



## Species sorting and seasonal dynamics primarily shape bacterial communities in the Upper Mississippi River



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### HIGHLIGHTS

- Upper Mississippi River bacterial communities were characterized over three years.
- Community structure was correlated with changes in physicochemical parameters.
- A reproducible community structure was observed in the late summer.
- Species sorting and seasonal dynamics primarily drove shifts in community structure.
- Sediment communities may also contribute significantly to planktonic communities.

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### ABSTRACT

Bacterial community structure (BCS) in freshwater ecosystems varies seasonally and due to physicochemical gradients, but metacommunity structure of a major river remains understudied. Here we characterize the BCS along the Mississippi River and contributing rivers in Minnesota over three years using Illumina next-generation sequencing, to determine how changes in environmental conditions as well as inputs from surrounding land and confluences impacted community structure. Contributions of sediment to water microbial diversity were also evaluated. Long-term variation in community membership was observed, and significant shifts in relative abundances of major freshwater taxa, including  $\alpha$ -Proteobacteria, Burkholderiales, and Actinomycetales, were observed due to temporal and spatial variations. Environmental parameters (e.g. temperature, rainfall, and nutrient concentrations) primarily contributed to differences in phyla abundances (88% of variance), with minimal influence from spatial distance alone (< 1% of variance). Furthermore, an annually-recurrent BCS was observed in late summer, further suggesting that seasonal dynamics strongly influence community composition. Sediment communities differed from those in the water, but contributed up to 50% to community composition in the water column. Among water sampling sites, 34% showed significant variability in BCS of replicate samples indicating variability among riverine communities due to heterogeneity in the water column. Results of this study highlight the need for a better understanding of spatial and temporal variations in riverine bacterial diversity associated with physicochemical gradients and reveal how communities in sediments, and potentially other environmental reservoirs, impact waterborne BCS. Techniques used in this study may prove useful to determine sources of microbes from sediments and soils to waterways, which will facilitate best management practices and total maximum daily load determinations.

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### 1. Introduction

The emergence of high-throughput, next-generation sequencing technology has allowed for a better characterization of bacterial

communities from a variety of environments, including marine and fresh waters (Sogin et al., 2006; Gilbert et al., 2009; Fortunato et al., 2012; Staley et al., 2013), soils (Jones et al., 2009), wastewater (Sanapareddy et al., 2009), and the human microbiome (Peterson et al., 2009). The most common focus of these studies has been on the ecological biogeography of bacterial communities – how community structure varies within and between habitats in response to biotic interactions and shifts in abiotic environmental parameters (e.g. pH, temperature, etc.) (Horner-Devine et al., 2003; Pernthaler, 2005; Gilbert

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et al., 2009, 2012; Lindström and Langenheder, 2012). Bacterial communities in aquatic systems have been shown to fluctuate in response to physicochemical factors including temperature, day length, and nutrient concentrations (Gilbert et al., 2009, 2012), and these fluctuations have been demonstrated to be seasonally reproducible in both marine and freshwater ecosystems (Crump and Hobbie, 2005; Shade et al., 2007; Fortunato et al., 2012; Gilbert et al., 2012). Deep sequencing of a sample from the English Channel, however, has revealed that a persistent microbial seed bank may exist for particular ecosystems, e.g. marine waters (Caporaso et al., 2012b). This finding has generally been interpreted to support the Baas-Becking hypothesis that 'everything is everywhere, but the environment selects' (Baas-Becking, 1934), suggesting that due to the small size of microorganisms, their rapid rates of reproduction, and high dispersal ability, among other factors, the extinction of particular taxa is unlikely (Lindström and Langenheder, 2012).

A metacommunity framework has been proposed for exploring the role of environmental variation as well as population dispersal dynamics in shaping bacterial community structure (Leibold et al., 2004). In this framework, a metacommunity consists of local communities of potentially interacting taxa that are linked by dispersal. Four perspectives have been presented to describe environmental and spatial influences on local community structure (Leibold et al., 2004), and these include: (1) the patch-dynamics perspective, (2) the species sorting perspective, (3) the mass-effect perspective, and (4) the neutral perspective. The species sorting and mass-effect perspectives are generally favored in most environmental studies of microbial biogeography, as the patch-dynamics and neutral theories are thought to be poorly applicable to environmental studies conducted over broad spatial scales (Lindström and Langenheder, 2012; Winter et al., 2013). Abundant evidence of bacterial biogeography structured along numerous gradients of environmental parameters suggests that the patch dynamics perspective can be ruled out as patches show apparent variation in physicochemical parameters and/or nutrient availability (Martiny et al., 2006). Furthermore, several studies have demonstrated that the habitat-specific distribution of bacterial populations suggests that the neutral perspective of the metacommunity framework can likely be excluded (Zwart et al., 2002; Nemergut et al., 2011).

