

Soil Type Modifies the Impacts of Warming and Snow Exclusion on Carbon and Nutrient Losses

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Abstract

The varied and wide-reaching impacts of climate change are occurring across heterogeneous landscapes. Despite the known importance of soils in mediating biogeochemical nutrient cycling, there is little experimental evidence of how soil characteristics may shape ecosystem response to climate change. Our objective was to clarify how soil characteristics modify the impact of climate changes on carbon and nutrient leaching losses in temperate forests. We therefore conducted a field-based mesocosm experiment with replicated warming and snow exclusion treatments on two soils in large (2.4 m diameter), in-field forest sapling mesocosms. We found that nutrient loss responses to warming and snow exclusion treatments frequently varied substantially by soil type. Indeed, in some cases, soil type nullified the impact of a climate treatment. For example, warming and snow exclusion increased nitrogen (N) losses on fine soils by up to four times versus controls, but these treatments had no impact on coarse soils. Generally, the coarse textured soil, with its lower soil-water holding capacity, had higher nutrient losses (e.g., 12-17 times more total N loss from coarse than fine soils), except in the case of phosphate, which had consistently higher losses (23-58%) from the finer textured soil. Furthermore, the mitigation of nutrient loss by increasing tree biomass varied by soil type and nutrient. Our results suggest that potentially large biogeochemical responses to climate change are strongly mediated by soil characteristics, providing further evidence of the need to consider soil properties in Earth system models for improving nutrient cycling and climate projections.

Introduction

Climate change is increasing air temperature, extending growing season length, and altering precipitation dynamics (Demaria et al. 2016; Hayhoe et al. 2008), but these changes are occurring across heterogeneous landscapes. Differences in ecosystem properties, such as parent material and soil type, could create substantial variation in ecosystem responses to climate change. By determining properties such as soil water-holding and sorption capacity (Mayes et al. 2012; Weil and Brady 2017), soil texture and composition control soil biogeochemistry and carbon (C) storage (Doetterl et al. 2015; González-Domínguez et al. 2019; Silver et al. 2000). Because soils are a critical component of the terrestrial C cycle with feedbacks to atmospheric carbon dioxide (CO₂) levels (Jobbágy and Jackson 2000; Köchy et al. 2015), researchers are increasingly calling for the inclusion of edaphic properties in Earth system models to improve C and climate projections (Doetterl et al. 2015; Todd-Brown et al. 2013).

Climate and soil properties control ecosystem processes and properties (Chapin III et al. 2011) by regulating resources that limit plant and microbial activity (LeBauer and Treseder 2008; Wang et al. 2019), such as soil moisture (Dai et al. 2004; Merz and Plate 1997) and nutrient availability (Ge et al. 2019; Melillo et al. 2011; Sanders-DeMott et al. 2018). Soil warming may increase plant and microbial activity, increasing decomposition and net nitrogen (N) mineralization (Melillo et al. 2011; Rustad et al. 2001), or decrease activity by reducing soil moisture availability (Rustad et al. 2001; Xu et al. 2013; Zhang et al. 2015). If, as in the first case, warming accelerates microbial processes and leads to greater soil

nutrient availability, it could also increase nutrient leaching losses, with variations depending on soil moisture and soil freezing (Groffman et al. 2009).

Climate change effects also vary seasonally, with increased wintertime temperatures impacting soil biogeochemistry and nutrient retention by shaping snow and soil freezing conditions. By providing insulation, snow maintains soil temperatures that can support microbial activity and lead to nutrient accumulation in the subnivean soil environment (Brooks et al. 2011; Hardy et al. 2001; Henry 2008; Schimel et al. 2004). However, warming winter temperatures have decreased snow cover extent and depth, and shortened snow seasons (Demaria et al. 2016; Hayhoe et al. 2008). With insufficient snowpack soils freeze more deeply (Decker et al. 2003; Groffman et al. 2001a), reducing microbial activity due to temperature (Kirschbaum 1995) and water limitations (Brooks et al. 2011). By changing the abiotic conditions of the soil environment, soil freezing can alter soil respiration (Blankinship and Hart 2012; Reinmann and Templer 2018), N cycling, and hydrologic losses of nitrate (NO_3^-), inorganic phosphorus (P), magnesium (Mg) and calcium (Ca) (Fitzhugh et al. 2003; Sanders-DeMott et al. 2019). Finally, the cycles of soil freezing and thawing that are more prevalent in warmer winters (Henry 2008) can lyse microbial cells and disrupt soil aggregates, plant litter, and plant roots (Campbell et al. 2014; Oztas and Fayetorbay 2003; Schimel and Clein 1996; Song et al. 2017). These disruptions can alter soil nutrient pools as well as biological nutrient uptake by plants and microbes, with the potential to influence soil nutrient retention.

