Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0388.R1
Manuscript Type:	Article
Date Submitted by the Author:	26-Jan-2017
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Is the invited manuscript for consideration in a Special Issue? :	
Keyword:	temporary ponds, longitudinal gradient, riparian wetlands, hierarchical model, site-occupancy

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Longitudinal variability in lateral hydrologic connectivity shapes fish occurrence in temporary floodplain ponds

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Key-words: temporary ponds, site-occupancy, longitudinal gradient, riparian wetlands, hierarchical model

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1 Abstract

2 Dynamic flow regimes maintain critical connections between main channel and adjacent
3 floodplain habitats that provide fish access to shelter, foraging, and spawning opportunities.
4 Our study advances the understanding of these processes by exploring the importance of
5 coupled longitudinal-lateral connectivity for determining species occurrence in headwater
6 streams of the Amazon. Using a multi-species occupancy model, we revealed a clear pattern
7 of species addition in the downstream direction in temporary floodplain ponds, associated
8 with changes in the pool of potential colonists present in the channel and with increasing
9 lateral hydrologic connectivity. Species that are more tolerant of stagnant waters and those
10 able to disperse in shallow habitats (e.g. *Anablepsoides micropus*) occurred frequently in
11 ponds along the entire longitudinal extent, whereas those species preferring lotic habitats
12 were present only in the most downstream sites. We also observed increasing similarity of
13 pond and channel communities with distance downstream. This study provides insights on
14 the spatial structuring of tropical fish communities in response to flood-induced hydrologic
15 connectivity, and further highlights the vulnerability of floodplain fishes to modification in
16 flooding regimes.

17 **Introduction**

18 Operating in longitudinal, lateral and vertical dimensions, connectivity is a fundamental
19 property of aquatic ecosystems (Ward 1989; Pringle 2003; Freeman et al. 2007). Ecologists
20 have long recognized the importance of these dimensions of aquatic connectivity in shaping
21 the distribution of freshwater fishes (Schlosser 1991). Many fish species have evolved
22 complex life histories, enabling them to colonize and utilize multiple habitats along
23 longitudinal gradients, including those needed during migration (McIntyre et al. 2016).
24 Stream flow provides lateral connections between the main channel and adjacent floodplains,
25 giving fish access to shelter, foraging, spawning and recruitment habitats (Junk et al. 1989;
26 Stoffels et al. 2015). Vertical exchange of surface and groundwater drives temperature and
27 productivity regimes of rivers, affecting the availability of food resources and the growth rate
28 of fish (Mejia et al. 2016). Consequently, there is considerable scientific interest and
29 management relevance in better understanding the ecological effects of multi-dimensional
30 reductions in riverine connectivity due to human activities (Fullerton et al. 2010; Olden et al.
31 2010; Jaeger et al. 2014).

32 Temporary pond habitats maintained by flooding regimes demonstrate marked
33 variability in connectivity in both time and space, yet our understanding of the consequences
34 of such variability for freshwater organisms remains limited (Leigh and Sheldon 2009;
35 Fullerton et al. 2010; Datry et al. 2014). For example, reduced opportunities for colonization
36 and the deterioration of water quality during dry periods are the primary drivers for fish
37 species loss in Australian waterholes (Arthington et al. 2010). Similarly, the persistence of
38 fish populations in spring-fed ponds in Japan was determined primarily by their proximity to
39 the mainstream channel, indicating that habitat accessibility defined by flooding regimes play
40 a fundamental role on shaping fish assemblages (Uchida and Inoue 2010). Other studies
41 conducted in floodplains also support that variation in lateral connectivity through time

42 promoted by floods produce fundamental changes in local fish assemblages (Fernandes et al.
43 2014; Stoffels et al. 2015). These examples highlight the fundamental ecological role of
44 hydrologic connectivity in temporary habitats such as intermittent streams and floodplains.
45 However, issues of spatial and temporal scale (e.g. dynamic of connections and
46 disconnections) and the inevitable limitations in sampling efficiency make the study of
47 habitat connectivity and its role in shaping fish species distribution a challenge.

48 The degree of lateral connectivity varies longitudinally in rivers. Thus, species
49 persistence, and likely meta-population and -community dynamics, may also change
50 predictably with longitudinal position. The flood pulse concept (Junk et al. 1989) predicts
51 that headwater streams are typified by low amplitude and high frequency flooding regimes
52 that are the result of local precipitation events. By contrast, large-river floods result in high-
53 amplitude and low-frequency variations in the water level, being determined by seasonal
54 precipitation regimes in the entire contributing drainage. Despite the recognition that this
55 gradient of flood amplitude and frequency represents a central component of floodplain
56 connectivity (Junk et al. 1989; Tockner and Stanford 2002; Ward 2002), the variation of
57 lateral connectivity along the longitudinal gradient and its implications for fish distributions
58 have received only limited attention. Addressing this issue is not trivial considering that
59 sampling efficiency of many aquatic organisms is affected by the water volume (Bayley and
60 Peterson 2001), which may bias the detection and interpretation of patterns along longitudinal
61 gradients (Gwinn et al. 2015).