The influences of environmental heterogeneity and dispersal effects on contemporary local community structures have been reviewed numerous times (Martiny et al., 2006; Hanson et al., 2012; Lindström and Langenheder, 2012). However, influences on community structure resulting strictly from variation in environmental parameters vs. that from spatial distance have been difficult to discern, in part due to the co-variation of physicochemical parameters with spatial distance in many recent studies (Lindström and Langenheder, 2012; Winter et al., 2013).

Temperature and salinity have been reported to be among the most influential physical and chemical parameters affecting the composition of bacterial communities in aquatic habitats (Tamames et al., 2010). However, many recent studies examining the effect of spatial distance on bacterial community composition have been confounded by co-variation of distance with temperature and/or salinity (Fortunato et al., 2012; Winter et al., 2013). Although all riverine systems will likely exhibit spatial and temporal heterogeneities in physical and chemical parameters (Winemiller et al., 2010), restriction of a study area and sampling period to a region with relatively consistent temperature and salinity may allow for better characterization of spatial variation within this system. Furthermore, while co-variation of environmental parameters, such as nutrient availability with distance, may occur as a result of a riverine continuum (Vannote et al., 1980), such factors will likely be offset by more significant terrestrial inputs such as agricultural runoff or wastewater effluent discharge (Pereira and Hostettler, 1993; Drury et al., 2013). These inputs may result in predictable variation in physicochemical parameters in local environments and bacterial communities may be shaped by anthropogenic impacts, as has been

previously suggested (Staley et al., 2013, 2014b). These local communities nevertheless remain interconnected by dispersal of upstream populations and may be influenced by communities in sediments, as well.

Here we hypothesized that species sorting dynamics would have a greater impact on community composition than spatial distance in a large riverine ecosystem, as has been previously demonstrated in a marine system (Winter et al., 2013). In order to evaluate effects of environmental parameters (i.e. rainfall, temperature, pH, and nutrient concentrations) and spatial distances on community structure, bacterial community structures were characterized annually from 2010 to 2012 at 11 sampling sites along the Upper Mississippi River using Illumina next-generation sequencing. Sampling was conducted during the early summer following annual flushing due to snowmelt in mid-late spring to avoid confounding effects of this temporally inconsistent event.

Furthermore, seasonally-associated variations of environmental parameters were anticipated to result in an annually reproducible community structure, as was observed in the English Channel (Gilbert et al., 2012). To evaluate these seasonal dynamics, samples were collected biweekly over a 12-week period in 2011 and 2012 to observe short-term seasonal progressions in community structure. In addition, since environmental reservoirs (i.e. sediments) and depth were suspected to be among variables that impacted the bacterial community structure, the influences of these parameters were evaluated in the later years of study. Results of this study elucidate processes controlling and shaping bacterial community structure in a riverine ecosystem over a relatively large spatial area (>400 km), and reveal potentially significant influences of environmental reservoirs influencing community composition.

## 2. Materials and methods

### 2.1. Sample collection

Water samples were collected in the early summer of 2010 to 2012 from 8 sites along the Upper Mississippi River in Minnesota, one site near the confluence of the Minnesota River with the Mississippi, and one site on the St. Croix River near its confluence with the Mississippi River, as described previously (Staley et al., 2013, 2014a). In 2011 and 2012, an 11th sampling site was added on the Zumbro River [44.314, -91.996]. Sampling sites were selected to span the entirety of the Mississippi River in Minnesota and to capture unimpacted communities as well as potential variations due to major agricultural and urban inputs and variation at confluences. Briefly, 40 l of water was collected at each site from the water's surface, transported back to the lab in sterile 20 l carboys, and either processed immediately or stored <24 h at 15 °C. In 2011 and 2012, samples (20 l) were collected from both the surface and at a depth of approximately 1.5 m using a canoe pump at the Twin Cities site, on six dates each year, two weeks apart. In 2012, sediment samples (approximately 5 cm depth) were also collected using an ethanol-sterilized, stainless steel soil auger, approximately 0.5 m from the river bank at the same time of water sample collection.

Water temperature and pH were measured at the surface at each sampling date in the field. Rainfall data, up to three days prior to sampling, was also obtained from Weather Underground [<http://www.wunderground.com>]. Site locations and physical data are summarized in Supplementary Table S1. Water stage data, monitored by the Army Corps of Engineers [[www.rivergages.com](http://www.rivergages.com)], was collected from stations near each sampling site, and variability in water stage varied  $\leq 0.21$  m from the day prior to sampling. As all sediment samples were collected at a depth of at least 0.5 m, samples were presumed to be inundated for at least 24 h.

In 2011 and 2012, at the time of collection of the 40 l sample, additional 1 l water samples were collected at all sites in sterile amber bottles and stored at 4 °C for nutrient analyses. From these samples, total carbon, colorimetric nitrite/nitrate, total phosphorus, and total

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