

Biogeochemical Effects of a Forest Understory Plant Invasion Depend More On Dissimilar Nutrient Economies Than Invader Biomass

Laura Y Podzikowski (✉ lpodziko@ku.edu)

University of Kansas College of Liberal Arts and Sciences <https://orcid.org/0000-0002-4787-4210>

Marissa Lee

Duke University

Catherine Fahey

University of Florida

Justin Wright

Duke University

S. Luke Flory

University of Florida

Richard P. Phillips

Indiana University Bloomington

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Abstract

There is an increasing need to better understand how and why invasion impacts differ across heterogeneous landscapes. One hypothesis predicts invader impacts are greatest where the invader is most abundant (the mass ratio hypothesis; MRH). Alternatively, invader impacts may be greatest in communities where the nutrient acquisition strategies of the invader are most dissimilar from those of native species (the nutrient economy dissimilarity hypothesis; NEDH). We tested whether the effects of an invasive grass, *Microstegium vimineum*, on soil biogeochemistry were best explained by MRH, NEDH, or both. At three locations (Indiana, North Carolina, and Georgia), invaded and reference plots were established across a nutrient economy gradient. Plots varied in the relative abundance of arbuscular mycorrhizal (AM) vs. ectomycorrhizal (ECM) associated overstory trees, reflecting gradients in biotic nutrient acquisition strategies and edaphic factors. At two locations, we found NEDH predicted invader effects on soil conditions. The net effect of *M. vimineum* homogenized soil properties across the nutrient economy gradient towards conditions consistent with AM-dominated stands; as such, the nutrient economy gradients observed in uninvaded plots were mostly absent in invaded plots. At one location with high N availability and intermediate acidity, both ECM-dominance (NEDH) and invader abundance (MRH) predicted differences in soil moisture, pH, and nitrification rates. Collectively, these results suggest the biogeochemical consequences of *M. vimineum* depend, in part, on pre-invasion soil nutrient economies. Where pre-invasion conditions are known, we provide a scalable and predictive approach to determine where impacts on biogeochemical cycling of C and N may be greatest.

Introduction

Determining the role of individual species in ecosystem processes is a primary need in ecology given the widespread changes in the distribution and abundance of species resulting from human activities (Naeem and Wright 2003, Hooper et al. 2005). Whereas considerable evidence suggests the addition or loss of species can significantly alter processes such as nutrient cycling or productivity, species effects in ecosystems are often highly contingent, which hinders our ability to predict the ecosystem consequences of species gains and losses (Chapin III et al. 1996, Cardinale et al. 2000, Cardinale et al. 2006, Wardle et al. 2011). It is particularly challenging to predict the impacts of non-native invasive species across heterogeneous environments (Strayer 2012) where individual species can have positive, negative, or no effect on carbon (C) and nitrogen (N) cycling (Dassonville et al. 2008, Vila et al. 2011, Castro-Diez et al. 2014, Stricker et al. 2015).

Historically, the magnitude of a species' effect on ecosystem processes has been predicted by its relative dominance within the community, assuming its traits will exert effects proportional to its abundance: the mass-ratio hypothesis (MRH) (Grime 1998, Mokany et al. 2008). While there is some evidence that supports MRH (Kramer et al. 2012, Lee et al. 2014), impacts do not always correlate with invader biomass (Peltzer et al. 2009, Sokol et al. 2017), casting doubt on the universality of this hypothesis. As an alternative, and perhaps not mutually exclusive hypothesis, a species could have its greatest effect when its nutrient acquisition strategy is most dissimilar from those of the existing species in the community:

the nutrient economy dissimilarity hypothesis (NEDH; Fig. 1c). While the MRH and NEDH are assumed to work in consort (Strayer et al. 2006), direct tests of their relative importance remain limited (Platt 1964, Quinn and Dunham 1983) and none have explored the hypotheses at the ecosystem scale. While there is evidence of these mechanisms acting as non-alternative hypotheses in lab microcosms (Kuebbing and Bradford 2019), laboratory, greenhouse, and common garden experiments often do not scale to whole ecosystems (e.g. a forest stand; (Kumschick et al. 2014, Stricker et al. 2015)). This knowledge gap has hindered development of models to predict how gains and losses of species influence ecosystem processes across a range of ecosystem types (Cardinale et al. 2012, Pyšek et al. 2012).

An abundance of research suggests that trees alter soil properties to confer an advantage in effectively obtaining limiting resources (Finzi et al. 1998, Read and Perez-Moreno 2003, Talbot and Treseder 2010, Phillips et al. 2013). Plants in AM-dominated communities usually have nutrient acquisitive traits (“fast cycling”), whereas those in ECM-dominated communities have nutrient conservative traits (McCormack et al. 2012, Chen et al. 2018, Zhang et al. 2018). As a result, forest plots dominated by trees associating with arbuscular mycorrhizal fungi (AM) typically have C and nutrient cycling rates that differ from plots dominated by trees that associate with ectomycorrhizal (ECM) fungi. Plots with high AM-dominance tend to be characterized by litter and soils with narrow C:N ratios (Read 1991, Midgley and Phillips 2016, Jo et al. 2018, Zhu et al. 2018, Ward et al. 2021) soils of intermediate acidity (Read 1991; Phillips et al. 2013), and fast rates of inorganic N cycling (Phillips et al. 2013, Lin et al. 2017, Craig et al. 2019), termed an inorganic nutrient economy (Fig. 1a). By contrast, ECM-dominated stands are characterized by litter and soils with wide C:N ratios (Read 1991, Midgley and Phillips 2016, Jo et al. 2018, Zhu et al. 2018), acidic soils (Read 1991, Phillips et al. 2013), and slow rates of inorganic N cycling (Phillips et al. 2013, Lin et al. 2017, Craig et al. 2019), an organic nutrient economy (Fig. 1a). Consequently, the dominant mycorrhizal association in a plot or stand may act as an integrative signal for soil nutrient cycling, microbial traits, and soil organic matter characteristics (Phillips et al. 2013, Craig et al. 2018, Craig et al. 2019). Because most plants and microbes have evolved strategies for scavenging and mining forms of nutrients that are most available (Read and Perez-Moreno 2003), we posit that differences in forest nutrient economies represent a useful framework for predicting the biogeochemical consequences of plant invasions (Fig. 1b). Despite this prediction, direct tests of the degree to which mycorrhizal dominance predicts invader effects are rare (Jo et al. 2018, Kuebbing and Bradford 2019).

