in 2015 associated to La Niña, this month was treated as an extension of the phase of low waters. November and July corresponded to the transitional seasons of falling and rising waters respectively (Fig. 2). The samplings were obtained with 10 gill nets of  $2 \text{ m} \times 30 \text{ m}$  each, eight of them were 4.5'' between knots, and four of them were 1.5'' between knots. During each month, the nets were put on the borders across the 15 km segment of Caño La Piedra and around the perimeter of Arenosa, with a distance of approximately 20 m between nets, and were left immersed during four hours between revisions in order to guarantee the independence of the samples. In both water bodies, the gill nets were revised five times during every month. During every revision, all fishes were extracted from the gill nets. Each one of these revisions was treated as an independent sample.

#### Statistical analyses

With the data of the fishes, incidence matrices of species per site in each water body separately for each month were prepared for the analyses. The co-occurrence patterns were explored based on these incidence matrices through pair-wise probabilistic analyses that test the hypothesis of dependence of co-occurrence between two species (Veech 2013, 2014). For the construction of these matrices, each revision of the entire set of gillnets in each water body was considered one site. All the analyses were based on presence/absence data. Therefore, for every water body, five monthly matrices of species per revision were built, and one with the data of all sampled months. These analyses were conducted using the package *co-occur* (Griffith et al 2016) of the R language (R Core Team 2014). The analyses rendered the probability of co-occurrence of each species pair and allowed to identify the species involved in significantly aggregated (positive) and segregated (negative) patterns of co-occurrence. The analyses also allowed us to calculate the total number of observed co-occurrences of every species pair in the two water bodies.

The total observed co-occurrences per species pairs for every month were used to construct co-occurrence networks

for each sampled month separately for Arenosa and Caño La Piedra, giving a total of ten networks. The observed co-occurrences of each species pair were used as edges and the species as nodes. The networks were constructed with the assistance of the package *igraph* (Amestoy et al. 2015) of the language R (R Core Team 2014), using the species weighed degrees as a scale for the size of the nodes in every case. The metrics weighed degrees and betweenness were calculated for each species within each one of the ten networks. The weighed degrees consist of the sum of observed co-occurrence of each species with all the other species of the community and indicate how well connected a network is, whereas betweenness is a measure of the extent to which a node is part of a transaction between other nodes, and it is calculated by dividing the binary shortest paths that go through a node by the number of binary paths between two nodes (Opsahl et al. 2010). The weighted degrees and betweenness were calculated using the package *met* (Opsahl 2015) of the R language. The local clustering coefficients were also computed as a measure of the nodes' weighted densities. The clustering coefficient is the fraction of the number of present links over the total number of possible links between a focal node (Opsahl and Panzarasa 2009). Networks with high clustering coefficients are more cohesive than networks with lower coefficients. We chose the measure proposed by Barrat et al. (2004) which applies to weighted networks. This approximation assigns to each edge of a graph a weight proportional to all possible connections among the various nodes of the network. The coefficients were also calculated using the package *met* (Opsahl 2015) in R.

Then, a generalized linear model was used to compare the weighted degrees among networks, accounting for the number of possible species associations within a network by using an  $n - 1$  offset, where  $n$  represented the number of nodes (Mokross et al. 2014). The model was based on a Poisson distribution and was calculated using the base commands of the R language (R Core Team 2014). A second generalized linear model was used to compare the clustering local coefficients among networks, and using the same  $n - 1$  offset. With the *intersection.by.name* code lines of *igraph*, we identified those species whose co-occurrences were consistent across month in each water body and therefore, are the core of the fish communities in the floodplain of Caño La Piedra.

#### Results

The total number of positive, negative and randomly associated species pairs within each water body is presented in Table 1. Most aggregated pairs were observed in the channel of Caño La Piedra. However, in both water bodies the numbers of random associations were high. This pattern was more evident when the analyses were conducted for every month separately in both water bodies, as can be seen in Table 2, for which March and May were the only months when Caño La Piedra exhibited non-random co-occurrence pairs, all positive, but very few when contrasting with the randomly associated pairs.

In Caño La Piedra, the species more frequently involved in significant associations were the catfish *Trachelyopterus*

**Table 1.** Number of pairs of fish species with positive, negative and random co-occurrence patterns in Caño La Piedra and Arenosa for the entire period of the study.

Water body	Habitat	Patterns of co-occurrence		
		Aggregated	Segregated	Random
Caño La Piedra	Stream	83	1	1746
Arenosa	Floodplain lake	21	1	881

