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Soil Nitrogen Cycling Following Invasive Shrub Removal

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Research Article

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Abstract

Invasive plants often alter ecosystem functions and processes, especially soil N cycling. In urban or recently disturbed forest stands, soil N is often more available and may facilitate plant invasion, which in turn increases N mineralization and available N. In eastern United States forests, the shrub *Rosa multiflora* (“rose”) is the dominant invader, yet potential effects on N cycling are poorly understood. Moreover, invasive plant management can impact soil N cycling by decreasing plant N uptake and disturbing the soil. The objectives of this study were to evaluate N cycling along a gradient of rose invasion and investigate potential changes to N cycling under four different management strategies: 1) do nothing (i.e., the control), 2) invasive plant removal, 3) removal followed by native seed mix addition, 4) removal, native seed mix, and chipped woody stem addition. We selected three forest sites experiencing a low, medium, or high amount of shrub invasion, and measured N cycling in the early (June) and late (September) growing seasons. We found N was immobilized in June and mineralized in September. One year after experimental management strategies were implemented, removal alone had no effect on N cycling compared to control plots, but addition of native seed mix and chipped stems reduced early-season nitrification in our medium invasion site. Our findings suggest that initial N cycling under different amounts of rose invasion and subsequent responses to management are complex, and that N cycling responds differentially to management in the year following invasive plant removal.

Introduction

Non-native invasive plants (hereafter “invasive”) pose a significant threat to biodiversity worldwide (e.g., Vitousek et al. 1997*a*), and the eastern U.S. is one of the most vulnerable regions (Early et al. 2016). In addition to negative effects on native biodiversity, invasive plants are often associated with alterations to ecosystem functions and processes, such as decomposition (e.g., Ashton et al. 2005, Heneghan et al. 2007, Trammell et al. 2012), plant productivity (Ladwig and Meiners 2009, León et al. 2018), and biogeochemical cycling of nutrients (Vitousek et al. 1997*c*, Liao et al. 2008). Changes in carbon (C) and nitrogen (N) cycling are cause for concern, as these cycles are inextricably linked. Nitrogen cycling has been greatly perturbed in the last 150 years (Vitousek et al. 1997*b*, Galloway et al. 2008, Fowler et al. 2013, Kanakidou et al. 2016), which can have cascading effects that ultimately impacts other ecosystems via eutrophication and atmospheric N deposition (Vitousek et al. 1997*a*, Galloway et al. 2003, Galloway et al. 2004, Clark et al. 2017).

Since 1900, atmospheric N deposition has more than doubled (Sutton et al. 2011, Fowler et al. 2013) leading to N saturation in many terrestrial ecosystems (Vitousek et al. 1997*b*, Aber et al. 1998). Global reactive N emissions now far exceed what is naturally produced (Fowler et al. 2013, Kanakidou et al. 2016), beyond what may be considered a “safe operating space” (Rockström et al. 2009, Steffen et al. 2015). Excess N in terrestrial ecosystems can have detrimental effects, leading to declines in native plant diversity (e.g., Stevens et al. 2010), increased invasive plant abundance (e.g., Corbin and D’Antonio 2004), shifts in species composition and/or ecosystem type (Gilliam 2006, Bobbink et al. 2010), direct plant toxicity (Bobbink et al. 2010, Pardo et al. 2011), increased susceptibility of plants to extreme weather

events (Grulke et al. 1998, Caporn et al. 2000, Friedrich et al. 2012), soil acidification (Stevens et al. 2010, Stevens et al. 2018), loss of soil cations and reduced cation uptake efficiency (Pardo et al. 2011), and eutrophication caused by leaching of NO_3^- (Stevens et al. 2018). While some of these environmental impacts have been addressed by enacting policies (Fowler et al. 2015, Gilliam et al. 2016, Reid and Aherne 2016) and regulations to control emissions (e.g., Clean Air Act), the effects of invasive plants have largely not been addressed and are often localized (e.g., Barney and Tekiela 2020, Pyšek et al. 2020). Therefore, there is a great need to understand how N cycling is altered in the presence and spread of invasive plants, and how restoration and management efforts can mitigate their effect.

In forests of the northeastern United States, the dominant invasive plant is *Rosa multiflora* (multiflora rose), a shrub native to eastern Asia (Kurtz and Hansen 2013, Schulz and Gray 2013, Trammell et al. 2020). Previous studies have found invasive shrubs are associated with changes in soil N cycling (e.g., Ehrenfeld et al. 2001, Ehrenfeld 2003) due to various plant traits such as higher leaf litter quality and quantity (Jo et al. 2015, Jo et al. 2017, Lee et al. 2017), accelerated decomposition rates (Hawkes et al. 2005, Trammell et al. 2012), or shifts in microbial communities (Kourtev et al. 2002, Elgersma and Ehrenfeld 2011, McLeod et al. 2016). However, most studies have focused on invasion in a single site, or comparisons between invaded and uninvaded habitat, and it remains uncertain how soil N cycling is altered along a gradient of invasion. Studying soil N cycling along a gradient of invasive plant abundance can identify thresholds of density that influence soil N cycling rates, and thus assist in prioritizing forests for management interventions.

While studies have examined vegetation responses following forest restoration (e.g., Hartman and McCarthy 2004, Johnson and Handel 2016, Hopfensperger et al. 2019), to our knowledge it remains unclear how soil N cycling in forest ecosystems may respond to invasive shrub removal, and specifically removal of *Rosa multiflora*. Moreover, additional management and restoration strategies after invasive shrub removal may lead to further changes in N cycling. For example, Clark et al. (2019) found that C addition was the only remediation approach that decreased soil N availability, while prescribed burning, thinning, and liming had no effect. Ultimately, we hope to understand whether soil N cycling can be altered to prevent or limit the spread of invasive shrubs in susceptible forests.

The overarching goal of this research was to study the abundance-impact of *R. multiflora* (hereafter “rose”) on soil N cycling using an observational (fine-scale) and manipulative experimental approach in three forests with varying invasion densities. In this study, we assessed soil N cycling rates (i.e., net mineralization and nitrification) and soil C:N under a gradient of rose cover, and we conducted a rose removal experiment to understand how short-term soil N processes respond to invasive plant removal. Specifically, we asked the following questions: 1) What are the fine-scale patterns (i.e., within forest sites) in potential mineralization rates under varying rose shrub density, total non-rose stem density, and soil water content?, 2) How will rose shrub removal influence mineralization rates?, 3) How will N mineralization rates respond to additional management strategies (i.e., native seed mix addition and C-rich soil amendment) within one year?, and 4) How does seasonality (early compared to late growing season) influence soil N cycling before and after management?

We expected soil N cycling (i.e., net N-mineralization) to be accelerated with increasing rose stem density and in forest sites with greater rose invasion. Following invasive plant removal, we expected larger reductions in N cycling rates where invasion density was greatest, with smaller reductions as invasion density decreased due to fewer shrubs affecting soil N cycling. Furthermore, we expected the addition of seed mix would lead to increased plant N uptake (from new grass and sedge germinants; Moore et al. 2023), thereby reducing nitrification rate via lower soil NH_3 pools. However, invasive plant removal is itself a disturbance which will result in seasonal and short-, mid-, and long-term soil N cycling responses, and some responses could take more than one year for soil N cycling to respond to the addition of native seeds. Nonetheless, we expected the application of C-rich chipped stems would directly increase soil C:N slowing N cycling rates, and the net change in %C (and thus molar C:N) would be positive and significantly greater than the control group, while net change in %N should decrease. We expected to see differences in soil N cycling rates between peak growing season (warm, wet) and late growing season (warm, dry), specifically if rose was influencing soil N cycling rates through soil moisture regimes.