62 Our study investigates patterns of fish species occurrence in temporary ponds and the
63 adjacent stream channel in response to longitudinal position in the drainage basin. We
64 explore three main predictions. First, because of longitudinal changes in the pool of species
65 available to colonize ponds from the main channel, we predict that pond occupancy
66 probabilities also vary along the longitudinal gradient. Second, we predict distinct

67 longitudinal patterns in fish occurrence between both habitats (i.e. channel vs ponds). Support
68 for this prediction would suggest that species occurrence in ponds is not merely a reflection
69 of channel occurrence, but also shaped by environmental and connectivity factors that vary
70 with longitudinal position. Third, following a downstream increase in channel-pond
71 hydrologic connectivity, we predict a downstream increase in species similarity of pond and
72 channel habitats. We test these three predictions using fish assemblages in upland headwater
73 streams of the Amazon Basin. Our study employs a hierarchical approach to account for
74 imperfect detection of fish (MacKenzie et al. 2002), as well as its variation among species,
75 habitats and longitudinal positions (Gwinn et al. 2015). By using such an approach we obtain
76 estimates of the probability of species occurrence and offer insights on how flood regimes
77 drive the distribution of freshwater fish species in temporary habitats.

78
79 **Material and methods**

80 **Study system**

81 The study was conducted in a pristine upland rainforest microbasin near “Camp 41” (Fig. 1)
82 of the Biological Dynamics of Forest Fragments Project (BDFFP), 70 km north of Manaus,
83 Amazonas state, Brazil (Bierregaard et al. 2001). The microbasin is part of the Urubu River
84 basin, a tributary of the Amazon River, where localized flooding supports both a permanently
85 flowing main channel and lentic temporary ponds (i.e. without or with negligible water flow)
86 scattered across the riparian floodplain (Wantzen et al. 2008). Ponds are filled by a
87 combination of rainfall, floodwater, and groundwater contributions, which tend to be more
88 frequent during the December–May rainy season (Tomasella et al. 2008; Espírito-Santo et al.
89 2009). Usually, the channel water recedes to pre-flood levels a couple of hours after flooding
90 events (Couto et al. 2015), forming temporary ponds that last from a few days to more than
91 11 months (Pazin et al. 2006). These ponds are typically shallow (1.3 to 35.0 cm deep) and

have small surface area individually (0.3 to 9.1 m²; Pazin et al. 2006), but they can be found in aggregations of up to dozens. The water connection between ponds and the main channel is very dynamic; while some ponds remain completely isolated, others maintain surface water connections with the channel for long periods.

Temporary ponds host a subset of the regional fish fauna composed of small-sized species (adults typically < 10 cm of standard length) that inhabit the channel and perform seasonal movements into ponds once they are formed in the rainy season (Pazin et al. 2006; Espírito-Santo and Zuanon 2016; Espírito-Santo et al. 2017). At least 64 species from 11 families are known to occur in temporary ponds of the Amazon Basin, ranging from killifishes that tolerate transient conditions of water availability to more rheophilic species that are recorded occasionally in ponds connected to the channel (Couto et al. 2015). The occurrence of stream fish species in ponds is partially explained by fish reproductive strategies (Espírito-Santo et al. 2013), but other factors may play a significant role in triggering pond colonization. For example, pond systems in Trinidad, similar to those in our study, are used by a killifish species to avoid predators in the channel (Gilliam & Fraser 2001). Other factors, such as resource availability in flooded areas and preference for slow-flow environments by some species may also be important.

Sampling design

The “Camp 41” microbasin was subdivided into 38 stream segments delimited by stream confluences (sensu Frissell et al. 1986; Fig. 1a); each segment had similar discharge throughout its length and was expected to contain both channel and temporary pond habitats. In two instances, we further divided a stream segment in two in order to ensure comparable segment lengths. We resampled each segment on four visits (i.e. sampling occasions) during the rainy season of 2012, between February 2 and May 17. During each visit we selected one

sampling location per segment at random and with replacement between visits (Fig. 1b; Kendall and White 2009). Each sample spanned a 15-m stretch of stream, located at most 30 meters from the selected location, so as to include, whenever possible, the two types of habitat. We took a total of 152 segment samples (four visits multiplied by 38 segments), of which 124 contained both habitats close enough to the pre-selected location. Only two segments (#13 and #35) had no ponds in any of the visits; the remaining 36 had an average of 3.4 visits containing pond habitats.