Microstegium vimineum, a plant invasive to the eastern United States (U.S.), is well suited to be a ‘model species’ for testing MRH and NEDH. It can form sparse to dense populations in forest understories (Flory 2010, Warren et al. 2011, Craig and Fraterrigo 2017, Sokol et al. 2017) dominated by a range of forest types and has well-documented and variable effects on soil biogeochemical cycling. Soils under *M. vimineum* tend to be wetter (Ehrenfeld et al. 2001, Fraterrigo et al. 2014), have higher pH (Kourtev et al. 1999), narrow soil C:N ratios (Ehrenfeld et al. 2001, Craig and Fraterrigo 2017), and higher rates of inorganic N cycling than uninvaded areas (Lee et al. 2014, Craig et al. 2019). These dynamics are consistent and similar with soils in inorganic nutrient economies (Fig. 1a). Both greenhouse (Kramer et al. 2012, Fraterrigo et al. 2014, Lee et al. 2014, Craig et al. 2015) and field (Phillips lab unpublished data) studies have reported that *M. vimineum* associates with AM fungi, further supporting the idea that the *M.*

vimineum has nutrient acquisition strategies most similar with those observed in AM-dominated stands. Previous work suggests *M. vimineum* may become dominate in both inorganic (Adams and Engelhardt 2009) and organic nutrient economies (Kourtev et al. 2002); though invasive plants might be more likely to invade AM-dominated forest stands (Jo et al. 2018). Therefore, we expect greater *M. vimineum* biomass in inorganic nutrient economies (Fig. 1b). However, evidence suggests both abundance and nutrient availability can predict *M. vimineum* effects on soil independently and collectively (Lee et al. 2014, Craig et al. 2015, Kuebbing and Bradford 2019), making it ideal for exploring MRH and NEDH as alternative and non-alternative hypotheses.

In this study, we evaluated the degree to which impacts of *M. vimineum* on various soil properties were explained by the ecosystem characteristics of the forest (i.e., supporting the NEDH), its biomass (i.e., supporting the MRH), or both (supporting NEDH and MRH as non-alternative hypotheses). We measured soil characteristics in reference and *M. vimineum* invaded plots across a gradient of AM- to ECM-dominated forest types (Fig. 1a). We determined whether *M. vimineum* abundance differed in AM- and ECM-dominated forest stands. Since invasion impacts differed across the ECM-dominance gradient, we use reference models to estimate the invader effect as the difference between invaded and reference conditions (Fig. 1b). We use these measures to directly ask whether ECM-dominance, *M. vimineum*, or both as proxies for MRH and NEDH best explain invasion effects on soil nutrient cycling (Fig. 1c). Finally, to evaluate if patterns are generalizable, we replicated the study at three locations (Indiana, North Carolina, and Georgia) across the invaded range of *M. vimineum* in the eastern U.S..

Methods

Study Locations

We selected three study locations across the distribution of invasive *M. vimineum* in the eastern U.S. (SI Fig. 1), including Moore's Creek Research and Teaching Preserve (IN; Bloomington, IN), Duke Forest (NC; Durham, NC), and Whitehall Forest (GA; Athens, GA). At each of the three locations, we established ~ 10 uninvaded plots (hereafter "reference plots") and ~ 10 *M. vimineum* invaded plots within mature forest stands (> 70 years old; Table 1). The 10 stands represented a mycorrhizal dominance gradient (i.e., shifts in the relative abundance of AM vs ECM tree basal area; Phillips et al. 2013) in order to capture a range of nutrient economies.

We established 60 plots total (IN = 18, NC = 22, GA = 20; SI Fig. 3), with equal number of reference and *M. vimineum* invaded plots at each location. Each plot consisted of three adjacent subplots (10m radius) within a single contiguous patch of *M. vimineum* and three subplots (10m radius) located nearby (i.e., within 40m) that lacked *M. vimineum* but was otherwise similar in slope, canopy coverage, and overstory and understory plant communities (SI Fig. 2). Within each subplot, we recorded the diameter at breast height and species (or genus) of all trees (≥ 5 cm DBH, 4.5ft above average ground level) to attribute a previously known mycorrhizal association to the tree community (Wang and Qiu 2006, Phillips et al. 2013). Overstory ECM tree dominance was calculated as a percentage of the total basal area within a

subplot (Phillips et al. 2013) and then averaged by invasion status across subplots to estimate ECM dominance for invaded and reference at each plot. Although ‘time-since-invasion’ can mediate invasion effects (Strayer et al. 2006, Flory et al. 2013, Stricker et al. 2016), our primary goal was to investigate invasion impacts across the forest nutrient economy gradient. We captured a range of ‘time-since-invasion’ at each location, while within location opted to capture the nutrient economy gradient rather than controlling for invasion age. More detailed information regarding ‘time-since-invasion’ for these locations is published in Craig et al. (2019).

