

# Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities

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The metacommunity framework has greatly advanced our understanding about the importance of local and regional processes structuring ecological communities. However, information on how metacommunity structure and the relative strengths of their underlying mechanisms change through time is largely lacking. Dynamic systems that undergo environmental temporal changes and disturbances, such as floodplains, serve as natural laboratories to explore how their metacommunity structure change in time. Here we applied the Elements of Metacommunity Structure framework and variation partitioning analysis to assess how temporal changes in the local environmental factors and regional dispersal processes in the rain season influence a seasonal floodplain-fish metacommunity. Across four months, relevant environmental factors were measured across 21 patches where over 3500 individual fish were sampled. Connectivity was measured using landscape resistance-based metrics and additional spatial variation in metacommunity structure was assessed via spatial autocorrelation functions. The metacommunity structure changed from nestedness, at the beginning of the flood season, to a quasi-Clementsian gradient at the end. Our analyses show that connectivity is only important in the beginning of the flood season whereas environment is only important at the end. These results suggest that this metacommunity is structured by changes between dispersal limitation and environmental filtering through time.

Understanding the mechanisms structuring how species from a regional pool assemble into local communities is a major goal of community ecology (Ricklefs 1987, Leibold et al. 2004). Patterns of species coexistence and distribution are affected mainly by two broad classes of factors that differ in the spatial and temporal scales at which they operate (Chase 2003). The first class is commonly referred as the ‘local factors’, such as local environmental conditions that species require in order to maintain a net positive population growth within the community (e.g. soil characteristics, temperature, habitat size) and biotic interactions that range from intraspecific and interspecific competition for local resources up to predator–prey relationships (Chase and Leibold 2003). The second class constitutes the ‘regional factors’, which operate at broader scales and regulate the arrival of organisms into the various local communities. They encompass dispersal filters, that dictate how permeable landscapes are to species movement and their probability of arriving at local communities (Taylor et al. 1993, Kennedy et al. 2011).

The metacommunity framework serves as a way to integrate both sets of factors (Leibold et al. 2004) and to

investigate their relative importance for the distribution of species and their co-existence (Cottenie 2005, Beisner et al. 2006, Peres-Neto et al. 2006). Insights regarding the relative importance of local and regional mechanisms underlying the composition of metacommunities may be obtained by analyzing non-random patterns of multi-species distributions across geographical and/or ecological gradients (e.g. nestedness, Clementsian gradients and others; Leibold and Mikkelsen 2002, Presley et al. 2009, Henriques-Silva et al. 2013). For any given landscape, the structural pattern that best fits a given metacommunity depends on the group of species being studied, as dispersal ability and environmental tolerance vary greatly across taxonomic classes (Presley et al. 2012). Additionally, it has been recently shown that these patterns are consistent and predictable on the basis of regional differences across large spatial extents (Henriques-Silva et al. 2013) and spatial scales (Meynard et al. 2013). Yet, these studies and other traditional analysis of metacommunity structure (Leibold et al. 2004, Presley et al. 2009) view these distributional patterns as static metacommunity properties. However, communities are dynamic, changing in richness and composition

even over very short timescales (Bloch et al. 2007, Azeria and Kolasa 2008).

On one hand, snapshot studies (one single sample in time) have assumed that the relative importance of underlying mechanisms dictating metacommunity structure is stable through time (but see Vanschoenwinkel et al. 2010, Erős et al. 2012). Given that natural systems may show considerable variability in environmental and spatial processes (Vanschoenwinkel et al. 2010, Pandit and Kolasa 2011) on a wide range of temporal scales, community studies based on single snapshots may misrepresent the importance of particular processes or factors, especially when communities are sampled across different periods and/or time scales. On the other hand, most studies analyzing metacommunity structures over time have focused on a single pattern (e.g. nestedness; Azeria and Kolasa 2008, Elmendorf and Harrison 2009) and whether these single patterns are different from random. Unfortunately, this approach may lack power in detecting structure in the sense that if the data do not fit the particular pattern of interest, the metacommunity structure may be interpreted as random whereas alternative non-random structures different from nested (e.g. Clementsian, Gleasonian, checkerboards) may well fit the data.

Hypotheses regarding the temporal stability of metacommunity structure and the relative importance of assembly processes can be tested using natural systems that undergo considerable ecological dynamics in a reasonable timescale, such as inter-tidal, rock-pool, temporary ponds or floodplains systems (McCauley et al. 2008, Fernandes et al. 2010, Vanschoenwinkel et al. 2010). One of the main consequences of perturbations is their effect on population densities, either directly through mortality or indirectly by changing habitat structure and resource availability. Floodplains differ from many temporary systems because they are characterized by temporal perturbations in the form of a recurrent and predictable dry phase dictating seasonal predictable changes in their habitats (Junk et al. 1989), which in turn affect the community structure of a wide range of organisms (Girard et al. 2010). In the wet phase, many terrestrial habitats are transformed into transient aquatic habitats by the expansion of permanent waterbodies (e.g. rivers, lakes) as well as by the local rainfall (Junk et al. 1989). Fish seek refugia in permanent ponds during the dry phase but can then expand their ranges into the temporary habitats, which are essential to feeding, growth and reproduction (Agostinho et al. 2001). Although these temporary waterbodies disappear for the most part during the dry season (seven months – June to December), they present regional persistence for about five months out of the year, thus forming to what we refer as a seasonal metacommunity. As such, these systems also serve as a natural system akin to defaunation experiments to understand the temporal dynamics in metacommunity structure in the good tradition of early experimental studies such as the seminal work of Simberloff and Wilson (1969).

During the beginning of the season, the landscape has a considerable degree of heterogeneity because each temporary habitat patch presents particular physicochemical characteristics, low connectivity and distinct biota that are recruited from nearby permanent ponds (Layman et al.

2010). Later in the flooding period, the ephemeral habitats become much more connected between them and with permanent waterbodies as well. Consequently, the among-habitat variability in limnological characteristics and dispersal limitation are reduced (Thomaz et al. 2007, Layman et al. 2010). In this study we set out to evaluate and quantify the structural changes in a floodplain-fish metacommunity throughout the wet season using the EMS approach (Presley et al. 2010, Henriques-Silva et al. 2013). We also quantified the overall importance of environmental and spatial factors over time as a way to determine how changes in these factors are associated to changes in metacommunity structure. We predict that spatial factors will be more important at the beginning of the wet season due to a lower connectivity and community composition will be highly constrained by dispersal limitation. Later in the wet season, environmental factors should predominate as species should be able to colonize all habitats and environmental filtering will be the main structuring factor. As a consequence, we predict that in the first months of the wet season the fish floodplain metacommunity structure should exhibit a nested structure where species that have low dispersal abilities or lack adaptations to tolerate hypoxic conditions will be present only in the deepest and more connected patches and thus have limited distributional ranges. Moreover, their narrow ranges should represent subsets of the broad-range species that have high dispersal ability (or adaptations against hypoxic conditions) and are found even in shallow or isolated patches. Throughout the wet season, we predict that the metacommunity structure should change from negative turnover (i.e. nested structure) to positive turnover across species ranges (i.e. Gleasonian gradients, Clementsian gradients or Evenly-spaced gradients) as species will be less constrained by dispersal limitation and will be sorted throughout habitats according to their environmental niches. Overall, we show that our results are in line with these expectations.