Environmental conditions of channel and ponds were assessed during the first and fourth visits to each segment. Water temperature, electric conductivity, dissolved oxygen (DO), and pH were measured in the field in both habitats with a multiparameter probe YSI Pro 1030. When possible, separate measurements were taken for ponds that were and that were not connected to the main channel. Connection is defined here as the presence of at least one surface water link between a pond and the channel. Habitat-specific measurements from different visits to the same segment were treated as independent data points in the construction of longitudinal profiles, since the location of each visit was randomly selected and no temporal change was detected in the data. Mean depth and water velocity were calculated for both channel and isolated ponds based on measurements taken during the fourth visit to each segment. Depth was measured in five equidistant points of the channel section and in the centre of three randomly selected ponds, adjusting a sampling design used by Mendonça et al. (2005) and Pazin et al. (2006). Mean water velocity was measured as the average time that a floating object took to travel one meter replicated three times. Our operational metric of pond connectivity for a given segment was the proportion of visits to that segment in which we found ponds connected to the channel. We adopted the cumulative distance from headwaters as the metric of longitudinal position in all profiles of environmental variables and in the occupancy analysis. This metric was calculated in ArcGIS

10.2 by summing the lengths of all upstream stream segments including the examined segment.

Fish samples of each stream segment were conducted separately for channel and pond habitats. Temporary pond samples involved a 10-minute visual assessment and 60 minutes of hand netting of all available ponds located adjacent to the randomly selected 15-m river stretch. Main channel samples involved 10 minutes of visual assessment, 40 minutes of hand netting and also included a single-pass seining of the 15-m stream stretch delineated by block nets at the upstream and downstream edge. All samples, regardless of habitat, were conducted simultaneously by two observers with field experience in the area. The visual assessments were performed to complement the fish sampling, especially for larger individuals that can be harder to catch using active methods. The two observers were positioned at both ends of the stream stretch, and in the case of ponds, the observers walked separately in the floodplain area searching for ponds and fish. In virtually all cases the species detection by visual assessments were later confirmed by active sampling. The active methods (i.e. fine-meshed hand nets and seine) were operated by both observers in the upstream direction along the 15-m stretch and were standardized by a time limitation that was sufficient to exhaust new catches in each habitat (adapted from Mendonça et al. 2005; Pazin et al. 2006; Espírito-Santo and Zuanon 2016). Approximately 97% of captured individuals were identified to species and released alive at the capture site. The remaining ~3%, which could not be reliably identified in the field were euthanized with Eugenol solution and preserved in 10% formalin for identification in the laboratory. The collected specimens were deposited in the fish collection of the Instituto Nacional de Pesquisas da Amazônia.

Data analysis

Our analysis models occurrence as a probability of site occupancy and examines the relationship between species-specific occupancy and the two site covariates of habitat and longitudinal position. We define a ‘site’ as a local habitat (i.e. channel or ponds) within a given stream segment and a ‘visit’ as one round of sampling to a site. Thus, every segment contains two sites of different habitat with the same longitudinal position. Absence of ponds in a visit was treated as a missing value in the pond-site. In order to estimate site occupancy, we account for the possibility of detection failure by considering that species i may occupy site j but go undetected on visit k (MacKenzie et al. 2002). We model the data from four visits to 74 sites, corresponding to 38 segments multiplied by two habitats minus two pond-sites where ponds were not found in any visit – the two channel sites were maintained. The model has a hierarchical structure that conditions the binary sampling process of species detection on the binary biological process of site occupancy (model diagram available in the online supplementary material, Fig. S1). Specifically, we model the occupancy probability with the logit function:

$$(1) \quad \text{logit}(\psi_{ij}) = u1_i \times C_j + u2_i \times P_j + u3_i \times D_j + u4_i \times C_j \times D_j$$

where ψ_{ij} is the probability that site j is occupied by species i . Covariates C_j and P_j act like dummy variables, with $C_j = 1$ when site j is a channel site and $C_j = 0$ otherwise. Similarly, $P_j = 1$ when site j is in temporary ponds and $P_j = 0$ otherwise. Covariate D_j is a metric of longitudinal position equal to the standardized log of the distance from headwaters of segment j . The product $C_j \times D_j$ codifies the interaction between habitat and longitudinal position. Parameters $u1_i$ and $u2_i$ are intercepts for channel and pond, respectively; $u3_i$ is the effect of longitudinal position and $u4_i$ is the interaction coefficient. The occupancy state of site j for species i is a Bernoulli distributed z_{ij} which equals 1 when the site is occupied and 0

189 when not. When $z_{ij} = 1$, the probability p_{ijk} of species detection at that site during visit k
190 follows the function:

191 (2) $\text{logit}(p_{ijk}) = v1_i \times C_j + v2_i \times P_j + v3_i \times C_j \times D_j$

192 where $v1_i$, $v2_i$ and $v3_i$ are detection coefficients, analogue to those of the occupancy
193 function. By including $v3_i$, the coefficient of interaction between channel and distance,
194 without the corresponding distance effect, we assume that detection varies with longitudinal
195 position only in the channel. The assumption that detection is constant in ponds along the
196 longitudinal gradient is based on the observation of very limited longitudinal variation in
197 depth and area of individual ponds. The estimation of both occupancy and detection
198 parameters for a given species requires data with species detections in both channel and
199 ponds; therefore, our analysis included only species that had at least two detections per
200 habitat.

