

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

Thiago Belisario d'Araújo Couto, Jansen Zuanon, Julian D. Olden, and Gonçalo Ferraz

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

Résumé : Les régimes d'écoulement dynamiqués maintiennent des connexions essentielles entre les habitats du chenal principal et ceux des plaines inondables attenantes qui fournissent aux poissons un accès à des abris et des possibilités d'approvisionnement et de frai. Notre étude élargit la compréhension de ces processus en explorant l'importance de la connectivité jumelée longitudinale–latérale pour déterminer la présence ou non d'espèces dans des cours d'eau d'amont de l'Amazonie. En utilisant un modèle d'occupation plurispécifique, nous révélons un motif bien défini d'ajout d'espèces vers l'aval dans des étangs de plaine inondable temporaires, associé à des changements dans le réservoir de colonisateurs potentiels présents dans le chenal et à l'augmentation de la connectivité hydrologique latérale. Les espèces présentant une plus grande tolérance aux eaux stagnantes et celles qui peuvent se disperser dans des habitats d'eau peu profonde (p. ex. *Anablepsoides micropus*) sont fréquemment présentes dans des étangs sur toute l'étendue longitudinale, alors que les espèces qui préfèrent des habitats lotiques ne sont présentes que dans les sites les plus en aval. Nous avons également observé une augmentation vers l'aval de la similitude entre les communautés d'étang et de chenal. L'étude fournit de l'information sur la structure spatiale des communautés de poissons tropicaux en réaction à la connectivité induite par les inondations et souligne la vulnérabilité des poissons de plaine inondable à la modification des régimes d'inondation. [Traduit par la Rédaction]

Introduction

Operating in longitudinal, lateral, and vertical dimensions, connectivity is a fundamental property of aquatic ecosystems (Ward 1989; Pringle 2003; Freeman et al. 2007). Ecologists have long recognized the importance of these dimensions of aquatic connectivity in shaping the distribution of freshwater fishes (Schlosser 1991). Many fish species have evolved complex life histories, enabling them to colonize and utilize multiple habitats along longitudinal gradients, including those needed during migration (McIntyre et al. 2016). Stream flow provides lateral connections between the main channel and adjacent floodplains, giving fish access to shelter, foraging, spawning, and recruitment habitats (Junk et al. 1989; Stoffels et al. 2015). Vertical exchange of surface water and ground water drives temperature and productivity regimes of rivers, affecting the availability of food resources and the growth rate of fish (Mejia et al. 2016). Consequently, there is considerable scientific interest and management relevance in better understanding the ecological effects of multidimensional reductions in

riverine connectivity due to human activities (Fullerton et al. 2010; Olden et al. 2010; Jaeger et al. 2014).

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

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

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

Our study investigates patterns of fish species occurrence in temporary ponds and the adjacent stream channel in response to longitudinal position in the drainage basin. We explore three main predictions. First, because of longitudinal changes in the pool of species available to colonize ponds from the main channel, we predict that pond occupancy probabilities also vary along the longitudinal gradient. Second, we predict distinct longitudinal patterns in fish occurrence between both habitats (i.e., channel versus ponds). Support for this prediction would suggest that species occurrence in ponds is not merely a reflection of channel occurrence, but is also shaped by environmental and connectivity factors that vary with longitudinal position. Third, following a downstream increase in channel-pond hydrologic connectivity, we predict a downstream increase in species similarity of pond and channel habitats. We test these three predictions using fish assemblages in upland headwater streams of the Amazon Basin. Our study employs a hierarchical approach to account for imperfect detection of fish (MacKenzie et al. 2002), as well as its variation among species, habitats, and longitudinal positions (Gwinn et al. 2015). By using such an approach, we obtain estimates of the probability of species occurrence and offer insights on how flood regimes drive the distribution of freshwater fish species in temporary habitats.

Materials and methods

Study system

The study was conducted in a pristine upland rainforest microbasin near “Camp 41” (Fig. 1) of the Biological Dynamics of Forest Fragments Project (BDFFP), 70 km north of Manaus, Amazonas state, Brazil (Bierregaard et al. 2001). The microbasin is part of the Urubu River basin, a tributary of the Amazon River, where localized flooding supports both a permanently flowing main channel and lentic temporary ponds (i.e., without or with negligible water flow) scattered across the riparian floodplain (Wantzen et al. 2008). Ponds are filled by a combination of rainfall, floodwater, and groundwater contributions, which tend to be more frequent during the December–May rainy season (Tomasella et al. 2008; Espírito-Santo et al. 2009). Usually, the channel water recedes to pre-flood levels a couple of hours after flooding events (Couto

et al. 2015), forming temporary ponds that last from a few days to more than 11 months (Pazin et al. 2006). These ponds are typically shallow (1.3 to 35.0 cm deep) and have small surface areas 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.