Field sampling

We collected soil and understory vegetation samples from invaded and reference subplots for three growing seasons from 2014–2016. All samples were collected during the time of peak biomass for *M. vimineum* (August in IN, and September in NC and GA). We collected soil cores using a slide hammer soil corer (5 cm in diameter) from each subplot, removing litter layers and collecting topsoil (0–5cm depth) including O horizons where present (e.g., in ECM-dominated plots) and (5-15cm depths). Since we saw no differences in 2014 and 2015 between the 0–5 and 5-15cm depths, we present the 0-5cm depths for simplicity. Cores collected from the three invaded and three reference subplots were composited at the plot level, totaling 30 invaded and 30 reference samples for each sampling year.

Samples were stored on ice, transported back to the lab, and sieved to 2mm to homogenate soils and remove fine roots. Sieved subsamples were reserved at 4°C for chemical assays and air-dried for total elemental analyses. At peak biomass, we also collected understory vegetation in subplots adjacent the soil samples by hand-clipping samples using 0.0625m² quadrats to quantify aboveground *M. vimineum* biomass on a grams per square meter basis (SI Fig. 3). Vegetation samples were sorted into *M. vimineum* and non-*M. vimineum* biomass, oven dried at 55C for at least 48hrs before being weighed. Aboveground biomass was averaged across subplots to obtain for comparison to the soil samples.

Laboratory analysis

Soil moisture content was determined gravimetrically. Soil pH was determined by measuring a 1:8 wet soil to 0.01M calcium chloride (CaCl₂) extract on a bench-top meter (VWR symphony pH meter; VWR international, West Chester, PA, USA). To quantify total soil C and N content, air-dried soils were ground to a homogenous powder and combusted on a Costech Elemental Analyzer 4010 (Costech Analytical Technologies Inc.; Valencia, CA, USA). Net nitrification potential (nitrification) and inorganic N concentrations were extracted in a 1:2.5 wet soil to a 2M potassium chloride (KCl) solution. Soil moisture was used to control for water content of soils in the extraction. Nitrification was quantified as the change in nitrate concentrations after 14-day aerobic incubations at 23°C. Inorganic N (KCl extractable N) was quantified as the initial concentration of ammonium and nitrate. Extracts were quantified for inorganic N, ammonium and nitrate + nitrite (henceforth described as nitrate), using salicylate and cadmium column reduction methods, respectively, on a Lachat QuikChem 8500 series 2 autoanalyzer (Lachat; Hach, Loveland, CO, USA).

Data analysis

To determine the role of invasion status, location, and position along the nutrient economy gradient on soil properties and processes, we used univariate linear models with the following fixed effects: invasion status (invaded, reference), location (IN, GA, NC), ECM%, and their interactions. Soil response variables were averaged across the three sampling time points (years 2014, 2015, 2016) and included soil pH, moisture (%), nitrification (ug per g*day), and soil C:N. To determine if *M. vimineum* differentially established across the ECM-dominance gradient, we test their correlation with Pearson's R test.

To estimate the impact of invasion on soil properties and processes, we originally intended to use a paired plot approach. However, we found that the ECM-dominance of invaded areas did not strongly correlate with those in nearby reference areas (SI Fig. 2), making the paired plot assumption impossible for these data. Instead, we used data from the reference plots to (1) establish a baseline relationship between ECM% and soil response variables at each location, (2) predict the soil response for all invaded areas based on measured ECM%, and (3) estimate the invasion impact by subtracting the predicted from the expected values at each plot (Fig. 1b). Each impact estimate is also accompanied by 95% prediction intervals to show our level of uncertainty in these estimates (SI Fig. 6). Though we acknowledge that we did not directly measure invader effects (e.g., a common garden) and did not manipulate the system, our observational data and modeling approach provide an critical insight into putative drivers. Using a well-established natural gradient as a hypothesis for expected soil conditions provides an informed prediction against which we can compare conditions under invasion, offering an alternative approach to estimate invader impacts that incorporates quantitative estimates of the ecological context.

We fit univariate linear regression models that used ECM-dominance, *M. vimineum* biomass and their interaction to explain Δ in soil conditions (i.e., the difference in soil characteristics between invaded and uninvaded reference plots across the mycorrhizal gradient; Fig. 1c). Results from the previous model showed that soil conditions and the baseline relationship between soil conditions and ECM% differed by location. For this reason, we fit separate models for each location. For each Δ soil property (Δ soil moisture, Δ pH, Δ soil C:N, Δ nitrification), we fit a linear regression with ECM-dominance, *M. vimineum* biomass, and their interaction as predictors. We standardized *M. vimineum* biomass values by dividing by 100, so values were in a comparable range as ECM-dominance. We partition the variation in our main effects (ECM-dominance and *M. vimineum* abundance) and their interaction by calculating eta-squared (η^2) to determine whether NEDH (described by ECM-dominance), MRH (described by *M. vimineum* abundance), or both explained the most variation in Δ soil property. All statistical analyses were performed in R version 3.4.1" (R Core Team 2017) and visualization of regression models were made in R Package visreg (Breheny and Burchett 2017).

Results

Site characteristics

Whitehall Forest had the highest N availability and more intermediate acidity, in comparison to Moore's Creek and Duke Forest. Locations differed in mean bulk density, texture, inorganic N, and soil pH.

Whitehall Forest had the highest mean KCl extractable nitrate and ammonium concentrations, as well as highest mean pH. Mean bulk density, percent clay, percent sand, and inorganic N were similar between reference and invaded conditions within location (SI Table 2).