## Methods

### Field survey

Located in the central portion of South America, the Pantanal is among the largest wetlands on the planet and its ecological dynamics are governed by a predictable monomodal flood pulse (Junk et al. 2006). The water expansion across a highly heterogeneous vegetation creates a high diversity of habitats for aquatic species (Fernandes et al. 2010). For this study, we used the Pantanal Long-Term Sampling Sites (PLTSS) dataset, which span an area of 25 km<sup>2</sup> (56°21'W, 56°18'E, 16°19'N, 16°22'S) and consists of 30 plots (250 × 1 m) that are distributed in a grid format (Fig. 1) and have a minimum distance of 1 km between each other (see Fernandes et al. 2010 for more details). We chose this particular size and shape of plots in order to minimize the variation of elevation within any plot. Within and around the PLTSS there are 26 permanent ponds, ranging from 0.01 to 0.36 ha as well as one lake with approximately 220 ha that act as colonization sources for the plots (Fernandes unpubl.). The fishing gear used in the

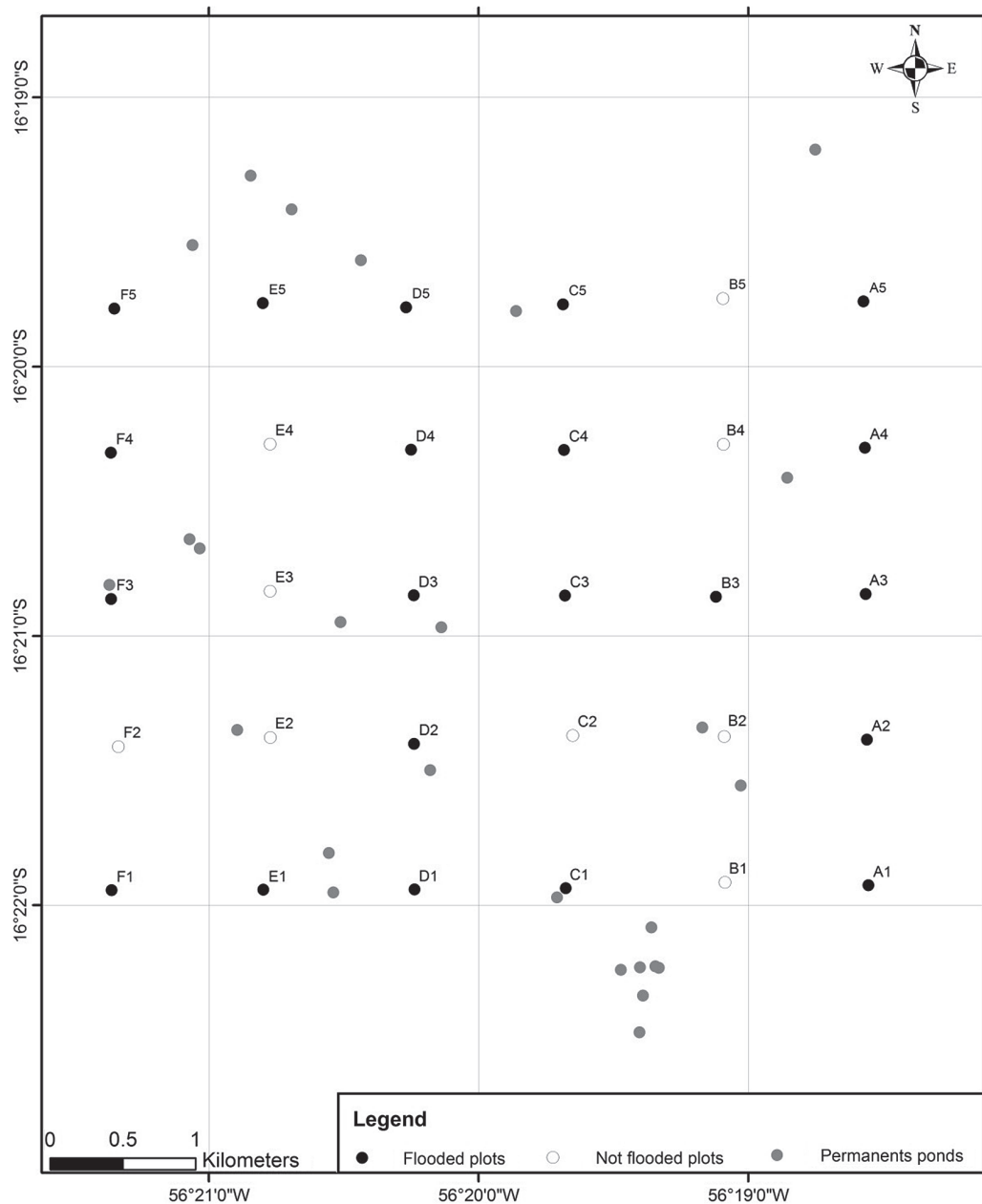


Figure 1. Map of the PLTSS grid. Dark and white circles represent plots that were flooded and not flooded, respectively, in 2009. Grey circles represent the permanent ponds. The code for each plot matches the ones from Fig. 2.

present study are known to efficiently sample strip-like plots such as ours (see Supplementary material Appendix 1 for a detailed description of the sampling protocol) and the distance among plots is large enough for them to be considered as separated fish communities, as the species in the region are mostly small and do not move across sampled plots for activities such as daily foraging. As such, we considered that each plot represented a sample of relatively distinct patches within this seasonal metacommunity. Among these plots, 21 (70%) became temporary aquatic habitats (Fig. 1) during the flood season and were surveyed monthly between January and July 2009. For the present study, we only used the data between January and April 2009 as most patches were dry in the remaining months. We also

considered additional data for the years of 2008, 2010 and 2011 for which a single sample was carried at the peak of the flood period (March). These data were used to assess whether metacommunity structure for this period was consistent across years and thus provided additional support for the temporal pattern uncovered in this study.