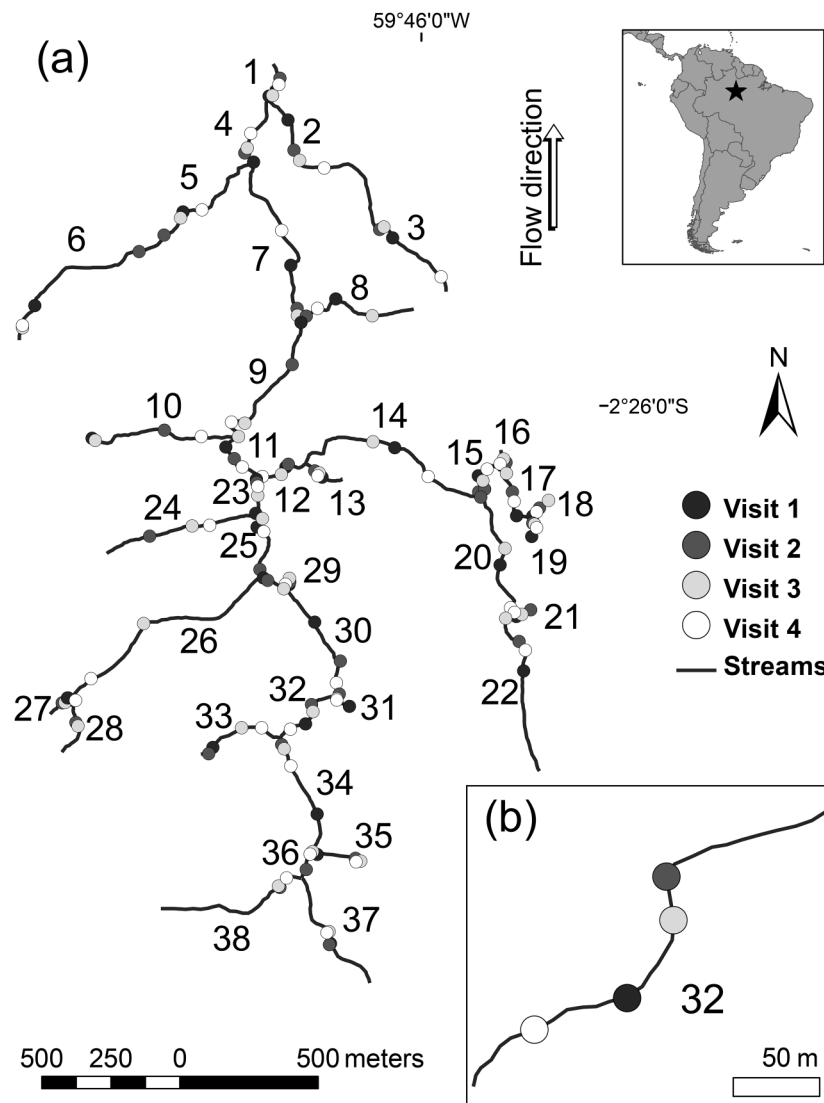
Temporary ponds host a subset of the regional fish fauna composed of small-sized species (adults typically <10 cm of standard length) that inhabit the channel and perform seasonal movements into ponds once they are formed in the rainy season (Pazin et al. 2006; Espírito-Santo and Zuanon 2016; Espírito-Santo 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 major 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 and 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 to ensure comparable segment lengths. We resampled each segment on four visits (i.e., sampling occasions) during the rainy season of 2012, between 2 February and 17 May. 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 m 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 preselected location. Only two segments (numbers 13 and 35) had no ponds in any of the visits; the remaining 36 had a mean 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 1 m 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

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 No. 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.



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.

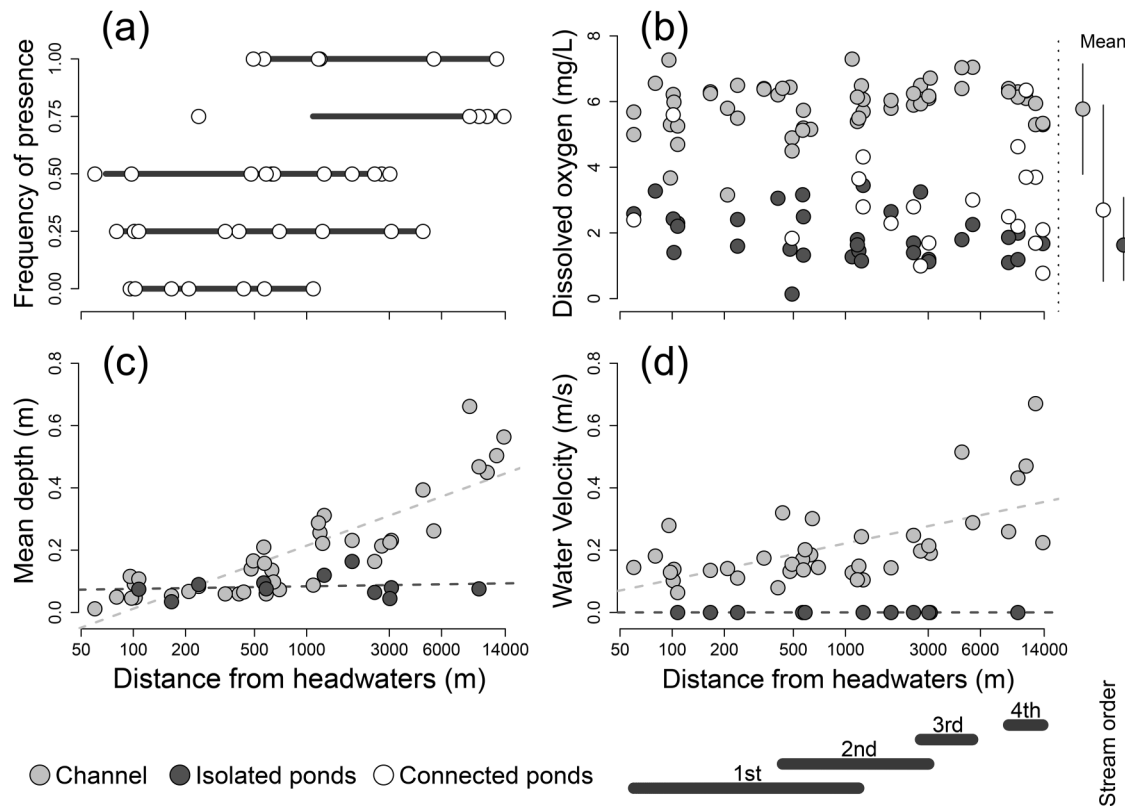
Fish samples of each stream segment were conducted separately for channel and pond habitats. Temporary pond samples involved a 10 min visual assessment and 60 min of hand-netting of all available ponds located adjacent to the randomly selected 15 m river stretch. Main channel samples involved 10 min of visual assessment, 40 min 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 edges. 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