Invasions across nutrient economies

We confirmed the presence of the nutrient economy gradient in reference plots at all three locations. ECM-dominance was a significant predictor of soil conditions at all locations. We observed significant negative relationships between ECM-dominance (Table 2, 'ECM') and pH ($p < 0.01$, Fig. 2a), soil moisture ($p < 0.001$, Fig. 2b), and nitrification ($p < 0.001$, Fig. 2c); soil C:N ratios increased with greater ECM-dominance ($p < 0.001$, Fig. 2d). Locations differed in their pre-invasion soil conditions, however, the magnitude of the relationship between ECM-dominance soil pH, moisture, and soil CN was consistent across varying soil types at all three locations (Fig. 2a,b,d). Location was a significant predictor in linear models, but ECM-dominance and location were not significant predictors of soil pH, moisture, or soil CN (Table 2).

Microstegium vimineum invaded forest stands across the ECM-dominance gradient, but it was not more likely to invade nutrient economies with similar conditions to those it promotes. ECM-dominance and *M. vimineum* biomass were not correlated (Pearson's $r = -0.18$, $t [0.05,87] = -1.7$, $p = 0.09$; SI Fig. 5).

Invasion promoted inorganic nutrient forms across the nutrient economy gradient

The effects of invasion status varied across the ECM-dominance gradient. The interaction between ECM-dominance and location was significant in all the models (Table 2), most often altering ECM-dominated soil conditions more than AM-dominated soil conditions (Fig. 2e-h). Under *M. vimineum* invasion the relationship between ECM-dominance (Table 2, 'ECM: invaded') and soil pH, soil C:N, and nitrification rates flattened (Fig. 2e-h); yet, the relative differences among locations were still evident in *M. vimineum* invaded plots (Table 2, 'invaded'). For example, in Whitehall forest, where reference pH (Fig. 2a), soil moisture (Fig. 2b), and nitrification (Fig. 2c) were greatest, we observed the highest soil pH (Fig. 2e), soil moisture (Fig. 2f), and nitrification (Fig. 2g) in the invaded locations.

Nutrient economy dissimilarity hypothesis

Of the two hypotheses, ECM-dominance (NEDH) explained the most variation in models predicting the difference in pH and soil C:N and at two sites for soil moisture and nitrification (Fig. 3). At Moore's Creek and Duke Forest, ECM-dominance consistently accounted for over 50% of the variation in the difference in soil moisture, pH, and nitrification under *M. vimineum* invasion, as well as soil CN at Moore's Creek. ECM-dominance explained a plurality of the variation in the change in soil CN at Duke Forest. At Whitehall Forest, ECM-dominance explained a plurality of the variation in difference in soil C:N. The interaction between ECM-dominance and *M. vimineum* biomass was significant for the difference in soil moisture at Moore's Creek and nitrification at Duke Forest. Where ECM-dominance positively predicts the change in soil moisture and nitrification, *M. vimineum* biomass is not correlated with the difference between

reference and invaded soil moisture or nitrification at both locations. This represents a significant difference between the slopes (SI Fig. 6), but not a synergistic or additive effect of both predictors.

Mass ratio hypothesis

Invader abundance, often along with ECM-dominance and the interaction, predicted the differences in soil conditions at one location, Whitehall Forest (Fig. 3). *M. vimineum* density positively predicted soil moisture, pH, and nitrification at Whitehall Forest (SI Fig. 7). *M. vimineum* biomass explained the most variation in models of change soil moisture ($\eta^2 = 0.37$; Fig. 3) and net nitrification ($\eta^2 = 0.60$; Fig. 3). *M. vimineum* density interacted with ECM-dominance to explain changes in soil pH at Whitehall Forest (Fig. 3), with both ECM-dominance and invader biomass as positive predictors (SI Fig. 6).

Discussion

We investigated whether invader biomass and ECM-dominance, as proxies for MRH and NEDH, operate as alternative and non-alternative predictors of invaded soil conditions. Overall, NEDH more often predicted differences between reference and invaded conditions, indicating that knowledge of the pre-invasion nutrient economy gradient may be a useful and scalable tool for predicting where a plant invasion may have the greatest impact on soil biogeochemistry. Notably, *M. vimineum* invasion across the mycorrhizal gradient was associated with homogenization of the ECM-dominance gradient, altering slow cycling organic soil conditions more than inorganic nutrient economies. To the extent that loss of heterogeneity in nutrient economies may promote a reduction in species richness (Scott and Baer 2019), which has known effects on ecosystem functioning (Hooper et al. 2005), the longer-term consequences of invasion may be greater than demonstrated here.

While it has been widely assumed that MRH and NEDH should operate additively to predict the effects of invasion (Strayer et al. 2006), we found more evidence that NEDH alone was a better predictor of invaded soil conditions. The MRH assumes the traits of the most dominant plant exert the greatest effects on the community. Studies often use measures of native and invasive plant height as a metric of dissimilarity, which are highly correlated with biomass (Martin et al. 2017). While it is true that MRH by definition incorporates some aspects of plant traits, which here we assume to exert a measurable effect on soil nutrient economies, it is surprising that nutrient economy dissimilarity (NEDH) alone, rather than *M. vimineum* abundance more often predicted invaded soil conditions. In contrast to our hypothesis, *M. vimineum* did not achieve higher biomass invade stands with nutrient economies it promotes, suggesting it is equally likely to form dense stands across forest types.

Our findings suggest that in forested communities, understanding the pre-invasion nutrient economy of soils may be a useful tool for predicting if and where invasion alters soil conditions. In direct tests using experimental microcosms, Kuebbing and Bradford (2019) found that biomass effects interacted with trait dissimilarity to alter C mineralization rates. The authors manipulated invader abundance by altering the percent of invasive plant litter in mesocosms containing maple–poplar and oak–hickory litter mixes.