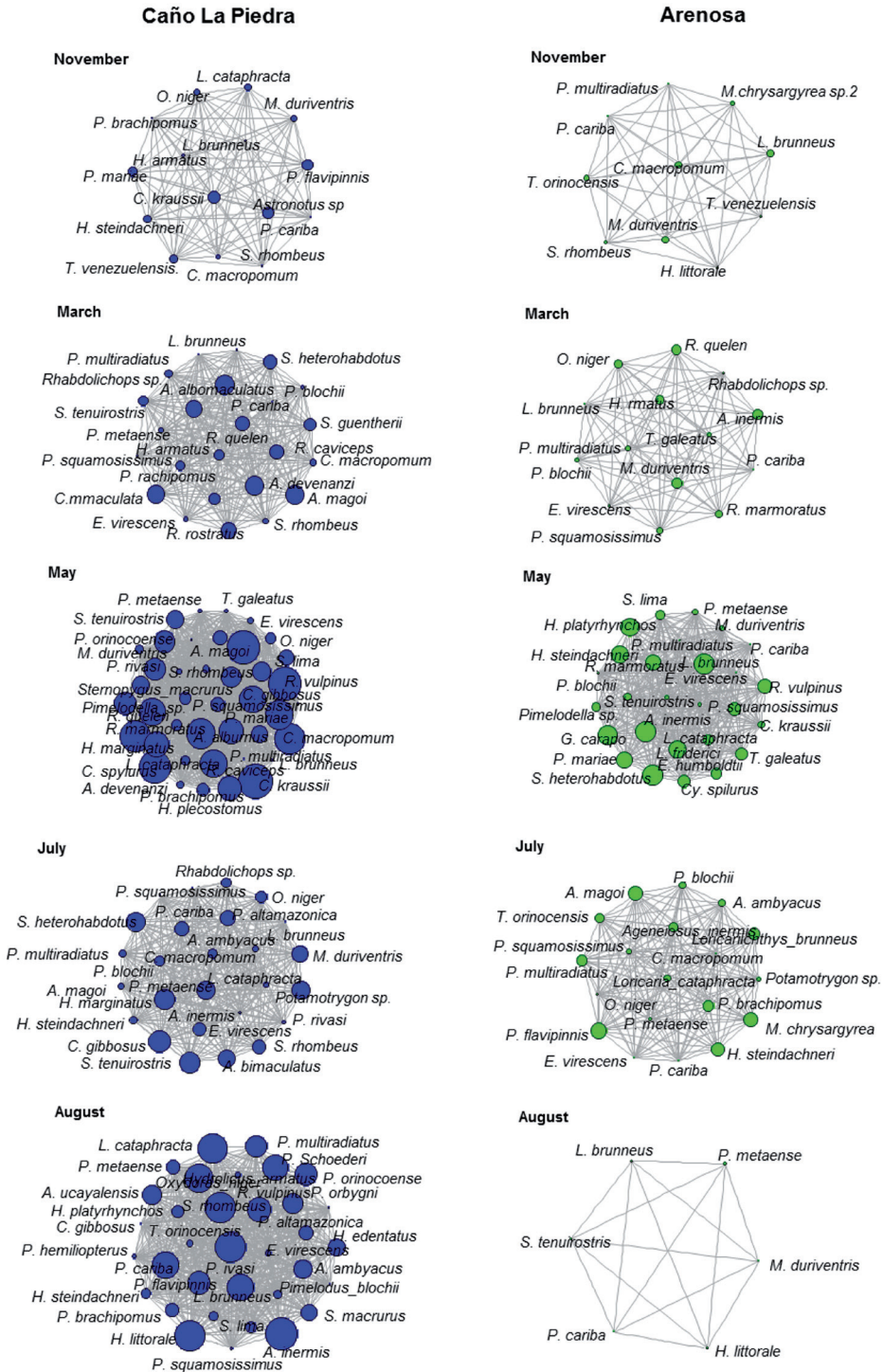
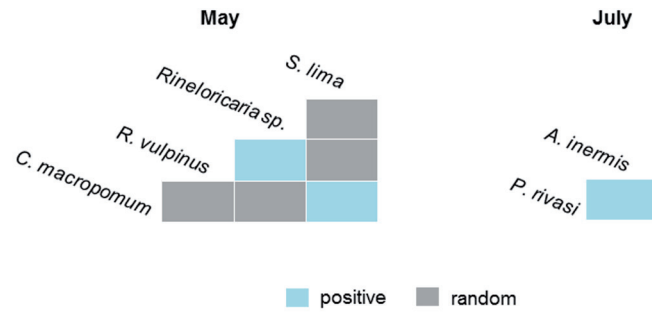
**Table 2.** Number of pairs of fish species with positive, negative and random co-occurrence patterns in Caño La Piedra and Arenosa per month.

	Stream			Floodplain lake		
	Caño La Piedra			Arenosa		
	Co-occurrence patterns					
	Aggregated	Segregated	Random	Aggregated	Segregated	Random
November	0	0	100	0	0	29
March	1	0	281	0	0	62
May	2	0	753	0	0	269
July	0	0	256	0	0	119
August	0	0	499	0	0	11



**Figure 3.** Co-occurrence patterns of fish species in the stream Caño La Piedra and the floodplain lake Arenosa during the entire period of the study.

**Figure 4.** Co-occurrence patterns of fish species in the stream Caño La Piedra during May and July.



**Figure 5.** Co-occurrence networks of fish species in the stream Caño La Piedra and the floodplain lake Arenosa during the sampled months. The circles represent the nodes (species) and the lines represent the links among nodes. The sizes of the nodes were scaled according to the species weighted degrees. The larger the circle the higher the species weighted degrees.

*galeatus* (12 aggregated pairs) and the knife fish *Adontosternarchus devenanzi* (9 aggregated pairs, 1 segregated) for the entire period of the study (Fig. 3). These two species tended to be aggregated with others such as *Pseudoplatystoma metaense*, *Schizodon heterohabdotus*, *Ageneiosus magoi*, *Pterygoplichthys multiradiatus*, *Loricariichthys brunneus*, *Eigenmannia virescens* and *Rineloricaria* sp. The only segregated pair was formed by *Hypoptopoma steindachneri* and *A. devenanzi*. The species involved in the significantly aggregated pairs in Caño La Piedra during March and July can be seen in Figure 4.

In the floodplain lake Arenosa, 21 species were involved in significantly associated pairs for the entire period, in contrast with Caño La Piedra, where the number of species was 83. The species most frequently involved in those pairs in La Arenosa was the small bodied loricariid *H. steindachneri* (3 aggregated pairs). The other species were involved in one or two significant pairs. The only segregated pair was represented by the piranha *Pygocentrus cariba* and the loricariid *Sturisoma tenuirostris*.