### Elements of metacommunity structure

We analyzed the incidence matrix (i.e. species-by-site matrix) of each month (March 2008, January–April 2009, March 2010 and March 2011) using the EMS framework developed by Leibold and Mikkelsen (2002) and improved

by Presley et al. (2010). In short, matrices were ordinated via correspondence analysis (CA) which maximizes the positioning of sites and species along the axes based on the degree to which their communities share similar species compositions and species share similar ranges, respectively. Then, three statistics (i.e. elements), namely coherence, range turnover and range boundary clumping, are evaluated under null models (1000 permutations,  $\alpha = 0.05$ ) that constrain site richness equal to the observed value, which has been shown to have appropriate type I error rates and adequate power (Gotelli and Graves 1996). Finally, the pattern that best fit the data is determined based on the comparison between the observed values of these elements with those obtained from the null matrices which are used to obtain significance values. See Supplementary material Appendix 2 for a detailed description on how the EMS statistics are computed and how results are interpreted. In order to apply the EMS framework, we used a matlab script made available by the authors from Presley et al. (2010) at <http://faculty.tarleton.edu/higgins/metacommunity-structure.html>.

In order to assess the mechanisms underlying species distributions and metacommunity structure we measured and computed a series of predictors that were grouped into three sets: environmental, spatial and connectivity factors. The rationale behind the subdivision between connectivity and spatial variables is explained further below in the 'Spatial factors' section.

## Environmental variables

Elevation, depth, patch age and vegetation cover were measured (see Supplementary material Appendix 1 for details) in each patch (plot) as these variables are known to be highly associated with fish biodiversity in floodplain systems (Crowder and Cooper 1982, Snodgrass et al. 1996, Baber et al. 2002). Elevation normally has a negative relationship with duration and magnitude of the inundation (Girard et al. 2010) whereas the patch age and water depth in temporary aquatic habitats are known to influence fish diversity through the probability of colonization for the former and habitat complexity for the latter (Snodgrass et al. 1996, Baber et al. 2002). Vegetation cover has been shown to be important in temporary aquatic habitats by creating habitat complexity while also influencing water quality (Crowder and Cooper 1982). We measured the percentage of each type of vegetation cover in a 450 m circular buffer around each plot. A principal component analysis (PCA) was applied on vegetation data in order to reduce the number of predictors. The first two PCA axes were used in further statistical analyses as they accounted for most of the variation (61.8%) in vegetation cover among plots (see Supplementary material Appendix 1 for more details). Prior to any statistical analysis, elevation, depth and patch age variables were log-transformed while arcsine transformation was applied to the square root of vegetation cover data in order to improve data normality.

## Connectivity factors

Landscape connectivity is the degree to which the landscape facilitates or precludes movement among patches (Taylor et al. 1993). Connectivity can be measured in different ways

(Prugh 2009) but can be broadly classified into two main classes namely structural and functional. While functional connectivity incorporates specific data about individuals moving in or out of focal patches, or throughout a landscape, structural connectivity measures the spatial arrangement of different types of habitat or patches in a landscape as a proxy of how these features may affect dispersal dynamics (Theobald et al. 2011). For each month, we measured the structural landscape connectivity by applying the '*Ti* metric' (Theobald et al. 2011), which is a modified version of Hanski's (1994) incidence function model:

$$Ti = \sum_{j=1}^n w_{ij} / (d_j \times d_i) \quad (1)$$

where  $w_{ij}$  is the effective distance between patches  $i$  and  $j$ ,  $d_j$  is the depth of patch  $j$ ,  $d_i$  is the depth of patch  $i$ . Lower values of  $Ti$  indicate less isolated (i.e. more connected) sites whereas high values suggest the opposite. Effective distance (least-cost distance) was calculated using information on vegetation cover, water level and elevation. Vegetation cover data was extracted from Google Earth while flood and elevation layers were constructed from the plot data through interpolation using ordinary kriging assuming a spherical model to build the semivariogram (Zimmerman et al. 1999). Effective distance is calculated based on factors that facilitate or restrict fish movement across the landscape as terrestrial areas increase the resistance and movement cost while flooded pristine vegetation increases landscape permeability thereby reducing movement cost. As such, effective distance between two patches represents the minimum cumulative effort (least-cost distance) for a fish to move across the resistance layer (Theobald et al. 2011). In order to create the resistance layer, the vegetation layer was classified by assigning a resistance value (cost) of 1 to wet forest and a value of 2 to wet pasture and wet grassland, while both dry forest and dry pasture received the maximum resistance value (100). We chose these resistance values because larger fish species are likely to avoid open habitats (i.e. wet pastures and wet grasslands) where terrestrial predators are more abundant (Fernandes unpubl.). The depth and elevation layers were reclassified with resistance values ranging from 1 to 10 where higher resistance values were assigned to shallower regions located at higher elevations. After reclassification, the three layers were combined to build the final resistance layer. Given its greater level of accuracy, vegetation data was given a higher weight (0.5) on the final resistance layer while depth and elevation, which were estimated via interpolation (0.4 and 0.1 respectively) were given a lower weight (see Adriaensen et al. 2003 for more details about these methods). All these analytical steps were performed in ArcGIS (ESRI 2006). The least-cost layer was calculated among plots and permanent ponds using the 'costDistance' function of the 'gdistance' package in the R Statistical Software.

Along with the  $Ti$  metric, we also computed two other metrics that account for the influence of potential sources of colonization for each plot: the number of ponds in a 1 km radius (hereafter named pond density) and the distance to the nearest neighboring pond weighted by its area (hereafter named  $NN$ ).



## Spatial factors

We constructed spatial predictors through spatial eigenfunction analysis using Moran's Eigenvector Maps (MEM), which allows representing complex spatial patterns at multiple spatial scales (Peres-Neto and Legendre 2010). We used the 'pcnm' package in the R Statistical Software in order to compute MEM. The procedure resulted in six positively autocorrelated MEM (due to a smaller number of sites in early season) for January and 10 for the remaining months. Note that MEM and other spatial predictors based on geographic positioning may be representing unmeasured environmental factors that are spatially structured (Peres-Neto and Legendre 2010) rather than the signature of dispersal per se (Moritz et al. 2013). If connectivity predictors and MEM represent dispersal processes, the fraction of their shared contribution should be much greater than their fraction of unique contribution in explaining species abundance patterns in variation partitioning analysis (see below). However, if MEM represents unmeasured environmental predictors, then their independent contribution should be relatively greater than their shared one.