201 Although we estimate different coefficients for every species, we also share
202 information across species by treating every u and v parameter as a random effect (Dorazio
203 and Royle 2005; Dorazio et al. 2006). This allows for joint inference about the set of all
204 species in the analysis, based on ‘hyper-parameter’ means ($\mu u1, \mu u2, \mu u3, \mu u4, \mu v1, \mu v2$
205 and $\mu v3$) and standard deviations ($\sigma u1, \sigma u2, \sigma u3, \sigma u4, \sigma v1, \sigma v2$ and $\sigma v3$) of the normally
206 distributed random effects (Zipkin et al. 2009). To infer assemblage-wide differences
207 between habitats, we computed a Sorensen index of similarity between channel and pond
208 sites of the same segment based on the imputed “true” occupancy state (z_{ij}) for all species i
209 and site j . Similarly, by summing z_{ij} values across species, we obtained estimates of the
210 expected number of species occurring at each site. Inference based on z_{ij} values afforded the
211 opportunity to evaluate similarity and number of species in different positions along the
212 longitudinal gradient. We fit our model to data in a Bayesian framework using a Markov

Chain Monte Carlo (MCMC) algorithm implemented with the freely available software JAGS 4.2.0 (Plummer 2003) in connection with R 3.3.1 (R Development Core Team 2016) through the “rjags” package (Plummer 2016). We used non-informative normal and gamma priors, respectively, for mean and standard deviation hyper-parameters (code available in Fig. S1). Posterior summaries were based on three chains with 72,000 iterations per chain, with a burn-in of 27,000 iterations and thinning of five. We tested the convergence of chains with Gelman and Rubin’s convergence diagnostics (Gelman and Rubin 1992).

Results

Connectivity between the main channel and floodplain ponds increased with distance downstream, whereas little longitudinal variation in other pond environmental variables was detected (Fig. 2). Connected ponds were more frequently found in the most downstream segments (Fig. 2a). Stream channel waters were warm (mean of 24.7° C and 95% confidence intervals: 23.6-25.6), moderately acidic (pH = 4.9: 4.7-6.0), oxygenated (5.9 mg/L: 4.9-7.2) and with low conductivities (8.3 µS/cm: 6.3-10.9). By contrast, isolated pond waters were more acidic (pH = 4.4: 2.9-4.9), less oxygenated (1.9 mg/L: 0.9-3.3), and had higher conductivities (12.8 µS/cm: 8.6-18.7). Ponds connected to the channel had intermediate levels of DO (3.0 mg/L: 0.9-6.0), pH (4.9: 4.6: 6.4), and conductivity (11.5 µS/cm: 7.0-21.8), indicating the influence of waters from the main channel. Water temperatures in isolated and connected ponds (24.6° C: 23.5-25.5) were quite similar to channel temperatures. There was little evidence of downstream trends in water characteristics for both isolated and connected ponds. The concentrations of dissolved oxygen, for example, were much higher in the channel than in isolated ponds, but with no clear longitudinal variation (Fig. 2b). Water velocities and depth increased with the longitudinal position in the channel, but did not vary

in ponds (Figs. 2c and 2d). Water temperature, DO, pH, and conductivity did not vary along the longitudinal gradient in any habitat.

Fish surveys resulted in the detection of 39 species, of which 16 were captured only in channel habitats and two captured only in temporary ponds (see Table S1). Eighteen species were detected at least twice in both habitats and were included in the hierarchical occupancy model. Eighteen out of the 23 species captured in pond habitats had more detections in connected than in isolated ponds. The only exception was the killifish *Anablepsoides micropus*, which had more than twice as many detections in isolated than in connected ponds. The species *Aequidens pallidus*, *Hyphessobrycon agulha*, *Hyphessobrycon* aff. *melazonatus*, *Nemuroglanis pauciradiatus*, *Helogenes marmoratus* and *Ancistrus* aff. *hoplogenyis* were only captured in connected ponds, with the last three only found very close to the channel. The vast majority of individuals of *A. pallidus*, *Callichthys callichthys*, *Erythrinus erythrinus* and *Hoplias malabaricus* captured in pond habitats were juveniles. Additionally, young of the year of *A. pallidus*, *C. callichthys*, *E. erythrinus*, *Hemigrammus* cf. *pretoensis*, *H. malabaricus*, *H. aff. melazonatus* and *Megalechis picta* were captured in ponds.

Site occupancy increased downstream for all 18 species (Fig. 3), as shown by the positive values of $u3_i$ for every species i and by the positive value of the hyper-parameter $\mu u3 = 1.74 \pm 0.34$ (mean $\pm$ standard deviation; Table 1). On average, site occupancy was two times higher in the channel than in ponds, represented by a positive difference between hyper-parameters $\mu u1 - \mu u2 = 3.90 \pm 1.17$, as well as by a positive difference $u1_i - u2_i$ for every species i (Table 1). This finding includes not only species that are rarely detected in ponds like *H. agulha* and *H. marmoratus*, but also pond-specialists like *A. micropus* and *Pyrrhulina* cf. *brevis*. Overall, site occupancy probability increases downstream at a faster rate in channel habitats than in ponds (Fig. 3; $\mu u4 = 1.07 \pm 0.71$), but no strong interaction

was identified for individual species. All 18 species had positive occupancy interaction coefficients u_{4i} , but the 95% credible intervals overlapped zero in all cases (Table 1).