In general terms, Caño La Piedra exhibited the most complex co-occurrence networks in terms of number of edges, nodes and the species degrees (Fig. 5), but these tendencies were more evident during May and August, the months with the lowest and the highest water levels respectively. In Arenosa, the most complex co-occurrence network was observed in May. In contrast to Caño La Piedra, in Arenosa the co-occurrence network observed in August was the simplest with respect to the other months. Considering the two water bodies together, the co-occurrence networks observed during the transitioning phases of falling waters in November and rising waters in July respectively tended to be simple in comparison to the networks observed during May. In Caño La Piedra as well as in Arenosa, the species showed the higher degrees during May, although in the former the species degrees were higher (Fig. 5).

The species with the highest degrees varied between water bodies and across month within them. In Caño La Piedra, during November these were *Caquetaia kraussi* (12), *Pellona flavipinnis* (12) and *Astronotus* sp. (10) and in Arenosa *L. brunneus* (9) and *C. macropomum* (8), (Fig. 4). During March, the species with high degrees in Caño La Piedra were the small bodied *Agamyxis albomaculatus* (25), *Adontosternarchus devenanzi* (23) and *Curimatella incompta* (20), in Arenosa it was the medium sized frugivore piranha *Mylossoma duriventris* (13). The species with high degrees varied again in May, represented by *L. brunneus* (40), *H. steindachneri* (40) and *C. kraussi* (40) in Caño La Piedra and the catfishes *Sorubim lima* (26), *Ageneiosus inermis* (26) and the small curimatid *Cyphocharax spilurus* (24) in Arenosa. During July, the small bodied insectivores *Charax gibbosus* (12), *A. bimaculatus* (12), the herbivorous anostomid *Schizodon heterohabdotus* (10) and the planktivorous catfish *Hypophthalmus marginatus* (8) showed high degrees in Caño La Piedra, whereas in Arenosa these were *P. flavipinnis*, another migratory catfish, *Ageneiosus magoi* and the knife fish *E. virescens*, all with degrees equal to 18. Finally, during August, the species with higher degrees in La Piedra,

**Table 3.** Estimates and p-values from generalized linear models of co-occurrence networks weighted degrees (top) and weighted densities (bottom) explained by water body and by month. Models based on 2760 observations.

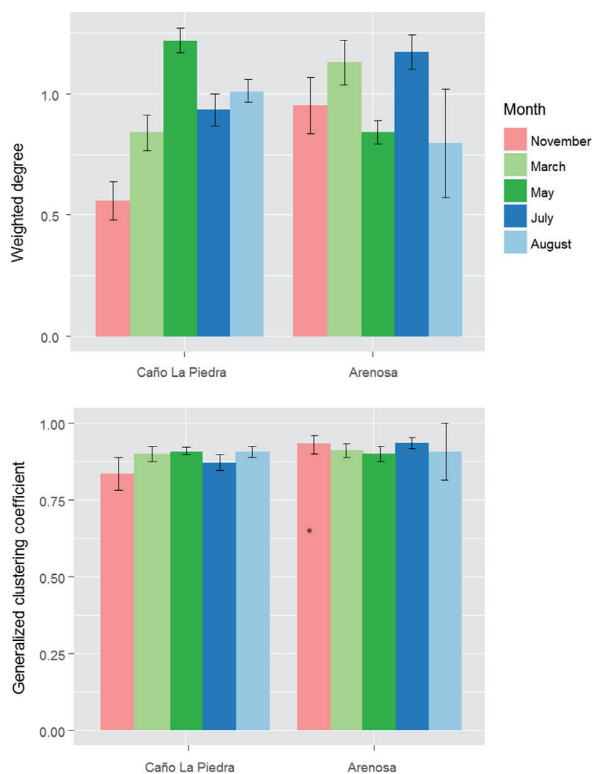
Weighted Degrees		
Water body	$\beta$	P - value
Caño La Piedra	-0.8499	2e-16
Month	$\beta$	P - value
November	1.28401	2e-16
March	0.6103	7.72E-14
May	-0.3525	2.45E-08
July	0.41407	4.94E-08
Generalized local clustering coefficients		
Water body	$\beta$	P - value
Caño La Piedra	-1.18672	2e-16
Month	$\beta$	P - value
November	1.14073	<2e-16
March	0.30823	0.0022
May	-0.89085	<2e-16
July	-0.686	0.4937

all of 18, were the croaker *Plagioscion squamosissimus*, the curito *Hoplosternum littorale*, the loricariid *Pterygoplichthys multiradiatus* and the small bodied *Triporthus orinocensis*, whereas in Arenosa the higher degree was showed by the predator catfish *Pseudoplatystoma metaense* (5), and the other five species showed low degrees, from two to three.

The species with high betweenness also varied spatial and temporally but in a much lesser extent. During November, *P. cariba* (41.25) showed the highest score in Caño La Piedra and *P. multiradiatus* (8.83) in Arenosa. During March, the species with high betweenness was *L. brunneus* in both Caño La Piedra (134.4) and Arenosa (31.01). In May, *P. cariba* was again the species with highest betweenness in Caño La Piedra (114.91) whereas *L. brunneus* (58) was so in Arenosa. In July, *P. cariba* again exhibited the higher betweenness score in Caño La Piedra (41.25) and in Arenosa (49.56). During August, *P. blochii* exhibited the highest betweenness in Caño La Piedra and *M. duriventris* (7) in Arenosa.