Fig. 2. Longitudinal profile of environmental variables. The longitudinal gradient is represented by cumulative distance from headwaters, and its equivalent stream order is represented by the dark grey bars below. (a) The presence of connected ponds (white dots) tends to increase in a downstream direction; 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 lines, respectively), (c) water depth, and (d) water velocity.



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. 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 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. S1¹). Specifically, we model the occupancy probability with the logit function

$$(1) \quad \text{logit}(\psi_{ij}) = u_{1i} \times C_j + u_{2i} \times P_j + u_{3i} \times D_j + u_{4i} \times C_j \times D_j$$

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 a pond site 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 u_{1i} and u_{2i} are intercepts for channel and pond, respectively; u_{3i} is the effect of longitudinal position and u_{4i} is the interaction coefficient. The occupancy state of site j for species i is a Bernoulli

distributed z_{ij} that equals 1 when the site is occupied and 0 when not. When $z_{ij} = 1$, the probability p_{ijk} of species detection at that site during visit k follows the function

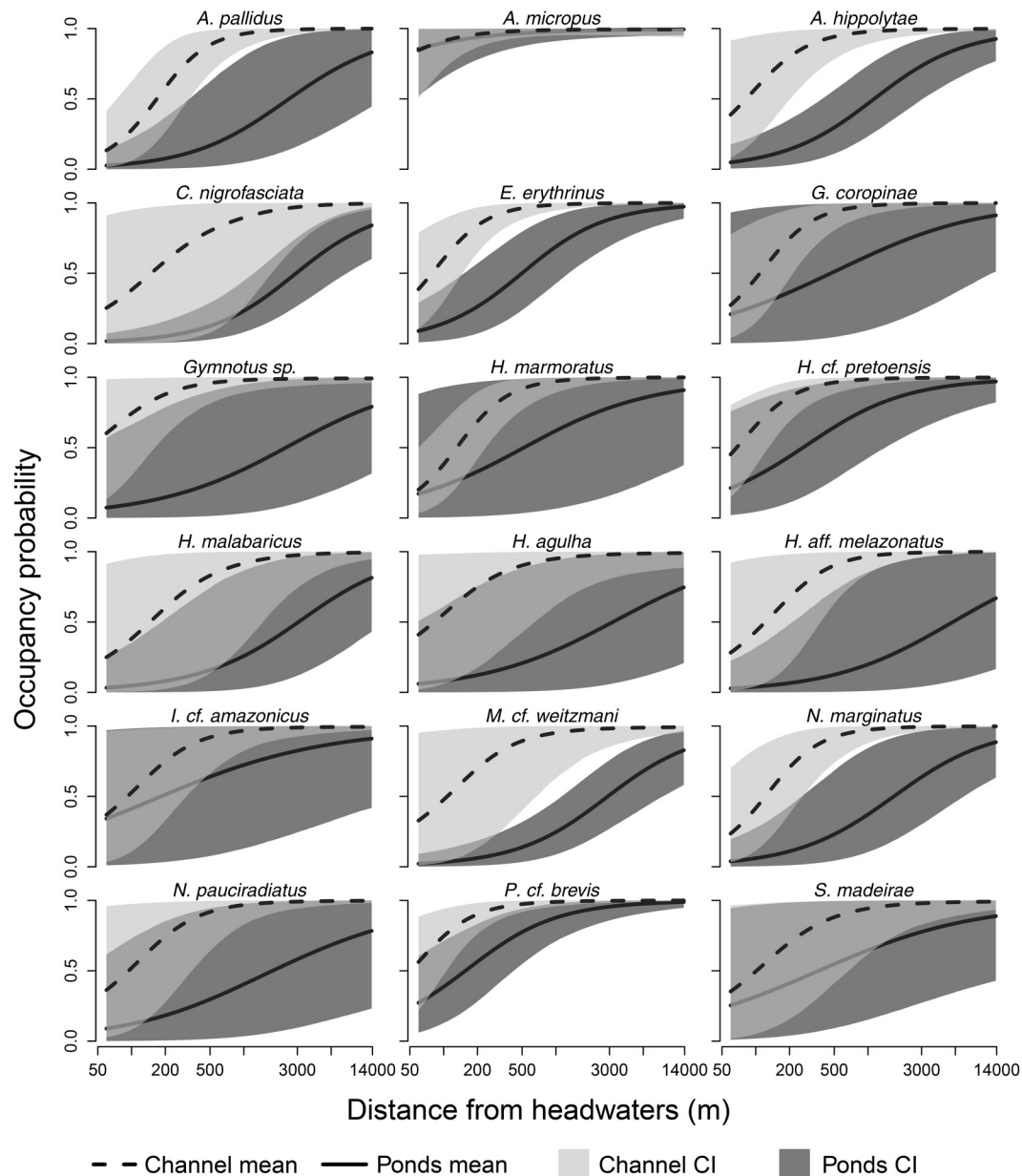
$$(2) \quad \text{logit}(p_{ijk}) = v_{1i} \times C_j + v_{2i} \times P_j + v_{3i} \times C_j \times D_j$$