In contrast to the occupancy part of the model, the average interaction between longitudinal position and habitat was moderately negative ($\mu v_3 = -0.19 \pm 0.23$). This is caused by a strong pattern of downstream decrease in detection probability in the channel that can be observed in the negative v_{3i} coefficients for five species (Fig. 4; Table 1). Conversely, detection probability of the two species of the genus *Hyphessobrycon* increases steeply in the most downstream channel sites (Fig. 4; Table 1). On average, detection probability is similar between channel and ponds ($\mu v_1 - \mu v_2 = -0.27 \pm 0.55$), but the difference is highly variable among species (Table 1). Six species had positive values of $v_1 - v_2$ with 95% credible intervals not overlapping zero, indicating markedly higher detection in ponds. They are *A. micropus*, *Apistogramma hippolytae*, *Copella nigrofasciata*, *E. erythrinus*, *Microcharacidium cf. weitzmani* and *P. cf. brevis*. Only *H. marmoratus* and *H. cf. pretoensis* are significantly more detectable in the channel.

Species composition in the main channel and ponds became increasingly similar downstream (Fig. 5a). The most upstream ponds are occupied by fewer species (Fig. 5b), consisting predominantly of the pond-specialist killifish *A. micropus* but also the pencilfish *P. cf. brevis* and a small number of other species (Fig. 3). Species richness of ponds gradually increased downstream (Fig. 5b), as species that rely on high connectivity were added (e.g. *H. aff. melazonatus*, *H. agulha*, *M. cf. weitzmani* and *N. pauciradiatus*; Fig. 3). A similar pattern of downstream increase in the number of species was observed in the channel (Fig. 5b), but species addition tended to be more pronounced in the most upstream segments when compared to ponds. The most upstream channel segments are also occupied by *A. micropus* and *P. cf. brevis*, but other species like *E. erythrinus*, *H. cf. pretoensis*, *Gymnotus coropinae*, *Gymnotus sp.1*, *H. marmoratus*, *A. pallidus* and *Nannostomus marginatus* were rapidly added

by moving downstream (Fig. 3). In general, site-occupancy probabilities in the same longitudinal position tended to be higher in the channel than in ponds (Fig. 3), but this difference narrowed in a downstream direction, leading to an increase in species similarity (Fig. 5a).

Discussion

This study supports that lateral hydrologic connectivity varies longitudinally and is a fundamental determinant of fish assemblage composition in temporary pond habitats. We found that species occurrence in ponds changed with longitudinal position, but did so differently when compared to main channel habitats, resulting in species composition becoming increasingly similar between pond and channels moving downstream. Thus, species composition in ponds was not independent from the immediate source of available colonists present in the main channel, but slight differences in longitudinal trends between habitats highlight the role of both dispersal barriers and local environmental filtering at the pond scale. Increasing magnitude of floods in the downstream direction can create additional opportunities for colonization and establishment of more species, which lead to a steady increase in assemblage similarity between pond and channel habitats. Taken together, our results contribute to a better understanding of the role of spatial variation in lateral connectivity in shaping the composition of fish assemblages in floodplain habitats.

The consistently lower occupancy probabilities in temporary ponds are driven, in part, by the periodic drying of these habitats and their dependence on colonists from the main channel. The importance of channel colonists is also supported by the pattern of seasonal differences in species composition and counts in both habitats, where directional movement by fish to the ponds is evident in the rainy season (Espírito-Santo et al. 2009, 2013; Espírito-Santo and Zuanon 2016). Although recent studies have highlighted how spatial and temporal

changes in hydrologic connectivity determine community assembly in floodplains (Fernandes et al. 2014; Stoffels et al. 2015), the role played by the longitudinal variation in the pool of potential colonizers present in the channel is rarely appreciated. This is particularly relevant given that the effect of longitudinal gradients in fish species composition is a global phenomenon (Jackson et al. 2001; Ibañez et al. 2009). In addition, after the primary role of the pool of colonizers, barriers to dispersal and environmental filters are typically the determinants of community composition (Cornell and Harrison 2014). Indeed, habitat characteristics have been reported to be a major driver of community assembly in floodplain waterbodies (Rodríguez and Lewis 1997; Winemiller et al. 2000; Pazin et al. 2006). Thus, other abiotic and biotic conditions of ponds that vary with longitudinal position will play an important moderating role in shaping fish assemblage composition.