Despite the high number of species involved in the co-occurrence networks across the study period, the intersection networks indicated that only three species maintained interactions across months in Caño La Piedra, and therefore are the core of the fish community in that stream. These were represented by the piranhas *Serrasalmus rhombeus* and *Pygocentrus cariba* and the loricariid *Loricariichthys brunneus*. Likewise, two of these species: *L. brunneus* and *P. cariba*, also represent the core of the fish community in the floodplain lake Arenosa.

The model constructed to test the effect of the water bodies and the months on the structure of the co-occurrence networks indicated that both factors influenced the networks at the species level when accounting for the sample size (Table



**Figure 6.** Bar plots of means  $\pm$  SEM of weighted degrees (top) and local clustering coefficients (bottom) per month in the stream Caño La Piedra and the floodplain lake Arenosa.

3, top). The weighted degrees tended to vary across months. The results indicated that, when accounting for the samples sizes, the weighted degrees were higher in Arenosa during November, March and July (Fig 6, top). On the contrary, during May and August Caño La Piedra exhibited higher weighted degrees. The second model indicated a significant effect of the water bodies and also of the months, with the exception of July, on the generalized local clustering coefficients (Table 3, bottom). In general terms, the clustering coefficients were slightly higher in Arenosa in comparison to Caño La Piedra (Fig. 6, bottom), but in both water bodies the coefficients were relatively high across months. In Caño La Piedra, the lowest clustering coefficients were observed during November and July, whereas in Arenosa the lowest values were observed during May and August, although in the latter the standard error was higher in comparison to the other months.

## Discussion

The analysis of temporal patterns of co-occurrence provides a deeper insight of communities as they are highly dynamic systems (Veech 2006). The co-occurrence patterns across water bodies and months floodplain segment of the Arauca River showed that both the stream and the floodplain lake are very dynamic and their fish communities are influenced by the spatial features of their habitats as well as by the temporal variation. Contrary to the first prediction of this study, there were not more segregated pairs of fish species

during the months of low waters either in the stream or in the floodplain lake. In fact, the monthly co-occurrence patterns of fish species were all random in the floodplain lake Arenosa, and only two significantly aggregated patterns were observed in Caño La Piedra. During the months of November and July, when the transitional phases of falling and rising waters take place, respectively, no significantly associated pair of species was observed in any of the water bodies. These results coincide with other researches in that the influence of the biotic interactions on the species co-occurrence patterns is only temporary (Townsend 1989, Arrington et al. 2005) and that it is prone to take place when the hydraulic stress is lower (Thorp et al. 2008), which is most likely why the significantly associated pairs were observed only in the stream during March and May. In tropical floodplains, predation can influence greatly the structure of fish communities during the months of falling and low waters by changing the species abundances and spatial distributions (Winemiller 1996, Petry et al. 2003a, Scarabotti et al. 2011). In contrast, during the transitional phases, the aquatic environment can change rather swiftly, which would increase the influence of stochastic factors. In this respect, our results do not agree with those which have found predominantly segregated patterns of co-occurrence (Connor and Simberloff 1979, Hoeinghaus et al. 2006). The predominantly random patterns that we observed might be the result of stochastic factors driven by the drastic variations in the water level across hydrological seasons, and we can only speculate that possibly also by the influence of predation, whereas the aggregated patterns might reflect similar environmental requirements among species, as indicated by Peres-Neto (2004).

On the other hand, the second prediction of this study stated that there would be more significantly associated species pairs in the stream Caño La Piedra. This pattern was observed in the analysis of the entire period of study as well as in the monthly analyses. However, the number of significant pairs in the latter was negligible in comparison to the randomly associated pairs of fish species, which suggests a considerable neutral element in the assembly of local fish communities in the floodplain of the Arauca River, manifested in a way that the presence of a species in a local community is maintained by a small amount of dispersal and by a reasonable abundance of such species in the meta-community (Hubbel 2001). This pattern likely reflects the high diversity of fish species at the whole floodplain level (Reis et al. 2016) and the influence of habitat connectivity during high waters, which contributes to the incidence of a high number of species, at least temporarily, in the local communities of each water body.

Nevertheless, these results seem to indicate that the co-occurrence patterns of fish species in the floodplain of the Arauca River are also mediated by the characteristics of the habitats as it has been observed in other similar aquatic systems (Arrington and Winemiller 2006). The lack of significantly associated fish species pairs in the floodplain lake Arenosa evidences that the drastic variations in water depth and the consequent hydrological stress impede the establishment of deterministic processes, because the fish communities are not able to reach an equilibrium state (Montaña et al.



2015). On the contrary, the more favorable conditions in the channel of Caño La Piedra favored more pairs of aggregated species.

In Caño La Piedra, the only pair of segregated species was represented by the invertibore knife fish *A. devennanzi* and the small detritivore loricariid *H. steindachneri*. The inspection of the incidence matrices indicated that both species were present in the stream during most sampled months. However, they were never present simultaneously in the same revision, which suggests that these species might be active at different hours of the day, occasioning a pattern of temporal segregation. In the floodplain lake Arenosa, the only segregated pair was represented by the piranha *P. cariba* and the detritivore loricariid *Sturisoma tenuirostris*. The inspection of the incidence matrices indicated that these species were present in the lake during different months, causing a temporal segregation at a longer time scale in comparison to the segregated species observed in Caño La Piedra. Considering the species involved in the segregated pair in Arenosa, this might be the result of a temporal segregation to avoid predation, as it has been observed in other aquatic systems (Jackson et al. 1992; Jackson et al. 2001, Layman and Winemiller 2005, Hoehinghaus et al. 2006). In the floodplain of the Cinaruco River, for instance, the presence of small sized species is influenced by that of top predators such as the peacock bass *Cichla intermedia* (Layman and Winemiller 2005). Our results point towards the influence of top predators such as the piranha *P. cariba* on the distribution of certain prey species, and thus its importance for the ecosystems (Wisz et al. 2013). This is probably a consequence of the high abundances of this species in the area and its constant presence throughout the hydrological cycle.

