



Persisting responses of salt marsh fungal communities to the Deepwater Horizon oil spill

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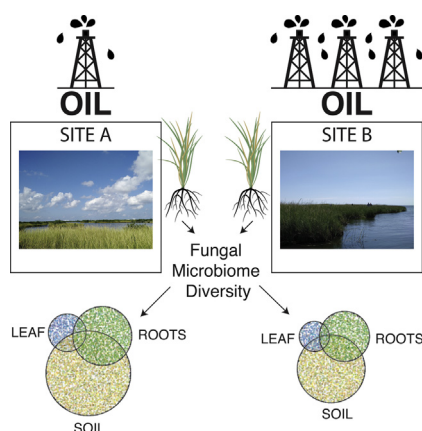
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HIGHLIGHTS

- Effects of oil spill on plant-associated microbiomes in salt marshes were investigated.
- Nature and magnitude of oiling effects assessed between sites and across plant host compartments
- Fungal communities inhabiting leaf, root and soil show distinct responses to oiling.
- Magnitude of fungal community responses to oiling constrained by local environment
- Oil pollution effects on plant microbiomes persist six years after initial exposure.

GRAPHICAL ABSTRACT



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ABSTRACT

The plant microbiome, composed of diverse interacting microorganisms, is thought to undergird host integrity and well-being. Though it is well understood that environmental perturbations like oil pollution can alter the diversity and composition of microbiomes, remarkably little is known about how disturbance alters plant-fungal associations. Using Next-Generation sequencing of the 18S rDNA internal transcribed spacer (ITS1) region, we examined outcomes of enduring oil exposure on aboveground leaf and belowground endophytic root and rhizosphere fungal communities of *Spartina alterniflora*, a highly valued ecosystem engineer in southeastern Louisiana marshes affected by the 2010 Deepwater Horizon accident. We found that aboveground foliar fungal communities exhibited site-dependent compositional turnover with consequent loss in diversity according to oiling history. Rhizosphere soil communities also exhibited shifts in community composition associated with oiling history, whereas root endophytic communities did not. Oiling did not increase or decrease similarities among aboveground and belowground communities within an individual host, indicating that host plant characteristics exert stronger control than external factors on fungal community composition. These results show that fungal community responses to oiling vary within tissues of the same host plant, and that differences in the local environment, or alternatively, site-specific differences in residual oil constrain the magnitude of exposure responses. Our study offers novel perspectives on how environmental contaminants and perturbations can influence plant microbiomes, highlighting the importance of assessing long-term ecological outcomes of oil pollution to better

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understand how shifts in microbial communities influence plant performance and ecosystem function. Our findings are relevant to coastal management programs tasked with responding to oil spills and increasing pressures arising from intensifying development and climate change. Understanding how modification of plant-microbiome associations influences plant performance, particularly of ecosystem engineers like *S. alterniflora*, can help guide efforts to protect and restore at-risk coastal ecosystems.

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1. Introduction

Plants host diverse complements of microorganisms, with distinct communities inhabiting aboveground and belowground tissues (Mishra et al., 2012; Christian et al., 2015). The diversity and composition of microbes can alter host fitness and behavior (Vandenkoornhuys et al., 2015), and can have direct and indirect feedbacks on ecosystem processes like carbon and nitrogen cycling (e.g., Saleem et al., 2017). Despite the recent explosion of work on microbial diversity (Vorholt, 2012; Tian et al., 2015), the mechanisms by which environmental perturbations affect plant-microbe interactions are not well understood, particularly for aboveground and belowground fungal communities.

Environmental disturbances can alter plant-microbe interactions by modifying microbial assemblages. Oil pollution, a prevailing environmental concern in industry-laden areas like the Gulf of Mexico, can reduce diversity of plant-associated fungal communities via increased abundance of oil-degrading taxa with consequent loss of diversity, which can persist for years after initial exposure (e.g., Kandalepas et al., 2015; Bourdel et al., 2016). The magnitude of shifts in plant-associated fungal communities, however, can vary across plants (e.g., Bourdel et al., 2016; Rietl et al., 2016) and even among assemblages within plant host tissues. For example, leaf fungal communities can suffer near complete diversity loss compared to more modest responses of root fungal assemblages to oiling (Kandalepas et al., 2015), suggesting that different mechanisms underlie responses to stressor exposure.

