Received: 4 March 2018 | Revised: 3 September 2018 | Accepted: 15 September 2018

DOI: 10.1111/fwb.13198

STANDARD PAPER

WILEY Freshwater Biology

Flood pulse regulation of bacterioplankton community composition in an Amazonian floodplain lake

Michaela L. de Melo[1] | Stefan Bertilsson[2] | João Henrique F. Amaral[3] | Pedro M. Barbosa[4] | Bruce R. Forsberg[3] | Hugo Sarmento[1]

[1]Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, Brazil

[2]Limnology and Science for Life Laboratory, Department of Ecology and Genetics, Uppsala University, Uppsala, Sweden

[3]Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

[4]Centro de Ciências da Saúde, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

Correspondence
Michaela L. de Melo, Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, Brazil.
Email: michaelaldemelo@gmail.com

Funding information
Conselho Nacional de Desenvolvimento e Científico e Tecnológico (CNPq), Grant/Award Number: 458036/2013-7, 482004/2012-6 and 309514/2017-7; Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Grant/Award Number: 2014/14139-3

Abstract

1. Understanding spatial and temporal dynamics of microbial communities is a central challenge in microbial ecology since microorganisms play a key role in ecosystem functioning and biogeochemical cycles. Amazonian aquatic systems comprise a dynamic mosaic of heterogeneous habits but are understudied and there is limited information about the mechanisms that shape bacterial community composition (BCC).
2. There is a consensus that environmental selection (species sorting) and dispersal processes (source–sink dynamics) act in concert to shape the composition of these communities, but the relative importance of each mechanism may vary dramatically through time and between systems.
3. Applying 16S rRNA gene amplicon high-throughput sequencing, we studied factors and processes that modulate BCC in an Amazonian floodplain lake and used source-tracking models to trace the main dispersal sources of microorganisms in the whole floodplain system during a full hydrological cycle.
4. Our source-tracking models indicated that dispersal processes were predominant, explaining most of the BCC variability throughout the study period. We observed more sources contributing to the sink community during the falling water than rising water period, when contributions from the Solimões River dominated.
5. There was a clear seasonal pattern in BCC, closely related to environmental variables, suggesting that the successful establishment of dispersing bacteria also depends on environmental filtering that is linked to water flow.
6. In summary, source–sink dynamics and species sorting were strongly affected by water exchange and connectivity with the main river that varied throughout the flood pulse cycle. Our results demonstrated the influence of lateral transport and temporal dynamics on BCC in Amazonian floodplain lakes that could ultimately impact regional carbon budgets and biogeochemical cycles.

KEYWORDS
16S rRNA gene, high-throughput sequencing, metacommunity, source–sink dynamics, spatiotemporal dynamics

 © 2018 John Wiley & Sons Ltd

1 | INTRODUCTION

Microbes are the most diverse and ubiquitous organisms within our biosphere. In aquatic systems they play key roles in ecosystem functioning and biogeochemical cycles, nutrient remineralisation and primary production (Cotner & Biddanda, 2002). Understanding how microbial communities are structured is one of the greatest challenges in aquatic microbial ecology. The development of high-throughput sequencing techniques is now allowing us to unravel this hitherto unexplored biodiversity and understand the processes behind temporal and spatial patterns observed across various habitats (Humbert et al., 2009; Read et al., 2015; Xu, 2006).

Microbial ecologists have been testing whether ecological theories and concepts originally developed for macro-organisms also apply to microorganisms. The metacommunity concept (Leibold et al., 2004) came from metapopulation theory (MacArthur & Wilson, 1967), and makes predictions about a set of local communities with a pool of potentially interactive species that are linked by dispersal (Leibold et al., 2004). The metacommunity concept considers habitat heterogeneity and describes how communities are structured by species responses to environmental filters and local selection (species sorting), and also the role of dispersal processes, immigration and emigration, to rescue species from local competitive exclusion (mass effect, source–sink dynamics).

The metacommunity concept has previously been applied to investigate factors that structure aquatic bacterial community composition (BCC) (Comte, Berga, Severin, Logue, & Lindstrom, 2017; Langenheder & Ragnarsson, 2007; Langenheder & Szekely, 2011; Lindstrom & Langenheder, 2012; Szekely & Langenheder, 2014; Zha, Berga, Comte, & Langenheder, 2016). In general, BCC is shaped by a combination of different mechanisms, which might vary with the environmental characteristics of each system (Szekely & Langenheder, 2014). However, few studies have addressed these questions in tropical river–floodplain systems (but see Lemke et al., 2009; Tessler et al., 2017) where high temporal variability and spatial heterogeneity add additional layers of complexity.

A good framework for addressing this topic is the source–sink theoretical model that describes how variations in environmental conditions may affect population growth or decline (Mouquet & Loreau, 2003; Mouquet, Miller, Daufresne, & Kneitel, 2006). Source-sink dynamics have been successfully applied to aquatic microbial communities, but their role seems to be smaller than that of resident bacterial growth (species sorting). A study conducted in a complex boreal aquatic network along an entire terrestrial/aquatic continuum found that BCC followed a directional spatial structure driven by the soil species recruitment (source–sink dynamics) and that these species were filtered by environmental conditions along the gradient (species sorting—Ruiz-González, Niño-Garcia, & del Giorgio, 2015). Another study, which also considered seasonal variations, investigated the importance of external and internal dispersal sources (precipitation, inlet inflow, sediment resuspension and mixing) to the BCC of a dimictic temperate lake and found that previous community structure had a more important role in determining the recent community composition than dispersal sources (Comte et al., 2017).

The Amazon River basin contains a complex hydrological network, with large main river channels and floodplains containing numerous interconnected subsystems, including lakes, vegetated wetlands (flooded areas occupied with a mixture of herbaceous macrophytes and woody vegetation), *paranás* (connecting channels) and *igarapés* (local upland streams), forming the world's largest river system with a drainage basin area of 6.1×10^6 km^2 (Richey et al., 1990). The connectivity and material exchange between floodplain systems and the river are strongly affected by water flux direction and relative contribution of different water inputs, which depend on the floodplain catchment area and the flood pulse (the annual variation in the water level), as demonstrated for the same study area (Lake Janauacá) (Bonnet et al., 2017).

A range of studies has demonstrated that floodplain systems play a crucial role in the structure and dynamics of the Amazon River system (Abril et al., 2014; Melack & Forsberg, 2001). Usually, these complex systems have high primary and secondary production (Forsberg, Melack, Richey, & Pimentel, 2017; Melack & Forsberg, 2001). The flooded vegetation produces and exports large amounts of inorganic and organic carbon to the river that can be transported over great distances before being metabolised and released to the atmosphere (Abril et al., 2014).

In the Amazon basin, most studies have investigated only the spatial dynamics of BCC (Tessler et al., 2017) or were restricted to sampling either the river's main channel and tributaries or the plume/estuary (Ghai et al., 2011; Satinsky et al., 2015). In contrast, few studies have considered both spatial and seasonal scales (Doherty et al., 2017). Most importantly, no studies have evaluated the mechanisms that shape bacterial community assemblages in floodplain systems and how local communities are connected into a regional metacommunity.

Given the importance of large tropical floodplain river systems, and the key role of bacteria in the degradation of the organic matter and other globally relevant biogeochemical cycles, this study aimed to: (a) track the relative contribution of bacterial dispersal sources into a sink community in an Amazonian floodplain lake (AFL); (b) investigate how the flood pulse changes environmental conditions and how these changes in turn affect BCC; and (c) identify key taxa involved in the major shifts in BCC throughout the hydrological cycle of an AFL. To accomplish this, we sampled monthly between June 2015 and May 2016 in the channel that formed the only permanent surface connection between the lake and the main river. We sampled this site because it showed the microbiota entering or leaving the lake. We hypothesised that the flood pulse strongly affects environmental conditions, as well as the relative contribution of the different sources of bacteria to the channel. During high water periods, when water from the Solimões River enters the lake through the channel, we expected an increase in bacterial sources from the river and a decrease in contribution from other sources, while in drier conditions when river discharge is lower, waters from the local upland drainage basin and from the channel's previous community were expected to be the main contributors to BCC.

2 | METHODS

2.1 | Study area and sampling

Lake Janauacá (3°23′ S; 60°18′ W; altitude 32 m) is an AFL located 40 km southeast of Manaus, in the middle of the Amazon basin (Figure 1). With a local watershed area of 770 km^2 and a floodable area ranging between 23 km^2 at low water to 390 km^2 at high water (Pinel et al., 2015). The lake is located along the south margin of the Solimões River and is permanently connected to it by a 12-km-long channel. The channel is the main connection (ground water is another less important permanent connection) and water-exchange path between lake and river during most of the year. The exceptions are high-water periods (May–August), when other connections are established along the riverbank in the northern part of the lake (open lake—northern area). The southernmost portion of the lake is characterised by a dendritic shape (Figure 1), which drains predominantly upland forests and agricultural areas. In the northern part, there is a larger portion forming a large open water lake (Figure 1), with strong influence from the river during high water periods, as the river floods into the lake. This portion is also dominated by herbaceous macrophytes and the dominant species vary throughout the year.