## Statistical analyses

We used two complementary statistical analyses to uncover the underlying drivers of metacommunity structure and their relative importance at each month. We first computed Spearman-rank correlations ( $\alpha = 0.05$ ) between each variable from the three sets of predictors (environmental, spatial and connectivity) and the canonical scores extracted from the correspondence analysis used in EMS framework. Secondly, we used variation partitioning (Borcard et al. 1992) to assess the relative contribution of environmental, connectivity ( $Ti$  metric, pond density and  $NN$ ) and spatial predictors (MEMs) on the species distribution matrix at each sampling period. This analysis decomposes the total variation of multi-species distributional tables into shared and unique contributions of these sets of variables. The analysis was based on a redundancy analysis (RDA) on Hellinger-transformed abundance data (Legendre and Gallagher 2001), as it has been shown to provide unbiased estimates in variation partitioning (Peres-Neto et al. 2006). A separate variable selection within each group (i.e. environmental, MEM and connectivity) was performed using the 'forward.sel' function of the 'packfor' library for (Peres-Neto and Legendre 2010). Variable selection was based on a Monte Carlo test based on 1000 permutations and the contribution of each set of predictors was reported using adjusted values based on the number of predictors and sampling sites (Peres-Neto et al. 2006).

## Results

### Elements of metacommunity structure

A total of 3538 individuals distributed across 58 species and 17 families were collected throughout the sampling period in 2009 (Supplementary material Appendix 3). Species richness at the metacommunity level, as well as abundance,

increased throughout the wet season from January (26 species and 460 individuals) to April (50 species and 1631 individuals). During the sampling period, species richness across patches throughout the sampling period varied between 1 and 20 species, with an average value ranging from  $5.11 \pm 4.48$  in January to  $14.09 \pm 5.17$  in April. The average plot depth across months varied between  $15.86 \pm 10.16$  cm and  $26.24 \pm 13.79$  cm. In the peak of the flood period for the other years, a total of 56 species (across 2104 individuals), 49 (887) and 55 (1320) were sampled in March 2008, 2010 and 2011, respectively. The EMS analysis revealed significant changes in the fish floodplain metacommunity structure throughout the four sampling periods of 2009 (Fig. 2, Table 1). At each month, the metacommunity structure was significantly different from random and assigned to a particular pattern according to our early predictions (Introduction). Coherence was statistically significant in all months, indicating that species in general responded to the major gradient of variation (i.e. first CA axis; Supplementary material Appendix 2). In January, the pattern that best characterized the metacommunity structure was nestedness (Table 1, Fig. 2a), with significantly negative range turnover and clumped species loss (Supplementary material Appendix 2). In February, species range turnover was negative but not significant as in the previous month and as a result the metacommunity structure was found to be quasi-nested with clumped species loss (Table 1, Fig. 2b). The clumped species loss pattern suggests that species have common tolerances to the environmental gradient depicted by the correspondence analysis and quasi-structures emerge when the overall range turnover is not distinguishable from randomness and indicate weaker structuring factors than in regular structures (Presley et al. 2010). Finally, the metacommunity structure in both March and April showed positive range turnovers, with a larger value in April; however neither was significant and the pattern that best fitted both months was quasi-Clementsian (Table 1, Fig. 2c, d). For the years in which only the flood peak was sampled (March), the pattern that best fit the metacommunity structure was Clementsian (2008), quasi-nested (2010) and quasi-Clementsian (2011) (Table 1, Fig. 3).

### Relative contribution of structuring factors to species distributions

Variation partitioning indicated that the relative contribution of environmental factors [E] to the variation in species abundances across the metacommunity remained mostly constant, decreasing only slightly in the last month (Table 3, Fig. 4). However, the contribution of spatial factors [S] and connectivity [C] changed through time (Table 3, Fig. 4). In January and February, only environmental factors and connectivity were significant. The unique contribution of environmental factors throughout the season was mainly due to depth and the second vegetation axis PC2 (Table 3, Fig. 4). Connectivity metrics decreased in contribution from 14% of the explained variation in January ( $Ti$  and pond density were selected as significant predictors) down to 4% in April