Methods

Study Area and Design

We chose three forest sites that are part of a long-term urban forest network called the FRAME (FoRests Among Managed Ecosystems; https://sites.udel.edu/frame/) for soil analyses and invasive plant removal. The selected sites were located in the piedmont region of northern Delaware and extreme southeast Pennsylvania within 13 km of one another. For the region, mean annual temperature is 13.2°C and mean annual precipitation is 119.3 cm year^{-1} (NOAA 2020). Soils in this Piedmont region are mostly ultisols, and our sites were Fallsington loam, Brinklow channery loam, and Glenelg silt loam soil series.

In 2015, vegetation was sampled in all 38 FRAME sites, and sites were classified along an invasion gradient (Trammell et al. 2020) based on the abundance of non-native woody plants (i.e., number of non-native woody stems). Sites were classified as experiencing no invasion (0 non-native stems ha^{-1}; n = 5), low invasion (0.2–25 non-native stems ha^{-1}; n = 11), medium invasion (26–80.5 non-native stems ha^{-1}; n = 11), or high invasion (> 80.5 non-native stems ha^{-1}; n = 11). We selected one forest site from the low, medium, and high invasion categories to assess initial woody stem density and soil C and N content, to be followed by an invasive plant removal experiment.

In March of 2017, we surveyed each study forest for invasive plant removal locations (the “management zone”). At each forest site, the management zone had to meet the following criteria: **1**) invasive shrub cover, particularly rose, must be dense enough to establish nine 4 m^2 (2 m × 2 m) treatment plots within the zone, plus three additional 4 m^2 control plots just beyond the zone, **2**) plots must be at least 1 m away from any other plots and/or trees, and **3**) invasive shrub cover must be greater than 75% in all plots. Within each forest site, we established 12 1-m^2 plots for the manipulative experiment (see below for

further details on the treatments), and assessed the plant communities and soil N cycling rates in each plot.

Vegetation Sampling

In 2017, prior to invasive plant removal, we sampled all tree, shrub, and herbaceous vegetation in each control (n = 3 site^{-1}) and treatment plot (n = 9 site^{-1}) at each forest site (n = 3). All plots were revisited for post-removal vegetation sampling in 2018 and 2019 to assess plant density following invasive plant removal (Moore et al. 2023). Trees, shrubs, and herbaceous species were counted as the number of stems across all individuals of a given species during peak growing season, beginning in July. If identification to species was not possible, individuals were identified to genus. Data were divided into total rose stem density and total non-rose stem density as potential drivers of soil N cycling rates.

Experimental Removal

Our experimental design incorporated a control and three manipulative treatments (hereafter "management strategies"). The goal of the manipulations was to conduct "easy-to-implement" and "cost-effective" strategies for landowners, managers, and restoration professionals. Due to the constraints of the management zone and number of management strategies, sample sizes at each forest site were small (n = 3 per management strategy). Within each site, 12 plots were established for a total of 36 plots across the three forest sites. Treatment strategies were *additive*, such that each subsequent treatment augmented the methods of the previous strategy. They were:

1) control – no invasive plant removal,

2) removal – hand pulling or cutting invasive plants, followed by stump treatment with the herbicide glyphosate,

3) seed mix – removal strategy with native plant seed mix amendment, and

4) mulch – removal and seed mix strategy with the addition of chipped invasive stems applied as mulch.

Implementation of Management Strategies

In February and March 2018, the removal zone was cleared of all invasive shrubs at each of our forest sites. Small plants were hand pulled, while larger plants were cut at approximately 10 cm above ground. Herbicide (50.2% glyphosate solution) was applied to the resulting stump immediately afterward. Invasive stems were collected and allowed to air-dry at the study site for at least 6 weeks prior to mulching.

In March 2018, a native seed mix (Prairie Moon Nursery, Winona, MN 55987) was applied to plots in management strategies (3) and (4). The seed mix was customized to include native plant species present in or near our forest sites, and excluded species known to be palatable to deer (e.g., *Trillium* spp.) The

seed mix consisted of 29 herbaceous and 7 graminoid species in quantities based upon seed size (Moore et al. 2023). Treatment plots (6 site^{-1}) were seeded by hand with 26.96 g of seed (6.74 g/m^2).

In May 2018, dried rose stems were mulched on-site using a Tazz K32 Chipper Shredder. Due to the large number of entangled stems, other woody invasive species may have unintentionally been mulched (e.g., Japanese barberry [*Berberis thunbergii*]), though care was taken to exclude them to the best of our ability. The resulting mass of mulched stems was similar at each site (Low = 10.55 kg, Medium = 10.65 kg, and High = 10.55 kg). Within three days of mulching, 3.5 kg of mulched stems were applied by hand to each plot in the mulch treatment group (n = 3 site^{-1}), forming a layer approximately ¼ inch thick on the soil surface.

Soil Sampling and In Vitro Laboratory Incubation

Soils were collected in June and September of 2017 (pre-removal year) and 2018 (first season post-removal) at each forest site. Our initial goal was to sample soils in 2019 (two seasons post-removal) as well, but due to building renovations and lab relocation in 2019, and the COVID-19 pandemic in 2020, we were unable to sample more than 1 year post-removal. In each plot (n = 13 site^{-1}), leaf litter was removed prior to sampling, and a soil push probe was used to collect 2-cm diameter cores from the top 15 cm of soil. Three cores were taken per plot, bagged and homogenized. Soil cores were transported and stored at 4°C until processing either upon arrival at the lab or within 48 hours after collection. Soils were sieved (2 mm) to remove rocks, roots, leaves, and other debris. Three 10 g (± 0.1 g) subsamples were weighed and used for determining soil moisture content, initial nitrate (NO_3^-) and ammonium (NH_4^+) content, and a 30-day *in vitro* lab incubation to determine potential N mineralization rates.

For gravimetric determination of soil field moisture content, soils were oven dried at 105°C for 72 hours, then removed and placed in a desiccator to allow cooling before re-weighing. Oven-dried soil mass was used to calculate the fresh-weight-to-dry-weight conversion factor and gravimetric soil moisture content. For the 30-day incubation, 10 g (± 0.1 g) of soil were placed into a tared, 250 mL Erlenmeyer flask, then sealed with parafilm. Parafilm was punctured with a small syringe needle to allow gas exchange. Flasks were placed in an incubator and kept at 25°C for the duration of the incubation. To ensure that soil moisture was maintained at field moisture content values, flasks were weighed at least once per week. If the weight decreased by more than 1 gram, an equivalent amount of DI water was injected into the flask through the parafilm using a small syringe. After approximately 30 days, soils were removed from the incubator and prepared for extraction.

