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Dry-wet cycles of kettle hole sediments leave a microbial and biogeochemical legacy

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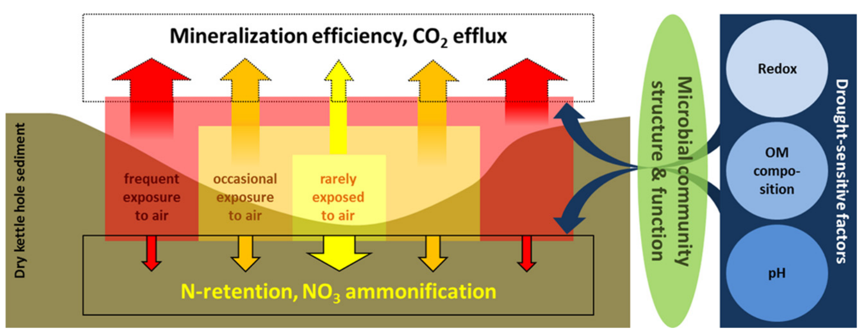
HIGHLIGHTS

- Dry-wet cycling leaves a microbial and biogeochemical legacy in kettle hole sediments.
- The legacy is driven by redox conditions, pH and organic matter properties.
- Carbon mineralization peaks in dry sediments with a less stable hydrological past.
- Nitrogen loss is potentially highest in hydrologically less stable sediments.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding interrelations between an environment's hydrological past and its current biogeochemistry is necessary for the assessment of biogeochemical and microbial responses to changing hydrological conditions. The question how previous dry-wet events determine the contemporary microbial and biogeochemical state is addressed in this study. Therefore, sediments exposed to the atmosphere of areas with a different hydrological past within one kettle hole, i.e. (1) the predominantly inundated pond center, (2) the pond margin frequently desiccated for longer periods and (3) an intermediate zone, were incubated with the same rewetting treatment. Physicochemical and textural characteristics were related to structural microbial parameters regarding carbon and nitrogen turnover, i.e. abundance of bacteria and fungi, denitrifiers (targeted by the *nirK* und *nirS* functional genes) and nitrate ammonifiers (targeted by the *nrfA* functional gene). Our study reveals that, in combination with varying sediment texture, the hydrological history creates distinct microbial habitats with defined boundary conditions within the kettle hole, mainly driven by redox conditions, pH and organic matter (OM) composition. OM mineralization, as indicated by CO_2-outgassing, was most efficient in exposed sediments with a less stable hydrological past. The potential for nitrogen retention via nitrate ammonification was highest in the hydrologically rather stable pond center, counteracting nitrogen loss due to denitrification. Therefore, the degree of hydrological stability is an important factor leaving a microbial and biogeochemical legacy, which determines carbon and nitrogen losses from small lentic freshwater systems in the long term run.

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1. Introduction

A changing climate with an increased likelihood of extreme events such as high temperature periods or precipitation events has been forecasted for the near future (Fischer and Knutti, 2015). Therefore, the hydrology and physicochemistry of global freshwater systems is expected to become more dynamic and variable, increasing the occurrence of semi-aquatic environments with intermittent stages (i.e. drying and rewetting).

Sequences of inundation and desiccation come along with changes in physicochemical conditions (i.e. redox potential, pH), organic matter (OM) and nutrient (e.g. nitrogen) availability (Reverey et al., 2016). This increased variability will have profound consequences for the ecosystem's microbial community structure and functioning and thus gear cascades of biogeochemical responses. For example, the OM turnover rate in kettle holes was found to be enhanced in systems with a temporal hydroperiod (Nitzsche et al., 2017). Thus, frequent dry-wet cycles of sediments are hypothesized to boost loss of previously stored carbon (C) to the atmosphere. Accordingly, increased CO_2 emissions were measured in desiccated temporary streambeds (Gómez-Gener et al., 2016). Further, CO_2 outgassing in temporary ponds was shown to be highest in OM-rich sediments that were repeatedly exposed to the atmosphere (Catalan et al., 2014), and incubations of littoral lake sediment revealed that dry treatments released significantly more CO_2 than wet controls (Weise et al., 2016).

Whereas it seems that organic carbon is preferentially released from drying sediment, the question remains whether nitrogen is lost or retained in the system. This uncertainty is mainly due to the fact that nitrogen (N) dynamics in sediments are determined by a complex interplay between different N transformation processes. For example, coupled nitrification and denitrification will lead to N outgassing, whereas dissimilatory nitrate reduction to ammonium (DNRA) can compete with denitrification, and thus retains N in the system (Burgin and Hamilton, 2007). These different processes all depend on redox states and fluctuations, as induced by dry-wet cycles. It has been shown that, for example, microbial communities responsible for nitrogen transformations in wetland ecosystems readjust their structural and functional equilibrium as a consequence of repeated moisture and hence redox fluctuations (Peralta et al., 2013).

