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Nitrogen enrichment shifts functional genes related to nitrogen and carbon acquisition in the fungal community

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ABSTRACT

To better understand mechanisms of carbon (C) and nitrogen (N) dynamics under anthropogenic N enrichment, we examined frequencies of C- and N-targeting genes in litter fungi. In particular, we tested the hypothesis that N enrichment selects for C-targeting genes but against N-targeting genes, if fungi preferentially invest resources in acquisition of growth-limiting nutrients. We conducted a fully-factorial litter and microbial transplant in a N fertilization experiment in Southern California grassland. The transplant design enabled us to contrast direct effects of N fertilization in the environment, indirect effects of N-induced shifts in the microbial community, and indirect effects of N-induced changes in plant litter chemistry. For each treatment, we assessed frequencies of select well-annotated fungal functional genes: cellulose-targeting AA9 genes (for C acquisition) versus ammonium transporter genes and amino acid permease genes (for N acquisition). We found that our hypothesis was upheld only with regard to shifts in the microbial community. Specifically, when grown in the same environment and litter, fungi from the N-fertilized plots displayed greater frequencies of cellulose-targeting AA9 genes from basidiomycetes, but smaller frequencies of ammonium transporter genes and amino acid permease genes, when compared to fungi from the control plots. In contrast, N fertilization in the plot environment was associated with higher frequencies of amino acid permease genes and ammonium transporter genes. Likewise, plant litter from the N-fertilized plots selected for higher frequencies of ammonium transporter genes. Altogether, we found fairly inconsistent effects of N enrichment on fungal functional genes related to C and N acquisition. Even if the genetic capacity of the fungal community to acquire C versus N changes owing to shifts in the microbial community, direct effects of N fertilization and indirect effects of litter chemistry may offset the response.

1. Introduction

Nitrogen (N) and carbon (C) are critical nutrients for fungi (Griffin, 1996). For example, fungi require C for energy and biomass production, and N for protein construction (Sinsabaugh et al., 2009). Fungi can acquire C by releasing extracellular enzymes into the environment to break down complex organic molecules such as crystalline cellulose (Lynd et al., 2002; Langston et al., 2011). They can also obtain N by incorporating transporter enzymes into their cell membranes to take up N-containing compounds like amino acids and ammonium (Grenson et al., 1970; Chalot and Brun, 1998; Mitsuzawa, 2006). In doing so, they contribute to C respiration, N mineralization, and microbial N immobilization within ecosystems (Dighton, 2016). A number of genes controlling these functions have been identified in fungi (Treseder and Lennon, 2015). Accordingly, we can assess the genetic potential of the fungal community to influence N and C cycling by examining the distribution of selected functional genes in fungi growing in the environment.

In fact, we can examine fungal functional genes in natural ecosystems to understand how these physiological capacities of fungi respond to N enrichment (Berlemont et al., 2014; Myrold and Nannipieri, 2014; Myrold et al., 2014). Nitrogen enrichment is an important element of global change, because human activity has about doubled the amount of biologically available N worldwide (Vitousek et al., 1997; Galloway et al., 2008). For example, in Southern California, anthropogenic N deposition adds more than 25 kg N ha^{-1} y^{-1}. It can be challenging to predict how soil C dynamics respond to N enrichment (Fog, 1988; Knorr et al., 2005; Hyvonen et al., 2007; Janssens et al., 2010). We may improve our understanding of links between N enrichment and C cycling by examining in detail the relevant processes governed by fungi.

For instance, since N is a macronutrient for fungi (Griffin, 1996), its enrichment could alter fungal investment in N versus C acquisition.