While this manipulation provides clear evidence that these processes can and do operate together, our observations in the field are an interesting contrast. We only found evidence at one site for one variable of a possibly synergistic interaction between both mechanisms. There were no live plants in the Kuebbing and Bradford (2019) lab mesocosms, while in the field in our study, plant interactions with soils and thus rhizosphere processes were present. Roots can alter soil microbial communities in many ways, for example, by altering the quantity (Phillips et al. 2011) and quality (de Vries et al. 2019) of root exudates that, in turn, can affect soil microbial respiration and rates of nutrient mineralization. Some of these processes may mask the direct effects of aboveground biomass on belowground processes in our observational study—perhaps making NEDH a better predictor of the differences between references and invaded conditions, as it inherently integrates both above and below ground plant-soil interactions. In a study of a northeastern forest in Connecticut, Ward et al. (2021) reported that understory shrubs associating with ericoid mycorrhizae weakened the negative relationship between soil CN and ECM-dominance in forests. While it's unlikely ericoid associating shrubs had similar effects in our plots (since only one site – Whitehall Forest, GA – has an abundant ericoid shrub layer), the findings of Ward et al. (2021) highlight that understory plants can have disproportionately large effects on soil processes and in some cases, modulate the impacts of MANE. Whether other understory plants - invasives or native – can have such effects warrants further study.

Pre-invasion soil conditions may help explain when MRH and NEDH drive invasion effects. While we observed nutrient economy gradients that were consistent with the predictions based on ECM% of the overstory trees across all three locations, soil pH and inorganic N at the GA location were higher in both reference and invaded plots than at the other two locations. This result may explain, in part, why Whitehall Forest, GA, was most sensitive to invader-induced changes in nitrification. In reference plots in GA, for example, we observed soil pH consistently above 4.75, which are conditions favorable to nitrifying bacteria (Vitousek et al. 1982, Mushinski et al. 2019). Given that high *M. vimineum* abundance can increase pH (Ehrenfeld et al. 2001, Kourtev et al. 2002, Lee et al. 2014), inorganic N availability (Craig and Fraterrigo 2017), and moisture (Fraterrigo et al. 2014), all of which are drivers of nitrification, the conditions in invaded plots may have become even more favorable for nitrification. This result could be due to increases in other limiting substrates such as organic matter, which was higher in invaded plots in GA (SI Table 2). Conversely, in landscapes with lower available N and greater soil acidity, strong limiters of nitrification rates and thus N cycling, the nutrient economy dissimilarity gradient was of greater importance for determining where the invader had the greatest effects on biogeochemical cycling. This result is in line with previous findings where invader effects on soil conditions were greatest in sites with low soil fertility and high acidity prior to invasion (Dassonville et al. 2008). Nitrification and soil moisture change on a faster temporal scale (days or months) in comparison to pH and soil CN (years or decades). The temporal scale may make moisture and nitrification more responsive to inputs from an annual plant.

The outcome of *M. vimineum* invading AM- and ECM-dominated stands in equal densities and NEDH driving effects, appears to result more uniform soil conditions across the nutrient economy gradient. The ultimate effect homogenizes a once biogeochemically diverse landscape, making pre-invaded organic nutrient economies indistinguishable from an inorganic nutrient economy within each location. Invasive

plants have been shown to promote the homogenization of plant communities (McKinney 2004), and these results suggest an invasive plant can also have similar impacts on soil conditions. Our results are consistent with findings from other studies that suggest invasive plants differentially affect high and low fertility soils, resulting in a convergence of soil conditions (Dassonville et al. 2008).

The disproportionate effect of *M. vimineum* on soils of ECM compared to AM dominated stands could have broad implications for soil nutrient cycling. Greater demand for inorganic N in soils that, under pre-invasion conditions, would have contained high quantities of accessible carbon could stimulate the breakdown of those unprotected carbon pools (Craig et al. 2019, Kumar et al. 2019). There is evidence of this phenomenon in soils from IN where in ECM-dominated plots the increased respiration from soils was perhaps due to greater demand for N (Kumar et al. 2019). We also observed changes in the composition of soil organic matter pools in ECM-dominated plots across all locations in this study, while concentrations in AM-dominated plots were unchanged (Craig et al. 2019). The potential to release stored, but unprotected, soil organic matter from ECM-dominated soils, and alter the form of stored carbon in soils, provides further evidence in support of preventing *M. vimineum* establishment in ecosystems dominated by ECM-associating trees (Craig et al. 2019, Kumar et al. 2019).

Of MRH and NEDH, our data suggest NEDH most often predicts *M. vimineum* impacts on soils. Under this mechanism, ECM-dominated forest stands are ultimately most at risk of ecosystem impacts due to *M. vimineum* invasion, where a positive feedback on soils creates a fast-cycling inorganic nutrient economy. The ultimate result may be to homogenize topsoils across forests that promote diversity biogeochemical cycling in soils. There are now maps of mycorrhizal dominance for the entire US (Jo et al. 2019), which could make our findings scalable to the landscape level. In the few instances where MRH best explained changes in soil conditions, reference soils were more fertile (higher inorganic N) with intermediate acidity, suggesting, as others have demonstrated (Dassonville et al. 2008), understanding ecological context is of the utmost importance for predicting spatial impacts of plant invasion. Our work elucidates where impacts of invasive plants on biogeochemical cycling may be idiosyncratic or unidirectional, with potential to be both predictive and scalable for other invasive species, as well.

Declarations

The authors declare no conflict of interest.