Determination of Nitrate, Ammonium, and Nitrogen Mineralization Rates

Prior to analysis, NO_3^- and NH_4^+ were extracted from soil using a 2 M KCl solution. For the soil samples collected in 2017, the extract was analyzed for NO_3^- and NH_4^+ by colorimetric spectrophotometry using a SEAL AQ2 Discrete Analyzer (SEAL Analytical, Mequon, Wisconsin 53092). Due to instrument down time,

the SEAL AQ2 was used only for NH_4^+ quantification for June 2018 soil samples. For NO_3^- analyses on the June 2018 soil samples, a spectro::lyser V2 (s::can Messtechnik GmbH, Vienna, Austria) was used to measure nitrate via UV-Vis spectrometry. The September 2018 soil samples were analyzed for NH_4^+ and NO_3^- by colorimetric spectrophotometry using a SEAL Analytical AutoAnalyzer 3 flow injection analyzer at the University of Delaware Soil Testing Lab.

To ensure that nitrate concentration results were comparable across the analytical instruments, a randomly chosen subsample of soil extracts (n = 14) previously analyzed on the AQ2 in 2017 were analyzed on the other two instruments as well. Results of one-way ANOVA indicated no significant difference ($P = 0.875$) in the measured nitrate concentrations among these three instruments.

Potential net nitrification rate was calculated as the net change in soil NO_3^--N between initial soil collection and incubated extract following 30-day incubation. Potential net N mineralization was calculated as the net change in soil NO_3^--N plus NH_4^+-N between initial soil content and incubated extract.

Soil C and N

To determine total soil C and N, all soils from September 2017 and the control and mulch treatment group from September 2018 were ground using a ball mill (Mixer Mill MM200, Retsch, Haan, Germany). Soil C (%), N (%), and C:N were measured using an elemental combustion system (4010 CHNSO analyzer, Costech Analytical, Costech Valencia, CA, USA) interfaced with a Thermo Delta V Ratio Mass Spectrometer (Thermo, Bremen, Germany) at the University of Maryland Center for Environmental Science's Appalachian Laboratory (Frostburg, MD). Soil C:N ratio was expressed on a molar basis.

Statistical data analysis

All data analyses were performed in R version 4.1.0 (R Core Team 2021) using the rstatix (Kassambara 2021) and relaimpo (Grömping 2006) packages. Significance was considered at the $\alpha = 0.05$ level, and in some cases the $\alpha \leq 0.10$ critical values are reported as marginally significant to identify potential trends. After confirming normality and homoscedasticity of the data, we performed one-way analysis of variance (ANOVA) followed by Tukey's post-hoc multiple comparisons test to determine potential differences between forest sites in soil N cycling metrics (i.e., nitrification and N-mineralization rates) and soil C and N metrics (i.e., soil %C, %N, and molar C:N) prior to restoration; June and September N cycling metrics were analyzed separately. We used the 'calc.relimp' function of relaimpo to assess relative importance of explanatory variables (total rose density, total non-rose density, and soil water content [SWC]), and to determine R^2 of the model for each month (June and September) by N cycling metric (nitrification and N-mineralization rates) combination. For models that explained a considerable amount of variance (i.e., with R^2 above 0.3 threshold), we report 'lmg' (partitioned R^2) for each explanatory variable and perform simple linear regressions between explanatory variables (i.e., rose stem density, non-rose stem density, and SWC) and soil N cycling rates.

To assess differences in soil N cycling among management strategies following invasive plant removal, we calculated the net change between pre- and post-removal (2017 to 2018) nitrification and net N-mineralization rates. Then, we performed one-way ANOVA followed by Tukey's post-hoc test to determine significant differences among management strategies, analyzing each site and month of sampling separately. We also calculated net change in soil water content (SWC) and analyzed the change between years with a paired *t*-test for June and September separately. To determine potential differences in soil C and N metrics between the control and mulched treatment (i.e., C amendment) groups, we calculated the net change between the pre- and post-removal (2017 to 2018) soil %C, %N, and molar C:N, then used Welch's *t*-test due to small sample sizes (n = 3 plots strategy^{-1}; 6 plots site^{-1}) and differences (> 3-fold) in standard deviations between groups.

Results

Initial site conditions

Prior to invasive plant removals, we analyzed differences in soil N processes across forests (Fig. 1a-d; Table 1 for means and Table S1 for results of one-way ANOVA and post-hoc analyses). In June, the low invasion site had significantly lower nitrification and N-mineralization compared to the medium and high invasion sites ($P < 0.01$; Fig. 1a, b). In September, there was a shift from N immobilization to N mineralization (Fig. 1). Nitrification was higher in the low invasion site compared to the medium ($P < 0.001$) and high invasion sites ($P = 0.021$; Fig. 1c). Furthermore, net N-mineralization was lower in the medium invasion site compared to the low invasion site ($P = 0.060$), though neither differed from the high invasion site (Fig. 4d).

Table 1
– Means (± 1 SE) of nitrification and net N-mineralization rates in June and September 2017.

Month	Invasion	Nitrification	N Mineralization
		μg NO_3^--N	μg [NO_3^- + NH_4^+]-N
		g^{-1} DW soil d^{-1}	g^{-1} DW soil d^{-1}
June	Low	-1.21 (0.18) [A]	-1.31 (0.22) [A]
	Medium	-0.36 (0.07) [B]	-0.46 (0.10) [B]
	High	-0.65 (0.09) [B]	-0.63 (0.09) [B]
September	Low	0.66 (0.08) [A]	0.91 (0.10) [A]
	Medium	0.25 (0.05) [B]	0.66 (0.06) [B]
	High	0.40 (0.06) [B]	0.73 (0.06) [AB]

* Letters indicate significant differences ($P < 0.10$) between sites.

Prior to experimental manipulation, soil %C ($F_{2,33}$ = 36.52, $P < 0.001$), %N ($F_{2,33}$ = 25.18, $P < 0.001$), and molar C:N ($F_{2,33}$ = 84.09, $P < 0.001$) significantly differed across the sites ($P < 0.05$; Table 2). Soil C (%), N (%), and molar C:N were significantly highest in the low invasion site, followed by the medium invasion site, and lowest in the high invasion site.

Table 2 – Means (± 1 SE) of soil C and N metrics, results of one-way ANOVA, and Tukey-Kramer post-hoc analysis across the Low, Medium, and High Invasion forest sites in September 2017, prior to invasive plant removal. *F*- and *P*-values are reported for the omnibus test; adjusted *P*-values are reported for each pairwise comparison.

Metric	Invasion	Mean (±1 SE)	*F*	*P*	Comparison	adjusted *P*
% C	Low	4.07 (0.26)	36.52	< 0.001	Low-Medium	0.003
	Medium	3.17 (0.13)			Low-High	<0.001
	High	1.92 (0.10)			Medium-High	<0.001
% N	Low	0.28 (0.02)	25.18	< 0.001	Low-Medium	0.029
	Medium	0.24 (0.01)			Low-High	<0.001
	High	0.17 (0.01)			Medium-High	<0.001
molar C:N	Low	16.62 (0.19)	84.09	< 0.001	Low-Medium	<0.001
	Medium	15.35 (0.22)			Low-High	<0.001
	High	13.16 (0.16)			Medium-High	<0.001

Fine-scale Soil N Cycling

Relative importance analysis indicated that the models (i.e., rose stem density, non-rose stem density, and SWC) explained a considerable amount of variance (i.e., R^2 = 0.349 to 0.651) for N process rates (i.e., potential nitrification and N mineralization) in June and for nitrification in September. However, for N-mineralization in September, the proportion of variance explained by the model was considerably low (i.e., R^2 < 0.18; Fig. S1). In June, soil water content (SWC) was most important for explaining N process rates (lmg; nitrification = 0.38, N-min. = 0.51), while rose stem density was most important for explaining nitrification rate in September (lmg = 0.15).

