



## Response of soil microbial community composition and function to a bottomland forest restoration intensity gradient



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### ABSTRACT

Terrestrial ecosystems are globally under threat of loss or degradation. To compensate for the impacts incurred by loss and/or degradation, efforts to restore ecosystems are being undertaken. These efforts often focus on restoring the aboveground plant community with the expectation that the belowground microbial community will follow suit. This ‘Field of Dreams’ expectation – if you build it, they will come – makes untested assumptions about how microbial communities and their functions will respond to aboveground-focused restoration. To determine if restoration of aboveground plant communities equates to restoration of belowground microbial communities, we assessed the effects of four forest restoration treatments – varying in intensity from unmanaged to interplanting tree species – on microbial (i.e. prokaryotic and fungal) community composition and function (i.e. catabolic profiles and extracellular enzyme activities). Additionally, effects of the restoration treatments were compared to both degraded (i.e. active arable cultivation) and target endpoint communities (i.e. remnant bottomland forest) to determine the trajectory of intensifying aboveground restoration efforts on microbial communities. Approximately 16 years after the initiation of the restoration treatments, prokaryotic and fungal community composition, and microbial function in the four restoration treatments were intermediate to the endpoint communities. Surprisingly, intensification of aboveground restoration efforts led to few differences among the four restoration treatments and increasing intensification did not consistently lead to microbial communities with greater similarity in composition and function to the target remnant forest communities. Together these results suggest that belowground microbial community composition and function will respond little to, or will lag markedly behind, intensifying aboveground restoration efforts. Reliance on a ‘Field of Dreams’ approach, even if you build it better, may still lead to belowground microbial communities that remain uncoupled from aboveground communities. Importantly, our findings suggest that restoring aboveground vegetation may not lead to the intended restoration of belowground microbial communities and the ecosystem processes they mediate.

### 1. Introduction

Terrestrial ecosystems across the globe are becoming increasingly human-dominated, leading to declines in their biodiversity and ecosystem functioning (Theobald, 2010). Efforts to restore these properties of systems primarily focus on the aboveground plant community (Callaham et al., 2008; Stanturf et al., 2014; Suding et al., 2015). This restoration focus has often led to many positive outcomes, from

increases in the strength of carbon (C) and nitrogen (N) sinks (Hooker and Compton, 2003; Houghton and Hackler, 2000) to recovery of herbaceous understories in forests (Duffy and Meier, 1992; Holl and Aide, 2011). Yet, this focus on aboveground plant restoration has also met with failure when soils are ignored (Kardol and Wardle, 2010; Ohsowski et al., 2012). Such failures have led researchers to question the efficacy by which passive (i.e. abandonment) or active restoration might return degraded ecosystems to states more representative of a

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system's previous structure and function when belowground components are ignored (Chazdon, 2008; Eviner and Hawkes, 2008; Holl and Aide, 2011).

By overlooking soils and belowground communities (Callahan et al., 2008), particularly soil microbial communities, restoration efforts may fail to restore the major heterotrophs in terrestrial ecosystems and hence system carbon and nutrient cycling (Fierer et al., 2009). In addition, these restoration efforts take a 'field of dreams' approach, that is the restoration of the soil communities will follow aboveground restoration (i.e. planting trees to restore a forest will lead to a forest soil community). As such, knowledge of relationships between aboveground and belowground communities (e.g. plant-soil feedbacks) are ignored, as are the functional implications of effectively restoring soil microbial communities (Strickland et al., 2009; van der Putten et al., 2013; Wubs et al., 2016). For instance, depending on the aboveground community there is the potential that differences in ecosystem function may arise due to differences in the types of mycorrhizal associates, competition between mycorrhizae and saprotrophic fungi, and differing modes of nutrient acquisition (Averill and Hawkes, 2016; Phillips et al., 2013). Ignoring these relationships and their importance to ecosystem function may limit the effectiveness of ecosystem restoration efforts (Callahan et al., 2008; Harris, 2009).

The need to explicitly consider belowground microbial communities in designing restoration efforts is apparent given the fundamental roles played by soil microbial communities. For instance, soil microbial communities are major contributors to the formation of stable soil organic matter, which is a property fundamental to ecosystem health (Cotrufo et al., 2013; Schmidt et al., 2011). Additionally, it is important to consider that belowground microbial communities may be slow to respond to changes in the aboveground community (Kulmatiski and Beard, 2011). This slow response will be particularly apparent when considering slow-growing or dispersal limited microbial groups, such as taxa within the bacterial phylum Verrucomicrobia (Brewer et al., 2016), which are often found in high abundance in undisturbed soils (Fierer et al., 2013). Additionally, legacies of the disturbed condition may lead to unsuitable environmental conditions for some microbes and suitable conditions for others (Hovatter et al., 2011). Intensifying aboveground restoration efforts, then may have little immediate influence and lag in their effect on belowground microbial communities, especially if agricultural legacies and/or soil degradation precede such restoration efforts.