Subsurface (50 cm) water samples were collected monthly at the channel site (Figure 1) between June 2015 and May 2016, covering a full hydrological cycle (totaling nine field campaigns—with gaps in the monthly sampling only in November and December 2015 and April 2016; Figure 2). We chose this channel sampling site to address questions about the seasonal dynamics in BCC and environmental drivers (species sorting). To track the sources of microorganisms dispersing to the sink community (channel) we sampled the BCC at four additional sites (in campaigns 4, 6, 7 and 9; Supporting Information Table S1): (a) open lake, a site located in the northern region of the floodplain lake that is influenced by the Solimões River; (b) drainage basin, a site located in the southern portion of the lake that is influenced by a forest stream receiving black and clear waters (Sioli, 1984); (c) macrophyte banks located near the margin of the basin in a wind protected area; and (d) Solimões River, the river mainstream (Figure 1).

The study period included an extreme high-water period (starting in June 2015; Figure 2) that was followed by an atypically dry period in November and December 2015 (the latter not covered in the present study). During this period, the lake was reduced to a draining channel, and it was not possible to sample some of the sites because they had dried out (see satellite images of high and low waters in Supporting Information Figure S1).

2.2 | Environmental variables, DNA extraction and purification

Water temperature and electrical conductivity were measured using a CTD profiler (CastAway; SonTek, San Diego, CA, USA) sampling at 4 Hz with data reported at 0.3 m intervals. Other physical variables such as pH and dissolved oxygen (DO) were determined using specific probes (YSI ProODO, Yellow Springs, OH, USA). Water transparency was determined with a Secchi disc. Water sampling and in situ measurements were taken in the morning (between 9 and 12 a.m.). Water level was noted twice a day by local residents using a

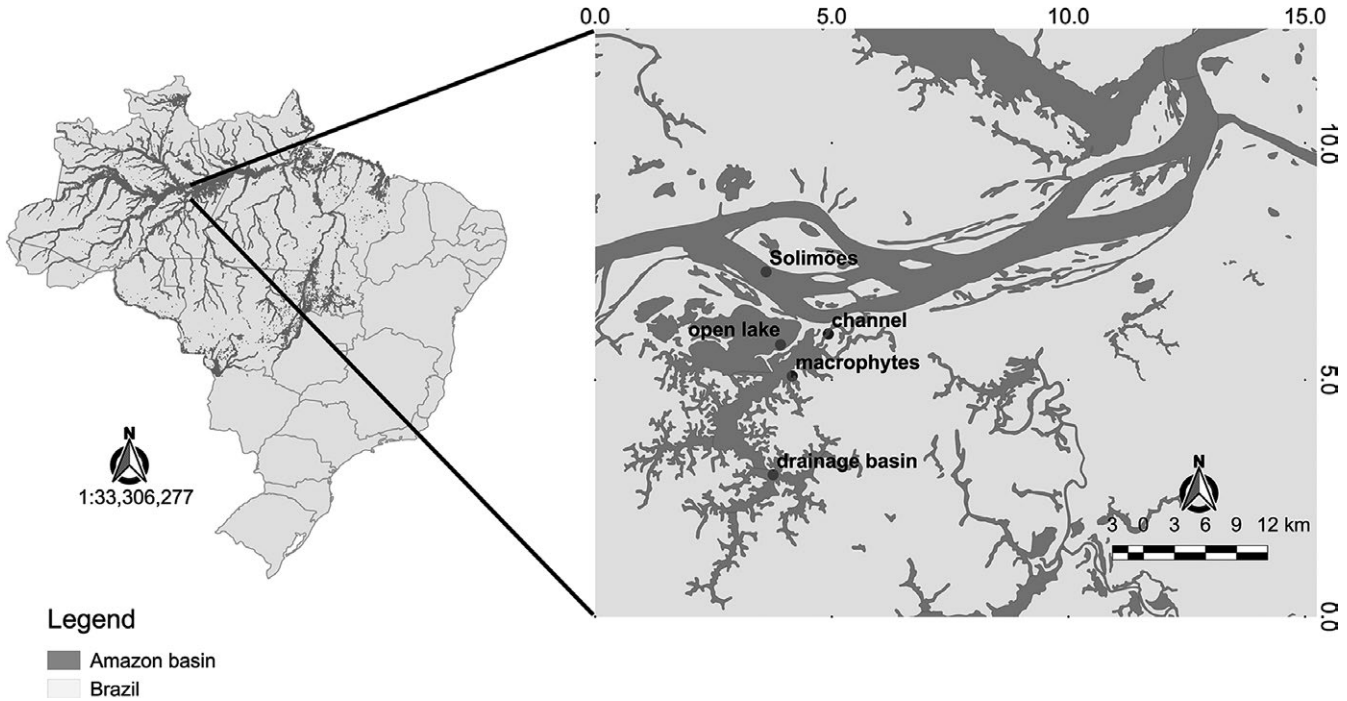

FIGURE 1 Map of the study area Lake Janauacá showing sampling sites: open lake, drainage basin, macrophytes, channel, Solimões. This map represents the lake in the high-water period

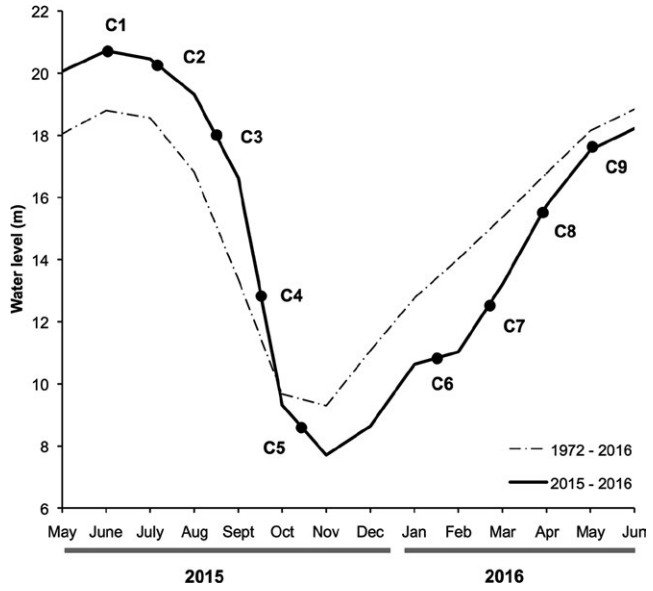

FIGURE 2 Dashed line shows the historical water level (m) based on 44 years of daily records for the Solimões River at the Manacapuru gauging station. Solid line represents mean monthly water levels from May 2015 to June 2016. Numbers indicate campaigns that took place in different periods of the flood pulse, grouped as: high (Campaigns C1, C2), falling (C3, C4, C5) and rising (C6, C7, C8, C9) water periods. Source: Brazilian National Agency of Waters (http://www.snirh.gov.br/hidroweb/)

metric ruler fixed in a series of wood frames distributed along the channel banks.

Samples for chemical analyses were stored in clean insulated flasks kept in thermal boxes until processing (for a maximum of 4 hr). Water for chlorophyll-*a* (Chl-*a*) was filtered through Whatman® GF/F filters using a vacuum pump and the filters were frozen and stored in the dark until analysis. Chl-*a* was determined spectrophotometrically, following filter maceration and extraction in 90% acetone (Wetzel & Likens, 2000). For TSS. we weighed the filters (Millipore® 0.45 μm pore size) before and after filtration, once dried at 60°C, and used the subtracted value (in mg) per litre of water volume filtered.

For BCC, lake water was filtered sequentially though 3 μm (Whatman® Nucleopore, UK; particle-attached fraction—PA) and 0.2 μm pore-size, 47 mm diameter (Millipore® Isopore, USA; free-living fraction—FL) and DNA samples were stored at −20°C in the field station and subsequently at −80°C in the laboratory. Total DNA was extracted directly from the filters using phenol–chloroform extraction followed by purification in Amicon columns (Millipore® 100KDa/100.000MWCO). We were not able to extract high-quality DNA from our samples with the widely used MoBio PowerSoil DNA isolation kit (MO BIO Laboratories, Inc, Carlsbad, CA, USA), probably because of the humic-rich nature of Amazonian waters. An additional purification step with 10% cetyl trimethyl ammonium bromide (CTAB) was carried out for a few samples where necessary (samples 1FL, 4PA) to remove humic substances (Schneegurt, Dore, & Kulpa, 2003), when the extract was not susceptible to polymerase chain reaction (PCR) amplification.