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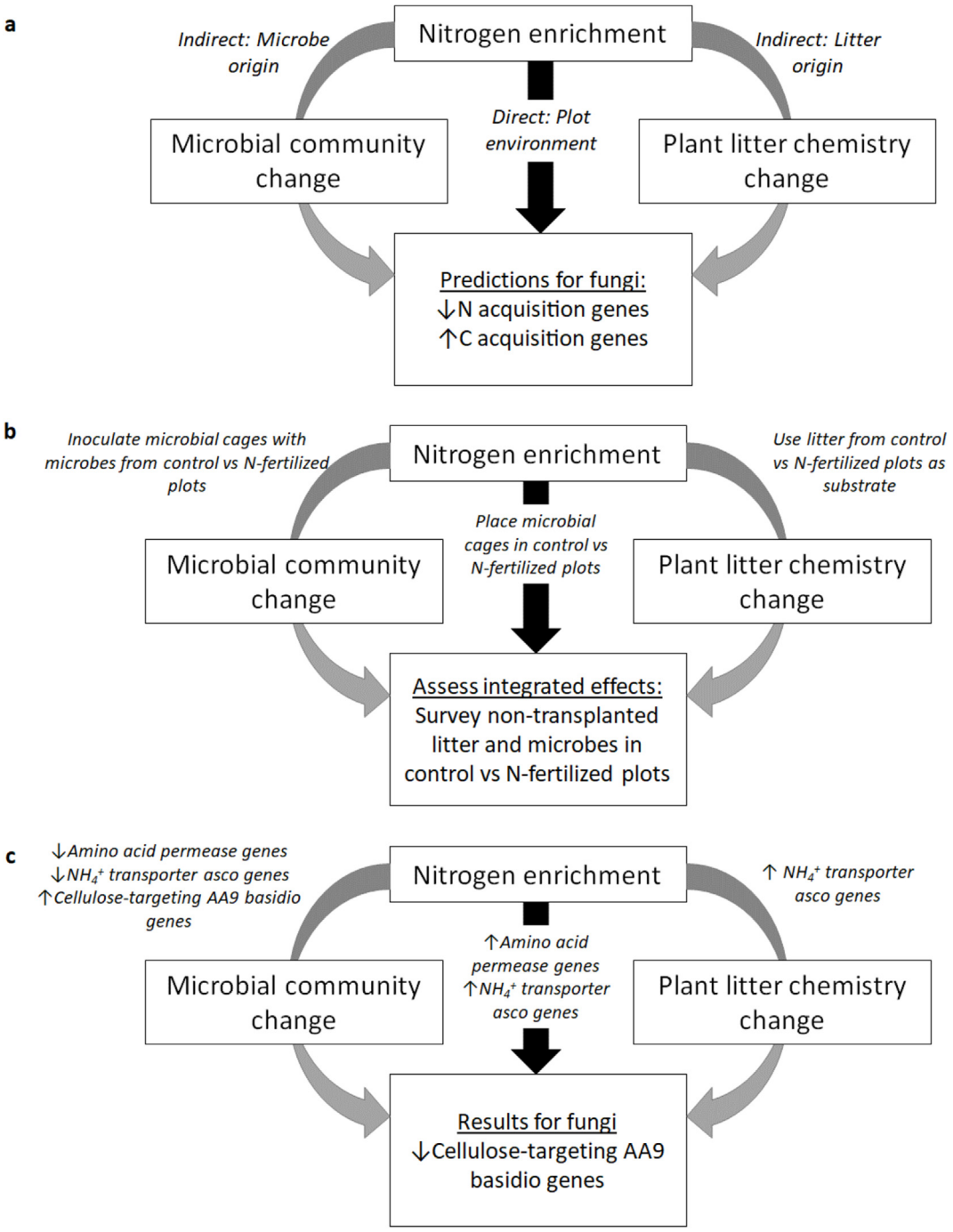

Fig. 1. Hypothesized effects of N enrichment (a), approaches for testing effects (b), and observed effects (c) on the frequency of fungal functional genes related to N acquisition and C acquisition. For observed effects, only significant responses are shown. The decrease in cellulose-targeting AA9 basidiomycete genes in "Results for fungi" refers to results from a survey of unmanipulated litter. All other results are from a reciprocal transplant experiment.

Extracellular enzymes and transporters are proteins, which require N and C to construct (Elser et al., 2000). If a fungus allocates N and C to construction of an N-acquiring enzyme, those resources become unavailable for production of a C-acquiring enzyme. Thus, this allocation constraint creates a trade-off between the ability to acquire N versus C (Allison et al., 2010). Accordingly, we hypothesize that N enrichment will select for C acquisition genes, and against N acquisition genes, if fungi preferentially invest resources in enzymes that target growth-limiting nutrients. If such a trade-off exists, then we can consider it when predicting fungal contributions to C dynamics under N enrichment.

A trade-off between fungal genetic capacity for N versus C acquisition could manifest via several ecological pathways (Fig. 1a). First, N additions could *directly* increase the growth of fungi with greater genetic capacity for C acquisition, allowing them to outcompete individuals that invest instead in greater genetic capacity for N acquisition. Second, over a longer term, N enrichment could select for fungal species that favor C acquisition over N acquisition. In this way, N additions could *indirectly* influence the genetic capacity of the fungal community via shifts in species composition. Third, N enrichment could *indirectly* alter the genetic capacity of fungi via changes in plant litter chemistry. For instance, N concentrations in plant litter often—though not always—increase after N enrichment (Ostertag and DiManno, 2016). Thus, we extend our hypothesis to specify that N enrichment