Our study suggests that hydrologic connectivity of ponds, in the absence of clear longitudinal changes in depth, flow, and water characteristics, best explains the downstream increase in species occurrence. Other studies in analogous systems support structural connectivity as a primary determinant of the richness and composition of fish assemblages (Arthington et al. 2010; Uchida and Inoue 2010; Fernandes et al. 2014; Stoffels et al. 2015). In addition, water permanence and volume have been reported to affect fish species composition of temporary ponds in Amazonian streams (Pazin et al. 2006; Espírito-Santo and Zuanon 2016). Considering that the magnitude of floods and the alluvial area increases downstream (Ward et al. 2002; Barker et al. 2009), longitudinal differences in number, permanence, and connectivity of ponds are expected.

We suggest that upstream floodplains are characterized by a small number of ephemeral and isolated ponds, whereas the number and connectedness of ponds increase rapidly in the downstream direction. This increase in the hydrologic connectivity in ponds creates conditions for the colonization and establishment of more species in the ponds of

downstream segments. The faster downstream addition of species in the channel than in ponds indicates that low hydrologic connectivity can limit the colonization and establishment of some species in the most upstream pond habitats, in agreement with some species' natural history traits. For example, in contrast to all other species, the killifish *A. micropus* was predominantly found in ponds across the entire longitudinal extent of the study. *A. micropus* is the only species able to move actively outside the water and survive days in ponds that are virtually dry (Couto et al. 2015; Turko & Wright 2015). These adaptations provide remarkable advantages for the species to occur in the most upstream pond systems that are ephemeral and more rapidly disconnected from the main channel. Anecdotally, the considerable higher number of detections of *A. micropus* in isolated ponds also suggests a preference for this kind of insulated habitat even in the most downstream sites, where it was generally captured in small isolated ponds in the boundaries of alluvial areas. This pattern is likely shaped, at least in part, by active predator avoidance; a phenomenon also observed for other rivulids in the Pantanal (Fernandes et al. 2014).

Progressing downstream, we found that pond systems became more likely to support species with more strict requirements for perennial water. For example, although the cichlids *A. pallidus* and *A. hippolytae* are frequently found in lentic and low oxygenated waterbodies, they depend on surface water connectivity to colonize these habitats. Other species like the tetra *H. aff. melazonatus* and the South American darter *M. cf. weitzmani* are less tolerant to hypoxic waters, depending on higher rates of water exchange with the main channel. Our occupancy estimates reveal that these species are unlikely to occur in ponds located in first-order streams, but tend to be present in the most downstream pond sites. In an equivalent system of Amazon riparian floodplains, a similar gradient of species addition was reported to be correlated with hydrological attributes of individual ponds such as surface area and water permanence (Pazin et al. 2006). Although more mobile and tolerant species occur in smaller

and more ephemeral ponds (e.g. *A. micropus*), other species are added to larger and more stable ponds present at the same site. In summary, downstream increases in the magnitude of floods and alluvial areas explain the greater frequency of connected ponds and the more diverse, and similar to the main channel, fish assemblages that they support.

We also observed variation in species detection between habitats and along the longitudinal gradient, which can be attributed to changes in sampling efficiency, and changes in species abundance. It is reasonable to expect that fish sampling efficiency may decrease with increasing water volume due to a dilution effect (Bayley and Peterson 2001; Falke et al. 2010; Gwinn et al. 2015). This would explain, at least in part, why the detection probability of five species decreases considerably downstream in the channel. Additionally, the probability of detection may be directly related to the abundance of a given species (Royle and Nichols 2003). Changes in abundance could explain why the congeneric tetras *H. aff. melazonatus* and *H. agulha* are more detectable downstream in the channel. Both species form schools that are likely to become larger downstream. Remarkably, the killifish *A. micropus* is much more detectable in ponds than in the channel, most likely as a result of abundance patterns. Some studies suggest that rivulids tend to have higher densities in shallower waters as a result of predator avoidance behavior (Gilliam & Fraser 2001; Fernandes et al. 2014). *Anablepsoides micropus* was caught in considerable higher numbers in ponds and just few individuals were captured in the most downstream channel sites, perhaps as a response to longitudinal changes in predation risk (Power 1984).

In conclusion, our study provides insight into the importance of coupled longitudinal-lateral connectivity in shaping fish assemblages of stream-floodplain systems. Our results show a clear longitudinal trend of species addition in temporary pond habitats, which is associated with variation in the availability of fish colonists in the adjacent main channel habitats and with longitudinal changes in hydrologic connectivity. Although our study

focused on headwater streams, we provide empirical evidence that fish assemblages respond predictably to longitudinal variation in floodplain connectivity (Junk et al. 1989). This emphasizes the importance of the channel on sustaining aquatic communities in temporary floodplain systems, and highlights the spatial dependence of such relationship. Therefore, modifications in the dynamics of floods (e.g. climate change and flow control) that exceedingly enhance or reduce hydrologic connectivity have the potential of promoting changes in community assembly not only in local floodplain habitats, but also in the entire basins. A novel approach to understanding the interface between river channels and floodplains as a complex spatial-temporal outcome of flooding waves has been recently proposed (Humphries et al. 2014). This framework will likely guide future research examining the relationship between lateral connectivity and freshwater communities, and its variation through space and time.