2.3 | DNA amplification and sequencing

The V3/V4 region of the 16rRNA gene was amplified with the bacterial primers 341F (5′-CCTACGGGNGGCWGCAG-3′) and 805R (5′-GACT ACHVGGGTATCTAATCC-3′) (Herlemann et al., 2011). PCRs were performed twice in a 25 μl reaction volume containing 12.5 μl of KAPA High-fidelity Hotstart ready mix (KAPA Biosystems, Boston, MA, USA), 0.3 μM of each primer (forward and reverse), 10 μl of PCR-grade water, and 10 ng of DNA. Reactions were started with an initial step of 95°C for 3 min, followed by 25 cycles of 98°C for 20 s, 62°C for 15 s, 72°C for 15 s and finally 72°C for 60 s.

Subsequently, PCR products were purified with magnetic beads AMPURE XP kit (Beckman Coulter) and indexed with Nextera XT kit V2 (Illumina, Inc, San Diego, CA, USA). An additional step of purification with magnetic beads was performed, and then a combined pool was prepared by mixing 5 μl from each library. High-throughput sequencing was performed on an Illumina Miseq2000 instrument (Laboratório Multiusuário Centralizado para Sequenciamento de DNA em Larga Escala e Análise de Expressão Gênica, Univerdade Estadual Paulista, Jaboticabal, SP, Brazil). All sequences were submitted to the BioSample database (https://www.ncbi.nlm.nih.gov/sra/SRP127556).

2.4 | Sequence processing and exploratory analyses

We performed the quality filtering, denoising and removal of potential chimeras and non-bacterial sequences using UPARSE (Edgar, 2013) in a previously implemented pipeline (Logares, 2017; Logares et al., 2014). Paired-end reads were merged with PEAR (Zhang, Kobert, Flouri, & Stamatakis, 2014). All sequences shorter than 100 bp (base pairs) were discarded and the full-length dereplication was carried out with USEARCH. Merged sequences were clustered into operational taxonomic units using UPARSE, applying a threshold of 97% identity (Quast et al., 2012). Chimeric sequences were filtered out with USEARCH (Edgar, 2010). Taxonomic classification was done with BLASTn against SILVA 119.1 (Zhang & Fang, 2000) with at least 75% of similarity. For further analyses, all chloroplasts and Archaea sequences were removed and to enable comparisons between samples, the OTU table was randomly subsampled (rarefied) based on the sample with the least number of reads (10,341 sequences). Then, we calculated the relative abundance by dividing the number of reads of each OTU by the total number of reads in each rarefied sample (10,341).

To assess the effect of environmental variables (log transformed) on channel BCC we used the distance-based redundancy analysis (dbRDA) based on Bray–Curtis dissimilarity measure. Hypotheses about differences in the structure of bacterial communities between FL and PA and among seasons were evaluated using permutational multivariate analysis of variance (PERMANOVA) and the results visualised using ordination (non-metric multidimensional scaling).

All data analyses were carried out in R version 3.3.3 (R Core Team, 2016) using the R package vegan (Oksanen et al., 2015). Figures were drawn using the package ggplot2 (Wickham, 2009).

2.5 | Identifying the sources of dispersing bacterial

To identify and determine the contribution of a set of sources to the bacterial community in the channel (sink) we used a Bayesian approach. Analyses were conducted in SourceTracker 0.9.5 software with MacQIIME (version 1.9.1, Knights et al., 2011). For each campaign, we ran a different model with a specific set of sinks and sources, considering also the size fraction (FL and PA), resulting in four models: FL fraction in falling (campaign 4—model 1) and rising waters (campaigns 6, 7 and 9, models 2, 3 and 4, respectively). The same procedure was used for the PA size fraction: PA fraction in falling (campaign 4—model 1) and rising waters (campaigns 6, 7 and 9, models 2, 3 and 4, respectively). For all models (FL and PA), the sink was always the bacterial community in the channel and the potential sources were: the resident communities sampled at the same site during the preceding campaign (e.g. for campaign 4, the preceding community was that collected during campaign 3), or bacterial communities sampled in macrophyte banks (ma), open lake (la), drainage basin (ba), Solimões River (sol) or unknown sources.

2.6 | Differences in BCC between seasons

A group significance test was used to compare the number of reads of various taxonomic levels in sample groups and to check whether they were significantly different (Kropf, Heuer, Grüning, & Smalla, 2004). The tests were performed in MacQiime (script group_significance.py—http://qiime.org/scripts/group_significance.html) using rarefied tables to compare all taxonomic levels (Phylum, Class, Order, Family and Genus) between fractions (PA and FL) and among seasons (high, falling and rising waters) in channel samples. Firstly, we removed taxa that were not present in at least 10% of our samples. Subsequently, the group significance test showed which taxa were differentially represented in each group based on a Kruskal–Wallis test, and calculated a p value corrected (using the Benjamini-Hochberg false discovery rate procedure) for multiple comparisons. We considered p-values ≤ 0.1 as significantly different. We did not consider unclassified taxa in this analysis.

3 | RESULTS

3.1 | Tracking sources of bacteria during the flood pulse

The sampling design had a good coverage of the possible sources of dispersal to the bacterial communities observed in the channel, as the proportion of unknown sources was low, averaging <7.5% (excepting model 1—PA fraction with 16.7% from unknown sources). Bacterial dispersal sources, as well as their contributions to the sink communities varied according to the size fraction and season (Table 1, Figure 3).

The sources for the BCC observed at the Lake channel were more diverse during the falling water period (campaign 4) than in other periods. The lowest source-diversity was registered during the rising water period.

During the falling water period, the drainage basin had the largest contribution to BCC in both PA and FL, followed by the open lake. The previous community and Solimões River were important sources for PA but not FL communities (Table 1), whereas during the rising water period (campaigns 6, 7 and 9), we observed only a few dominant sources. Firstly, the contribution from Solimões River increased for both PA and FL. In contrast, open lake, macrophytes and drainage basin communities had no or very low contributions to the sink for both PA and FL. The contribution of the previous community was especially high in campaign 7.

3.2 | Environmental variables and their relationship with bacterial communities

The flood pulse clearly affected the physical and chemical properties of the channel water (Supporting Information Table S2). The high-water period was characterised by increased water level and decreased DO (average of 1.76 mg/L). During this period, we registered low concentrations of TSS, intermediate Chl-*a* concentrations (3.73 and 16.2 μg/L, compared with the maximum and minimum 65.26 and 0.90 μg/L, respectively; Supporting Information Table S2) and higher water transparency (Secchi depth > 1 m) compared to the other periods investigated. During the falling water period, Chl-*a* concentration reached the annual maximum value (65.26 μg/L) in our study. Consequently, DO concentrations increased slowly from campaign 4 to reach a maximum value at the end of the season (campaign 5). During the rising water, conductivity and TSS increased to values ranging between 48.7 and 72.1 μS/cm and 102 to 162 mg/L, respectively. In contrast, water transparency and Chl-*a* concentrations reached their lowest annual values during this period (average Secchi disk depth of 14 cm and Chl-*a* *c.* 2.5 μg/L). DO concentrations decreased again towards the end of the rising water period (campaigns 8 and 9).

The dbRDA model with temperature, pH, DO, Chl-*a*, conductivity, Secchi and water level (Figure 4, note that TSS was excluded because it was correlated with conductivity) explained 72% of the variation in channel BCC for all campaigns and size fractions (all seven axes, constrained proportion = 0.72) in the channel site. Most variation was explained by the first and second axes (CAP1 = 35.5%; CAP2 = 15.6%). Campaigns 1, 2 and 3 (both PA and FL) were grouped together and were associated with lower temperatures and high-water level (Figure 4). At the beginning of the falling water period (campaign 3), an inverse relationship with low DO concentrations was observed. Campaigns 4 and 5 were grouped together and were positively related with transparency and Chl-*a* concentrations. During early rising water, campaigns 6 and 7 were positively associated with DO concentrations and high temperatures. Samples from the end of the rising waters (campaigns 8 and 9), were positively related with pH, conductivity, DO and low transparency.