For models with R^2 > 0.3, relationships between rose density, non-rose stem density, SWC and soil N cycling rates are reported. In the early growing season (June), potential nitrification (R^2 = 0.271, P = 0.001) and net N mineralization (R^2 = 0.116, P = 0.042) decreased as rose density increased (Fig. 2a, b). Similarly, nitrification (R^2 = 0.451, P < 0.001) and net N mineralization (R^2 = 0.566, P < 0.001) decreased with increasing SWC (Fig. 3a, b). The relationship between non-rose stem density and soil N cycling were opposite to the relationships observed with rose density; nitrification (R^2 = 0.238, P = 0.003) and net N mineralization increased (R^2 = 0.158, P = 0.016) as non-rose stem density increased (Fig. 4a, b). Patterns in the late growing season (September) were mostly opposite those found in the early growing season. Potential nitrification increased with increasing rose density (R^2 = 0.284, P < 0.001; Fig. 2c) and SWC (R^2 = 0.146, P = 0.022; Fig. 3c), yet decreased as non-rose stem density increased (R^2 = 0.225, P < 0.01; Fig. 4c).

Soil N Responses to Invasive Plant Management

Within each of our forest sites, we found that removing invasive plants (i.e., strategy #2) had no effect on soil N cycling (i.e., nitrification and N-mineralization) when compared to control plots (i.e., strategy #1; $P > 0.10$; Figs. 5, S2, S3; Tables S2) after one year. However, post-removal treatments (i.e., addition of native seed mix [strategy #3] and invasive stems as mulch [strategy #4]) resulted in greater soil N cycling responses in the *medium* invasion site in June (Fig. 5). Net change in nitrification rate was positive under all management strategies, though the net increase was smaller in the seed mix ($P = 0.067$) and mulched ($P = 0.061$) treatment groups compared to the control group (Fig. 5a). There were no differences in N cycling metrics among management strategies at the low and high invasion sites in either the early or late growing seasons ($P > 0.10$; Figs. S2, S3).

Within each forest site, amending the soil with carbon-rich, chipped invasive stems resulted in site-specific changes in soil C and soil N metrics (%C, %N, and molar C:N) when compared to the control strategy (Fig. 6). In the low invasion site, there were net decreases in mean soil C (%) and N (%) in the mulched treatment group (%C = -0.66 ± 0.19% ; %N = -0.01 ± 0.02%) compared to the control group (%C = 0.22 ± 0.32%, $P = 0.091$; %N = + 0.05 ± 0.02%, $P = 0.073$; Fig. 6a, b). In the high invasion site, there was a net increase in mean soil N (%) and a significant net decrease in mean soil C:N in the mulched treatment group (%N = 0.08 ± 0.03%; C:N = -1.029 ± 0.423) compared to the control group (%N = -0.003 ± 0.012, $P = 0.074$; C:N = 0.392 ± 0.262, $P = 0.057$; Fig. 6h, i). There were no differences in the medium invasion site ($P > 0.10$).

Discussion

In general, we found differences in N cycling across forests along a gradient of rose density (Fig. 2), soil water content (SWC; Fig. 3), and non-rose total density (Fig. 4) as expected. Assessing N cycling during early and late growing seasons also revealed differences in nitrification and net N-mineralization rates. Across sites, rose density was a better predictor of N cycling in September (Fig. 2), while SWC was a better predictor in June (Fig. 3). N cycling responses following invasive plant removal varied by site and among management strategies (Figs. 5, S1, S2). The addition of the seed mix, both with and without mulched stems, resulted in decreases in June nitrification rate at the medium invasion site compared to control plots (Fig. 5). Variation in N cycling responses to different management strategies emphasizes the importance of studying forests that differ along a gradient of invasion and understanding N cycling within invaded forests prior to management.

N Cycling within and across Forests

Across our forest sites, N cycling was significantly related to rose invasion (i.e., rose stem density) during both seasons prior to invasive plant removal (Fig. 2). Previous studies have found increased rates of nitrification and N-mineralization in the presence of invasive shrubs (e.g., Ehrenfeld 2001, Ehrenfeld 2003, Jo et al. 2015), though we found this relationship was only true in September, and potential nitrification and N-mineralization *decreased* with increasing rose stem density in June. In contrast, patterns between N cycling and non-rose total stem density were opposite (Fig. 4) the patterns observed with rose stem

density. Thus, rose invasion influences soil N cycling rates in an opposite direction than all other plants in the same location. These findings provide evidence that rose is driving changes in N cycling since the relationship between rose and N cycling rates are not a consequence of plant abundance, but the presence of rose shrubs specifically.

In the early growing season, rose density ($P < 0.05$) was less important than soil water content ($P < 0.01$) in explaining variation in N cycling (June; Figs. 2, 3, S1). Additionally, N cycling rates decreased as SWC increased within our forest sites, suggesting that denitrification led to gaseous losses of N in the early growing season. All three sites had low C:N values (< 17:1) indicative of microbial C-limitation and net N-mineralization prior to invasive plant removal. Therefore, organic matter quality may not explain the patterns we observed in N immobilization in the early growing season. Water quantity may be an important mechanism and high SWC suggests these soils may be saturated contributing to denitrification (Myers 1982, Robertson and Groffman 2015, De Neve 2017). Thus, more study is needed to understand the influence of rose on the water cycle across spatial and temporal scales. Other factors which we did not consider in this study, such as soil pH/texture and microbial community composition, may promote N immobilization under the lab conditions, and future studies could investigate these potential relationships.

The proportion of net N-mineralization due to nitrification differed among our sites prior to management (Fig. 4). At the low and high invasion sites, more than 90% of net N-mineralization rate in June and 55–70% in September was due to nitrification. In contrast, nitrification was proportionately less important, and accounted for approximately 75% and 40% of the net N-mineralization rate in June and September in the medium invasion site. This suggests that microbial communities in the low and high invasion sites may be more similar, and conditions in these sites favor increased importance of nitrification to N cycling.

N Cycling Responses to Management Strategies

Overall, responses to management strategies varied within our forest sites, and did not support our hypothesis that removing invasive plants would decrease N cycling rates in the most invaded site within the time period of the experiment. Furthermore, unmanipulated control plots exhibited unexpected changes in all N cycling metrics across sites. For example, in 2018, all sites experienced a net increase in potential N-mineralization in June, but a net decrease in September (Figs. 5, S2, S3). Changes in soil water availability between the two years may be responsible for these patterns, as SWC was lower in June but higher in September in 2018 (Fig. S4). Post-removal treatments (i.e., seed mix addition, seed mix plus mulched stem amendment) at the medium invasion site led to a smaller net increase in nitrification rate compared to the control group, but the seed mix and mulch treatments were not significantly different from one another (Fig. 5a). We suggest that a single year of management may not be sufficient to observe changes in N cycling among the various strategies, and continued management over subsequent years may be necessary to observe differences in N cycling. Over time, net changes in plant communities (Moore et al. 2023) and soil amendments may increasingly influence N cycling post invasive plant removal.