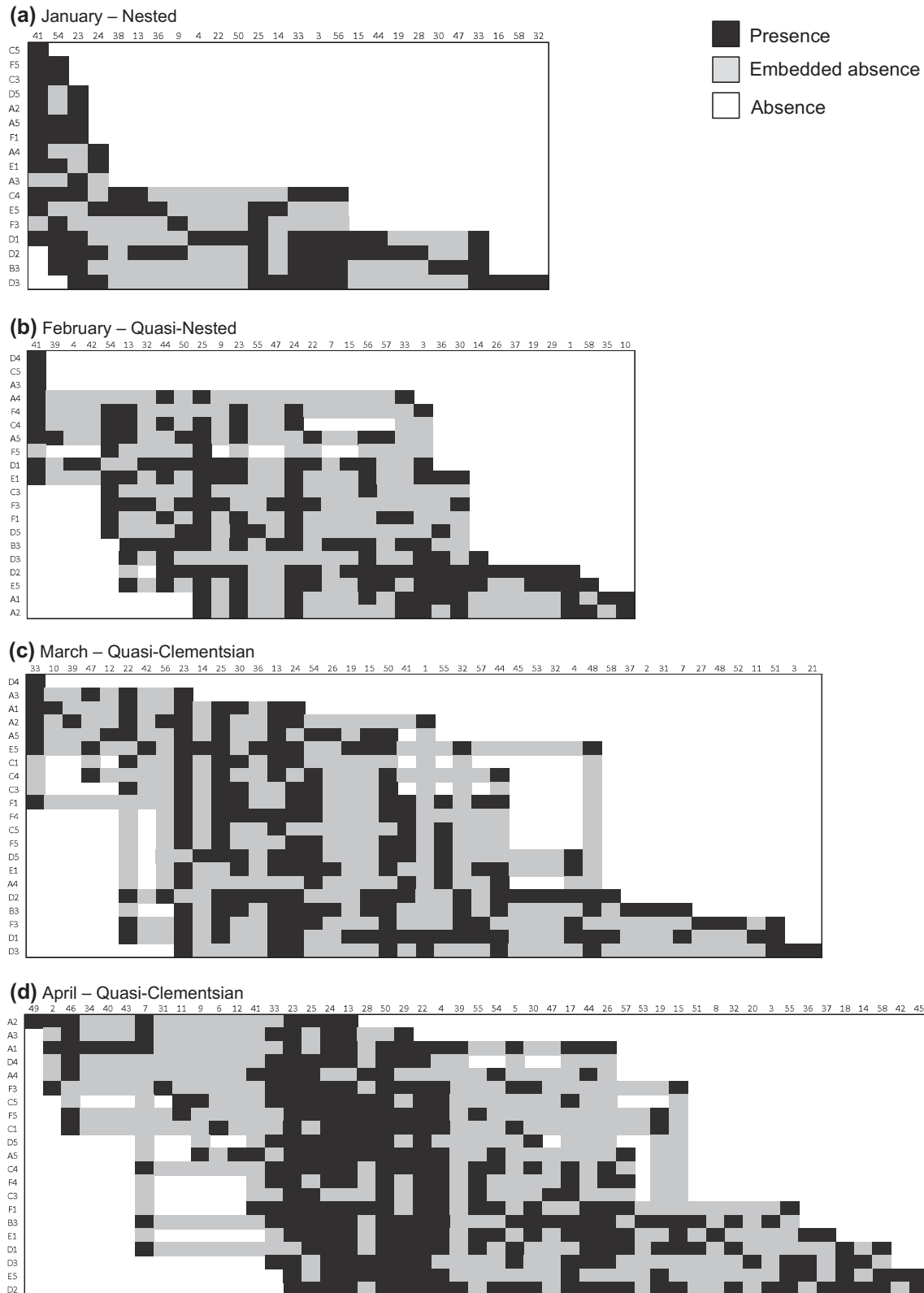


Figure 2. Distributional profiles of species as ordered via analysis of correspondence for (a) January, (b) February, (c) March and (d) April. Species and plots are presented in columns and rows, respectively. See Supplementary material Appendix 3 for species names. Black and white areas represent species presence and absence, respectively while gray areas represent embedded absences within species ranges (Supplementary material Appendix 2).

Table 1. Results for the EMS framework for each month from the wet season in 2009 and for March of 2008, 2010 and 2011. Abs = number of embedded absences, Re = number of replacements, Mo = Morisita index,  $p$  = probability,  $\mu$  = mean value for the null model,  $\sigma$  = standard deviation value for the null distribution. Significant ( $p \leq 0.05$ ) results are bold. Jan = January, Feb = February, Mar = March and Apr = April.

Elements	Parameters	Jan 2009	Feb 2009	Mar 2009	Apr 2009	Mar 2008	Mar 2010	Mar 2011
Coherence	Abs	81	201	287	333	514	323	435
	$p$	<b>0.0253</b>	<b>0.0104</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
	$\mu$	131.29	261.01	415.46	540.93	696.52	405.52	633.90
	$\sigma$	22.48	23.46	25.67	22.33	25.57	23.04	27.99
Range turnover	Re	684	2625	4939	6097	15110	5033	8226
	$p$	<b>&lt;0.0001</b>	0.0944	0.6622	0.2156	<b>&lt;0.0001</b>	0.33	0.30
	$\mu$	1503.44	3690.62	4600.11	5185.50	9577.57	5865.30	7178.49
	$\sigma$	189.59	637.02	775.73	757.85	1429.68	859.78	757.85
Boundary clumping	Mo	2.41	1.68	1.77	1.61	2.07	1.56	1.36
	$p$	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
	Structure	nested	quasi-nested	quasi-Clementsian	quasi-Clementsian	Clementsian	quasi-nested	quasi-Clementsian

(only  $T_i$  was selected as significant). Finally, in March and April, spatial predictors were significant and accounted for 4% (MEM2) and 15% (MEM 1, MEM 6 and MEM10) of the variation in species abundances, respectively.

### Drivers of metacommunity structure

The results from the correlation are fairly similar to those obtained via variation partitioning. The correlation between January canonical scores and depth was extremely high ( $r = -0.81$ ;  $p < 0.001$ ), thus supporting our hypothesis that depth should be one of the main factors influencing the metacommunity structure at the beginning of the wet season. The strength of this correlation decreased somewhat over the following months: February ( $r = -0.67$ ;  $p < 0.001$ ), March ( $r = -0.40$ ;  $p = 0.019$ ) and April ( $r = -0.71$ ;  $p < 0.001$ ), indicating that water depth became less important for metacommunity structure as the season advanced (Table 3). Pond density was significantly related to the main gradient of variation as well in January ( $r = -0.58$ ;  $p = 0.014$ ), March ( $r = -0.52$ ;  $p = 0.015$ ) and April ( $r = -0.49$ ;  $p = 0.023$ ) while the  $T_i$  metric contributed significantly correlations across all months (Table 3). Finally, between one and three MEM were significantly related to the metacommunity's major gradient of variation in March and April, respectively and none in the first two months (Table 3). Overall, the major difference in contrast to the variation partitioning results was the absence of correlation with PC2 (vegetation gradient), suggesting that vegetation is more related to species' abundances rather than their distribution.

## Discussion

### Metacommunity structure

Different metacommunity structures can emerge from the relationship between species distributions and environmental gradients (Presley et al. 2010) and in this study we showed that metacommunity structure may also change over time due to structural changes in their landscapes. Moreover, these structural changes can be related to predictable ecological processes related to the flood regime in this

system, which directly affects the degree of environmental heterogeneity and landscape connectivity (Layman et al. 2010). The floodplain fish metacommunity went from nested to quasi-nested in the beginning of the wet season up to quasi-Clementsian during the peak of the flood. In January, and to a lesser degree in February, the metacommunity was characterized by a hierarchical structure of narrow-range species whose occurrences represented subsets of broadly distributed species (Fig. 2a, b). However, during subsequent months some of the broadly distributed species retreated their ranges (e.g. *Neofundulus parvipinnis*; *Stenolebias damascenoi*; species 41 and 54 on Fig. 2, respectively) while some narrow-range species (e.g. *Hemigrammus tridens*; species 22 on Fig. 2) dispersed across the landscape. This process accounted for the change in range turnover that, as predicted, was negative at the beginning of the wet season but gradually increased through time (Fig. 2; Table 1). Finally, the consistency of significant positive boundary clumping across all months (Table 1) indicates that species might be sharing physiological and/or evolutionary constraints resulting in a shared response to a common environmental gradient (Presley et al. 2010). Indeed, throughout all months the vegetation axis (PC2) was a significant factor explaining fish abundance distribution (Table 2). This axis represents a gradient of vegetation variation from wet grasslands to wet forests (Supplementary material Appendix 1) which associated with the flood regime, creates contrasting habitats that are likely to select different groups of fish species depending on their habitat preferences.