3.3 | Features of Amazonian bacterioplankton

BCC in the channel varied throughout the year, with a clear seasonal pattern partitioning the communities into three different groups

TABLE 1 Results from Source-Tracker analysis showing the contribution of different sources to the sink (channel community) in both size fractions (free-living [FL] and particle-attached [PA]) across four campaigns (falling 4, rising 6, 7 and 9)

Model	Season	Sources	Sink: channel FL Contribution (%)	Sink: channel PA Contribution (%)
1	Falling 4	Previous PA	0.3	10.3
		Previous FL	0.2	8.8
		Drainage basin PA	8.9	23.6
		Drainage basin FL	49.8	0.7
		Open lake PA	2.7	9.8
		Open lake FL	25.5	9.0
		Macrophytes PA	4.0	0.0
		Macrophytes FL	0.0	3.8
		Solimões PA	0.2	12.7
		Solimões FL	3.9	4.9
		Unknown	4.6	16.7
2	Rising 6	Previous PA	10.7	11.1
		Previous FL	0.0	0.3
		Macrophytes PA	0.0	0.0
		Macrophytes FL	0.2	0.1
		Solimões PA	52.8	60.5
		Solimões FL	29.9	21.7
		Unknown	6.5	6.4
3	Rising 7	Previous PA	23.7	42.6
		Previous FL	14.3	28.2
		Drainage basin PA	0.0	0.0
		Drainage basin FL	6.1	0.6
		Open lake PA	0.0	0.0
		Open lake FL	0.0	0.0
		Macrophytes PA	0.0	0.0
		Macrophytes FL	0.0	0.0
		Solimões PA	48.7	24.3
		Solimões FL	0.0	0.0
		Unknown	7.2	4.3
4	Rising 9	Previous PA	5.8	8.6
		Previous FL	14.5	24.4
		Drainage basin PA	0.0	0.1
		Drainage basin FL	0.0	0.0
		Open lake PA	0.0	0.0
		Open lake FL	0.0	0.0
		Macrophytes PA	0.1	0.4
		Solimões PA	20.3	14.6
		Solimões FL	55.3	44.7
		Unknown	3.9	7.4

(Figure 5). These groups were high water (campaigns 1 and 2), falling water (campaigns 3–5) and rising water periods (campaigns 6–9; Figures 2 and 5). In contrast, BCC in FL and PA fractions were not separated in the non-metric multidimensional scaling bidimensional plot (Figure 5). This was confirmed by the PERMANOVA analysis, where seasons were strongly associated with patterns in BCC, explaining 45% of the variation ($R^2 = 0.45$, $p \leq 0.001$), but size fractions (FL versus PA) did not differ.

Few differences were observed between FL and PA fractions, but there were clear seasonal patterns for several phyla (Figure 6). Phyla Actinobacteria, Proteobacteria (classes Alpha-, Beta-, Gammaproteobacteria), Planctomycetes and Cyanobacteria had

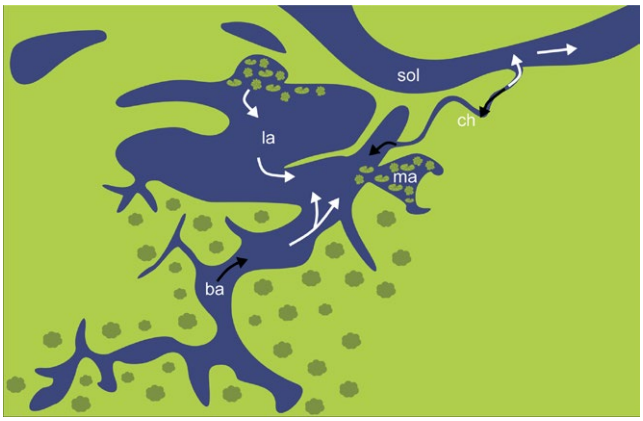

FIGURE 3 Schematic illustration of Lake Janauacá showing the sink (ch) and dispersal sources. The white arrows indicate the typical water flux dynamics in falling water and the black arrows in rising water periods. ba, drainage basin; ch, channel; ma, macrophytes; sol, Solimões; la, open lake

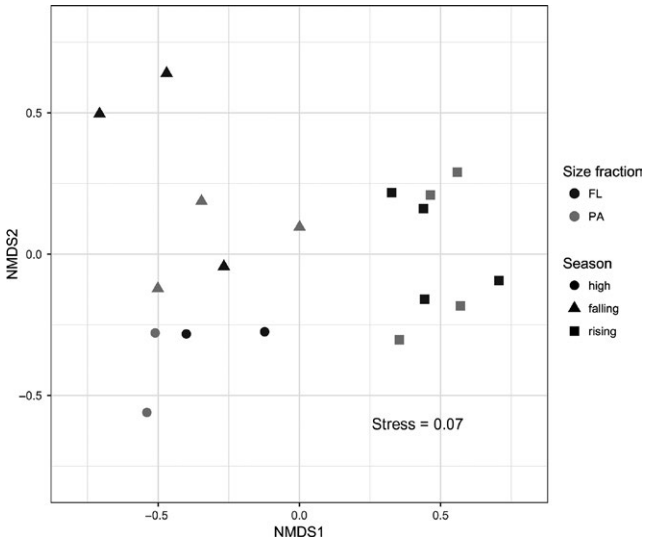

FIGURE 5 Two-dimensional plot of non-metric multidimensional scaling (NMDS) ordination of bacterial operational taxonomic units in the channel. Symbols shape are indicating seasons, high, falling and rising water periods, and colours (grey and black) are indicating the size fraction, free-living (FL) and particle-attached (PA)

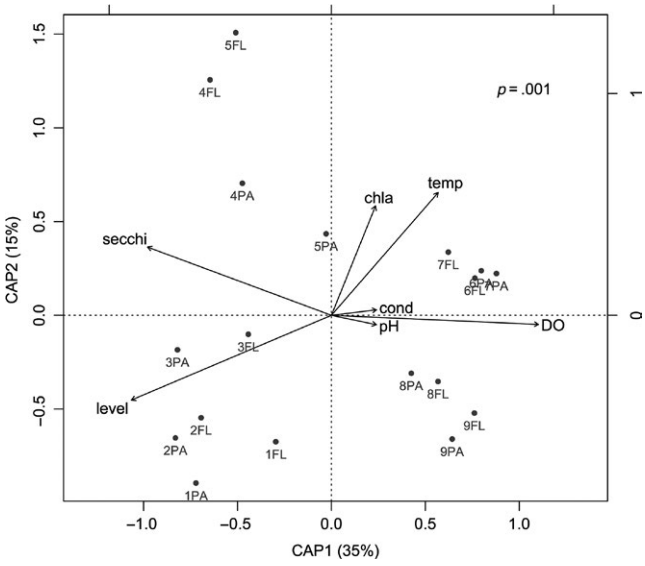

FIGURE 4 Distance-based redundancy analysis of operational taxonomic units in bacterial communities and environmental variables at the channel site. Samples are identified with the number of the campaign and the size fraction, free-living (FL) and particle-attached (PA). DO, dissolved oxygen; cond, electrical conductivity; temp, water temperature; chl-*a*, chlorophyll-*a*; level, water level

the highest relative abundances on all campaigns, accounting for at least 75% of the total community (Figure 6). Other phyla such as Chloroflexi, Verrucomicrobia, Acidobacteria, Bacteriodetes and Parcubacteria fluctuated seasonally. Saccharibacteria, Firmicutes, Armatimonadetes, Gemmatimonadetes and Chlorobi had relative abundances typically ranging from 0.1 to 1%.

PA and FL fractions did not differ in taxonomic composition (as also pointed out in the community analyses). However, there were seasonal differences for both fractions for all taxonomic levels (phylum, class, order, family and genus; Supporting Information Table S3). We found two main patterns: (a) Taxa with significant differences for more than one taxonomic level due to their dominance. For example, *Synechococcus* was an overrepresented genus in our samples, especially during the falling water period. This pattern was also reflected at other levels—*family I*, order *Subsection I*, class and phylum *Cyanobacteria*. (b) Taxa with significant differences for only one taxonomic level. This was the case for the genus *Planctomyces*, which was overrepresented in high water but with no significant differences manifested at higher taxonomic ranks. We found significant differences in the seasonal pattern at different taxonomic levels in the following phyla: Cyanobacteria, Actinobacteria, Proteobacteria (Alpha, Beta and Gamma), Planctomycetes, Verrucomicrobia, Armatimonadetes and Chlorobi.

The phylum Armatimonadetes, the genus *Planctomyces*, classes Alphaproteobacteria (most represented by the family Methylocystaceae) and Gammaproteobacteria (most represented by the family Methylococcales) were significantly overrepresented at high water (Supporting Information Table S3). In contrast, Cyanobacteria (genus *Synechococcus* and *Merismopedia*) and Chlorobi were significantly more highly represented during falling water. Members of Verrucomicrobia (genus *Opitutus*) and Betaproteobacteria (family Comamonadaceae were significantly overrepresented during rising water compared to other seasons (Supporting Information Table S3).

Overall, Actinobacteria tended to be the phylum with highest relative abundances across all samples, but also increased during rising water, mostly related to an increase in the *AcI clade (hgcI)*. In contrast, the Actinobacteria class Thermoleophilia and Acidimicrobiia were overrepresented during falling water.