where v_{1i} , v_{2i} , and v_{3i} are detection coefficients, analogous to those of the occupancy function. By including v_{3i} , the coefficient of interaction between channel and distance, without the corresponding distance effect, we assume that detection varies with longitudinal position only in the channel. The assumption that detection is constant in ponds along the longitudinal gradient is based on the observation of very limited longitudinal variation in depth and area of individual ponds. The estimation of both occupancy and detection parameters for a given species requires data with species detections in both channel and ponds; therefore, our analysis included only species that had at least two detections per habitat.

Although we estimate different coefficients for every species, we also share information across species by treating every u and v parameter as a random effect (Dorazio and Royle 2005; Dorazio et al. 2006). This allows for joint inference about the set of all species in the analysis, based on “hyperparameter” means (μu_1 , μu_2 , μu_3 , μu_4 , μv_1 , μv_2 , and μv_3) and standard deviations (σu_1 , σu_2 , σu_3 , σu_4 , σv_1 , σv_2 , and σv_3) of the normally distributed random effects (Zipkin et al. 2009). To infer assemblage-wide differences between habitats, we computed a Sorensen index of similarity

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0388>.

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). See Table 1 for full species names.



between channel and pond sites of the same segment based on the imputed “true” occupancy state (z_{ij}) for all species i and site j . Similarly, by summing z_{ij} values across species, we obtained estimates of the expected number of species occurring at each site. Inference based on z_{ij} values afforded the opportunity to evaluate similarity and number of species in different positions along the 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 Core Team 2016) through the “rjags” package (Plummer 2016). We used noninformative normal and gamma priors, respectively, for mean and standard deviation hyperparameters (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 °C), moderately acidic (pH = 4.9: 4.7–6.0), oxygenated (5.9 mg·L⁻¹: 4.9–7.2 mg·L⁻¹), and with low conductivities (8.3 μS·cm⁻¹: 6.3–10.9 μS·cm⁻¹). By contrast, isolated pond waters were more acidic (pH = 4.4: 2.9–4.9), less oxygenated (1.9 mg·L⁻¹: 0.9–3.3 mg·L⁻¹), and had higher conductivities (12.8 μS·cm⁻¹: 8.6–18.7 μS·cm⁻¹). Ponds connected to the channel had intermediate levels of DO (3.0 mg·L⁻¹: 0.9–6.0 mg·L⁻¹), pH (4.9: 4.6–6.4), and conductivity (11.5 μS·cm⁻¹: 7.0–21.8 μS·cm⁻¹), indicating the influence of waters from the main channel. Water

Table 1. Hyperparameters and species-specific parameters estimated with data from 18 fish species.

Species	Hyperparameters						
	$\mu u1$	$\mu u2$	$\mu u3$	$\mu u4$	$\mu v1$	$\mu v2$	$\mu v3$
	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-specific parameters							
	$u1$	$u2$	$u3$	$u4$	$v1$	$v2$	$v3$
<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 sp.1</i>	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 cf. 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 aff. 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 cf. 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 cf. 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 cf. 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)

Note: Values in parentheses are 95% credible intervals for parameter estimates. Parameters $\mu u1$ – $\mu u4$ and $u1$ – $u4$ describe longitudinal variation in occupancy, while parameters $\mu v1$ – $\mu v3$ and $v1$ – $v3$ do so for detection. Extreme variation in these parameters is highlighted in bold, whenever the credible intervals do not overlap zero.

temperatures in isolated and connected ponds (24.6 °C: 23.5–25.5 °C) 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 DO, 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 S1¹). 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. hoplogenys* were only captured in connected ponds, with the last three only found very close to the channel. The vast majority of individuals of *Aequidens pallidus*, *Callichthys callichthys*, *Erythrinus erythrinus*, and *Hoplias malabaricus* captured in pond habitats were juveniles. Additionally, young of the year of *Aequidens pallidus*, *Callichthys callichthys*, *Erythrinus erythrinus*, *Hemigrammus cf. pretoensis*, *Hoplias malabaricus*, *Hyphessobrycon aff. melazonatus*, and *Megalechis picta* were captured in ponds.