We did not find evidence of spatial segregation due to interspecific competition (Gotelli 2000). For instance, we failed to observe segregated patterns among the congeners predator catfish species *P. metaense* and *P. orinocoense*. In our study, this species were randomly associated in the two water bodies and across months, even though it has been pointed out that these species occupy distinct positions in the water column (Barbarino and Winemiller 2003). Nevertheless, *P. metaense* was more abundant through the entire period of sampling. The same pattern was observed for the three species of *Ageneiosus*: *A. magoi*, *A. inermis* and *A. ucayalensis*.

As a matter of fact, most significantly associated pairs were aggregated, particularly in Caño La Piedra. Aggregated patterns of co-occurrence in general have been attributed to the species sharing the same habitat affinities and adaptations to environmental conditions (Benedito-Cecilio and Agostinho 1999, Peres-Neto 2004, Bell 2005). This seems to be the case for the aggregated patterns observed in this study, which were composed by a variety of species from diverse trophic guilds. These patterns also reflect the species temporal occupation of the floodplain.

On the other hand, the overall randomness in the co-occurrence patterns of the fish communities across hydrological phases deviates from what has been observed in other systems (Jackson et al. 1992; Arrington et al. 2005). In

this regard, other factors different from biotic interactions, such as stochastic processes of colonization and extinctions (Townsend 1989) might shape the spatial distribution of the species across months, giving way to an organization of the fish communities under mobility control, as it has been found in other tropical floodplains (Arrington and Winemiller 2006, Jackson et al. 2013). In other biotic communities, segregated patterns have been detected and they have been attributed to the effects of predation (Connor and Simberloff 1979). In our study, the species of the fish communities in Caño la Piedra and Arenosa were mainly randomly associated, although one of the segregated pairs could possibly be the result of predator avoidance, indicating that this biotic interaction acts upon the species level and not upon entire communities. These results also highlight the advantage of the pair-wise approach to analyze the co-occurrence patterns of fish communities. This allowed us to identify that there is an important random component in the species associations within the communities. It also showed that deterministic processes may not be the dominant force behind community organization, unlike in other studies where the use of different statistical methods have led to assume that deterministic processes are the main component in the assemblage of fish communities (Rodríguez and Lewis. 1994, Lewis et al. 2000), but at the same time that fish communities are not random associations of species (Petry et al. 2003b).

The third prediction of more complex co-occurrence networks in the stream Caño La Piedra was also met in general terms. This is probably the consequence of higher species abundances and richness in the stream. However, when accounting for sample sizes, the networks were less connected in terms of the species degrees in in the floodplain lake Arenosa during November, March and July. In both water bodies, the networks tended to be more complex during May, when they exhibited more edges, nodes and degrees, but this tendency is lost when the sample sizes are considered, in which case the co-occurrence network of July showed the higher species degrees in Arenosa. In Caño La Piedra the clustering coefficients tended to be lower during November, reflecting the same pattern as the weighted degrees and suggesting a less connected network during that month, whereas during the others most potential connections between species actually took place, indicating more cohesive networks, particularly from May to August. The clustering coefficients in Arenosa indicated that most of the potential connections between species were actually met during November and July. Therefore, even though the number of nodes was lower during November in Arenosa, that network was more cohesive in comparison to the other months. These results show that the co-occurrence networks are influenced by the hydro-geomorphological features of the distinct habitat types, even at very local scales, and also that the structure of these networks can vary according a natural source of disturbance, the seasonal hydrological variation (Widder et al. 2014) across the hydrological cycle. This was also evident in the spatial and temporal replacements of the species that exhibited the highest degrees, demonstrating that these fish communities are highly

dynamic. These replacements may also have caused the high number of randomly associated pairs of species.

In the aquatic habitats of the Arauca floodplain, the co-occurrence networks seem to be affected by the hydrological stability of the water bodies. In that sense, within La Arenosa, the most variable water body in terms of its water depth, the species tended to associate with each other less frequently, as shown by their lower weighted degrees. In contrast, in the channel of Caño La Piedra the species weighted degrees were not only higher, but also there were more species with high degrees. Therefore, and even though the small sample size in terms of the number of water bodies analyzed in this study may represent a shortcoming, these results are consistent with the riverine ecosystem synthesis precept that the biotic interactions are dependent on the habitats characteristics (Thorp et al. 2008). In a similar fashion, the differences in the networks structure across months show the influence of the temporal variation on the incidence of biotic interactions and consequently on the structure fish communities.

In general terms, during November, May, July and August, the species that had higher degrees in both water bodies belonged to two groups: small bodied herbivores – detritivores and top predators, which might reflect the interactions between predators and their prey. During March, when the water level was the lowest, these were represented by small bodied invertivores, frugivores and detritivores, which reflects the seasonal movements of some predators from the floodplains to the main channels during falling waters (Lowe-McConnell 1975) and possibly the effects of predation (Taphorn and Lylestrom 1985, Scarabotti et al. 2011).