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Tables

Table 1: Location characteristics, including stand age, soil type, canopy cover (mean(SE)), *M. vimineum* densities (mean (SE)), ECM-dominance in reference and invaded plots (range), and dominant ECM and AM taxa. The dominant trees listed combined accounted for greater than 75% of the total basal area in

all locations. An extensive species list and mycorrhizal characterization can be found in the supplemental materials (Supplemental Table 2).

	<i>Moore's Creek, IN</i>	<i>Duke Forest, NC</i>	<i>Whitehall Forest, GA</i>
latitude	39° 5'N	36° 1' N	33°53' N
longitude	86° 27'W	78° 59'W	83°22' W
stand age	~80 years old	~ 70 years old	~ 80 years old
soil type	Inceptisols	Georgeville	Congaree
canopy cover (%)	80.7 (1.11)	75.9 (2.0)	86.7 (0.75)
<i>M. vimineum</i> (g m⁻²)	104.3 (11.1)	147.3 (20.8)	103.4 (7.4)
ref. ECM-dom. (%)	23.6 - 82.9	18.3 – 82.9	15.2 - 63.3
inv. ECM-dom. (%)	7.8 – 68.5	0 – 69.3	13.3 – 76
dominant ECM taxa	<i>Fagus grandifolia</i>	<i>Pinus taeda</i>	<i>Quercus nigra</i>
	<i>Quercus alba</i>	<i>Quercus phellos</i>	<i>Pinus taeda</i>
	<i>Quercus rubra</i>		<i>Quercus rubra</i>
dominant AM taxa	<i>Acer saccharum</i>	<i>Liquidambar styraciflua</i>	<i>Liriodendron tulipifera</i>
	<i>Liriodendron tulipifera</i>	<i>Liriodendron tulipifera</i>	<i>Liquidambar styraciflua</i>

Table 2: Regression models describing soil moisture (%), pH, soil C:N, and net nitrification rates ($\mu\text{g g}^{-1}\text{d}^{-1}$) as a function of ECM-dominance, with location and invasion status as fixed factors.

	<i>Soil pH</i>	<i>Soil Moisture</i>	<i>Net Nitrification</i>	<i>CN</i>
<i>P-values</i>				
ECM	0.0009	1.6e-05	9.9e-07	1.1e-05
state	0.0004	0.0005	3.9e-11	2.9e-06
invasion status	0.001	0.47	0.003	0.049
ECM:state	0.32	0.07	0.02	0.57
ECM:invasion	0.004	0.002	0.05	0.02
state:invasion	0.83	0.19	0.03	0.90
ECM:state:invasion	0.80	0.94	0.69	0.72
<i>Coefficients</i>				
Intercept	5.733***	0.364***	1.508***	13.139***
ECM	-2.003*	-0.374***	-1.833**	4.169
IN	-0.733	-0.134*	-0.668	-1.327
NC	-1.028*	-0.064	-1.008**	-0.464
invaded	-0.311	-0.067	0.151	-0.069
ECM:IN	1.101	0.263*	1.074	0.028
ECM:NC	1.508	0.151	1.192	2.951
ECM:invaded	1.755	0.254	0.891	-1.517
IN:invaded	-0.176	-0.008	-0.735	1.769
NC:invaded	0.277	-0.052	-0.319	1.728
ECM:IN:invaded	0.005	-0.059	0.546	-3.745
ECM:NC:invaded	-0.649	-0.028	-0.165	-3.555
Observations	60	60	60	60
R²	0.54	0.56	0.75	0.59
F Statistic	5.057***	5.589***	13.059***	6.313***