Although changes of species distributions are expected in such dynamic systems, this may not necessarily impose changes to the overall metacommunity structure. For instance, a study performed on terrestrial gastropods within tropical forests that are frequently disturbed by hurricanes and logging activities found that the degree of nestedness changed through time but the pattern, in general, was persistent (Bloch et al. 2007). Nestedness was also found to be temporally stable in invertebrate communities inhabiting rock pools, despite it being a dynamic system with high temporal turnover (Azeria and Kolasa 2008). However, because these studies only considered nestedness, the possibility that other patterns with different structuring

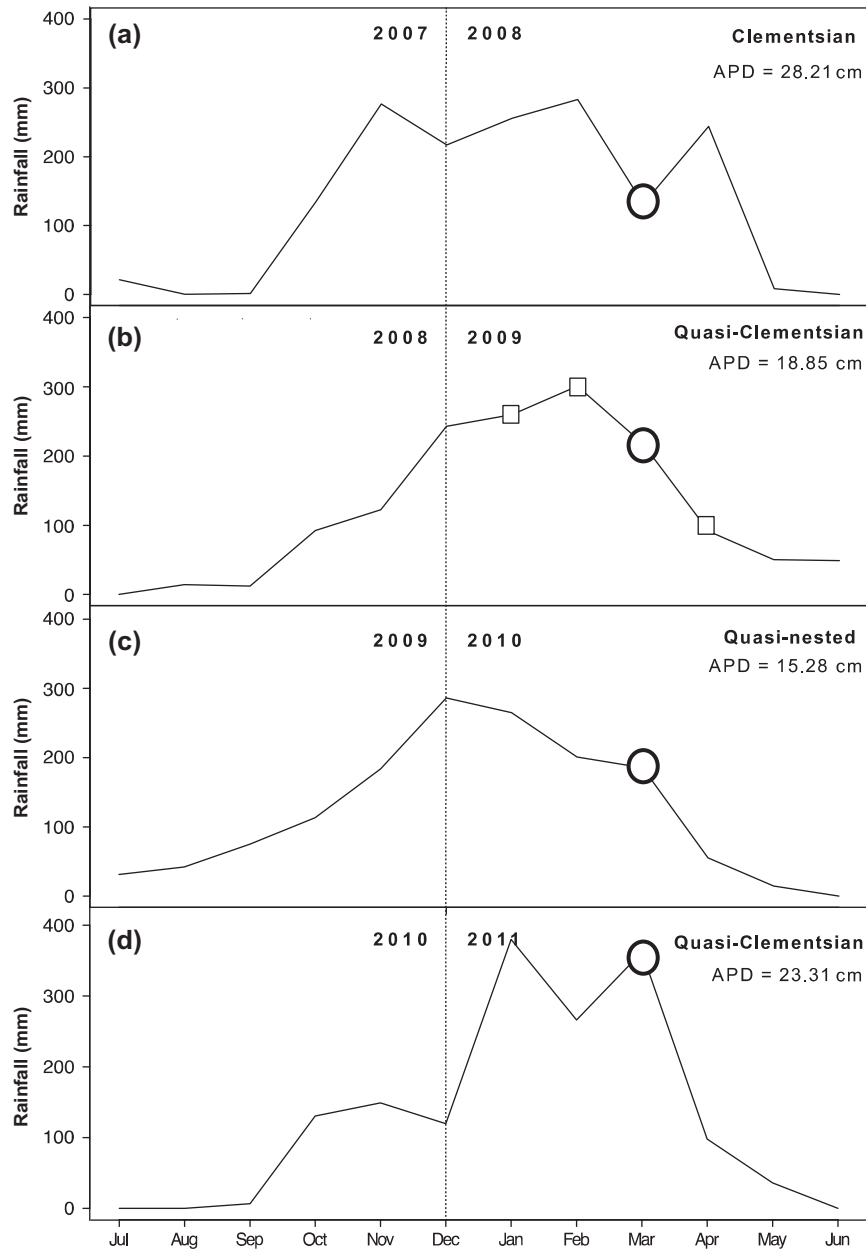


Figure 3. Average monthly rainfall across years from 2007 to 2011. Black circles represent the sampling dates in March. The metacommunity structure found in each year is depicted in the top-right corner. (a) July 2007–June 2008; (b) July 2008–June 2009; (c) July 2009–June 2010; (d) July 2010–June 2011. White squares in (b) indicate the sampling campaigns from January, February and April 2009. APD = average plot depth.

mechanisms could fit even better their data was not considered. Other studies such as Keith et al. (2011) and Newton et al. (2012) applied the EMS technique in order to assess the temporal variability in the structure of English woodland and calcareous grassland metacommunities, respectively. Both studies reported that these plant metacommunities followed a Clementsian structure and, more importantly, that these structures were stable for a relatively long period (i.e. 70 yr). Surprisingly, these results were found despite the fact that significant changes in both local and regional diversity occurred over this period of time, casting doubt on the utility of EMS approach as a broad indicator of conservation status (Keith et al.

2011, Newton et al. 2012). However, metacommunity structures not only depend on species diversity but also on the processes underlying landscape-scale community organization. Although apparently long, 70 yr were probably not enough to account for meaningful temporal variability in the fundamental mechanisms that influence plant metacommunities, which might explain the lack of structural changes. In stark contrast, we were able to detect significant changes in metacommunity structure in an extremely short term because the structural changes in our landscape are massive as these systems go from flooded to dry within a single year. We also applied the EMS analysis using the pooled fish distribution data across all four months and



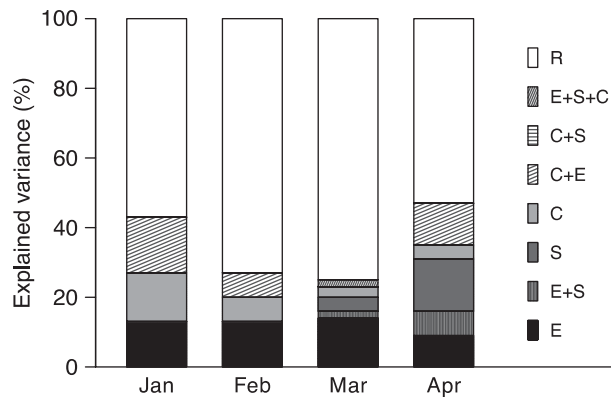


Figure 4. Result of the variation partitioning analysis showing the contribution of environmental factors [E], spatial factors [S] and connectivity [C] to the variation in species abundances across the metacommunity through the four months of 2009 wet season. Components with a + sign indicate the shared contribution of two or more sets of predictors (see also Table 2). Jan = January, Feb = February, Mar = March and Apr = April.

detected a quasi-Clementsian structure. Therefore, if we had not taken into account the temporal dynamics of this system we would have missed a signal suggesting that dispersal limitation is important at the beginning of the wet season.