In other ecosystems, it has been demonstrated that the structure of co-occurrence networks can be affected by habitat degradation (Mokross et al. 2014). We believe that might have been the case of the low degrees, clustering coefficients, nodes and edges of the co-occurrence network of Arenosa during August. During that sampling period, residual waters were discharged upstream in the channel of Caño La Piedra. This caused an episode of fish mortality that was more intense in Arenosa due to the lack of water flow, therefore decreasing the species richness and abundances in this water body, which was reflected in its co-occurrence network.

The co-occurrence network approach is useful to identify keystone species across ecosystems (Williams et al. 2014). In the floodplain of the Arauca River, three nuclear species were identified through the intersection of the networks of Caño La Piedra and two of Arenosa. These species are the core of the fish communities of their respective habitats and at least two of them, the predator piranha *P. cariba* and the detritivore loricariid *L. brunneus*, contribute to the connection of the networks by having a series of links with less frequent species, as indicated by their betweenness scores. Species that exhibit high betweenness are considered crucial because they hold the ecological networks together and contribute to the transfer of organic matter and energy (Widder et al. 2014). This is evident in the case of these two species. Loricariids such as *L. brunneus* play an important role in the aquatic ecosystems by regulating the amount of sediment and detritus in the benthos

of the water bodies (Flecker 1992), whereas *P. cariba* as a predator, contributes to the regulation of its preys populations (Wiszniewski et al. 2013). Therefore, the removal of any of these species can have serious implications at the community and at the ecosystem level.

Finally, our results highlight the importance of the spatial and environmental variability in the maintenance of fish diversity. In other riverine ecosystems, the hydrological variability controls the co-occurrence patterns of biofilm communities (Widder et al. 2014). We found that this is also the case for the fish communities in the floodplain of Caño La Piedra. The variations in the water level across months in combination with the distinct conditions within the two water bodies mediate the species distribution of the fish communities (Thorp et al. 2008), consequently determining their co-occurrence patterns. This also implies that the species interactions in the fish communities in the floodplain of Caño La Piedra are likewise habitat dependent. Similarly, this study, even though encompasses a small number of water bodies and encompass a local scale, provides the first analysis of co-occurrence networks of Neotropical fish communities. The co-occurrence networks represent a new approach for the study of freshwater fish communities that offers opportunities to make comparisons of composition and structure across ecosystems, levels of integrity and more.

**Acknowledgements:** INSOPESCA granted the scientific fish permits N°404442 and N°455934. The authors wish to thank A. Machado–Allison for facilitating the use of the Laboratory of Ichthyology of the Institute of Tropical Zoology and Ecology of the Central University of Venezuela, C. Rodríguez for his hospitality in Hato Santa Luisa and the staff of this ranch for their invaluable assistance in the field, particularly E. Romero. The funds for this project were given by The Rufford Small Grant and Neotropical Grassland Conservancy. Thanks also to Provita for the administration of the funds and to Idea Wild for the donation of equipment necessary for the samplings. G. Echevarría also wants to thank G. Buitrón–Jurado for his helpful comments for the improvement of this paper.

## References

- Adlte, A. and K.O. Winemiller. 1996. Trophic ecology and ecomorphology of fish assemblages in coastal lakes of Benin, West Africa. *Ecoscience* 4:6–23.
- Amestoy, P., A. Azzalini, T. Badics, G. Benison, A. Bowman, W. Böhm and K. Briggs. 2015. Package “igraph.” CRAN.
- Araújo, M.B., A. Rozenfeld, C. Rahbek and P.A. Marquet. 2011. Using species co-occurrence networks to assess the impacts of climate change. *Ecography* 34:897–908.
- Arrington, D.A. and K.O. Winemiller. 2003. Diel changeover in sandbank fish assemblages in a Neotropical floodplain river. *J. Fish Biol.* 63:442–459.
- Arrington, D. A. and K. O. Winemiller. 2006. Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. *J. North Amer. Benthol. Soc.* 25:126–141.