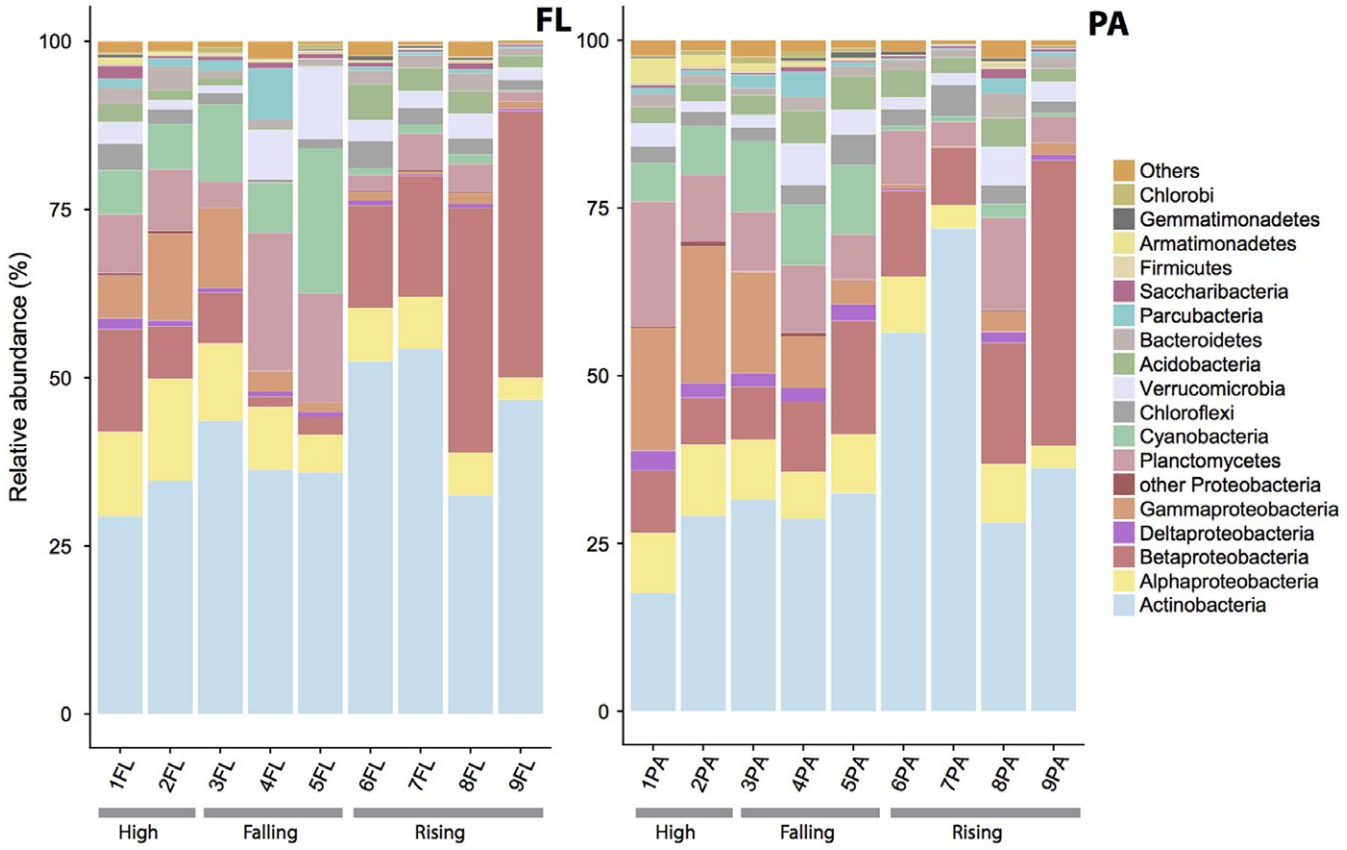

FIGURE 6 Average relative abundance (%) of the main phyla in the channel's bacterial community in each campaign, 1–9 in free-living (FL) and particle-attached (PA) communities. Note that *Proteobacteria* are divided among *Alphaproteobacteria*, *Betaproteobacteria*, *Deltaproteobacteria*, *Gammaproteobacteria* and other *Proteobacteria*

4 | DISCUSSION

We evaluated the mechanisms that shaped BCC in this AFL and tracked the main dispersal sources of microorganisms, considering the whole river–floodplain system in different phases of the annual hydrological cycle. We found that different bacterial sources contributed to the BCC over the year and that the importance of each source was related to the specific stage of the hydrological cycle. The changes triggered by the flood pulse shifted environmental conditions, which in turn altered dispersing bacterial communities.

4.1 | Tracking sources of bacteria along the flood pulse

A water balance for the fluxes between the mainstream (Solimões River) and Lake Janauacá, revealed that the contribution of different water inputs varied seasonally with contributions from more diverse inputs during the rising water period (Bonnet et al., 2017). Considering a complete annual cycle, the Solimões River was the main source of water to the lake (*c.* 87%), followed by upland water from the drainage watershed (1–9%). Ground water (<1%) and direct precipitation (<5%) had lower contributions. During the low water and early rising water periods, local waters and water remaining from the previous year were the main components of the lake. Their relative contribution to the water budget decreased as Solimões River water entered the lake through the channel (Bonnet et al., 2017). Therefore, dispersal sources were expected to contribute differently throughout the year because of changes in water flow. For bacterial communities, our models revealed a greater contribution from a more diverse range of dispersal sources during the falling water period. The main explanation for this pattern is the direction of water flow during this period, flowing from the southern portion (draining basin) to the river through the channel. BCC from different habitats located in the watershed could be transported by flow into the channel and subsequently to the main river. At this stage, the lake was a probable source of nutrients, organic matter and bacterial taxa for the river. When the water was flowing in the opposite direction with the Solimões feeding the lake, the main source of water to the lake was the main river and the inputs from the local watershed became less important. At this stage we observed an increase in the contribution of Solimões bacterial dispersal sources.

Previous studies reported the directional structuring of BCC along the gradient of the river continuum, with a loss of abundant taxa from headwaters and a decreased taxonomic richness downstream (Ruiz-González, Niño-García, Berggren, & del Giorgio, 2017; Ruiz-González et al., 2015). Here, we found that the flood pulse controlled not only the transport downstream, but also lateral exchange between the main river (Solimões) and the associated floodplain lake

(Janauacá). These results suggest that all systems in this complex landscape (and their microbiomes) are linked by water flows and driven by river flood-pulses, promoting exchange and dispersal at least during some periods of the hydrological cycle.

An earlier study in two boreal lakes showed that the most important source of bacteria was the previous (resident) community, while all other dispersal sources (sediments, inlets, the other strata of the lake and precipitation) appeared to have limited immediate effects on the community (Comte et al., 2017). These results suggested that species sorting was more important than dispersal in those lakes. In contrast, we observed that the previous community contributed significantly as a source only during rising water (campaigns 7, 9). Rising water led to longer water residence time (Bonnet et al., 2017; this study), and this provided more time for bacterial communities to adapt to local conditions and persist in the lake, leading to a higher contribution by previous communities as a source. With increased river discharge and water level, resident bacteria are flushed from the system and dispersing bacteria are exposed to environmental filtering by the new local conditions.

Although the proportion of unknown sources was very low, these sources may represent soil bacteria that enter the system during flooding and that are not filtered by species sorting at that time. Soil bacteria are known to be important sources for downstream temperate aquatic habitats (Crump, Amaral-Zettler, & Kling, 2012; Ruiz-González et al., 2015). While this topic has not been explored in tropical river systems and floodplains, we know that the flood pulse is a strong force in controlling the linkage between aquatic and terrestrial systems (through the formation of aquatic/terrestrial transition zones (Junk, Bayley, & Sparks, 1989) and further research is required to fully describe this relationship.

Even in periods with high densities (for example, June, July and January), macrophytes were not an important source of dispersal to the bacterial community in the channel in any of our models. Special chemical and physical conditions in these microhabitats create an environmental filter that hinders the colonisation of non-adapted bacterial taxa. Additionally, there are highly diverse and host-specific BCC forming biofilms attached to plants (Crump & Koch, 2008; Pang et al., 2016; Zhao et al., 2017) that may be less susceptible to transport to surrounding waters.

Here, we found that dispersal processes had a predominant role in shaping BCC in the highly connected hydrological network of the Lake Janauacá. Considering the dynamic hydrology and hydraulic flows in AFLs (e.g. Bonnet et al., 2017; Lesack & Melack, 1995) and that the flux is not directional, a more complex conceptual framework is needed, where the main river is also an important lateral bacterial source to floodplain systems and to the exchange of microorganisms throughout the annual hydrological cycle.