Acknowledgements

The authors thank Ocírio Pereira, Osmaildo da Silva, Alaércio dos Reis, Francisco Diniz and the BDFFP logistics team for help during fieldwork. Marc Kéry, Henrique Giacomini, Murilo Dias, Helder Espírito-Santo and two anonymous reviewers provided valuable suggestions to the manuscript. This study was carried out under permits by ICMBio (10199-1/2007) and by the INPA Animal Use Ethics Committee (CEUA/INPA, 014/2013). The Brazilian CNPq provided financial support in the form of research grants, TBAC's MSc scholarship, and GF's (#312606/2013-3) and JZ's (#313183/2014-7) productivity grant. This is contribution #710 of the BDFFP Technical Series and #48 of the Igarapés Project.

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Table 1. Hyper- and species-specific parameters estimated with data from 18 fish species. Values in the parentheses are 95% credible intervals for parameter estimates. Parameters $\mu u1-4$ and $u1-4$ describe longitudinal variation in occupancy, while parameters $\mu v1-3$ and $v1-3$ do so for detection. Extreme variation in these parameters is highlighted in bold, whenever the credible intervals do not overlap zero.

Hyper-parameters	$\mu u1$	$\mu u2$	$\mu u3$	$\mu u4$	$\mu v1$	$\mu v2$	$\mu v3$
	3.9 (2.1, 6.1)	0.0 (-1.2, 1.3)	1.7 (1.1, 2.5)	1.1 (-0.2, 2.6)	-1.4 (-2.0, -0.7)	-1.1 (-2.0, -0.3)	-0.2 (-0.6, 0.3)
Species	$u1$	$u2$	$u3$	$u4$	$v1$	$v2$	$v3$
<i>Aequidens pallidus</i>	3.3 (1.5, 5.8)	-1.3 (-3.2, 1.1)	1.9 (1.0, 3.2)	1.4 (-0.2, 3.3)	-0.4 (-0.9, 0.1)	-1.3 (-2.5, -0.1)	-0.2 (-0.7, 0.3)
<i>Anablepsoides micropus</i>	5.2 (2.9, 8.9)	4.4 (2.2, 8.0)	1.3 (0.0, 2.4)	0.5 (-1.7, 2.5)	-0.3 (-0.7, 0.1)	3.0 (2.2, 4.0)	-1.7 (-2.3, -1.2)
<i>Apistogramma hippolytae</i>	4.1 (1.9, 7.1)	-0.4 (-1.4, 0.8)	1.8 (1.0, 2.7)	1.0 (-0.8, 2.8)	-1.2 (-1.7, -0.8)	0.0 (-0.7, 0.6)	-0.3 (-0.8, 0.2)
<i>Copella nigrofasciata</i>	3.1 (-1.5, 6.6)	-1.5 (-2.7, -0.4)	1.9 (1.0, 2.9)	1.2 (-0.7, 3.3)	-3.0 (-4.1, -1.4)	0.3 (-0.4, 1.1)	0.8 (-0.3, 1.7)
<i>Erythrinus erythrinus</i>	4.5 (2.6, 7.0)	0.6 (-0.5, 2.0)	2.0 (1.1, 3.1)	1.1 (-0.6, 2.9)	-1.2 (-1.6, -0.8)	-0.3 (-0.9, 0.2)	-0.9 (-1.4, -0.4)
<i>Gymnotus coropinae</i>	4.0 (2.1, 6.4)	0.8 (-2.5, 5.8)	1.7 (0.7, 2.9)	1.4 (-0.3, 3.3)	-1.3 (-1.8, -0.8)	-2.6 (-3.9, -1.2)	-0.5 (-1.0, 0.1)
<i>Gymnotus</i> sp.1	4.6 (1.9, 8.2)	-1.0 (-3.6, 2.7)	1.7 (0.6, 2.7)	0.7 (-1.5, 2.6)	-3.5 (-4.5, -2.6)	-2.4 (-3.9, -0.8)	-0.9 (-1.8, 0.0)
<i>Helogenes marmoratus</i>	3.7 (1.8, 6.0)	0.6 (-2.8, 5.0)	1.8 (0.7, 3.1)	1.3 (-0.3, 3.2)	-0.5 (-0.9, 0.0)	-3.2 (-4.7, -1.5)	-0.8 (-1.3, -0.3)
<i>Hemigrammus</i> cf. <i>pretoensis</i>	4.5 (2.5, 7.0)	1.3 (-0.5, 4.0)	1.8 (0.8, 2.9)	1.0 (-0.6, 2.9)	0.0 (-0.4, 0.4)	-1.4 (-2.0, -0.7)	-0.8 (-1.3, -0.4)
<i>Hoplias malabaricus</i>	3.3 (-1.0, 6.7)	-1.6 (-4.0, 1.6)	2.0 (1.0, 3.2)	1.2 (-0.8, 3.3)	-2.9 (-4.0, -1.5)	-2.0 (-3.4, -0.7)	0.7 (-0.3, 1.5)
<i>Hyphessobrycon agulha</i>	3.9 (0.2, 7.4)	-1.4 (-4.4, 2.5)	1.7 (0.6, 2.9)	0.9 (-1.5, 2.9)	-1.9 (-2.5, -1.1)	-2.6 (-4.4, -0.7)	1.2 (0.6, 1.8)
<i>Hyphessobrycon</i> aff. <i>melazonatus</i>	3.7 (1.4, 6.8)	-2.1 (-4.8, 1.5)	1.8 (0.8, 3.0)	1.2 (-0.6, 3.2)	-1.0 (-1.6, -0.4)	-1.8 (-3.7, 0.1)	0.9 (0.3, 1.4)
<i>Ituglanis</i> cf. <i>amazonicus</i>	3.8 (1.3, 6.8)	1.6 (-2.1, 6.5)	1.5 (0.3, 2.7)	1.2 (-0.7, 3.1)	-1.9 (-2.5, -1.3)	-2.7 (-4, -1.2)	-0.1 (-0.8, 0.5)
<i>Microcharacidium</i> cf. <i>weitzmani</i>	3.8 (0.3, 7.0)	-1.4 (-2.6, -0.3)	1.8 (0.9, 2.7)	1.1 (-0.9, 3.2)	-3.1 (-4.1, -2.1)	0.2 (-0.5, 0.9)	0.1 (-0.8, 1.0)
<i>Nannostomus marginatus</i>	3.8 (1.7, 6.4)	-0.8 (-2.4, 1.4)	1.9 (1.0, 2.9)	1.3 (-0.4, 3.2)	-1.1 (-1.6, -0.6)	-1.1 (-2.0, -0.2)	-0.3 (-0.9, 0.2)
<i>Nemuroglanis pauciradiatus</i>	3.9 (1.3, 7.0)	-0.7 (-3.6, 3.4)	1.7 (0.5, 2.9)	1.1 (-0.8, 3.1)	-1.6 (-2.2, -1.0)	-2.1 (-3.7, -0.1)	0.4 (-0.2, 0.9)
<i>Pyrrhulina</i> cf. <i>brevis</i>	4.8 (2.9, 7.5)	1.9 (0.7, 3.5)	1.8 (1.0, 2.8)	0.9 (-0.7, 2.7)	1.3 (0.9, 1.8)	0.6 (0.2, 1.1)	-0.7 (-1.1, -0.3)
<i>Synbranchus madeira</i>	3.5 (0.2, 6.8)	1.0 (-1.9, 6.0)	1.5 (0.3, 2.7)	1.1 (-0.8, 3.1)	-2.4 (-3.1, -1.5)	-1.9 (-3.0, -0.6)	-0.3 (-1.2, 0.4)