Amending the soil with C-rich mulched stems (plus hand-sowing the native seed mix) after invasive plant removal resulted in changes to soil C and N metrics yet the observed changes differed by site and did not follow our expectations. In the low invasion site, mulched stem amendment reduced soil N (%) as expected, yet also reduced soil C (%) unexpectedly ($P < 0.10$). The low invasion site primarily consisted of small rose shrubs that were hand pulled (Moore et al. 2023), which could have caused the decreased soil C via belowground root removal. We cannot rule out the possibility there was not enough time for decomposition of mulch amendments to increase soil C content within one year. However, in the medium invasion site, soil C increased and C:N decreased in the mulch treatment, though these patterns were not significant due to high variation and low sample size. In the high invasion site, soil C had a non-significant increase with the mulch addition and soil N (%) significantly increased ($P < 0.10$) leading to decreased C:N ($P < 0.10$) compared to control plots in the first year following management. The rose stem mulch was more N-rich in the high invasion site compared to the other sites, which may have caused these observed changes in soil N (%) and C:N following the soil amendment management technique. This further suggests a positive feedback loop with N, as rose litter and stem quality may have had a long-term influence on soil conditions (higher available N) in the high invasion site with legacies of rose invasion. Thus, differences in C:N of the rose mulch between invasion densities suggests a possible threshold for management.

In this manipulated experiment, we found that addition of mulched stems reduced invasive shrubs in our highly invaded forest site (Moore et al. 2023), but we caution land managers to consider potential adverse effects on soil C and N if employing this strategy short-term, especially since it did not result in significant changes to N cycling that we expected to observe after one year of management in the high invasion site. Moreover, C:N declined under both control and mulched management strategies in the low and medium invasion sites suggesting that C-rich mulched stem addition following invasive plant removal is likely not enough to offset potential changes in soil C and N cycling due to other processes, such as decomposition, microbial respiration, or changes in soil moisture due to climate change. Thus, more time may be needed to incorporate this C-rich organic matter into soil C and N pools.

Conclusion

We found N cycling was related to rose invasion and SWC within sites, but these relationships varied by season. Rose density and SWC were unrelated in June 2017 (when soils were very wet); however, SWC increased with increasing rose density in September 2017 when soils were drier. Therefore, rose may be mediating nitrification, and thus N mineralization, via SWC under less soil saturated conditions, and invasion may have a more pronounced effect on soil N cycling in climates predicted to receive more moderate rainfall. Amending the soil with C-rich mulched stems did not increase soil C:N within our sites, and is likely not a viable management strategy, if the goal is to reduce nitrification and losses of N from the system, given the additional cost and labor. While this study examined potential N cycling responses only in the year following invasive plant removal, it is possible that these changes take more time to occur. Our goal was to sample soils in 2019 as well, but we were unable to sample more than 1 year post-removal. However, in our assessment of the plant community in 2019 (Moore et al. 2023), we found

greater differences two years post removal. Thus, long-term research could uncover meaningful patterns that may be associated with different management strategies. Continued research in forests along a gradient of invasion and evaluation of management strategies will be necessary to further comprehend the relationships between invasive shrubs and soil N cycling.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Study conception and design, formal analysis, and investigation were performed Eric R. Moore, Tara L. E. Trammell, and Richard V. Pouyat. Methodology was developed by Eric R. Moore and Tara L. E. Trammell. The first draft of the manuscript was written by Eric R. Moore. Tara L. E. Trammell and Richard V. Pouyat assisted with manuscript revisions. Funding, resources, and supervision were provided by Tara L. E. Trammell.

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Data Availability Statement: The datasets generated and analyzed during the current study are available from the corresponding author upon request, and will be made publicly available on EDI post-review.

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Figures

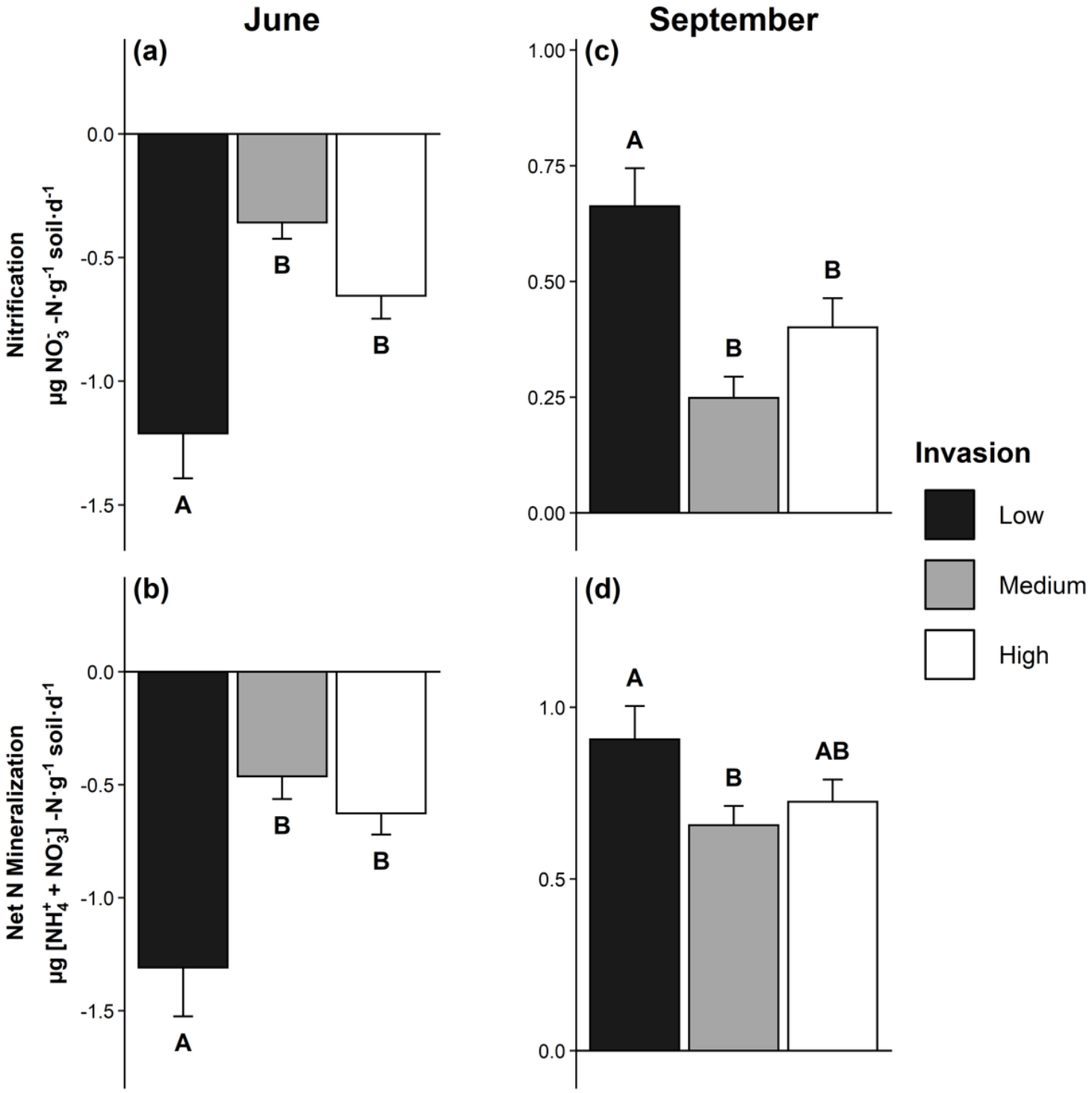

Figure 1

Means (± 1 SE) of potential nitrification and net N-mineralization rates in the early (June) and late (September) growing season of 2017. Letters indicate significant differences ($P < 0.10$) between sites. Note the different y-axes and units.