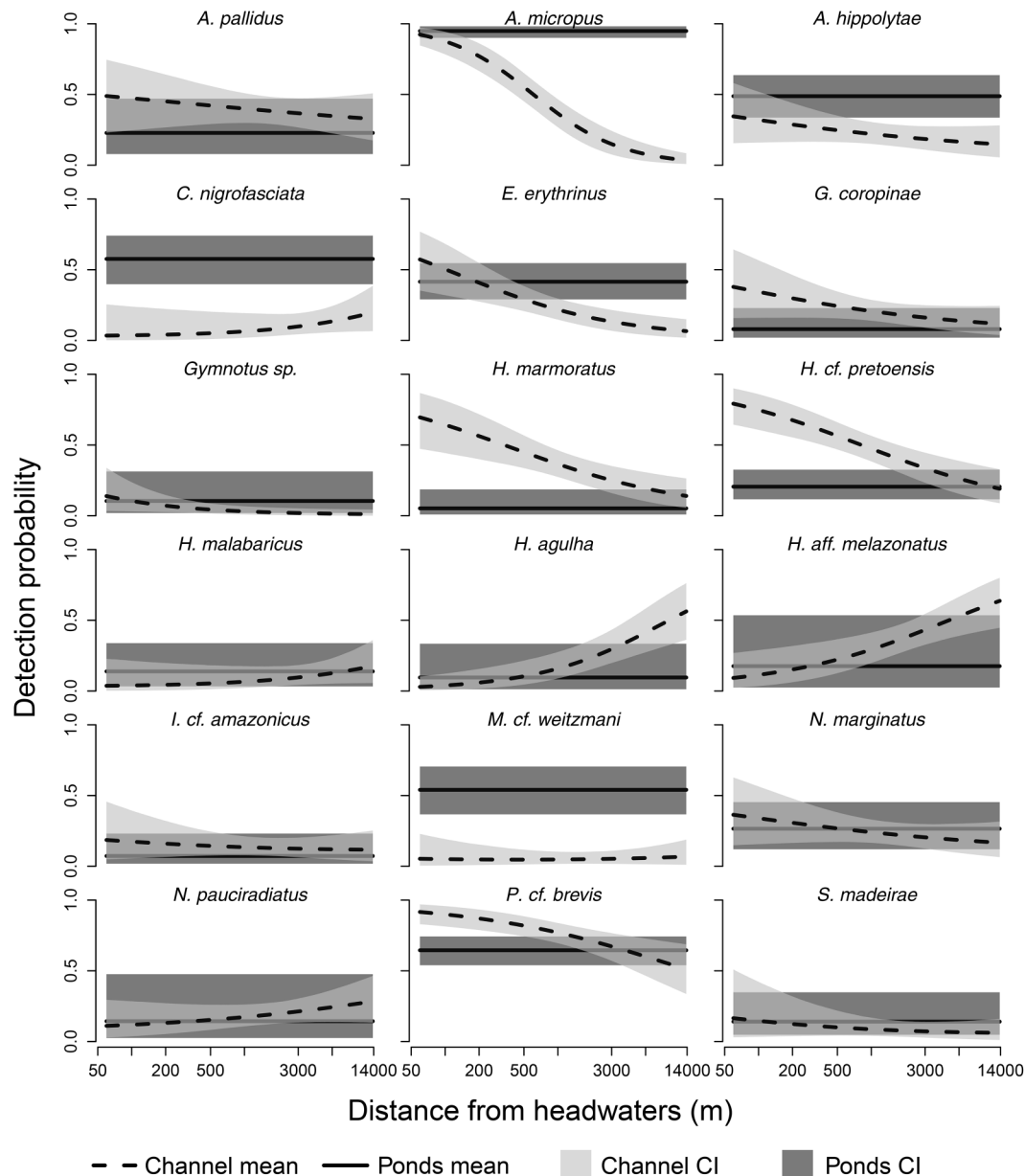
Site occupancy increased downstream for all 18 species (Fig. 3), as shown by the positive values of $u3$, for every species i and by the positive value of the hyperparameter $\mu u3 = 1.74 \pm 0.34$ (mean \pm standard deviation; Table 1). On average, site occupancy was two times higher in the channel than in ponds, represented by a positive difference between hyperparameters $\mu u1$ and $\mu u2 = 3.90 \pm 1.17$, as well as by a positive difference for $u1_i - u2_i$ for every species i (Table 1). This finding includes not only species that are rarely detected in ponds like *Hyphessobrycon agulha* and *Helogenes marmoratus*, but also pond specialists like *Anablepsoides 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 $u4_i$, but the 95% credible intervals overlapped zero in all cases (Table 1).

