



The role of ammonium oxidizing communities in mediating effects of an invasive plant on soil nitrification



Sarah Shannon-Firestone ^{a,*}, Heather L. Reynolds ^a, Richard P. Phillips ^a, S. Luke Flory ^b, Anthony Yannarell ^c

^a Department of Biology, Indiana University, 1001 East Third Street, Bloomington, IN, USA

^b Agronomy Department, University of Florida, Gainesville, FL, USA

^c Department of Natural Resources and Environmental Science, University of Illinois, Urbana-Champaign, IL, USA

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ABSTRACT

Invasive plants often benefit from changes that they impose on soil microbes via positive plant–soil feedback, but the mechanisms that underlie these changes, and the legacy of their effects, remain poorly quantified. We investigated the impacts of an invasive annual grass, *Microstegium vimineum*, on the structure and functioning of soil microbial communities in a multi-year, field-based common garden experiment. Given previous reports that *M. vimineum* can both elevate nitrification rates in soil and benefit from enhanced nitrate availability, we sought to answer the following questions: 1) Does *M. vimineum* alter the abundance or composition of soil nitrifying microbial communities (ammonia oxidizing archaea and bacteria, AOA and AOB, respectively)? 2) Are such effects reversible or do soil legacy effects persist after *M. vimineum* is no longer present? After three years, invaded plots had greater AOA abundances than uninvaded native dominated plots, as well as different AOA community structure. However, after seven years, and following a period of *M. vimineum* replacement by native plants in the invaded plots, AOA abundances and nitrification rates declined toward levels found in uninvaded plots. Collectively, our results suggest that while the impacts of *M. vimineum* invasions on nitrogen cycling likely relate to their association with AOA, these effects may not persist if *M. vimineum* declines over time and native plants and their associated microbes are able to re-establish.

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1. Introduction

Invasive plants can change microbial communities in ways that impair ecosystem services (e.g., soil carbon storage, Strickland et al., 2013), alter plant community dynamics (Stinson et al., 2006) and promote invasions through positive feedbacks (van der Putten et al., 2013). Plant–soil feedbacks can involve both abiotic changes to the soil environment and biotic changes to soil communities, and the latter can involve both direct interactions between plants and soil organisms (i.e. pathogens or mutualists) or indirect interactions resulting from changes in functional groups of soil microorganisms (van der Putten et al., 2013). Such changes to the activities, abundances, or community composition of nutrient-cycling microorganisms can alter ecosystem function in ways that support invasive plant success and inhibit native plant species.

* Corresponding author. Tel.: +1 530 574 7071.

E-mail address: smshanno@indiana.edu (S. Shannon-Firestone).

The restoration of ecosystem functions following invasive plant removal or the natural decline of invasions is determined, in part, by whether soil microbial communities can return to their pre-invasion structure and activity (Wolfe and Kironomos, 2005; Corbin and D'Antonio, 2012). In some cases, legacy effects of invasions on soil microbial communities persist long after removal of the invasive plants (Corbin and D'Antonio, 2012). In other cases, the soil microbial community is able to return to its pre-invasion structure and activities (van der Putten et al., 2013). It can be difficult to predict whether an invasive species will have soil legacy effects, especially if the mechanism behind the invader's impact is not clear.

One mechanism for invasive plant impacts is altered nutrient cycling processes (Liao et al., 2008). It is critical to understand how invasions that alter nutrient cycling processes affect specific microbial functional groups and their activities, which could in turn assist in predicting the likelihood of soil legacy effects. *Microstegium vimineum* is a highly invasive grass in forests of the eastern

U.S. (Fairbrothers and Gray, 1972; Barden, 1987; Flory and Clay, 2010) that alters soil nitrogen cycling by promoting the conversion of ammonia to nitrate through the process of nitrification (Kourtev et al., 2003; Lee et al., 2012). The increased availability of nitrate can benefit *M. vimineum* more than co-occurring native plants (Lee et al., 2012), and thus *M. vimineum* dominance appears to be promoted by plant–soil feedback associated with an altered soil nitrogen cycle (Ehrenfeld et al., 2001; Kourtev et al., 2003; Lee et al., 2012). This plant–soil feedback is also associated with changes in soil pH, with higher pH often found in invaded soils (Ehrenfeld et al., 2001; McGrath and Binkley, 2009). In addition, *M. vimineum* has been associated with shifts in the overall community structure of soil microbial communities (Kourtev et al., 2002, 2003). It is possible that these changes are due to root exudation or chemicals released from *M. vimineum* litter as it decomposes (Elgersma et al., 2012). Alteration of microbial communities did not promote *M. vimineum* growth when used as inoculum in a recent plant–soil feedback study (Shannon et al., 2012). However, such inoculum-based studies may not adequately represent the full functional potential of microbial communities under field conditions because they favor fast-growing microbes with short-term impacts over slow-growing microbes with longer-term, more cumulative impacts (Brinkman et al., 2010). Nitrification is a microbial process, and so nitrifying microorganisms may play a central functional role in nitrate-associated plant–soil feedback. Yet, the impact of *M. vimineum* on nitrifying microorganisms has not been investigated.