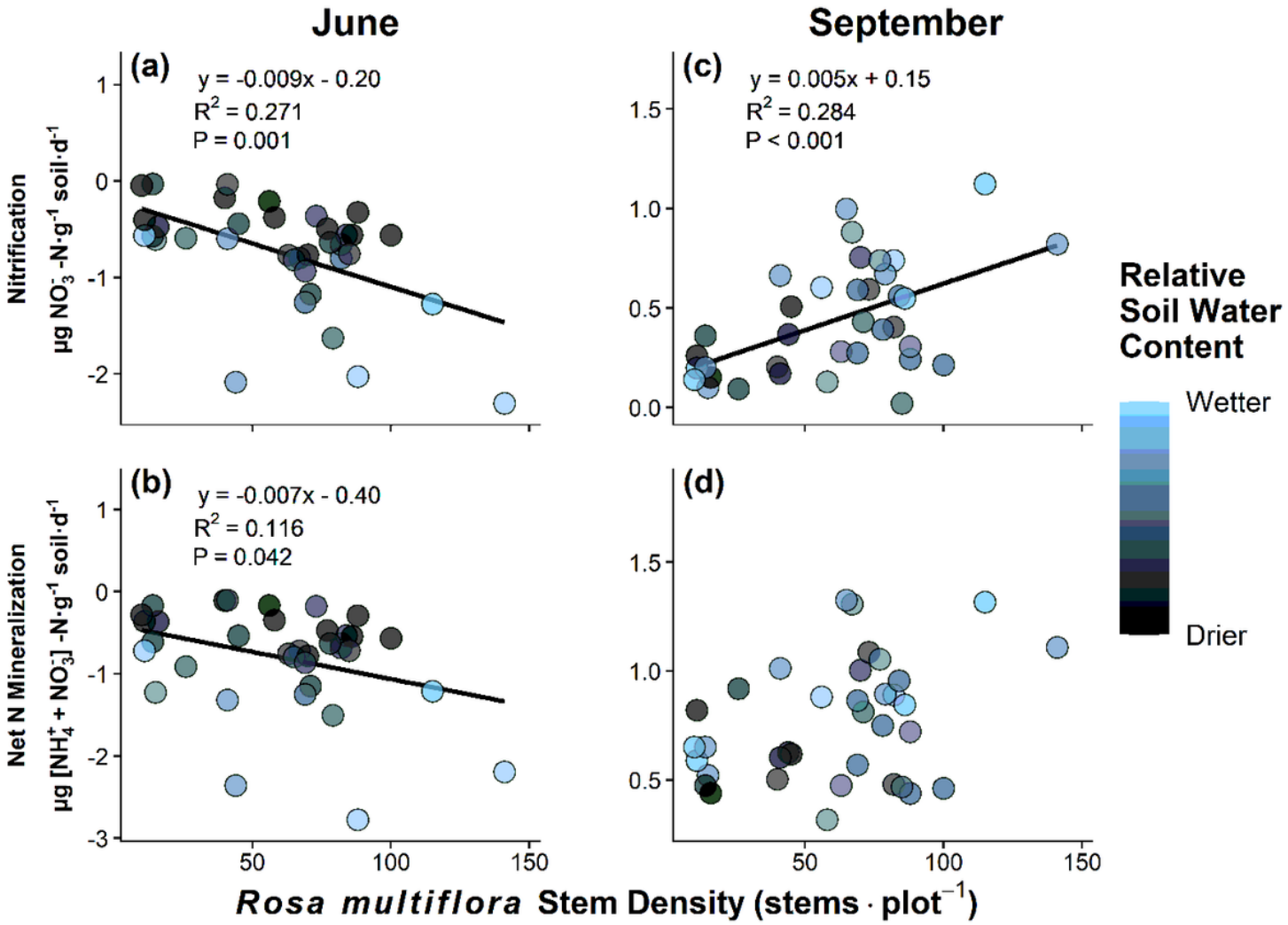

Figure 2

Potential nitrification and net N mineralization as a function of *R. multiflora* stems in the early (June) and late (September) growing season across all three forest sites. Equation, R^2, *P*-value and trendline are shown for $R^2 > 0.30$ as indicated by R package 'relaimpo'. Note the different axes.