In contrast with the occupancy part of the model, the mean interaction between longitudinal position and habitat was moderately negative ($\mu v3 = -0.19 \pm 0.23$). This is caused by a strong pattern of downstream decrease in detection probability in the channel that can be observed in the negative $v3$, 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 ($\mu v1 - \mu v2 = -0.27 \pm 0.55$), but the difference is highly variable among species (Table 1). Six species had positive values of $v1-v2$ with 95% credible intervals not overlapping zero, indicating markedly higher detection in ponds. They are *Anablepsoides micropus*, *Apistogramma hippolytae*, *Copella nigrofasciata*, *Erythrinus erythrinus*, *Microcharacidium cf. weitzmani*, and *Pyrrhulina cf. brevis*. Only *Helogenes marmoratus* and *Hemigrammus 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 *Anablepsoides micropus* but also the pencilfish *Pyrrhulina 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., *Hyphessobrycon aff. melazonatus*, *Hyphessobrycon agulha*, *Microcharacidium cf. weitzmani* and *Nemuroglanis 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 *Anablepsoides micropus* and *Pyrrhulina cf. brevis*, but other species like *Erythrinus erythrinus*, *Hemigrammus cf. pretoensis*, *Gymnotus coropinae*,

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).



Gymnotus sp.1, *Helogenes marmoratus*, *Aequidens 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).

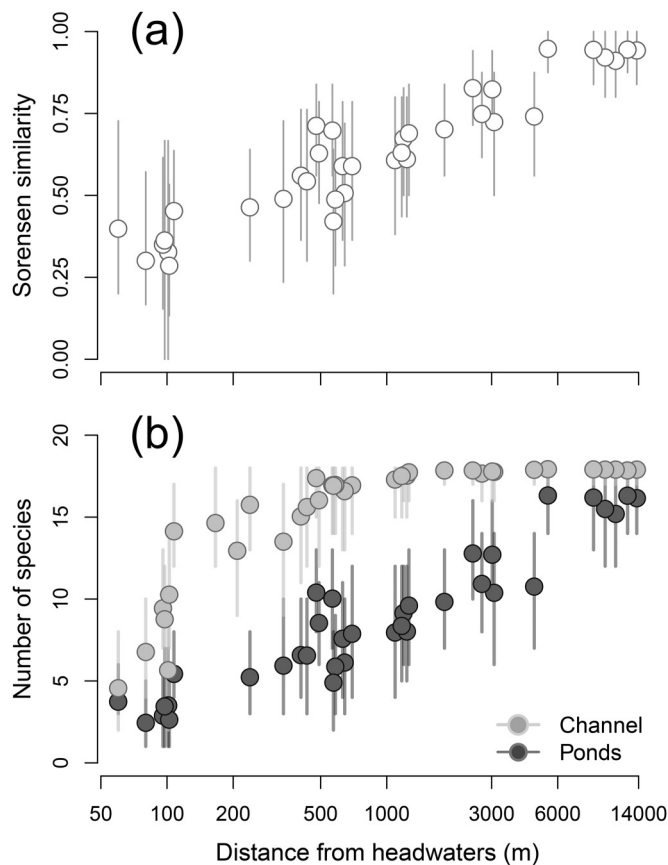
Discussion

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 with 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

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



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 with all other species, the killifish *Anablepsoides micropus* was predominantly found in ponds across the entire longitudinal extent of the study. *Anablepsoides 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 and 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 considerably higher number of detections of *Anablepsoides 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 *Aequidens pallidus* and *Apistogramma 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 *Hyphessobrycon* aff. *melazonatus* and the South American darter *Microcharacidium* 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., *Anablepsoides 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 *Hyphessobrycon* aff. *melazonatus* and *Hyphessobrycon* *agulha* are more detectable downstream in the channel. Both species form schools that are likely to become larger downstream. Remarkably, the

killifish *Anablepsoides 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 and Fraser 2001; Fernandes et al. 2014). *Anablepsoides micropus* was caught in considerable higher numbers in ponds and just a 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 a 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 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.

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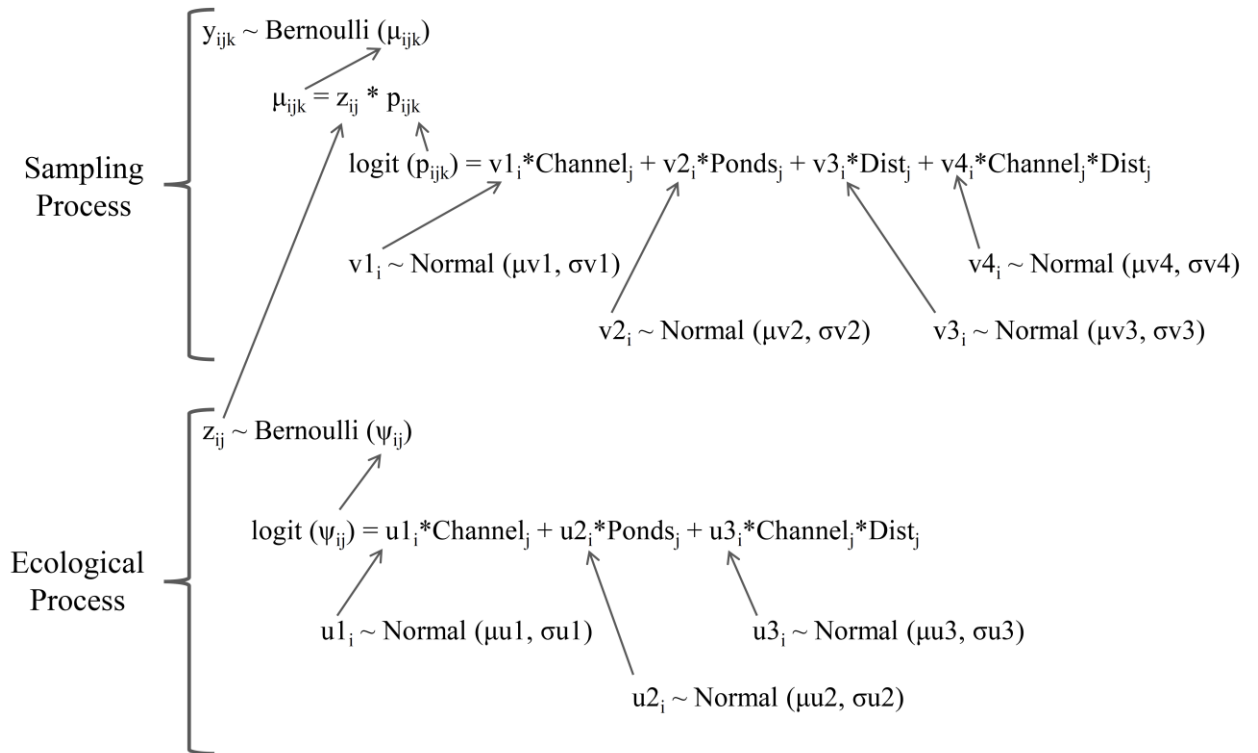
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Supplementary material