Figures

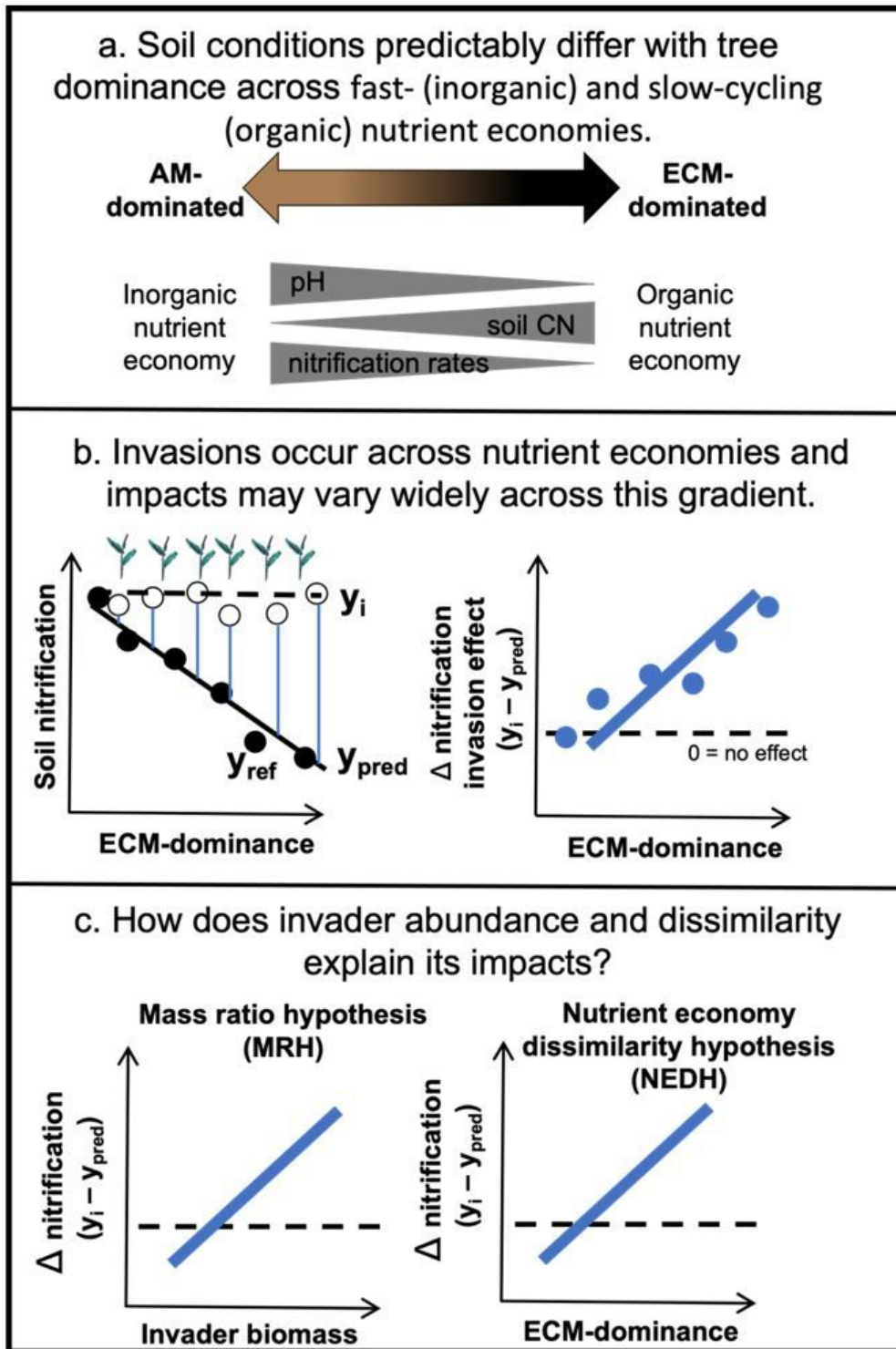


Figure 1

a) Soil nutrient economies vary across an AM to ECM tree dominance gradient. AM associating trees promote fast-cycling, nutrient acquisitive conditions (inorganic nutrient economies), while ECM associating trees promote slow cycling conditions (organic nutrient economies). This gradient provides a well-established predictable backdrop upon which we can compare the differences between invaded and uninvaded (reference) conditions. b) Invasion can occur across the gradient their impacts can vary across

the gradient. To quantify invader effects, we use reference models to estimate an invader effect as the difference between invaded and predicted reference conditions. c) Where mass ratio hypothesis (MRH) drives invader impacts, we expect invader effects to increase with invader abundance. Where nutrient economy dissimilarity hypothesis (NEHH) is driving the effects of invasion, we expect the greatest invasion effects in ECM-dominated soils. Where both operate in consort, we expect the effects to be greatest in ECM-dominated plots with greater *M. vimineum* biomass.