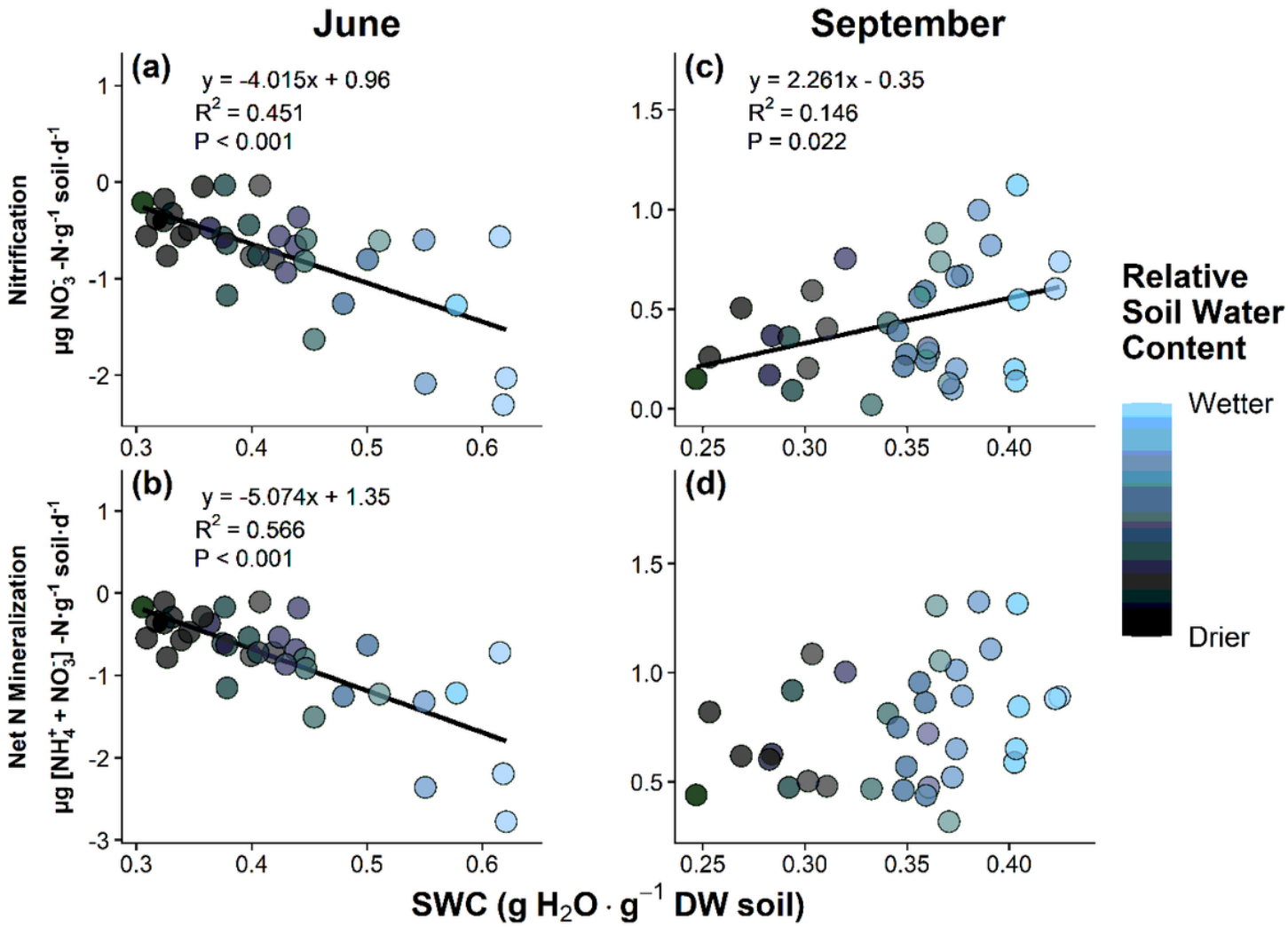

Figure 3

Potential nitrification and net N mineralization as a function of Soil Water Content (SWC) in the early (June) and late (September) growing season across all three forest sites. Equation, R^2, *P*-value and trendline are shown for $R^2 > 0.30$ as indicated by R package 'relaimpo'. Note the different axes.

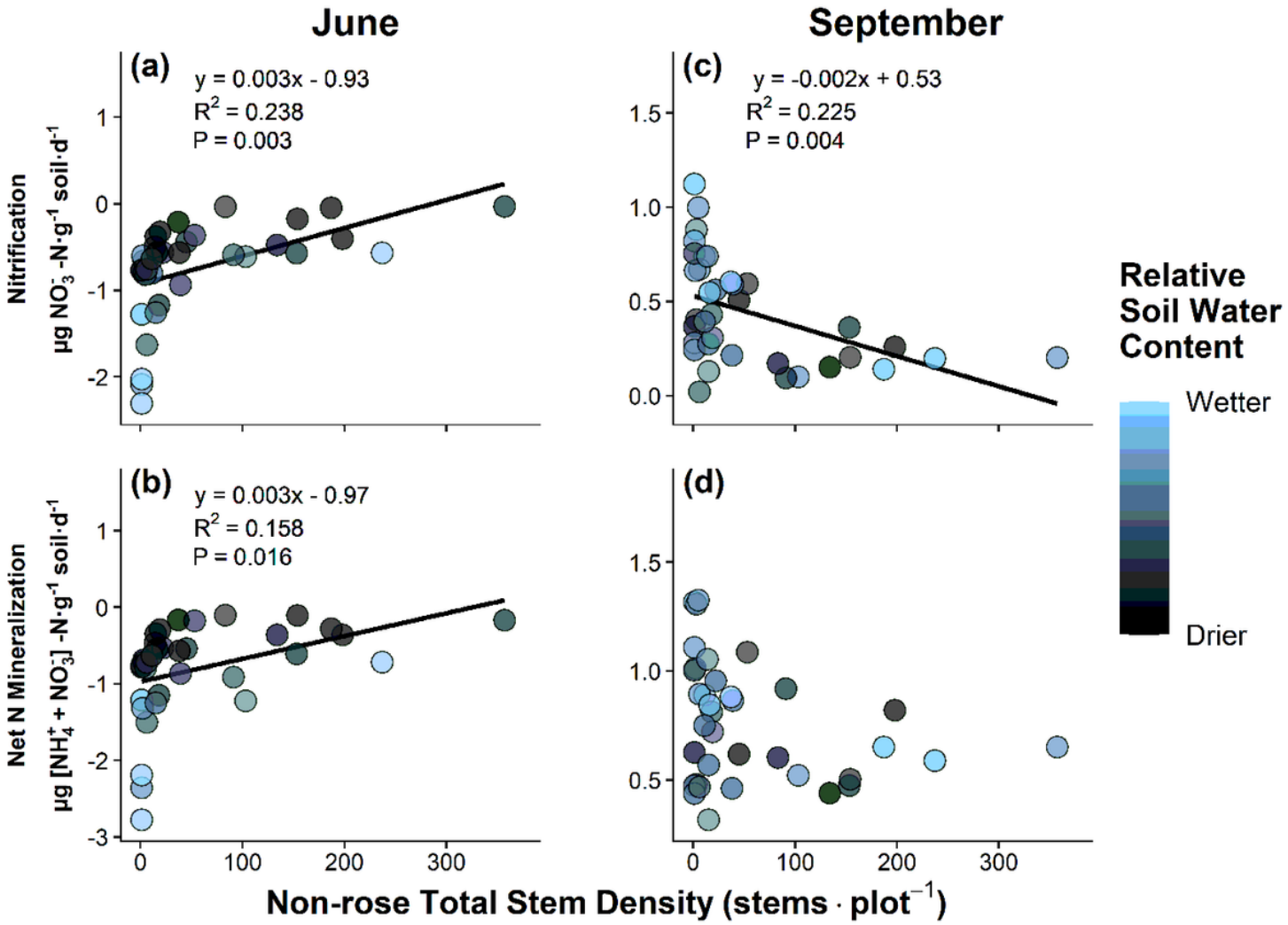

Figure 4

Potential nitrification and net N mineralization as a function of non-rose stem (all herbs, shrubs, and trees except *R. multiflora*) density in the early (June) and late (September) growing season across all three forest sites. Equation, R^2, *P*-value and trendline are shown for $R^2 > 0.30$ as indicated by R package 'relaimpo'. Note the different axes.