4.2 | Seasonal variations in environmental conditions and BCC

The flood pulse produces changes in riverine systems four-dimensionally (in space and time), affecting biogeochemical cycles, productivity, animal and plant distributions and interactions (Ferreira, 1997; Oliveira & Calheiros, 2000; Thomaz, Bini, & Bozelli, 2007). Despite this understanding, little is currently known about how bacterioplankton responds to the flood pulse. We observed a clear seasonal pattern in environmental variables followed by changes in BCC. Seasonal patterns in BCC are well documented in some temperate aquatic systems, where temperature appears to be the main force shaping BCC (Poretsky, Rodriguez-R, Luo, Tsementzi, & Konstantinidis, 2014; Rösel, Allgaier, & Grossart, 2012; Staley et al., 2015). However, few comparable studies have been carried out in tropical systems (Doherty et al., 2017; de Oliveira & Margis, 2015) so it remains unclear whether temperature is also the driving force there.

The low DO concentration found during the high-water period is related to the flooding of large lateral areas and the increased surface area of aquatic vegetation subjected to sedimentation, decomposition and planktonic respiration which reduces DO (Devol, Forsberg, Richey, & Pimentel, 1995). Also, daily stratification is commonly observed in the Amazon region due to slight and temporary changes in water temperature and density (Lewis, 1987; Sarmento, 2012; Tundisi et al., 1984) that could contribute to these low DO concentrations. These conditions may have facilitated the establishment of bacteria belonging the families Methylocystaceae (Alphaproteobacteria) and Methylococcaceae (Gammaproteobacteria). Both are obligate methanotrophs that play an important role as biological filters for methane emissions, supporting high rates of biological methane oxidation, as previously reported for Lake Janauacá (Barbosa et al., 2018).

During the falling water period, depth decreased and the water column mixed, allowing nutrient remobilisation from bottom waters and sediments, which culminated in phytoplankton proliferation and an increase in DO concentrations (rapid increase in Chl-*a* concentrations). The relative abundance of photoautotrophs such as *Cyanobacteria* (e.g. genus *Synechococcus* and *Merismopedia*) and *Chlorobi* increased although cyanobacteria are important community members in Lake Janauacá all year round.

Synechococcus was amongst the most abundant genera in our study, being significantly overrepresented in communities during falling water. This genus also had high relative abundances in other AFLs (Toyama et al., 2017), but not in rivers (Doherty et al., 2017; Toyama et al., 2017). High temperatures and the food-web structure of tropical aquatic environments enhance the contribution of these phototrophic picoplankton to primary production (Domingues et al., 2017; Sarmento, 2012). This is due to their higher surface:volume ratio compared to larger phytoplankton cells, which confers an advantage under the oligotrophic conditions common in Amazon waters (Lewis, 1976).

The genus *Planctomyces* (phylum *Planctomycetes*) also featured higher relative abundances during the falling water period. They are found in many aquatic and terrestrial environments but are usually not very abundant in oxic freshwater ecosystems (Newton, Jones, Eiler, McMahon, & Bertilsson, 2011). Members of Planctomycetes together with other quite abundant phyla found here (Betaproteobacteria, Gammaproteobacteria and Verrucomicrobia)

have been reported in association with cyanobacteria blooms in tropical lakes (Woodhouse et al., 2016).

During the rising water period the expansion of flooded areas increases inputs of allochthonous materials from the river and surrounding areas into AFLs (Melack & Forsberg, 2001; Moreira-Turcq et al., 2013). As a consequence, the terrestrial genus *Opitutus* (Verrucomicrobia) probably entered the lake with a temporary increase in relative abundance. At that moment, the high TSS concentration in the turbid Solimões River flowing into the lake had a direct impact on water transparency, which resulted in a drop in cyanobacteria and Chl-*a* concentrations, also reported in other AFLs (Barbosa, de Moraes Novo, Melack, Gastil-Buhl, & Filho, 2010; Forsberg et al., 2017).

Although differences between PA and FL fractions are commonly observed (Jackson, Millar, Payne, & Ochs, 2014; Savio et al., 2015), other Amazon studies have not shown such differences (Doherty et al., 2017; Satinsky et al., 2015), and we did not find differences in BCC between FL and PA size fractions here (supported by any of the statistical tests performed). These results could be result from the pore-size of the filters used, which may have been inadequate to separate the full range of particle size in Amazon waters. The concentrations and sizes of particulate and colloidal organic matter in Amazon basin is variable and depends on the system and season analyzed (Benedetti, Ranville, Ponthieu, & Pinheiro, 2002; Hedges et al., 2000). For example, the average concentration of fine particulate organic matter (0.1–63 μm) was six times higher than the coarse particulate concentrations (>63 μm) in the Amazon River during a low water period (Hedges et al., 2000). Here, we used 3-μm membrane filters and we acknowledge that this may have been too large a pore-size to separate smaller particles with bacteria attached from their FL counterparts. We did not test other filter pore sizes here, but we recommend their use to investigate size-specific patterns in future studies.

Overall, despite growing interest and efforts to study the composition of aquatic bacterial communities, the ecology and function of many components of the microbiota are still largely unknown, especially in structurally complex and inaccessible systems such as the Amazon. This makes it difficult to characterise seasonal and spatial patterns in the BCC. From our results, it is clear that the flood pulse controls fluxes of water and materials and environmental conditions that ultimately influence bacterial community assembly. In our metacommunity approach, dispersal processes were predominant and hydrology was the main driving force controlling the contribution of different bacterial sources to the sink community through the year. Lateral exchange with the main river was an important mechanism shaping BCC in the studied AFL, shown by its increased contribution during the rising water period. In addition, changes in environmental conditions during the flood pulse appeared to determine the successful establishment of dispersing bacteria, which showed seasonal differences at all taxonomic levels (from phylum to genus). In conclusion, our study presents strong evidence that bacterial dispersal between local communities plays a large role in highly connected hydrological networks like Amazonian floodplain–river systems and reinforces the need for further studies.

ACKNOWLEDGMENTS

Financial support was provided by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP - process 2014/14139-3) and Conselho Nacional de Desenvolvimento e Pesquisa Tecnológica (CNPq/LBA-Edital.68/2013 – process 458036/2013-7 and CNPq-Universal – process 482004/2012-6), and the Swedish Research Council (grant to S.B.). H.S.'s work was supported by CNPq (grant 309514/2017-7). Post-graduate scholarships were provided to MLM, JHFA and PMB by CNPq and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). M.L.M. is thankful to Uppsala Universitet for receiving her as a guest PhD student at the Limnology Program and CAPES for the grant "Programa de Doutorado Sanduíche no Exterior – 88881.132280/2016-01" and to Dr Eva Lindström and Dr Yianghua Zha for valuable analysis suggestions. The authors would like to thank Universidade Estadual Paulista – UNESP, Laboratório Multiusuário Centralizado para Sequenciamento de DNA em Larga Escala e Análise de Expressão Gênica for DNA sequencing (process 2009/53984-2 and 2016/07679-7). We also thank Instituto Nacional de Pesquisas na Amazônia (INPA) for the logistical support, João B. Rocha and Jonismar Sousa da Silva for the field support and Laboratório de Ficologia – UFSCar for laboratory infrastructure (Dr Inessa Bagatini).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Michaela L. de Melo http://orcid.org/0000-0002-8545-4153

REFERENCES

Abril, G., Martinez, J. M., Artigas, L. F., Moreira-Turcq, P., Benedetti, M. F., Vidal, L., … Roland, F. (2014). Amazon River carbon dioxide outgassing fuelled by wetlands. *Nature*, *505*, 395–398. https://doi.org/10.1038/nature12797

Barbosa, C. C. F., de Moraes Novo, E. M. L., Melack, J. M., Gastil-Buhl, M., & Filho, W. P. (2010). Geospatial analysis of spatiotemporal patterns of pH, total suspended sediment and chlorophyll-a on the Amazon floodplain. *Limnology*, *11*, 155–166. https://doi.org/10.1007/s10201-009-0305-5

Barbosa, P. M., Farjalla, V. F., Melack, J. M., Amaral, J. H. F., da Silva, J. S., & Forsberg, B. R. (2018). High rates of methane oxidation in an Amazon floodplain lake. *Biogeochemistry*, *137*, 351–365. https://doi.org/10.1007/s10533-018-0425-2

Benedetti, M., Ranville, J. F., Ponthieu, M., & Pinheiro, J. P. (2002). Field-flow fractionation characterization and binding properties of particulate and colloidal organic matter from the Rio Amazon and Rio Negro. *Organic Geochemistry*, *33*, 269–279. https://doi.org/10.1016/S0146-6380(01)00159-0

Bonnet, M. P., Pinel, S., Garnier, J., Bois, J., Resende Boaventura, G., Seyler, P., & Motta Marques, D. (2017). Amazonian floodplain water balance based on modelling and analyses of hydrologic and electrical conductivity data. *Hydrological Processes*, *31*, 1702–1718. https://doi.org/10.1002/hyp.11138