### Drivers of metacommunity structure

The major distributional gradient in our system was highly correlated with depth and connectivity (Table 3). Spatial factors modeled by MEM, which were non-significant in the beginning of the season, ended up explaining 15% of species variation in the last month (April). In contrast, the connectivity factors were important mostly in January and explained over 14% of the variation in species abundances (Fig. 4, Table 2), decreasing drastically in the subsequent months. Therefore, because the effects of connectivity and MEM contrasted across months, we suspect that the lat-

Table 2. Result of the variation partitioning analysis showing the contribution of environmental factors [E], spatial factors [S] and connectivity [C] to the variation in species abundances across the metacommunity through time. Components with a + sign indicate the shared contribution of two factors (Fig. 2). *Ti* = connectivity metric; Age = patch age; PC2 = 2 axis of the PCA for the vegetation data; Pond. den. = number of ponds in a 1 km buffer around each plot.

Component	January		February		March		April	
	R <sup>2</sup>	p	R <sup>2</sup>	p	R <sup>2</sup>	p	R <sup>2</sup>	p
E	0.13	0.006	0.13	0.001	0.14	0.001	0.09	0.001
E + S	0.0	–	0.0	–	0.02	–	0.07	–
S	0.0	–	0.0	–	0.04	0.026	0.15	0.001
C	0.14	0.002	0.07	0.01	0.03	0.015	0.04	0.001
C + E	0.16	–	0.07	–	0.0	–	0.12	–
C + S	0.0	–	0.0	–	0.0	–	0.0	–
E + S + C	0.0	–	0.0	–	0.02	–	0.0	–
R	0.57	–	0.73	–	0.75	–	0.53	–
Variables selected	Depth [E] PC2 [E] <i>Ti</i> [C] Pond den. [C]		Depth [E] PC2 [E] <i>Ti</i> [C]		Depth [E] PC2 [E] Age [E] <i>Ti</i> [C] MEM2 [S]		Depth [E] PC2 [E] <i>Ti</i> [C] MEM1 [S] MEM6 [S] MEM10 [S]	

ter are not related to dispersal processes. This conclusion is further supported by the fact that the shared contribution between connectivity and MEM [C + S] was null across all months (Fig. 4, Table 3). Therefore, metacommunity variation related to MEM in our study system is likely to represent unmeasured environmental factors that are themselves spatially structured (see Peres-Neto and Legendre 2010 for a discussion on this matter). As such, by adding the fractions explained by environmental factors and spatial eigenvectors [E] + [E + S] + [S] together in March and April, there is a substantial increase in the importance of environment, which accounts for more than 20% (March) and 30% (April) of the variation in species abundances, respectively. This result strengthens our predictions, where

Table 3. Spearman-rank correlation between predictors and canonical scores extracted from the first axis of the correspondence analysis used to ordinate species distribution in the EMS framework. Significant relationships are depicted in bold.

Variables	January 2009		February 2009		March 2009		April 2009	
	r	p	r	p	r	p	r	p
Altitude	<b>0.50</b>	<b>0.018</b>	<b>0.46</b>	<b>0.039</b>	0.14	0.523	0.25	0.266
Depth	<b>–0.81</b>	<b>&lt;0.001</b>	<b>–0.67</b>	<b>0.001</b>	<b>–0.50</b>	<b>0.019</b>	<b>–0.71</b>	<b>&lt;0.001</b>
Age	<b>–0.59</b>	<b>0.012</b>	<b>–0.44</b>	<b>0.052</b>	<b>–0.44</b>	<b>0.042</b>	<b>–0.72</b>	<b>&lt;0.001</b>
PC1	0.32	0.206	0.42	0.065	0.19	0.395	0.35	0.109
PC2	–0.17	0.500	–0.30	0.187	0.28	0.212	0.06	0.784
Pond density	<b>–0.58</b>	<b>0.014</b>	–0.30	0.197	<b>–0.52</b>	<b>0.015</b>	<b>–0.49</b>	<b>0.023</b>
NN	–0.37	0.141	0.10	0.644	<b>–0.55</b>	<b>0.010</b>	–0.35	0.108
Ti metric	<b>0.76</b>	<b>&lt;0.001</b>	<b>0.62</b>	<b>0.003</b>	<b>0.52</b>	<b>0.016</b>	<b>0.75</b>	<b>&lt;0.001</b>
MEM1	0.13	0.59	–0.004	0.984	–0.19	0.398	<b>–0.43</b>	<b>0.047</b>
MEM2	0.31	0.217	–0.03	0.894	0.35	0.109	<b>0.52</b>	<b>0.016</b>
MEM3	0.24	0.352	–0.20	0.389	0.28	0.206	0.35	0.113
MEM4	0.03	0.888	–0.16	0.477	<b>0.44</b>	<b>0.045</b>	0.24	0.282
MEM5	–0.20	0.418	–0.31	0.170	–0.34	0.122	–0.35	0.118
MEM6	0.02	0.936	–0.09	0.676	–0.20	0.361	–0.30	0.172
MEM7	–	–	–0.12	0.599	0.94	0.682	<b>0.43</b>	<b>0.048</b>
MEM8	–	–	0.01	0.959	0.04	0.850	–0.03	0.885
MEM9	–	–	–	–	0.031	0.894	–0.29	0.192
MEM10	–	–	–	–	–0.053	0.819	0.06	0.775

dispersal processes, estimated by connectivity factors, are important at the beginning of the wet season whereas the environment (represented by environmental predictors and MEM) are relevant at the end.