Fig. 1. Map depicting the study microbasin near Manaus, Brazil, with details of the sampling design showing (a) 38 individually-numbered stream segments delimited by channel confluences, with grey-scale dots representing the four sampling visits to each segment. Inset (b) shows a detailed view of all visit locations on segment #32; each visit (i.e. sampling occasion) covered a 15-m-long stretch of stream, where fish were sampled both in the channel and temporary ponds.

Fig. 2. Longitudinal profile of environmental variables. The longitudinal gradient is represented by cumulative distance from headwaters and its equivalent stream orders is represented by the dark grey bars below. (a) The presence of connected ponds (white dots) tends to increase in a downstream direction and black bars represent the 95% confidence intervals for each value of frequency of presence. Remaining panels show longitudinal profiles of (b) dissolved oxygen (mean estimates and 95% confidence intervals are represented on the right by dots and by lines, respectively), (c) water depth and (d) water velocity.

Fig. 3. Changes in occupancy probabilities along the longitudinal gradient for the 18 species analysed in the model. Mean probabilities estimated for the main channel and temporary ponds are represented by dashed and continuous black lines, respectively. The grey scale polygons represent the 95% credible intervals (CI).

Fig. 4. Changes in detection probabilities along the longitudinal gradient for the 18 species analysed in the model. Mean probabilities estimated for the main channel and temporary ponds are represented by dashed and continuous black lines respectively. The grey scale polygons represent the 95% credible intervals (CI).

588

589 **Fig. 5.** Changes in similarity of species composition and richness between habitats along the
590 longitudinal gradient. Estimates were based on the 18 species that dwell in both channel and
591 temporary ponds. (a) Downstream increase in Sorensen Similarity Index between channel and
592 ponds of each sampled segment. White dots represent mean estimates and lines are the
593 corresponding 95% credible intervals. (b) Downstream increase in the number of species in
594 both habitats. Light and dark grey dots represent the mean estimates for channel and ponds in
595 each stream segment; lines are the corresponding 95% credible intervals.

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59°46'0"W

Occupancy probability

-- Channel mean — Ponds mean Channel CI Ponds CI

Detection probability

-- Channel mean

<https://mc06.manuscriptcentral.com/cjfas-pubs>

— Ponds mean

Channel CI

Ponds CI