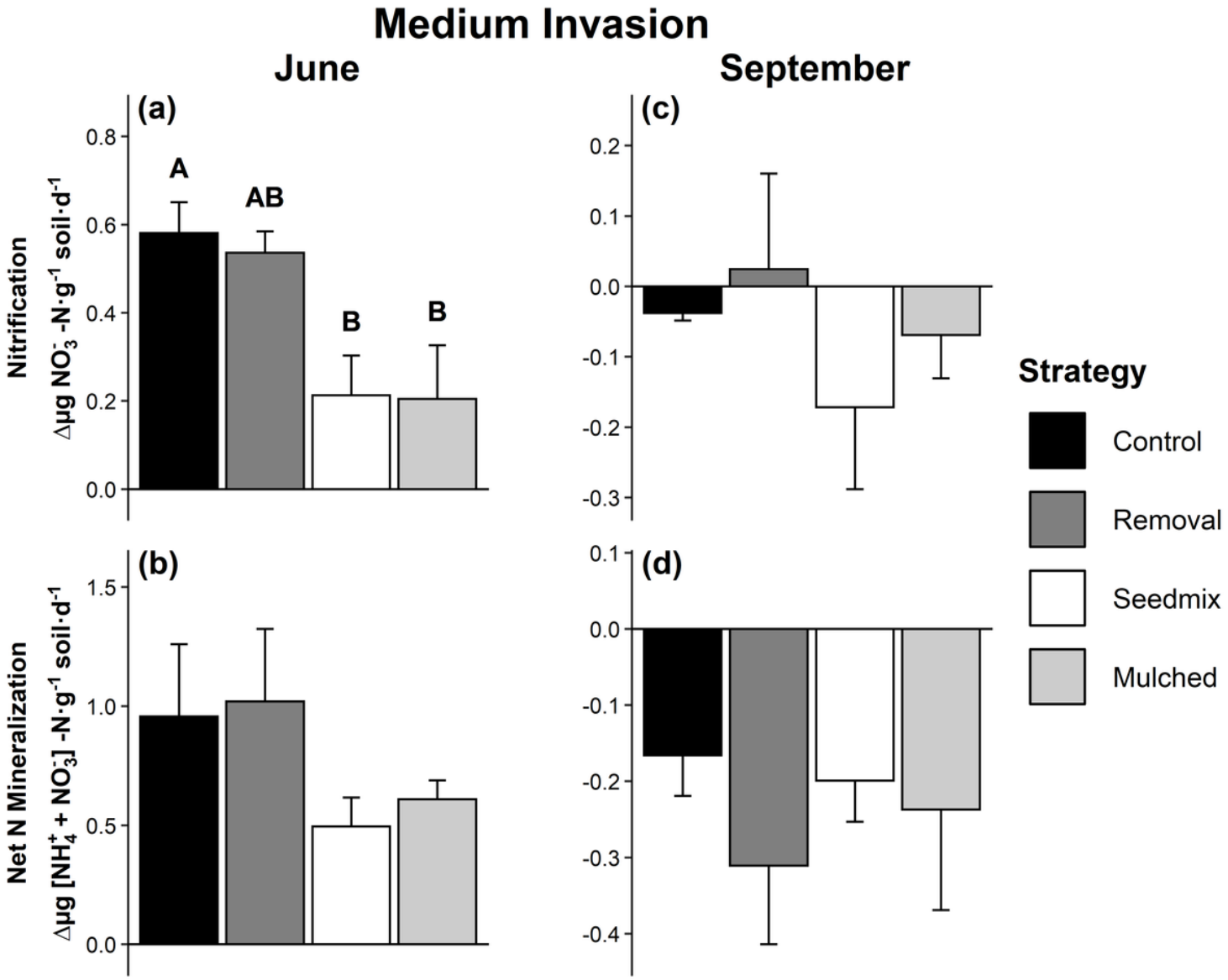

Figure 5

Mean net change (± 1 SE) in potential nitrification and net N-mineralization rates during early (June) and late (September) growing season in plots at the **Medium Invasion** site following management in 2018. Letters indicate significant differences ($P < 0.10$) between groups.

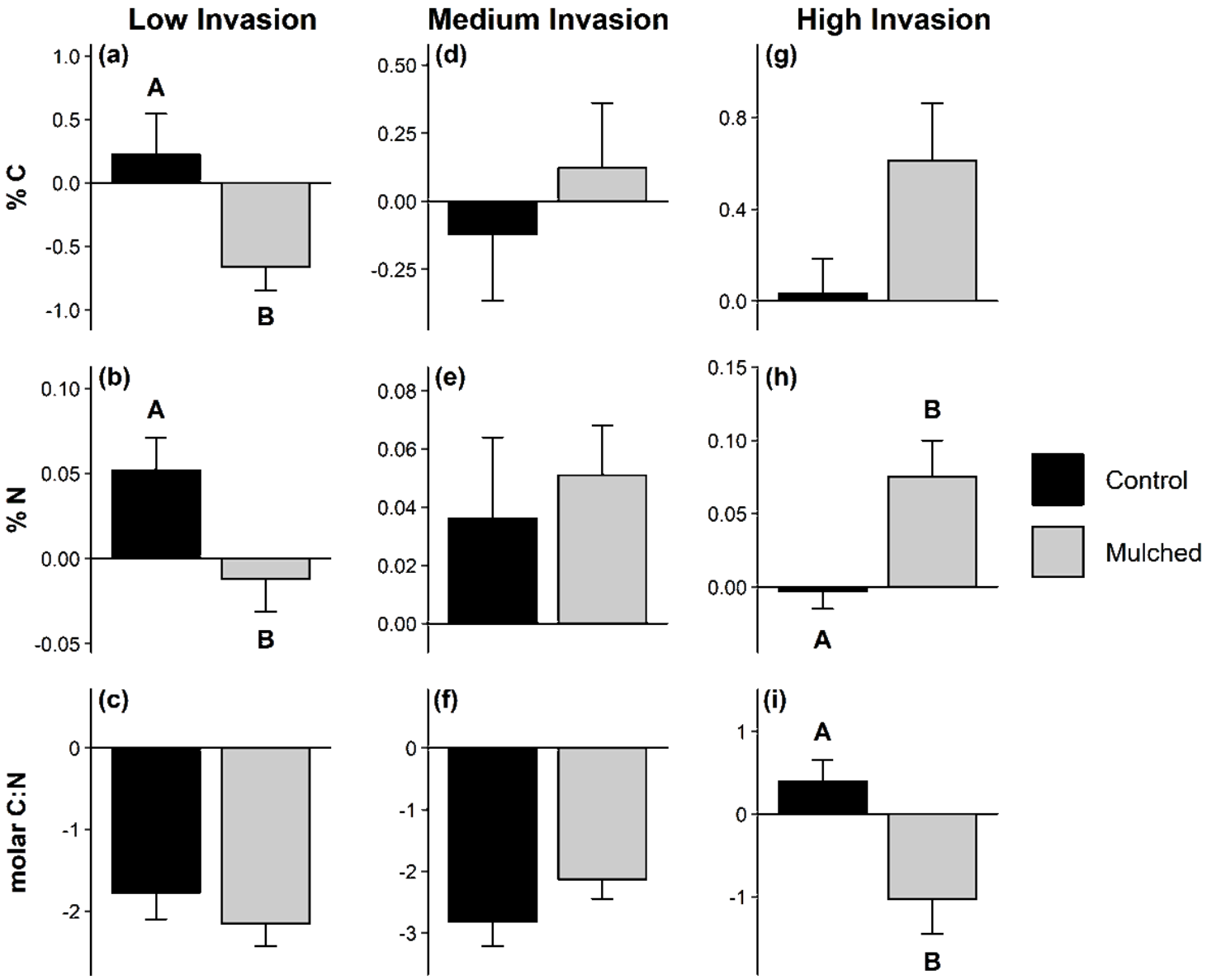

Figure 6

Mean net change (± 1 SE) in soil C and N metrics in control and mulched treatment plots at each forest site following invasive plant removal in 2018. Letters indicate significant differences ($P < 0.10$) between groups.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Mooreetal2023SoilNCyclingSupplementalInformation.pdf