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Bacterial community response to changes in soil redox potential along a moisture gradient in restored wetlands

Ariane L. Peralta [a,b,*], Sarah Ludmer [b], Jeffrey W. Matthews [a,c], Angela D. Kent [a,c]

[a] Program in Ecology, Evolution, and Conservation Biology, University of Illinois at Urbana-Champaign, 505 S. Goodwin Ave. Urbana, IL 61801, USA
[b] School of Integrative Biology, University of Illinois at Urbana-Champaign, 505 S. Goodwin Ave. Urbana, IL 61801, USA
[c] Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 1102 S. Goodwin Ave. Urbana, IL 61801, USA

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ABSTRACT

Hydrology is greatly modified during wetland restoration, especially when restoration sites were previously under agricultural management. Fluctuations in hydrology affect soil redox potential, causing a shift in microbial metabolic pathways due to changes in nutrient and oxygen availability. We hypothesize that hydrologic variability influences microbial community composition. To evaluate the relationship between hydrology and bacterial community composition, we characterized soil redox potential and local soil factors along a hydrologic gradient at two floodplain wetland restoration sites. We collected soil samples along a gradient from upland to wetland, and monitored redox potential (*in situ* redox probes) and bacterial community composition (DNA fingerprinting) bi-weekly (June–October 2011). In addition, we measured soil organic matter, ammonium, nitrate, temperature, and pH along the moisture gradient. During these observations, both sites shifted from reducing to more oxidizing environments, based on changes in soil redox potential. At both sites, distinct bacterial communities were observed at each location along the moisture gradient, corresponding to spatial shifts in redox conditions. Additionally, we experimentally tested if hydrologic history constrained bacterial response to contemporary soil moisture conditions by exposing field soil collected from upland (dry) to wetland (saturated) plots at one wetland site to a range of moisture levels. Where soils originated from hydrologically variable field conditions, the experimental moisture additions resulted in distinct bacterial assemblages among moisture treatments. Our results revealed that bacterial communities originating from fluctuating hydrologic conditions in the field were more diverse and capable of greater changes in community composition in response to changes in soil moisture than bacterial communities shaped by stable, less dynamic, hydrologic conditions (*i.e.,* more permanently wet or dry conditions). As a consequence, land use changes that alter hydrologic conditions may impact soil microbial communities more when environmental conditions were historically more stable compared to fluctuating. Wetland management aimed at restoring microbial functions should consider ways in which management can be adapted to overcome biological, physical, and chemical legacies from prior land use that may constrain restoration of microbial ecosystem services.

1. Introduction

Differences among microbial populations in their physiological responses to environmental conditions can result in a shift in community composition and subsequent changes in biogeochemical processes (Picek et al., 2000; Pett-Ridge and Firestone, 2005; Mentzer et al., 2006; Nygaard and Ejrnæs, 2009). As a consequence, microorganisms vary in their tolerance to the range of oxidation–reduction (redox) conditions imposed by fluctuations in soil moisture (Truu et al., 2009). Hydrologic conditions directly impact soil redox conditions due to changes in local oxygen and nutrient

Abbreviations: Oxidation–reduction, redox; CTAB, cetyl trimethyl ammonium bromide; ARISA, automated ribosomal intergenic spacer analysis; PCR, polymerase chain reaction; ROX, rhodamine X-labeled; ANOVA, analysis of variance; NMDS, non-metric multidimensional scaling; OTU, operational taxonomic unit; PERMANOVA, permutational (nonparametric) multivariate analysis of variance.

* Corresponding author. Current address: Department of Biology, East Carolina University, Howell Science Complex, Mail Stop 551, Greenville, NC 27858, USA. Tel.: +1 252 328 2712.
E-mail address: peraltaa@ecu.edu (A.L. Peralta).

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availability (Keddy, 2000; Mitsch and Gosselink, 2007). An increase in soil moisture can shift the soil environment from oxic to anoxic conditions, resulting in a decreased redox potential (Picek et al., 2000). As conditions become more anoxic and reducing, soil microorganisms switch to using alternative electron acceptors (*e.g.*, nitrate, iron, sulfate), shifting the dominant metabolic activity in the soil (Keddy, 2000; Mitsch and Gosselink, 2007). The influence of fluctuating environmental conditions on microbial community structure over space and time can impact the range and magnitude of microbial functions. Understanding the extent to which microbes are sensitive to environmental fluctuations can enhance management of microbial ecosystem services in restored wetlands.

A hydrologic gradient within wetlands provides a variety of habitats, selecting for taxa capable of exploiting specific environmental conditions (Mentzer et al., 2006; Schimel et al., 2007). Fluctuations in hydrology can result in recharge of oxygen and nutrient pools, whereas less dynamic hydrology can result in a more stable and potentially more nutrient-limited condition for microorganisms (Keddy, 2000; Picek et al., 2000; Banach et al., 2009). These types of fluctuating hydrologic environments are seen within floodplain wetland areas where flooding is seasonal (Mentzer et al., 2006; Kim et al., 2008). Previous studies have demonstrated that environments subjected to drying–rewetting events support microorganisms capable of taking advantage of a wide range in redox conditions. Resilient microbial taxa that were better suited to dynamic hydrologic conditions were able to persist (Pett-Ridge and Firestone, 2005; Borken and Matzner, 2009; DeAngelis et al., 2010).