In this study, we consider stress to be a change in environmental conditions (e.g. drought) that triggers a physiological response threatening microbial functioning or survival (according to Schimel et al., 2007). Subsets of the microbial communities are able to tolerate the above-mentioned temporal dynamics, whereas others with more restricted physiological flexibility will be more sensitive to local disturbance (DeAngelis et al., 2010; Schimel et al., 2007). Basically, strategies of microorganisms to deal with such environmental stress include resistance or resilience mechanisms, which can be on the functional level and reversible or on the structural level, inducing the shift to a new equilibrium different from the initial state (Barthès et al., 2015). Whether loss of stress susceptible microbial species changes the community's functional traits or is compensated for by functional replacement with other taxa greatly depends on the degree of specialization of the lost species (Peralta et al., 2013) as well as on the biodiversity of the functional group, potentially buffering loss of individual species (Peralta et al., 2014). Drying and rewetting can lead to enrichment or depletion of specific compounds such as OM or nutrients and thus influence microbial activity, which does not necessarily coincide with a change in microbial community structure. The magnitude of microbial responses greatly depends on the duration and frequency of environmental changes, i.e. of drought or flood events. Short-term events will impact biogeochemistry on the process level, but might not change microbial community structure, whereas long-term events or a high frequency of short-term events can exert a much stronger selective pressure on microorganisms prone to stress (Fig. 1; Reverey et al., 2016). Consequently, adaptation of microorganisms to dry-wet cycling strongly depends on the sediment's hydrological history. For example, the microbial community was hypothesized to preadapt to a certain degree of moisture fluctuation, whereas extreme events outside an environment's historical range of variability lead to stronger functional and structural responses (Evans and Wallenstein, 2011). In soil incubation experiments, a soil microbial community was enriched mainly consisting of taxa that were more active under fluctuating than static redox conditions (DeAngelis et al., 2010). However, a change in microbial functioning and community structure in lake sediments was only observed after exposure to extended drought events (Weise et al., 2016). Historical preadaptation can form a microbial community which is more efficient regarding specific transformation processes. For example, the stimulus of microbial potentials upon rewetting of dry pond sediments was observed to be higher with frequent exposure to dry-wet cycling than with shorter and/or infrequent dry phases (Fromin et al., 2010).

Kettle holes are small, glacially created ponds, which generally have a highly variable hydroperiod (Kalettka and Rudat, 2006), leading to frequent dry-wet cycles and thus represent excellent model systems for our study. The question how variations in the duration and frequency of previous drought events impact sediment C and N losses to the atmosphere has been addressed by comparing selected biogeochemical and microbial variables between sediment areas with a different hydrological past within the same kettle hole. We hypothesize that prolonged drought increases sediment C and N losses due to increased OM mineralization, and decreases sediment C and N retention. Furthermore, the hydrological past of the sediment, i.e. the duration and frequency of previous dry-wet events, is suggested to determine future biogeochemical processes and microbial community structure by changing physicochemical boundary conditions such as water content, pH and OM composition.

2. Methods

2.1. Study site

The study site is located in the Quillow catchment (168 km^2) in North-East Brandenburg, Germany. The hummocky, young moraine landscape is coined by small, glacially created depression wetlands that are characterized by a highly variable hydroperiod. This variability is driven by water inputs mainly due to precipitation, snow melt, interflow, shallow groundwater discharge and surface runoff as well as water loss due to evapotranspiration, lateral subsurface flow, and shallow groundwater recharge (Reverey et al., 2016).

The kettle hole "Rittgarten" (N 53°23′22″ E 013°42′09″) is situated in the Uckermark region, mainly consisting of sandy soils (Kleeberg et al., 2016). The climate is sub-humid, with a mean annual temperature of 9.1 °C and a mean annual precipitation of 561 mm in 2015 (Nitzsche

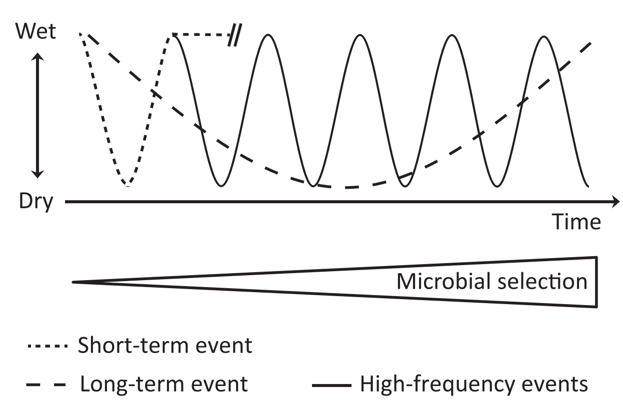

Fig. 1. Potential effect of different scenarios of dry-wet cycling on the degree of microbial selection.

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