- Arrington, D.A., K.O. Winemiller and C.A. Layman. 2005. Community assembly at the patch scale in a species rich tropical river. *Oecologia* 144:157–67.
- Barbarino, A. and K.O. Winemiller. 2003. Dietary segregation among large catfishes of the Apure and Arauca Rivers, Venezuela. *J. Fish Biol.* 63:410–427.
- Barrat, A., M. Barthélemy, R. Pastor-Satorras and A. Vespignani. 2004. The architecture of complex weighted networks. *PNAS* 101:3747–3752.
- Bell, G. 2005. The co-distribution of species in relation to the neutral theory of community ecology. *Ecology* 86:1757–1770.
- Benedito-Cecilio, E. and Á.A. Agostinho. 1999. Determination of patterns of ichthyofauna co-occurrence in the Paraná River basin, area of influence of the Itaipu reservoir. *Interciencia* 24:360–365.
- Blasina, G., J. Molina, A. Lopez Cazorla and J. D. Astarloa. 2016. Relationship between ecomorphology and trophic segregation in four closely related sympatric fish species (Teleostei, Sciaenidae). *Comptes Rendus Biologies* 339:498–506.
- Cecilio, E.B., A.A. Agostinho and C.S. Pavanelli. 1997. Colonizacão ictiofaunística do reservatório de Itaipu e áreas adjacentes. *Rev. Bras. Zool.* 14:1–14.
- Céréghino, R., F. Santoul, A. Compin, J. Figuerola and S. Mastrorillo. 2005. Co-occurrence patterns of some small-bodied freshwater fishes in southwestern France: implications for fish conservation and environmental management. *Ambio* 34:440–444.
- Connor, E.F. and D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132–1140.
- Diamond, J. 1975. Assembly rules. In: M. Cody and J. Diamond (eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Mass. pp. 342–444.
- Erős, T., P. Takács, A. Specziár, D. Schmera and P. Sály. 2016. Effect of landscape context on fish metacommunity structuring in stream networks. *Freshwater Biol.* 62:1–14.
- Eschmeyer, W.N., R. Fricke and R. van der Laan (eds). 2016. *Catalog Of Fishes: Genera, Species, References*. (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>). Electronic version accessed in 2017.
- Fernandes, I.M., R. Henriques-Silva, J. Penha, J. Zuanon and P.R. Peres-Neto. 2013. Spatiotemporal dynamics in a seasonal meta-community structure is predictable: the case of floodplain-fish communities. *Ecography* 37:464–475.
- Flecker, A.S. 1992. Fish trophic guilds and the structure of a tropical stream: Weak direct vs. strong indirect effects. *Ecology* 73:927–940.
- Girvan, M. and M.E.J. Newman. 2002. Community structure in social and biological networks. *PNAS USA* 99:7821–7826.
- Gotelli, N.J. and G. Graves. 1996. *Null Models in Ecology*. Smithsonian Institution Press, Washington and London. pp. 358.
- Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621.
- Gotelli, N.J., N.J. Buckley and J.A. Wiens. 1997. Co-occurrence of Australian land birds: Diamond's assembly rules revisited. *Oikos* 80:311–324.
- Gotelli, N.J. and D.J. McCabe. 2002. Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83:2091.
- Griffith, D.M., J.A. Veech and C.J. Marsh. 2016. cooccur: Probabilistic species co-occurrence analysis in R. *J. Stat.Softw.* 69:1–17.
- Hoehinghaus, D.J., K.O. Winemiller and J.S. Birnbaum. 2006. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *J. Biogeogr.* 34:1–15.
- Horner-Devine, M.C., J.M. Silver, M.A. Leibold, B.J.M. Bohannan, R.K. Colwell, J.A. Fuhrman, J.L. Green, C.R. Kuske, J.B.H. Martiny, G. Muyzer, L. Ovreås, A.-L. Reysenbach and V.H. Smith. 2007. A comparison of taxon co-occurrence patterns for macro- and microorganisms. *Ecology* 88:1345–53.
- Hubbell, S. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey.
- Jackson, A.T., A. Adite, K.A. Roach and K.O. Winemiller. 2013. Fish assemblages of an African river floodplain: a test of alternative models of community structure. *Ecol. Freshw. Fish* 22:295–306.
- Jackson, D., P.R. Peres-Neto and J.D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* 58:157–170.
- Jackson, D., K.M. Somers and H.H. Harvey. 1992. Null models and fish communities: evidence of nonrandom patterns. *Amer. Nat.* 139:930–951.
- Jordán, F., T.A. Okey, B. Bauer and S. Libralato. 2008. Identifying important species: Linking structure and function in ecological networks. *Ecol. Model.* 216:75–80.
- Junk, W., P. Bayley and E. Sparks. 1989. The Flood Pulse Concept in River - Floodplain Systems. In: P. Dodge, (ed.), *Proceedings of the International Large Rivers Symposium*. Canadian Special Publications in Fish and Aquatic Science. pp. 110–127.
- Keddy, P. and E. Weiher. 2004. Introduction: The scope and goals of research on assembly rules. In: E. Weiher and P. Keddy (eds.), *Ecological Assembly Rules. Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge, UK. pp. 1–20.
- Layman, C.A. and K.O. Winemiller. 2005. Patterns of habitat segregation among large fishes in a Venezuelan floodplain river. *Neotrop. Ichthyol.* 3:103–109.
- Lewis, W., S. Hamilton, M.A., Lasi, M. Rodríguez and F.J. Saunders. 2000. Ecological Determinism on the Orinoco Floodplain. *BioScience* 50:681–692.
- Lowe-McConnell, R.H. 1975. *Fish Communities in Tropical Freshwaters. Their Distribution, Ecology and Evolution*. Longman Inc., New York.
- MacArthur, R. H. and E. O. Wilson. 1967. *Theory of Island Biogeography*. Princeton University Press, Princeton.
- Mokross, K., T.B. Ryder, M.C. Côrtes, J.D. Wolfe and P.C. Stouffer. 2014. Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *Proc. Royal Soc. B: Biol. Sci.* 281:01–10.
- Montaña, C.G., C. Layman and K.O. Winemiller. 2015. Species-area relationship within benthic habitat patches of a tropical floodplain river: An experimental test. *Austral Ecol.* 40:331–336.
- Moruea-Holme, N., B. Blonder, B. Sandel, B.J. McGill, R.K. Peet, J.E. Ott, C. Violle, B. J. Enquist, P.M. Jorgensen and J.C. Svenning. 2016. A network approach for inferring species associations from co-occurrence data. *Ecography* 39:1–12.
- Mouchet, M.A., M.D.M. Burns, A M. Garcia, J.P. Vieira and D. Mouillot. 2013. Invariant scaling relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos Lagoon estuary (Brazil): Environmental filtering consistently overshadows competitive exclusion. *Oikos* 122:247–257.
- Mouillot, D., O. Dumay and J.A. Tomasini. 2007. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine, Coastal and Shelf Science* 71:443–456.