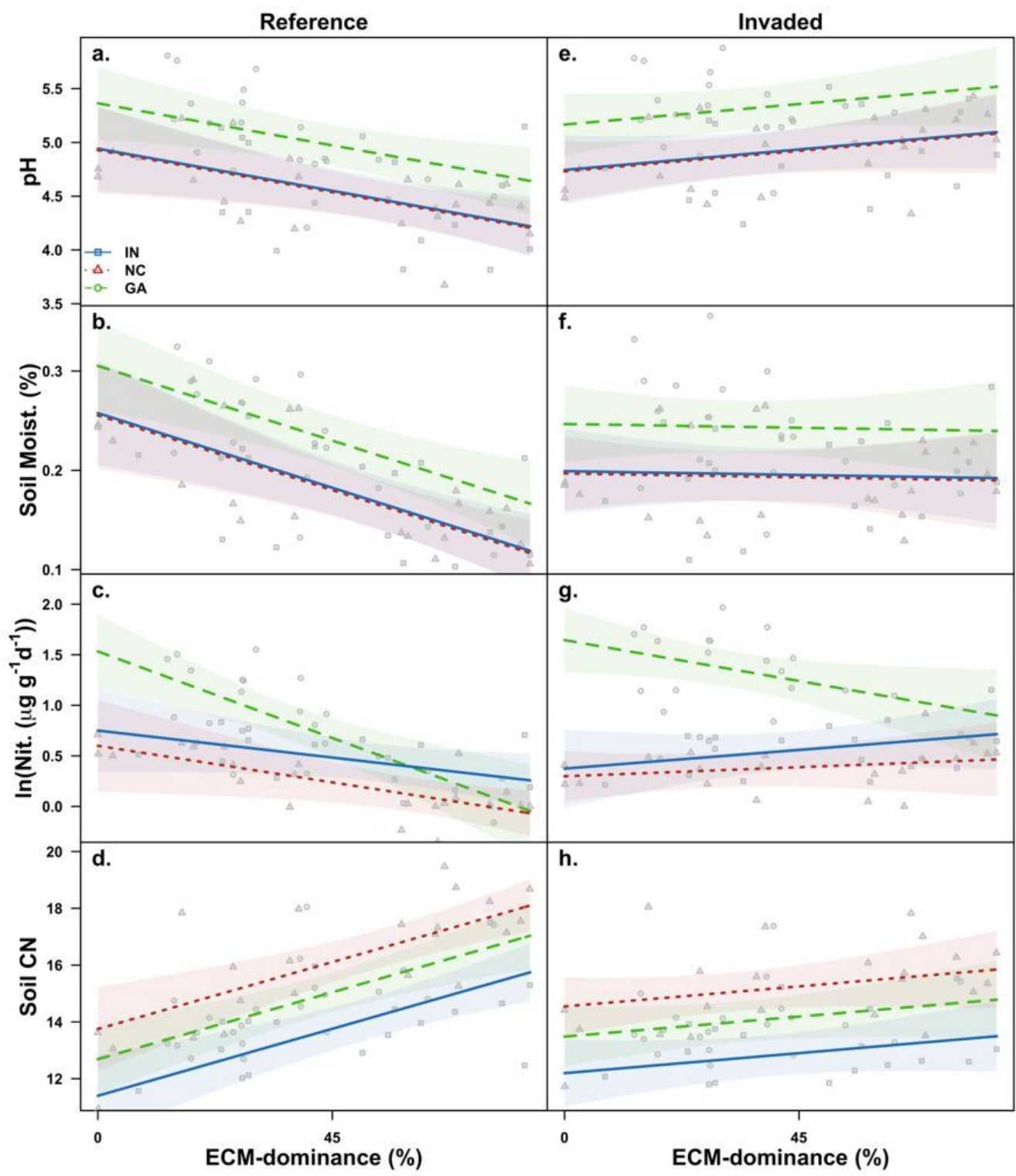


Figure 2

Forest ECM-dominance (aboveground community) predicts (a) pH, (b) soil moisture, (c) nitrification, and (d) soil C:N in reference plots. *M. vimineum*-invasion changes the relationships between ECM-dominance and (e) soil pH, (f) soil moisture, (g) nitrification, and (h) soil CN. IN as blue squares, NC as red triangles, and GA is depicted as green circles.

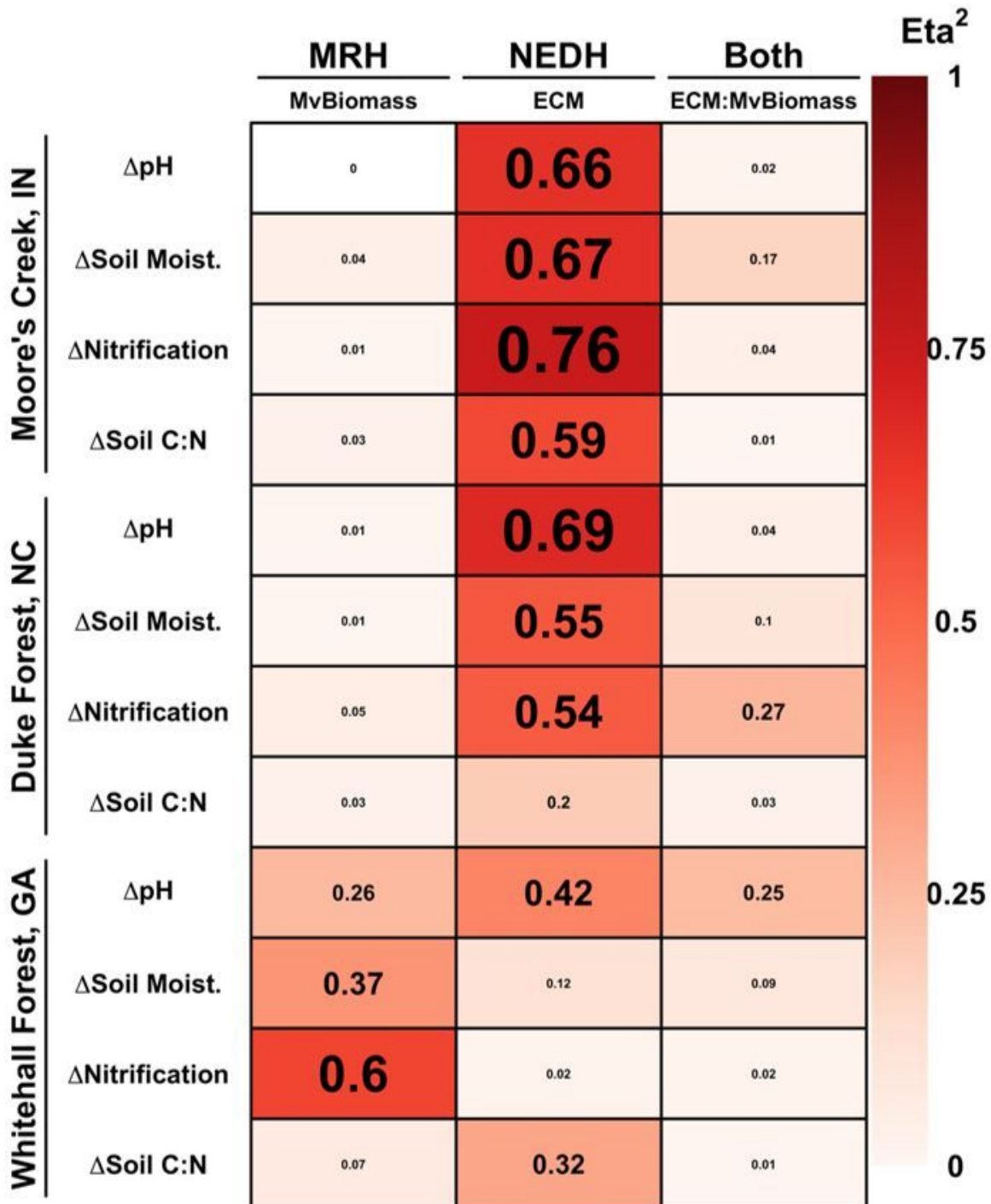


Figure 3

Model variance (eta-squared) explained by mass ratio hypothesis (*M. vimineum* biomass, left column), nutrient economy dissimilarity hypothesis (ECM-dominance, middle column), and the interaction (right column). Eta-squared values are scaled in color and size (darker red and larger font indicating a higher eta-squared) by their relative contribution to the total variation explained by the model predicting invader effects, Δ pH, Δ soil moisture, Δ nitrification, and Δ soil CN, for Moore's Creek, Duke, and Whitehall forests.

Supplementary Files

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- [Podzikowski et al. Oecologia SI Tables And Figures 25 Sept 2021.pdf](#)