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

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Figure S1. Diagram of the multi-species hierarchical model.



In the model, the indexes i, j and k designates species, sites and visits respectively. The ecological process (species site-occupancy) and the sampling process (species detection) are differentiated in the lower and upper bracket. Each process follows a Bernoulli distribution, with probability ψ for occupancy and μ (the product of detection probability p and z) for detection. The latent variable z represents the occupancy or non-occupancy of a site.

Considering that the species can only be detected when $z = 1$ (i.e. the species is present), the species detection is conditional on site occupancy. Both parameters ψ and p are described as logit-linear functions. We included as covariates in these functions the two habitat categories *Channel* and *Ponds* that compose differential intercept coefficients in each function (i.e. when *Channel* = 1, *Ponds* = 0 and vice-versa). In the occupancy function, we also included the additive effect of the distance from headwaters (*Dist*) and the interaction between the effects of habitat and distance (*Channel*Dist*). This combination permits not only to make inference on the general effect of the longitudinal position on occupancy, but also to examine the response of each habitat separately. For the detection function, we included only the interaction covariate, which is based on the assumption that detection probability can vary downstream in the channel but remain constant in ponds. The coefficients $u1_i$, $u2_i$, $u3_i$, and $u4_i$ describe effects of covariates on occupancy probability (ψ) for species i , while $v1_i$, $v2_i$ and $v3_i$ describe effects on detection probability (p). Species are modelled as random effects in normal distributions with mean μ and standard deviation σ constructed for each u and v parameter of the model. Each μ and σ describes the effect of a given covariate in the whole fish assemblage, which make them a superior class of parameters named by “hyper-parameters”. To run the model, we used uninformative priors for both mean and standard deviation of the hyper-parameters.

The multi-species hierarchical model code for the software JAGS:

```
model {
# Priors

# Set uninformative priors for the hyper-parameters
u.mean1 ~ dunif(0, 1)
muu1 <- log(u.mean1) - log(1 - u.mean1)
u.mean2 ~ dunif(0, 1)
muu2 <- log(u.mean2) - log(1 - u.mean2)
u.mean3 ~ dunif(0, 1)
```



```

muu3 <- log(u.mean3) - log(1 - u.mean3)
u.mean4 ~ dunif(0, 1)
muu4 <- log(u.mean4) - log(1 - u.mean4)
v.mean1 ~ dunif(0, 1)
muv1 <- log(v.mean1) - log(1 - v.mean1)
v.mean2 ~ dunif(0, 1)
muv2 <- log(v.mean2) - log(1 - v.mean2)
v.mean3 ~ dunif(0, 1)
muv3 <- log(v.mean3) - log(1 - v.mean3)

tau.u1 ~ dgamma(0.1, 0.1)
tau.u2 ~ dgamma(0.1, 0.1)
tau.u3 ~ dgamma(0.1, 0.1)
tau.u4 ~ dgamma(0.1, 0.1)
tau.v1 ~ dgamma(0.1, 0.1)
tau.v2 ~ dgamma(0.1, 0.1)
tau.v3 ~ dgamma(0.1, 0.1)

# Define the relationships between species-specific parameters and hyper-parameters
# Loop over species
for (i in 1: S) {

  u1[i] ~ dnorm(muu1, tau.u1)
  u2[i] ~ dnorm(muu2, tau.u2)
  u3[i] ~ dnorm(muu3, tau.u3)
  u4[i] ~ dnorm(muu4, tau.u4)
  v1[i] ~ dnorm(muv1, tau.v1)
  v2[i] ~ dnorm(muv2, tau.v2)
  v3[i] ~ dnorm(muv3, tau.v3)

  # Likelihood
  # Loop over sites
  for (j in 1: J) {

    # Ecological level
    logit(psi[j,i]) <- u1[i] * Chan [j] + u2[i] * Pond[j] + u3[i] * Dist[j] + u4[i] * Chan[j] * Dist[j]
    z[j,i] ~ dbern(psi[j,i])

    # Loop over visits
    for (k in 1: K[j]){

      # Sampling level
      logit(p[j,k,i]) <- v1[i] * Chan [j] + v2[i] * Pond[j] + v3[i] * Chan[j] * Dist[j]
      mup[j,k,i] <- p[j,k,i] * z[j,i]
      Y[j,k,i] ~ dbern(mup[j,k,i])
    }
  }
}

# Richness estimates - Sum all “true” occupancy state (z) for all species in each site