We examined the influence of four aboveground forest restoration treatments (established in 1995) of increasing intensity (Fig. 1) (Stanturf et al., 2009) on soil microbial community structure and function at a previously farmed bottomland site in the Lower Mississippi Alluvial Valley (LMAV). The restoration treatments, from least to most intensive, were i) unassisted recolonization, ii) direct-seeding Nuttall oak (*Quercus texana*) acorns, iii) planting bare-root Nuttall oak nursery stock, and iv) interplanting eastern cottonwood with oaks. We compared the response of these restoration treatments to adjacent active agricultural sites and remnant bottomland hardwood forest stands. These restoration treatments represented a gradient of restoration intensity from a labor perspective, from an ecological perspective these treatments represented a gradient of both aboveground vertical structure and attempts at jump-starting forest succession (Stanturf et al., 2009). When considering the aboveground restoration success for these treatments, by 1998, four growing seasons after initial establishment, biomass of ground-layer vegetation was highest in the recolonization (i) and direct seeded (ii) treatments and these two treatments had the lowest overstory tree density (De Steven et al., 2015). Plant species diversity changed over time, reflecting successional patterns, but restoration treatments had no significant effect on diversity. Finally, restoration treatments differed in how quickly the trees established forest-like conditions. The cottonwood/oak interplanting (iv) achieved canopy closure within two years (Stanturf et al., 2009), although the cottonwood canopy was relatively open such that sufficient light

reached the surface to allow herbaceous species to establish (De Steven et al., 2015). While there has been a significant emphasis on understanding the aboveground effects of restoration at these sites, little attention has been paid to the belowground components.

We determined the effects of intensifying restoration on soil prokaryotic and fungal community composition via marker gene sequencing. We also determined whole microbial community function via catabolic profiling (i.e. multiple substrate-induced respiration) and extracellular enzyme activity. Objectives for the study were to: 1) Determine how different restoration practices influence soil microbial communities in comparison to converted (arable) and target (forest) systems; 2) Determine whether restoration practices have equivalent effects on both the composition and functional capabilities of soil microbial communities; and 3) Determine whether more intense restoration efforts expedite 'recovery' of microbial community composition and function toward a reference end goal. We expected that there would be distinct differences between the restoration treatments, with the most intensive restoration efforts leading to microbial communities most similar to those found in the reference bottomland forest stands. That is, if you build it better, then this will expedite the 'recovery' of the microbial community because of aboveground effects on belowground community structure and function (Gellie et al., 2017; van der Putten et al., 2013; Wardle et al., 2004). Alternatively, we recognized that aboveground restoration intensity might have little influence on microbial community composition and function – potentially due to the primacy of land use legacies in shaping soil communities and processes (Grandy et al., 2009; Johnstone et al., 2016; Keiser et al., 2011). Under such a scenario there would be few differences observed between restoration treatments (i.e. building it better will not expedite the 'recovery' of the microbial community).

## 2. Materials and methods

### 2.1. Study site description and experimental design

For a complete description of the experimental design and establishment see Stanturf et al. (2009). Briefly, all experimental plots were established by May 1995 in Sharkey County, MS (32°58'N 90°44'W) located within the greater LMAV. Elevations in the experimental plots range from a maximum of 30.9 m MSL to a minimum of 28.5 m MSL. Soils at these sites are Vertisols of the Sharkey series (very-fine, smectitic, thermic chromic Epiaquerts) and these sites were historically dominated by bottomland hardwood forests (Stanturf et al., 2000). The entire experimental area was cultivated to soybean (*Glycine max*) in the year prior to establishment of the restoration treatments, and was disked immediately prior to establishment.

The experiment is a randomized complete block design, with blocks accounting for elevational variation. The treatment plots are ~8 ha in size and consist of four treatments ranging in restoration intensity from, i) unassisted recolonization, ii) direct-seeding Nuttall oak (*Quercus texana*) acorns, iii) planting bare-root Nuttall oak nursery stock (i.e. saplings), to iv) interplanting eastern cottonwood (*Populus deltoides*) with Nuttall oak (Fig. 1). Hereafter, we refer to these restoration treatments as recolonization (i), direct-seed (ii), planted oaks (iii), and interplanted (iv), respectively. In particular, the interplanted (iv) treatment aims to establish an early successional, arbuscular mycorrhizal (AM) fungal associated tree species, eastern cottonwood, along with the later successional, ectomycorrhizal associated Nuttall oak. This interplanting leads to a more rapid increase in vertical structure and a stratified canopy, which has been shown to increase bird species richness associated with this treatment (Hamel, 2003). Other than the interplanted (iv) treatment, the other treatments had not reached canopy closure at the time of sampling (i.e. 2010).

Soils were sampled in Spring 2010 and Winter 2011—to account for potential turnover in the microbial community between the growing and non-growing season – from 5 × 5 m subplots located within each

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