Autotrophic bacteria and archaea conduct ammonia oxidation, the rate-limiting step of nitrification (Hart et al., 1994). These ammonia oxidizing bacteria (AOB) and ammonia oxidizing archaea (AOA) thus control the rate of nitrification in soils. Changes in AOB abundance and community composition have been linked to increased nitrification rates under non-native grasses (Hawkes et al., 2005), but evidence suggests that AOA could also be involved (e.g., Eloy Alves et al., 2013). AOA are generally more abundant in soil than AOB (Leininger et al., 2006; Zhalnina et al., 2012), and AOA abundance—but not AOB abundance—tends to be positively correlated with nitrification rates (Zhang et al., 2010; Zhalnina et al., 2012). *M. vimineum*'s impacts on soil nitrification rates and soil pH suggest that it could be impacting the AOA or AOB communities. *M. vimineum* may stimulate the activity of ammonia-oxidizing archaea (AOA) or ammonia-oxidizing bacteria (AOB) without altering nitrifier community structure, but if this is the case, then elevated nitrification rates should drop once *M. vimineum* is no longer present. On the other hand, *M. vimineum* may disrupt ammonia oxidizer community structure. This altered community structure could result in soil legacies that persist beyond *M. vimineum* invasion or could be short-lived, if ammonia oxidizer structure can recover quickly.

While we know from previous studies that *M. vimineum* invasion is associated with coarse changes in soil microbial community structure (e.g., as determined by phospholipid fatty acid analysis; Kourtev et al., 2002), no studies have as yet examined whether *M. vimineum* alters ammonia oxidizer communities. Connecting *M. vimineum* invasion to changes in ammonia oxidizer community structure will help to elucidate the mechanism of *M. vimineum* invasion and associated increases in nitrification rates. Understanding this mechanism will help determine the likelihood of soil legacy effects after native plants are re-established in *M. vimineum*-invaded soils. To determine whether *M. vimineum* affects ammonia oxidizer communities, we measured the abundance and community composition of AOA and AOB in the soils of a common garden experiment with invaded and uninvaded plots. In 2009, nitrification rates in the invaded plots were 63% higher than in the uninvaded plots (Lee et al., 2012). We collected soil samples from these

plots in 2008, when *M. vimineum* was dominant in the invaded plots, and in 2011 and 2012, a period of declining *M. vimineum* dominance. Our goal was to evaluate changes in the soil microbial community over four years to determine whether *M. vimineum* invasions were associated with altered ammonia oxidizer abundance or community structure and whether *M. vimineum* decline had a residual impact on the soil microbial community and nitrification rate (soil legacy effects). We tested whether *M. vimineum*'s effects on ammonia oxidizer communities correlated with changes in nitrification rates, and explored effects of covarying factors such as soil moisture.

2. Materials and methods

2.1. Common garden invasion experiment and soil sampling

To evaluate the links between *M. vimineum*, soil microbial communities, and nitrification rates, we used a long-term common garden study containing control plots and plots experimentally invaded with *M. vimineum* at the Indiana University Research and Teaching Preserve (39°13'9"N, 86°32'29"W). This experiment has demonstrated effects of *M. vimineum* on native herbaceous species, forest succession, arthropod abundance and diversity, and N-cycling (Civitello et al., 2008; Flory and Clay, 2010; Simao et al., 2010). The study area was historically bottomland hardwood forest but has been maintained as grassland for biological research for many years. In 2005, after repeated tilling to diminish the resident species seed bank, thirty-two 5.25 m × 5.25 m (27.5 m²) plots were established and seeded with native herbaceous species (*Andropogon gerardii*, *Asclepias incarnata*, *Aster novae-angliae*, *Calamagrostis canadensis*, *Carex vulpinoidea*, *Elymus virginicus*, *Helenium autumnale*, *Panicum virginatum*, *Senna hebecarpa*, *Scirpus atrovirens*, *Verbena hastata*). Locally collected *M. vimineum* was randomly seeded into half (n = 16) of all plots. In the following three years, other woody and herbaceous species (both native and non-native) naturally recruited into the plots, including *Acer negundo*, *Acer rubrum*, *Ambrosia trifida*, *Carex* spp., *Cornus sericea*, *Lindera benzoin*, *Paspalum laeve*, *Rosa multiflora*, *Viola* spp., and *Vernonia gigantea*. In 2011, the plots were divided into four quadrants, three of which received additional experimental manipulations. Here, we restrict our analyses to the unmanipulated control quadrants.

2.2. Plant biomass

We quantified *M. vimineum* and total native biomass in each plot in fall 2008, when the invasion was fully established in experimental plots, and in 2011 and 2012, as *M. vimineum* biomass was declining and native species were reestablishing. We destructively harvested all aboveground herbaceous species within two to six haphazardly located 30 cm × 30 cm subplots within each plot. We separated *M. vimineum* and resident herbaceous biomass, dried it to constant mass at 60 °C, and recorded the weight. Biomass measurements were averaged across subplots and adjusted to grams per square meter per plot.

2.3. Soil sampling

We collected soil in spring, summer, and fall of 2008, 2011, and 2012 from seven invaded plots and seven uninvaded plots. Soil samples in 2008 were collected from eight soil cores (2 cm diameter × 10 cm deep) evenly distributed in a grid throughout the plots. All soil cores from a given plot were composited and sieved (2 mm mesh). A subsample of soil from each plot was stored at –80 °C for analysis of AO communities. In 2011 and 2012, nine soil cores (2 cm diameter × 15 cm deep) were taken from three

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