```

```

# Loop over sites
for (j in 1: J){
  rich[j] <- sum(z[j,])
}

# Similarity estimates between channel and ponds of each segment
# Estimates are based on the “true” occupancy state (z) for all species in each site

# Loop over segments
for (j in 1: W){

# Sorensen similarity index between adjacent sites
  similarity[j] <- 2 * (sum(z[j, ] * z[j + W, ])) / (sum(z[j, ]) + sum(z[j + W, ]))
}

}

```

Table S1. List of species sampled with their respective number of detections per habitat. The species marked with (*) were only captured in parts of connected ponds that were very close to the channel.

Species	Family	Channel	Ponds
<i>Aequidens pallidus</i> (Heckel, 1840)	Cichlidae	46	8
<i>Anablepsoides micropus</i> (Steindachner, 1863)	Rivulidae	71	120
<i>Acestrorhynchus falcatus</i> (Bloch, 1794)	Acestrorhynchidae	3	0
<i>Ancistrus</i> aff. <i>hoplogenys</i> (Günther, 1864)*	Loricariidae	6	1
<i>Apistogramma hippolytae</i> Kullander, 1982	Cichlidae	30	28
<i>Brachyglanis frenata</i> Eigenmann, 1912	Heptapteridae	4	0
<i>Brachyhypopomus beebei</i> (Schultz, 1944)	Hypopomidae	1	2
<i>Bryconops inpai</i> Knöppel, Junk & Géry, 1968	Characidae	40	0
<i>Callichthys callichthys</i> (Linnaeus, 1758)	Callichthyidae	0	7
<i>Copella nigrofasciata</i> (Meinken, 1952)	Lebiasinidae	8	21
<i>Crenicichla</i> cf. <i>alta</i> Eigenmann, 1912	Cichlidae	23	0
<i>Crenuchus spilurus</i> Günther, 1863	Crenuchidae	5	1
<i>Denticetopsis seducta</i> Vari, Ferraris & de Pinna, 2005	Cetopsidae	3	0
<i>Erythrinus erythrinus</i> (Bloch & Schneider, 1801)	Erythrinidae	34	29
<i>Gymnorhamphichthys rondoni</i> (Miranda Ribeiro, 1920)	Rhamphichthyidae	4	0
<i>Gymnotus coropinae</i> Hoedeman, 1962	Gymnotidae	27	4
<i>Gymnotus</i> sp.1	Gymnotidae	5	4
<i>Gymnotus</i> sp.2	Gymnotidae	1	0
<i>Helogenes marmoratus</i> Günther, 1863*	Cetopsidae	45	2
<i>Hemigrammus</i> cf. <i>pretoensis</i> Géry, 1965	Characidae	68	16
<i>Hoplerethrinus unitaeniatus</i> (Spix & Agassiz, 1829)	Erythrinidae	3	0
<i>Hoplias malabaricus</i> (Bloch, 1794)	Erythrinidae	8	4
<i>Hyphessobrycon agulha</i> Fowler, 1913	Characidae	26	2
<i>Hyphessobrycon</i> aff. <i>melazonatus</i> Durbin, 1908	Characidae	41	3
<i>Iguanodectes variatus</i> Géry, 1993	Characidae	24	0
<i>Ituglanis</i> cf. <i>amazonicus</i> (Steindachner, 1882)	Trichomycteridae	17	5
<i>Leporinus klausewitzii</i> Géry, 1960	Anostomidae	3	0
<i>Megalechis picta</i> (Müller & Troschel, 1849)	Callichthyidae	0	2
<i>Microcharacidium</i> cf. <i>weitzmani</i> Buckup, 1993	Crenuchidae	5	21
<i>Myoglanis koepckeii</i> Chang, 1999	Heptapteridae	7	0
<i>Nannostomus marginatus</i> Eigenmann, 1909	Lebiasinidae	30	12
<i>Nemuroglanis pauciradiatus</i> Ferraris, 1988*	Heptapteridae	23	4
<i>Parotocinclus longirostris</i> Garavello, 1988	Loricariidae	19	0
<i>Pyrhulina</i> cf. <i>brevis</i> Steindachner, 1876	Lebiasinidae	111	62
<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	Heptapteridae	4	0
<i>Rineloricaria heteroptera</i> Isbrücker & Nijssen, 1976	Loricariidae	9	0
<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	Sternopygidae	2	0
<i>Synbranchus madeirae</i> Rosen & Rumney, 1972	Synbranchidae	10	8
<i>Tatia brunnea</i> Mees, 1974	Auchenipteridae	1	0