Outcomes of perturbations like oiling might depend on several factors, including whether fungal communities are in aboveground and belowground plant tissues (Coince et al., 2014; Tardif et al., 2016) as well as local abiotic and biotic conditions. Fungal symbiont communities occupying different tissues of a host plant (e.g., aboveground vs. belowground, endophytic (inside plant tissues) vs. rhizosphere (surrounding roots)) exhibit distinct ecologies (Wearn et al., 2012; Christian et al., 2015). Each may interact idiosyncratically with different factors that may change according to local environmental conditions. The fungal community residing in host leaves may, for example, have relatively poor and variable nutrient supply (Lindow and Brandl, 2003) while rhizosphere communities draw from a stable and nutrient-rich environment (Badri et al., 2009). Consequently, perturbations can result in varying patterns and degrees of responses between fungal communities. For instance, oil contamination might promote selection of hydrocarbon-degrading microorganisms in the rhizosphere of plants for protection against contaminant toxicity (Siciliano et al., 2001; Bell et al., 2014), altering root endophytic and rhizosphere community composition while exerting little influence on leaf endophytes. It is possible, however, that predominantly belowground perturbations like oiling also alter foliar fungal communities via changes to host tissue chemistry and plant uptake of organic compounds (Desalme et al., 2013; Li et al., 2017).

The nature and magnitude of fungal community response to perturbations may also be due to different processes driving community assembly in different plant tissues. For example, the assembly of aboveground foliar fungal endophytes largely reflects airborne dispersal, while belowground communities are primarily influenced by local environmental filtering (David et al., 2016; Hendershot et al., 2017). Thus, fungal communities within the same plant host can have distinct responses to the same perturbation, especially when local

environmental conditions influence stressor exposure. Parallel responses may, however, arise following a disturbance. For example, communities throughout the host plant could be reduced to taxa that are tolerant to a specific disturbance type like oiling. Therefore, microbes generally associated within a particular plant tissue may not persist, where stressor exposure acts as a selective force resulting in greater similarity among communities across a plant host (Herren et al., 2016).

Characterizing exposure responses across tissues within and among plant hosts can offer insight into potential associations between aboveground and belowground processes (Wardle et al., 2004). It would also clarify how plant-microbiota interactions mitigate outcomes of environmental disturbances, including how associations feedback to influence higher-order processes ranging from host demography to ecosystem resilience (e.g., Rudgers and Orr, 2009). We examined the effects of oil exposure on aboveground foliar and belowground endophytic root and rhizosphere fungal communities of the foundational saltmarsh grass, *Spartina alterniflora*, at two sites in southeastern Louisiana six years after the Deepwater Horizon (DWH) oil spill. Through next-generation metabarcoding, we assessed whether (1) aboveground and belowground endophyte and rhizosphere fungal communities of *S. alterniflora* respond idiosyncratically to oiling within and among sites; (2) site differences influence the magnitude of fungal community responses to oiling; and (3) oil exposure alters associations between aboveground and belowground fungal communities. Given that different plant tissues may not be equally susceptible to (direct) oil exposure, we expected to find greater variation in response in aboveground versus belowground communities. Furthermore, we expected that belowground endophytic and rhizosphere communities would exhibit similar response profiles to site-level differences in oiling history given that the two communities are generally tightly linked (i.e. root endophytes are generally derived from the microbial pool inhabiting the rhizosphere zone).

2. Methods

2.1. Site and sample collection

Our two focal sites are located in southeastern Louisiana: Bay Jimmy and Fourchon (Fig. 1). Both sites were affected by the DWH oil spill in 2010, although the Bay Jimmy site experienced greater oil deposition than the Fourchon site (Michel et al., 2013). The Bay Jimmy site, located in Northern Barataria Bay, is salt marsh dominated by *S. alterniflora* with a few *Distichlis spicata* and *Salicornia virginica* occurring infrequently on the shoreline. The marsh is predominantly organic soil with some clay content. The Fourchon site, situated in the adjoining Carminada Bay, consists of organic soil with some sand content. The vegetation is predominantly *S. alterniflora* and *Avicennia germinans*. The two sites are 43 km apart. Our measurement of residual polycyclic aromatic hydrocarbon (PAH) levels in soils directly within the vicinity of our plant samples indicated that Bay Jimmy had significantly higher PAH levels than Fourchon at the time of our study (Fig. S1). Within each site, one transect was placed in an area that received oil (i.e., oiled area) and another transect was placed in a nearby area that did not receive oil (i.e., non-oiled area). The two transects (14 m each) were ca. 600 and 30 m apart in Bay Jimmy and Fourchon, respectively.

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