Comte, J., Berga, M., Severin, I., Logue, J. B., & Lindstrom, E. S. (2017). Contribution of different bacterial dispersal sources to lakes: Population and community effects in different seasons. *Environmental Microbiology*, *19*, 2391–2404. https://doi.org/10.1111/1462-2920.13749

Cotner, J. B., & Biddanda, B. A. (2002). Small players, large role: Microbial influence on biogeochemical processes in pelagic aquatic ecosystems. *Ecosystems*, *5*, 105–121. https://doi.org/10.1007/s10021-001-0059-3

Crump, B. C., Amaral-Zettler, L. A., & Kling, G. W. (2012). Microbial diversity in arctic freshwaters is structured by inoculation of microbes from soils. *ISME Journal*, *6*, 1629–1639. https://doi.org/10.1038/ismej.2012.9

Crump, B. C., & Koch, E. W. (2008). Attached bacterial populations shared by four species of aquatic angiosperms. *Applied and Environmental Microbiology*, *74*, 5948–5957. https://doi.org/10.1128/AEM.00952-08

Devol, A. H., Forsberg, B. R., Richey, J. E., & Pimentel, T. P. (1995). Seasonal variation in chemical distributions in the Amazon (Solimões) River: A multiyear time series. *Global Biogeochemical Cycles*, *9*, 307–328. https://doi.org/10.1029/95GB01145

Doherty, M., Yager, P. L., Moran, M. A., Coles, V. J., Fortunato, C. S., Krusche, A. V., … Crump, B. C. (2017). Bacterial biogeography across the Amazon River–ocean continuum. *Frontiers in Microbiology*, *8*, 882. https://doi.org/10.3389/fmicb.2017.00882 https://doi.org/10.3389/fmicb.2017.00882

Domingues, C. D., da Silva, L. H. S., Rangel, L. M., de Magalhães, L., de Melo Rocha, A., Lobão, L. M., … Sarmento, H. (2017). Microbial food-web drivers in tropical reservoirs. *Microbial Ecology*, *73*, 505–520. https://doi.org/10.1007/s00248-016-0899-1

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*, *26*, 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Edgar, R. C. (2013). UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nature Methods*, *10*, 996–998. https://doi.org/10.1038/NMETH.2604

Ferreira, L. V. (1997). Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jau′ National Park in floodplain forests in central Amazonia. *Biodiversity & Conservation*, *6*, 1353–1363. https://doi.org/10.1023/a:1018385529531

Forsberg, B. R., Melack, J. M., Richey, J. E., & Pimentel, T. P. (2017). Regional and seasonal variability in planktonic photosynthesis and planktonic community respiration in Amazon floodplain lakes. *Hydrobiologia*, *800*, 187–206. https://doi.org/10.1007/s10750-017-3222-3

Ghai, R., Rodriguez-Valera, F., McMahon, K. D., Toyama, D., Rinke, R., de Oliveira, T. C. S., … Henrique-Silva, F. (2011). Metagenomics of the water column in the pristine upper course of the Amazon River. *PLoS ONE*, *6*, e23785. https://doi.org/artn e2378510.1371/journal.pone.0023785

Hedges, J. I., Mayorga, E., Tsamakis, E., McClain, M. E., Aufdenkampe, A., Quay, P., … Maurice, L. (2000). Organic matter in Bolivian tributaries of the Amazon River: A comparison to the lower mainstream. *Limnology and Oceanography*, *45*, 1449–1466. https://doi.org/10.4319/lo.2000.45.7.1449

Herlemann, D. P. R., Labrenz, M., Jurgens, K., Bertilsson, S., Waniek, J. J., & Andersson, A. F. (2011). Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *ISME Journal*, *5*, 1571–1579. https://doi.org/10.1038/ismej.2011.41

Humbert, J. F., Dorigo, U., Cecchi, P., Le Berre, B., Debroas, D., & Bouvy, M. (2009). Comparison of the structure and composition of bacterial communities from temperate and tropical freshwater ecosystems. *Environmental Microbiology*, *11*, 2339–2350. https://doi.org/10.1111/j.1462-2920.2009.01960.x

Jackson, C. R., Millar, J. J., Payne, J. T., & Ochs, C. A. (2014). Free-living and particle-associated bacterioplankton in large rivers of the Mississippi River basin demonstrate biogeographic patterns. *Applied and Environmental Microbiology*, *80*, 7186–7195. https://doi.org/10.1128/AEM.01844-14

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. In D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium* (pp. 110–127). Ottawa: Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences.

Knights, D., Kuczynski, J., Charlson, E. S., Zaneveld, J., Mozer, M. C., Collman, R. G., … Kelley, S. T. (2011). Bayesian community-wide culture-independent microbial source tracking. *Nature Methods*, *8*, 761–763. https://doi.org/10.1038/nmeth.1650

Kropf, S., Heuer, H., Grüning, M., & Smalla, K. (2004). Significance test for comparing complex microbial community fingerprints using pairwise similarity measures. *Journal of Microbiological Methods*, *57*, 187–195. https://dx.doi.org///doi.org/10.1016/j.mimet.2004.01.002

Langenheder, S., & Ragnarsson, H. (2007). The role of environmental and spatial factors for the composition of aquatic bacterial communities. *Ecology*, *88*, 2154–2161. https://doi.org/10.1890/06-2098.1

Langenheder, S., & Szekely, A. J. (2011). Species sorting and neutral processes are both important during the initial assembly of bacterial communities. *ISME Journal*, *5*, 1086–1094. https://doi.org/10.1038/ismej.2010.207

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., … Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lemke, M. J., Lienau, E. K., Rothe, J., Pagioro, T. A., Rosenfeld, J., & DeSalle, R. (2009). Description of freshwater bacterial assemblages from the Upper Parana River floodpulse system, Brazil. *Microbial Ecology*, *57*, 94–103. https://doi.org/10.1007/s00248-008-9398-3

Lesack, L. F., & Melack, J. M. (1995). Flooding hydrology and mixture dynamics of lake water derived from multiple sources in an Amazon floodplain lake. *Water Resources Research*, *31*, 329–345. https://doi.org/10.1029/94WR02271

Lewis, W. M. J. (1976). Surface/volume ratio: Implications for phytoplankton morphology. *Science*, *192*, 885–887. https://doi.org/10.1126/science.192.4242.885

Lewis, W. M. (1987). Tropical limnology. *Annual Review of Ecology and Systematics*, *18*, 159–184. https://doi.org/10.1146/Annurev.Ecolsys.18.1.159

Lindstrom, E. S., & Langenheder, S. (2012). Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports*, *4*, 1–9. https://doi.org/10.1111/j.1758-2229.2011.00257.x

Logares, R. (2017, January 25). ramalok/amplicon_processing: Workflow for Analysing MiSeq Amplicons based on Uparse (Version v1.5). Zenodo. http://doi.org/10.5281/zenodo.259579

Logares, R., Sunagawa, S., Salazar, G., Cornejo-Castillo, F. M., Ferrera, I., Sarmento, H., … Acinas, S. G. (2014). Metagenomic 16S rDNA Illumina tags are a powerful alternative to amplicon sequencing to explore diversity and structure of microbial communities. *Environmental Microbiology*, *16*, 2659–2671. https://doi.org/10.1111/1462-2920.12250

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

Melack, J. M., & Forsberg, B. (2001). Biogeochemistry of Amazon floodplain lakes and associated wetlands. In M. E. McClain, R. L. Victoria & J. E. Richey (Eds.), *The biogeochemistry of the Amazon*

basin and its role in a changing world (pp. 235–276). Oxford: Oxford University Press.

Moreira-Turcq, P., Bonnet, M. P., Amorim, M., Bernardes, M., Lagane, C., Maurice, L., … Seyler, P. (2013). Seasonal variability in concentration, composition, age, and fluxes of particulate organic carbon exchanged between the floodplain and Amazon River. *Global Biogeochemical Cycles*, *27*, 119–130. https://doi.org/10.1002/gbc.20022

Mouquet, N., & Loreau, M. (2003). Community patterns in source–sink metacommunities. *The American Naturalist*, *162*, 544–557. https://doi.org/10.1086/378857

Mouquet, N., Miller, T. E., Daufresne, T., & Kneitel, J. M. (2006). Consequences of varying regional heterogeneity in source–sink metacommunities. *Oikos*, *113*, 481–488. https://doi.org/10.1111/J.2006.0030-1299.14582.X

Newton, R. J., Jones, S. E., Eiler, A., McMahon, K. D., & Bertilsson, S. (2011). A guide to the natural history of freshwater lake bacteria. *Microbiology and Molecular Biology Reviews*, *75*, 14–49. https://doi.org/10.1128/MMBR.00028-10

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P., O'Hara, R. B., … Wagner, H. (2015). *Vegan: Community ecology package*. R package vegan, vers. 2.2-1.