- Opsahl, T. 2015. *inet. V. 3.0.14. Software for Analysis of Weighted, Two-Mode, and Longitudinal Networks*. CRAN. Available at <http://toreopsahl.com>. United Kingdom.
- Opsahl, T., F. Agneessens, and Skvoretz, J. 2010. Node centrality in weighted networks: Generalizing degree and shortest paths. *Social Networks* 32: 245–251.
- Opsahl, T. and P. Panzarasa. 2009. Clustering in weighted networks. *Social Networks* 31: 155–163. doi:10.1016/j.socnet.2009.02.002
- Pease, A., J.M. Taylor, K.O. Winemiller and R.S. King. 2015. Ecoregional, catchment, and reach-scale environmental factors shape functional-trait structure of stream fish assemblages. *Hydrobiologia* 753:265–283.
- Peres-Neto, P.R. 2004. Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. *Oecologia* 140:352–60.
- Petry, A.C., A.A. Agostinho and L. C. Gomes. 2003a. Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year. *Neotrop. Ichthyol.* 1:111–119.
- Petry, P., P.B. Bayley and D.F. Markle. 2003b. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *J. Fish Biol.* 63:547–579.
- Power, M.E. and W.E. Dietrich. 2002. Food webs in river networks. *Ecol. Res.* 17:451–471.
- Proulx, S.R., D.E.L. Promislow and P.C. Phillips. 2005. Network thinking in ecology and evolution. *Trends Ecol. Evol.* 20:345–353.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Reis, R.E., J.S. Albert, F. Di Dario, M.M.M. Mincarone, P.L. Petry and L.R. Rocha. 2016. Fish Biodiversity and Conservation in South America. *J. Fish Biol.* 89:12–47.
- Rodríguez, M. and W. Lewis. 1994. Regulation and stability in fish assemblages of Neotropical floodplain lakes. *Oecologia* 99:166–180.
- Sampaio, A.L.A., J.P.A. Pagotto and E. Goulart. 2013. Relationships between morphology, diet and spatial distribution: testing the effects of intra and interspecific morphological variations on the patterns of resource use in two Neotropical Cichlids. *Neotrop. Ichthyol.* 11:351–360.
- Scarabotti, P., J. López and M. Pouilly. 2011. Flood pulse and the dynamics of fish assemblage structure from Neotropical floodplain lakes. *Ecol. Freshw. Fish* 20:605–618.
- Stone, L. and A. Roberts. 1992. Competitive exclusion, or species aggregation? An aid in deciding. *Oecologia* 91:419–424.
- Strange, E., P. Moyle and T. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. *Environ. Biol. Fishes* 36:1–15.
- Taphorn, D.C. and C. Lylestrom. 1985. *Revista UNELLEZ de Ciencia y Tecnologia* 3:55–85.
- Team, R.D.C. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Thorp, J.H., M.C. Thoms and M.D. Delong. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Res. App.* 22:123–147.
- Thorp, J., M. Thoms and M. Delong. 2008. Ecological implications of the Riverine Ecosystem Synthesis: Some proposed biocomplexity tenets. In: J. Thorp et al. (ed.). *The Riverine Ecosystem Synthesis*. Elsevier, London, UK. Chapter 6. pp. 103–131.
- Townsend, C. 1989. The patch dynamics concept of stream community ecology. *J. North Amer. Benthol. Soc.* 8:36–50.
- Ulrich, W. and N.J. Gotelli. 2013. Pattern detection in null model analysis. *Oikos* 122:2–18.
- Veech, J. 2006. A probability-based analysis of temporal and spatial co-occurrence in grassland birds. *J. Biogeogr.* 33:2145–2153.
- Veech, J. 2013. A probabilistic model for analyzing species co-occurrence. *Global Ecol. Biogeogr.* 22:252–260.
- Veech, J. 2014. The pairwise approach to analyzing species co-occurrence. *J. Biogeogr.* 41:1029–1035.
- Weiherr, E. and P. Keddy. 2004. Assembly rules as general constraints on community composition. In: E. Weiherr and P. Keddy (eds.), *Ecological Assembly Rules. Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge, UK. pp. 251–271
- Widder, S., K. Besemer, G.A. Singer, S. Ceolae, E. Bertuzzof, C. Quinceg, W.T. Sloang, A. Rinaldof and T.J. Battin. 2014. Fluvial network organization imprints on microbial co-occurrence networks. *Proc. Nat. Acad. Sci. USA* 111:12799–12804.
- Williams, R.J., A. Howe and K.S. Hofmockel. 2014. Demonstrating microbial co-occurrence pattern analyses within and between ecosystems. *Frontiers Microbiol.* 5:1–10.
- Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* 60:331–367.
- Winemiller, K.O. 1996. Dynamic diversity in fish assemblages of tropical rivers. In: M. L. Cody and J. A. Smallwood (eds.). *Long-Term Studies of Vertebrate Communities*. Academic Press, London. pp. 99–134.
- Wisz, M.S., J. Pottier, W.D. Kissling, L. Pellissier, J. Lenoir, C.F. Damgaard, C.F. Dormann, M.C. Forchhammer, J.-A. Grytnes, A. Guisan, R.K. Heikkinen, T.T. Høye, I. Kühn, M. Luoto, L. Maiorano, M.-C. Nilsson, S. Normand, E. Öckinger, N.M. Schmidt, M. Termansen, A. Timmermann, D.A. Wardle, P. Aastrup and J.-C. Svenning. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modeling. *Biol. Rev.* 88:15–30.
- Zaret, T.M. and S. Rand. 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. *Ecology* 52:336–342.

Received March 17, 2017  
 Revised March 31, June 1, 2017  
 Accepted June 2, 2017