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Shifts in fungal communities during decomposition of boreal forest litter

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ABSTRACT

We characterized changes in fungal communities over 2 yr of litter decomposition in an Alaskan boreal forest, and then related them to ecological and phylogenetic traits of taxa. Senescent leaves of *Populus tremuloides* and *Picea mariana* were placed on the forest floor during leaf fall, and were collected 9, 10, 12, and 24 months later to assess the abundance of active fungal taxa. Fungal community composition varied over time and between litter types. The preferred decomposition stage and preferred litter type of individual taxa were each phylogenetically conserved. Taxa that target glutamate and tannin-protein complexes were more common at later decomposition stages. Finally, communities were overdispersed phylogenetically and in terms of substrate use, indicating that competition may have occurred.

Introduction

Fungi break down plant litter as a nutrient and energy source. In doing so, they drive decomposition, which releases greenhouse gases such as CO_2 to the atmosphere. Decomposition is a dynamic process, with fungal community composition as well as litter chemistry changing over time. For instance, Frankland (1998) characterized fungal succession on decomposing leaves of four species in a temperate woodland, and found that certain ascomycetes (e.g., *Aureobasidium*, *Phoma*, and *Epicoccum*) were consistently present at early stages, whereas basidiomycetes dominated later. Indeed, numerous other studies have documented shifts in the community composition of fungal and other microbial groups (Ponge 1991; Paulus *et al.* 2006; Bray *et al.* 2012). Lindahl *et al.* (2007) also noted that fungal communities in soil organic matter varied with soil depth, which corresponded to age of soil carbon. What controls these patterns of succession? Environmental filtering (i.e., environmental constraints on the presence or absence of species) and biotic interactions (e.g., competition

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or facilitation) can influence the succession of plants and animals (Guisan & Thuiller 2005). These mechanisms may be important for fungi as well. In both cases, ecological traits of fungal taxa could determine their order of succession.

As leaf litter decomposes, the environment experienced by resident fungi changes. In particular, the chemical composition of plant litter shifts predictably as decomposition proceeds (Schlesinger 1977; Berg 2000; Herman et al. 2008). The major carbon components of fresh litter are soluble sugars, celluloses, lignocellulose, and condensed tannins; the most common organic nitrogen components are proteins and amino acids, particularly arginine and glutamine (Stevenson 1994). Soluble sugars are removed early in decomposition, then cellulose at more intermediate stages (Chapin et al. 2011). Lignocellulose is not broken down substantially until free cellulose becomes relatively scarce. In the meanwhile, tannins can bind proteins, forming complexes that resist decay (Basaraba & Starkey 1966; Talbot & Finzi 2008). Arginine and glutamine can remain present throughout stages of decomposition, as they are released from larger organic compounds and also produced by microbes.

Fungal taxa differ in the degree to which they target these organic compounds (Hanson et al. 2008; McGuire et al. 2010). As a result, the prevalence of a given fungal taxon may be determined to some extent by the availability of its preferred substrates (Ponge 2005). This type of environmental filtering might be partly responsible for fungal succession (Frankland 1998; Dighton 2003). Moreover, litter chemistry varies among plant species (e.g., Aber & Melillo 1982; Cornwell et al. 2008; Hattenschwiler et al. 2011), which could also contribute to observed differences in fungal communities across litter types (Frankland 1998; Chapman & Newman 2010; Bray et al. 2012). Since humans are altering the distributions of plant species in many ecosystems (Vitousek et al. 1997), the extent to which fungi specialize on litter types may influence belowground communities.

Interactions among fungal taxa could further modify the community. For instance, taxa compete for energy, nutrients, or space; and can interfere with one another's growth by releasing allelopathic compounds or chitinases (Holmer & Stenlid 1997; Baar & Stanton 2000; Boddy 2000; Heilmann-Clausen & Boddy 2005). Furthermore, saprotrophic microbes that colonize habitats relatively quickly can inhibit or facilitate later-arriving taxa, producing historical effects on community assembly (Fukami et al. 2010; Dickie et al. 2012; Peay et al. 2012). To some extent, limiting similarity in ecological traits may influence the degree of competition among taxa (Macarthur & Levins 1967; Kraft et al. 2007). In the case of microbial succession on plant litter, organic substrate use may be a particularly relevant trait. Competition between taxa for organic substrates can lead to a wider phylogenetic distribution of taxa, or a wider distribution of traits (i.e., overdispersion) than expected by random chance.

The evolutionary history of fungal taxa is germane to each of these issues. Fungal succession has primarily been documented in terms of the taxonomic identity of fungi, which is determined by evolutionary relationships. Furthermore, ecological and phenotypic traits are expected to be relatively similar in closely-related species (i.e., phylogenetically conserved) (Darwin 1859; Damerval et al. 1987). In particular, previous work has found that the use of organic substrates by microbes can be phylogenetically conserved (McGuire et al. 2010; Treseder et al. 2011; Peay et al. 2012). Phylogenetic conservation of these and other ecological traits could elicit the taxonomic shifts commonly documented during decomposition.

We examined these issues by characterizing changes in fungal communities on two common litter types (black spruce and aspen) decomposed in a boreal forest. We applied bromodeoxyuridine (BrdU) as a nucleotide analog to label DNA of fungi that were active during four decomposition stages. We tested four hypotheses. First, fungal community composition will shift as decomposition proceeds and will differ between litter types. Second, preference for decomposition stage, and for aspen versus black spruce litter, will be phylogenetically conserved. Third, the capacity for fungal taxa to use particular organic substrates will be related to preferences for early versus late stages of decomposition, and for aspen versus black spruce litter. Fourth, communities will be overdispersed within samples, potentially owing to competition among taxa.

Our study was designed to complement—but be independent from—that of McGuire et al. (2010), which tested functional diversity in organic substrate use by fungi. McGuire et al. (2010) used the same study site and identical molecular techniques, but with a separate set of litter bags exposed to different treatments (organic substrate additions) than in the current study.

Methods

Sites

Our study site was located in an upland boreal ecosystem near Delta Junction, Alaska (63°55′ N, 145°44′ W) detailed in Treseder et al. (2004). Briefly, this ecosystem is an 85-yr-old, mature forest dominated by *Picea mariana* (black spruce) with an understory of lichens, mosses, and shrubs. *Populus tremuloides* (quaking aspen) is also present. The mean annual temperature is −2 °C; the precipitation rate, 303 mm yr^{-1} (http://weather.noaa.gov/). Permafrost is discontinuous in this area and is not present in the site. Soils are well-drained. The growing season extends from bud break in mid May to leaf fall in mid Sep.

Experimental design

Senescent leaves were plucked directly from black spruce and quaking aspen (the most common coniferous tree and deciduous tree, respectively) in this site in Sep 2002, air dried, and stored at 20 °C. Litterbags were constructed with each bag containing either black spruce or aspen litter (but not both). Specifically, aspen or black spruce litter was placed in 1 mm mesh bags (4 g litter/bag), sterilized in a Cs-137 gamma irradiator overnight (2.5 total Mrad). There were six replicates per litter type per pickup time. We then embedded all litterbags in the organic layer at the site in Sep. 2005. Litterbags from the current study were placed adjacent to those from the McGuire et al. (2010) study. Litterbags were collected in Jun. 2006, Jul. 2006, Sep. 2006 and Sep. 2007, placed immediately on ice, and then transported directly to UC Irvine. Nucleotide analog labeling (below) was performed within 48 hr of litterbag collection.

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