Monitoring soil redox conditions over space and time can provide characterization of the range in potential terminal electron acceptor usage at a given site. Soil redox potential can be measured using various methods. One common method is the use of platinum electrodes for discrete measurements of redox potential. However, the single point measurement captured by platinum electrodes does not capture changes in redox potential over time (Cogger et al., 1992; Mansfeldt, 2003; Vorenhout et al., 2004). In contrast, other approaches can integrate redox potential over several days or weeks (*e.g.*, indicator of reduction in soils tubes (Jenkinson and Franzmeier, 2006)), and provide information about the longer-term redox conditions of a site. Neither point measures nor integrated assessments capture variability in hydrology (Vorenhout et al., 2004; Castenson and Rabenhorst, 2006; Jenkinson and Franzmeier, 2006). *In situ* soil redox probes can be used to address this issue by continuously monitoring temporal changes in redox potential over an extended time period in the field (Vorenhout et al., 2004). These data can provide information on potential electron acceptor availability that may affect microbial communities, and can serve as an indicator of potential microbial functions over both space and time.

In this study, we examined the relationship between hydrology and bacterial community composition to investigate how hydrologic differences influenced bacterial community structure and response to altered environmental conditions. In addition to characterizing microbial community composition across a hydrologic gradient, we aimed to characterize spatial and temporal variation in soil redox potential and local soil factors along a hydrologic gradient and to monitor the response of bacterial communities, developed under different hydrologic histories, to experimental manipulation of the moisture gradient. We hypothesize that hydrologic variability influences microbial diversity. Bacterial communities from a variable environment (*e.g.*, drying and re-wetting events) are more likely to be composed of populations capable of using multiple metabolic pathways (DeAngelis et al., 2010). When soil redox conditions are stable over time, bacterial community composition is expected to be distinct from bacterial communities experiencing a highly variable set of redox conditions.

2. Materials and methods

2.1. Site description

We conducted this study at Emiquon Preserve in Lewistown, Illinois (40° 20′ 24″, −90° 5′ 24″) and St. Joseph Wetland in St. Joseph, Illinois (40° 7′ 12″, −88° 2′ 60″). Both wetland sites were previously under conventional agricultural management. In 2006, the Champaign County Soil and Water Conservation District began restoration on the St. Joseph and in 2007, The Nature Conservancy began restoration efforts on the Emiquon Preserve.

2.2. Field sampling

We established two transects, 20 m apart, from upland to wetland areas at each site, spanning a hydrologic gradient. Along each transect, we established, based on distinct changes in plant community plots (A–D, from upland to wetland) that represented different hydrologic conditions. Plant community composition was significantly different at each plot along the hydrologic gradient at both wetland sites (comparison of plant communities along hydrologic gradient Emiquon: PERMANOVA $R^2 = 0.8408$, $P < 0.001$; St. Joseph: PERMANOVA $R^2 = 0.4721$, $P < 0.001$) (Fig. S1). Therefore, plant community composition was an appropriate initial proxy for changes in soil moisture conditions. We collected soil samples bi-weekly from each wetland from June 30, 2010 to October 17, 2010. On each sampling occasion, we collected a total of eight 3 cm diameter × 12 cm deep soil cores from each plot, two cores per 1-m^2 quadrat within the 4-m^2 plot. Cores from each plot were combined and homogenized, transported on ice, and stored at 4 °C for 24 h until processed in the laboratory. We passed soil through a 2.54 cm sieve and excluded roots from the final composite sample. A subsample of homogenized soil from each plot was stored at −20 °C awaiting microbial analysis. In addition, we measured soil temperature (averaged over 12 cm) *in situ* for each plot using a temperature probe (Campbell Scientific, Logan, UT, USA) at four locations within each plot and averaged for each plot. If plots were inundated with water, we recorded water depth.

2.3. Soil chemical analyses

For all samples, we assessed gravimetric soil moisture from a 20–30 g subsample from each plot for each sampling date. Field-moist soil was dried at 105 °C for 24 h and moisture content was determined from the proportion of water (by weight) to oven-dried soil. To assess inorganic N content, about 5 g of field-moist soil was extracted with 2 M KCl, and we measured available ammonium (NH_4^+) and nitrate (NO_3^-) in the soil extracts based on colorimetric analysis using an auto analyzer (Lachat Instruments/Hach Company, Loveland, CO, USA). For soil pH and soil organic matter analyses, we composited soil from each plot sampled over time so that a single, representative sample from each plot was analyzed. We determined the pH of the soil solution (10 g sample + 10 mL deionized water) for each soil sample by averaging three pH measurements per sample. We ground a subsample of air-dried soil into a fine powder and analyzed to determine total organic matter (total organic C and total N), based on elemental analysis (ECS 4010, Costech Analytical Instruments, Valencia, CA, USA).

2.4. Soil redox potential

To continuously monitor soil redox potential, we installed a HYPNOS III Data Logger System (MVH Consult, Utrecht, The