The nested pattern detected at the beginning of the wet season was influenced by a combination of local and regional factors. The importance of local environmental factors on wetland fish communities has been well documented (Baber et al. 2002). Depth and patch age are both positively related to wetland fish diversity, where the former can be viewed as habitat size because a greater water volume may provide more habitat diversity and complexity (Barbour and Brown 1974) while the latter is directly related to an increase in chance that fish disperse and successfully colonize patches through time (Baber et al. 2002, Arrington et al. 2005, Layman et al. 2010). Both factors have been reported to promote nestedness in wetland metacommunities for many taxa (Snodgrass et al. 1996, Baber et al. 2004) and it may be the case in the Pantanal wetland as well. Shallower patches (i.e. lower depth) or the ones that were flooded later (i.e. lower patch age) harbored fewer species than the ones that were flooded earlier or that were deeper. In addition, the species composition of poor-species patches represented subsets of richer sites, creating a nested structure (Fig. 2a). As for regional factors, connectivity or isolation associated with differential abilities among species to disperse have been found to underlie the nested structure in other systems as well (Kodric-Brown and Brown 1993). Indeed, variation partitioning indicated that pond density was only important in January (Table 2), suggesting that proximity to more sources of colonization was an important structuring factor during that month. Due to the low degree of connectivity among patches in the beginning of the rain season, only species with high dispersal abilities or specific adaptations can colonize most patches, while poor dispersers are restricted to dwell in the highly connected or deeper patches. For instance, both *Hoplerhythrinus unitaeniatus* and *Hoplias malabaricus* (species 23 and 24 in Fig. 2; Supplementary material Appendix 2) can tolerate hypoxic conditions by diffusing atmospheric oxygen into their bloodstream through a vascularised swim bladder and also perform overland movements using lateral body undulation (Kramer et al. 1978, Lima-Filho et al. 2012). Such traits may explain why these species have relatively larger distributional ranges during the initial months of the rainy season when most patches are poorly connected and shallow. Others, such as killifishes (i.e. species 38, 41, 53, 54 and 57 in Fig. 2; Supplementary material Appendix 2), have drought-resistant eggs that are deposited in the muddy substrate in the end of the wet season and remain buried during the dry period, waiting for the next wet season to hatch (Wourms 1972). In addition, these species present annual lifecycles, thus their larvae and juveniles have rapid growth rates, which allow them to quickly colonize newly formed habitats and explain their broad distribution in January and February (Fig. 2a, b). Evolutionary strategies that enable persistence or rapid colonization in systems affected by drought are common among fish species (Wourms 1972, Kramer et al. 1978) as well as for others taxa such as zooplankton, algae and macrophytes (Chase

2007). In contrast, species of the tetras lacking any of these adaptations such as *Aphyocharax anisti*, *Hemigrammus tridens* and *Serrapinnus* spp (i.e. species 4, 22 and 50 in Fig. 2; Supplementary material Appendix 2) were restricted to the deepest patches and had much smaller ranges.

During the last half of the wet season quasi-Clementsian structure was the pattern that best fitted the floodplain fish metacommunity. The rise of the water level increases the connectivity across habitat patches, providing opportunities for dispersion and thus reducing dispersal limitation, explaining the decrease in importance of connectivity metrics after January (Table 2). During this period, a highly connected landscape is formed, allowing the expansion of some species (e.g. tetras) ranges throughout March and April. Conversely, some broadly distributed species (e.g. killifish) observed their ranges reduced during these months (Fig. 2c, d), potentially excluded by competitive interactions with late colonizer species (Arrington et al. 2005). Indeed, the killifish, which were responsible for 47 and 36% of the total abundance of fish sampled in January and February, respectively, decreased to about 14 and 4% of the total abundance in the two last months. This process created some degree of turnover among species ranges and changed the pattern from nested to a quasi-Clementsian structure at the metacommunity scale (sensu Presley et al. 2010). A Clementsian structure is found on metacommunities where major suites of species replace each other as groups across space. Such pattern is generally due to joint responses of species to the environmental gradient (Presley et al. 2010). Although ephemeral habitats are more similar in their limnological characteristics during the late wet season, the growth of macrophytes, the vegetation gradient of the landscape and debris increase habitat complexity by creating microhabitats that select for different group of fish species (Arrington et al. 2005, Dibble and Pelicice 2010). If such habitat features are spatially structured they may be captured by the MEM that were found to be important during March and April. Indeed, the highest explained variation from environmental factors was found in April, thus supporting the hypothesis of environmental filtering regulating the floodplain fish metacommunity at the end of the wet season as indicated by the Clementsian structure. Alternatively, competitive interactions can also promote Clementsian pattern if pairs of competing species do not occur independently of each other, rather forming 'clusters of forbidden combinations' (Gilpin and Diamond 1982). However, in order to assess the possible role of competition further research is needed using phylogenetic or trait-based approaches (Ingram and Shruin 2009).

The analysis performed with the additional data from other years (Fig. 3) reinforces our general conclusions based on the 2009 data. In 2008, the year where the average plot depth (APD) was the highest (28.21 cm), the fish metacommunity exhibited a Clementsian structure, indicating that species experienced sufficient opportunity to disperse and consequently select for their preferred habitats, creating the significant range turnover, which was not found in 2009 (APD = 18.85 cm). In contrast, 2010 was the driest year (APD = 15.28 cm), which created limited opportunities for fish to disperse across plots. Consequently, up to March 2010 the fish metacommunity structure was still

quasi-nested while in the other years it had already changed to quasi-Clementsian or Clementsian structure (Fig. 3). These results suggest that the metacommunity structure in fish-floodplain systems is predictable and recurrent across years on the basis of the relative importance of environmental (local) versus connectivity (regional) factors. Indeed, it has been reported that cichlid assemblages in the Pantanal may undergo substantial changes over one season but have a low inter-annual variability (Lourenço et al. 2012) and a similar result was found for fish assemblages in a Venezuelan neotropical floodplain system (Rodriguez and Lewis 1994). One important point that cannot be investigated with our data is whether and how changes in the dynamics of this seasonal metacommunity through time affect the larger regional metacommunity. If dispersal limited species are precluded to expand their ranges due to low connectivity during one year they will not be able to take fully advantage of this temporary resource-rich landscape. This may have long-term consequences to their regional demographics, as they may not be able to grow and/or produce enough individuals to cope with the dry season.

The majority of the species that dwell in this system are small-sized fish (<30 cm; Fernandes unpubl.) and thus rarely perform long distance dispersal (i.e. dispersal distance is known to be correlated with body size in fish; Griffith 2006). Therefore, we consider that the sampling scheme used here was broad enough to encompass the dispersal processes, environmental heterogeneity and biotic interactions underlying the metacommunity structure of our study system. In addition, the findings from this study are not restricted to this system. Temporal variability in environmental and spatial processes is common in probably most ecological systems, as environmental variables changes across many different temporal scales and species tend to respond to these changes. The differences among systems will lie on which temporal scale these processes operate. Therefore, as long as the appropriate temporal and spatial scales are assessed for the particular system of interest, one can evaluate how the relative importance of different underlying factors will influence the metacommunity structure through time.

Finally, our results together with the findings of other studies (see results from Vanschoenwinkel et al. 2010, Erös et al. 2012) emphasize that many ecosystems undergo great temporal variability in the relative contribution of environmental and dispersal processes. In addition, others have found that the relative importance of these two types of processes also depend on the spatial scale (Meynard et al. 2013) and disturbance regimes (McCauley et al. 2008). Together, these findings suggest that the ongoing debate regarding neutral (i.e. spatial) versus niche (i.e. environment) factors for assembly processes (Cottenie 2005, Alonso et al. 2006, Ricklefs 2006) may only be relevant, if at all, for very large spatial scales.

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Supplementary material (Appendix ECOG-00527 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1–3.