Oliveira, D. M., & Calheiros, D. F. (2000). Flood pulse influence on phytoplankton communities of the south Pantanal floodplain, Brazil. *Hydrobiologia*, *427*, 101–112. https://doi.org/10.1023/a:1003951930525

de Oliveira, L. F. V., & Margis, R. (2015). The source of the river as a nursery for microbial diversity. *PLoS ONE*, *10*, e0120608. https://doi.org/10.1371/journal.pone.0120608

Pang, S., Zhang, S. H., Lv, X. Y., Han, B., Liu, K. H., Qiu, C. H., … He, Z. L. (2016). Characterization of bacterial community in biofilm and sediments of wetlands dominated by aquatic macrophytes. *Ecological Engineering*, *97*, 242–250. https://doi.org/10.1016/j.ecoleng.2016.10.011

Pinel, S., Bonnet, M. P., Santos Da Silva, J., Moreira, D., Calmant, S., Satgé, F., & Seyler, F. (2015). Correction of interferometric and vegetation biases in the SRTMGL1 spaceborne DEM with hydrological conditioning towards improved hydrodynamics modeling in the Amazon Basin. *Remote Sensing*, *7*, 15822.

Poretsky, R., Rodriguez-R, L. M., Luo, C. W., Tsementzi, D., & Konstantinidis, K. T. (2014). Strengths and limitations of 16S rRNA gene amplicon sequencing in revealing temporal microbial community dynamics. *PLoS ONE*, *9*, e93827. https://doi.org/10.1371/journal.pone.0093827 https://doi.org/10.1371/journal.pone.0093827

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., … Glockner, F. O. (2012). The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Research*, *41*, D590–D596. https://doi.org/10.1093/nar/gks1219

R Development Core Team (2008). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Read, D. S., Gweon, H. S., Bowes, M. J., Newbold, L. K., Field, D., Bailey, M. J., & Griffiths, R. I. (2015). Catchment-scale biogeography of riverine bacterioplankton. *ISME Journal*, *9*, 516–526. https://doi.org/10.1038/ismej.2014.166

Richey, J. E., Hedges, J. I., Devol, A. H., Quay, P. D., Victoria, R., Martinelli, L., & Forsberg, B. R. (1990). Biogeochemistry of carbon in the Amazon River. *Limnology and Oceanography*, *35*, 352–371. https://doi.org/10.4319/lo.1990.35.2.0352

Rösel, S., Allgaier, M., & Grossart, H. P. (2012). Long-term characterization of free-living and particle-associated bacterial communities in Lake Tiefwaren reveals distinct seasonal patterns. *Microbial Ecology*, *64*, 571–583. https://doi.org/10.1007/s00248-012-0049-3

Ruiz-González, C., Niño-García, J. P., Berggren, M., & del Giorgio, P. A. (2017). Contrasting dynamics and environmental controls of dispersed bacteria along a hydrologic gradient. *Advances in Oceanography and Limnology*, *8*, 222–234. https://doi.org/10.4081/aiol.2017.7232

Ruiz-González, C., Niño-Garcia, J. P., & del Giorgio, P. A. (2015). Terrestrial origin of bacterial communities in complex boreal freshwater networks. *Ecology Letters*, *18*, 1198–1206. https://doi.org/10.1111/ele.12499

Sarmento, H. (2012). New paradigms in tropical limnology: The importance of the microbial food web. *Hydrobiologia*, *686*, 1–14. https://doi.org/10.1007/s10750-012-1011-6

Satinsky, B. M., Fortunato, C. S., Doherty, M., Smith, C. B., Sharma, S., Ward, N. D., … Crump, B. C. (2015). Metagenomic and metatranscriptomic inventories of the lower Amazon River, May 2011. *Microbiome*, *3*, 39. https://doi.org/10.1186/s40168-015-0099-0 https://doi.org/10.1186/s40168-015-0099-0

Savio, D., Sinclair, L., Ijaz, U. Z., Parajka, J., Reischer, G. H., Stadler, P., … Eiler, A. (2015). Bacterial diversity along a 2600 km river continuum. *Environmental Microbiology*, *17*, 4994–5007. https://doi.org/10.1111/1462-2920.12886

Schneegurt, M. A., Dore, S. Y., & Kulpa, C. F. (2003). Extraction of DNA from soils for studies in microbial ecology. *Current Issues in Molecular Biology*, *5*, 1–8.

Sioli, H. (1984). The Amazon and its main affluents: Hydrography, morphology of the river courses, and river types. In H. Sioli (Ed.), *The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin* (pp. 127–165). Dordrecht, The Netherlands: Springer. https://doi.org/10.1007/978-94-009-6542-3

Staley, C., Gould, T. J., Wang, P., Phillips, J., Cotner, J. B., & Sadowsky, M. J. (2015). Species sorting and seasonal dynamics primarily shape bacterial communities in the Upper Mississippi River. *Science of the Total Environment*, *505*, 435–445. https://doi.org/10.1016/j.scitotenv.2014.10.012

Szekely, A. J., & Langenheder, S. (2014). The importance of species sorting differs between habitat generalists and specialists in bacterial communities. *Fems Microbiology Ecology*, *87*, 102–112. https://doi.org/10.1111/1574-6941.12195

Tessler, M., Brugler, M. R., DeSalle, R., Hersch, R., Velho, L. F. M., Segovia, B. T., … Lemke, M. J. (2017). A global eDNA comparison of freshwater bacterioplankton assemblages focusing on large-river floodplain lakes of Brazil. *Microbial Ecology*, *73*, 61–74. https://doi.org/10.1007/s00248-016-0834-5

Thomaz, S. M., Bini, L. M., & Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river–floodplain systems. *Hydrobiologia*, *579*, 1–13. https://doi.org/10.1007/s10750-006-0285-y

Toyama, D., Santos-Júnior, C. D., Kish, L. T., Oliveira, T. C. S., Garcia, J. W., Sarmento, H., … Henrique-Silva, F. (2017). A snapshot on prokaryotic diversity of the Solimões River basin (Amazon, Brazil). *Genetics and Molecular Research*, *16*, gmr16029567. https://doi.org/10.4238/gmr16029567

Tundisi, J. G., Forsberg, B. R., Devol, A. H., Zaret, T. M., Tundisi, T. M., Dossantos, A., … Hardy, E. R. (1984). Mixing patterns in Amazon lakes. *Hydrobiologia*, *108*, 3–15. https://doi.org/10.1007/Bf02391627

Wetzel, R. G., & Likens, G. E. (2000). *Limnological analyses*. New York, NY: Springer-Verlag. https://doi.org/10.1007/978-1-4757-3250-4

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag. https://doi.org/10.1007/978-0-387-98141-3

Woodhouse, J. N., Kinsela, A. S., Collins, R. N., Bowling, L. C., Honeyman, G. L., Holliday, J. K., & Neilan, B. A. (2016). Microbial communities reflect temporal changes in cyanobacterial composition in a shallow ephemeral freshwater lake. *ISME Journal*, *10*, 1337–1351. https://doi.org/10.1038/ismej.2015.218

Xu, J. P. (2006). Microbial ecology in the age of genomics and metagenomics: Concepts, tools, and recent advances. *Molecular Ecology*, *15*, 1713–1731. https://doi.org/10.1111/j.1365-294X.2006.02882.x

Zha, Y. H., Berga, M., Comte, J., & Langenheder, S. (2016). Effects of dispersal and initial diversity on the composition and functional

performance of bacterial communities. *PLoS ONE*, *11*, e0155239. https://doi.org/10.1371/journal.pone.0155239

Zhang, T., & Fang, H. H. P. (2000). Digitization of DGGE (denaturing gradient gel electrophoresis) profile and cluster analysis of microbial communities. *Biotechnology Letters*, *22*, 399–405. https://doi.org/10.1023/A:1005680803442

Zhang, J. J., Kobert, K., Flouri, T., & Stamatakis, A. (2014). PEAR: A fast and accurate illumina paired-end reAd mergeR. *Bioinformatics*, *30*, 614–620. https://doi.org/10.1093/bioinformatics/btt593

Zhao, D. Y., Wang, S. C., Huang, R., Zeng, J., Huang, F., & Yu, Z. B. (2017). Diversity and composition of bacterial community in the rhizosphere sediments of submerged macrophytes revealed by 454 pyrosequencing. *Annals of Microbiology*, *67*, 313–319. https://doi.org/10.1007/s13213-017-1262-6

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: de Melo ML, Bertilsson S, Amaral JHF, Barbosa PM, Forsberg BR, Sarmento H. Flood pulse regulation of bacterioplankton community composition in an Amazonian floodplain lake. *Freshwater Biol*. 2018;00:1–13. https://doi.org/10.1111/fwb.13198