The physical and chemical mosaic of soils across the landscape provides the foundation upon which climate change will act, giving soils the potential to mitigate or exacerbate the impacts of climate change on the soil water balance and soil nutrient retention or loss. For example, along with climatic conditions, soil texture and organic matter content determine soil moisture (Cosby et al. 1984; Jawson and Niemann 2007) and moist soils tend to warm more due to latent heat increases (Subin et al. 2013). But soil moisture also regulates microbial activity, with high soil moisture increasing microbial populations and enzyme activity (Prado and Airoldi 1999; Tiwari et al. 1987). In fine soils, high soil moisture may combine with high nutrient or C availability to enhance rates of decomposition, soil respiration, N mineralization, and denitrification (Hamarashid et al. 2010; Silver et al. 2000; Xu et al. 2016). Similarly, soil texture determines water available for soil activity during dry (Ritchie 1981) or frozen periods (Gray et al. 1985), as well as the extent of soil freezing in winter (Fuss et al. 2016). Therefore, fine soils, with higher soil moisture, carbon, and nutrient availability, may support greater levels of plant and microbial activity than coarse soils as the climate warms. In addition to soil texture, mineralogy also determines nutrient dynamics of soils. For example, soils with higher clay and iron/aluminum oxide contents have greater soil cation exchange capacity and thus nutrient retention and availability; conversely, nutrient leaching tends to be higher from coarse soils (Feng et al. 2013; Manrique et al. 1991; Silver et al. 2000; Tahir and Marschner 2017). Thus, while it is clear that many of the basic chemical and physical attributes of soils will interact with climate change to affect ecosystem processes, the compounded effects of soils and changing climate on ecosystem C and nutrient losses are poorly documented with few studies attempting to control for multiple interacting factors.

Here we experimentally tested the effects of warming and reduced snow on N mineralization and leachate loss of nutrients (C, N, P) and cations prone to mobilization following environmental perturbation (Ca, Mg, and aluminum, Al) from two different soil types. To fully quantify main and interactive effects, we examined loss dynamics in a field-based, replicated climate change mesocosm experiment that imposed aboveground warming and snow exclusion treatments on two soils that differed in texture and chemical composition. We chose this large, in-field mesocosm (2.4 m diameter) approach to reduce heterogeneity and allow quantification of annual aqueous losses of C and nutrients. We hypothesized that climate treatment impacts would vary substantially with soil type. Specifically, we expected that warming and snow exclusion would increase losses, but that losses would be greatest on the coarse-textured soil. Our in-field, forest mesocosm experiment provides direct quantitative evidence of the importance of soil characteristics in modifying and interacting with climate impacts to control C and nutrient losses.

Materials And Methods

Site description and climate treatments

We examined interactions among climate treatment and soil type in a replicated, in-field climate change mesocosm experiment at the George D. Aiken Forestry Sciences Laboratory in South Burlington, VT, USA (44°27' N, 73°12' W; 60 m elevation). Mean annual temperature in South Burlington is 7.2°C, and mean annual precipitation is 889 mm (Burlington International Airport, S. Burlington, VT; elevation 100 m; ~ 5.9 km from study site) (NOAA National Weather Service 2017). Using a factorial design, we imposed control, warming, and snow exclusion treatments on two soil types (fine and coarse) across 24 large mesocosms, resulting in four replicates of each soil type-climate treatment combination (i.e., fine-control, fine-warming, fine-snow exclusion, coarse-control, coarse-warming, coarse-snow exclusion).

Mesocosms were installed in 1995 as described in Beard et al. (2005). Briefly, the 2.4 m polyethylene mesocosms had a 1 m soil depth and a closed leachate drainage area with a vacuum extraction system (Fig. 1a-b, Fig. S2). Tanks were installed belowground with a 20 cm aboveground rim. Each mesocosm contained one of two randomly assigned mineral soils with distinct physical and chemical properties (Table S1-2). The “coarse” soil was a sandy clay loam with twice the fine gravel content (34%; 2-5 mm diameter; Soil Science Division Staff 2017) than the “fine” soil, a loamy sand with low fine gravel content (17%). Although we labeled the soil types as “coarse” and “fine,” they varied by multiple characteristics. The gravel content of the coarse soil reduced its water holding capacity, while its higher Ca availability increased its pH buffering capacity relative to the fine soil. Overall, the coarse soil (including gravel) had higher cation exchange capacity (11 vs 1), clay (1.15 vs. 0.95%), and percent C (0.7 vs 0.3%) than the fine soil (including gravel), but lower water holding capacity (9.6 vs. 14.1%). No significant differences were found in soil properties among treatments prior to treatment establishment ($p < 0.05$, Table S2).

Mesocosms were planted in spring 2013 (see Supplementary Methods and Figs. S1, S2). We used four deciduous tree species: paper birch (*Betula papyrifera* Marshall), quaking aspen (*Populus tremuloides*

Michx.), American chestnut (*Castanea dentata* (Marshall) Borkh.), and black cherry (*Prunus seronita* Ehrh). The selected species represented different rooting depths and geographic ranges to examine possible effects of future climate on range shifts (Table S3). Each mesocosm contained 20 tree saplings per species. Equally spaced and randomly distributed planting locations resulted in an inter-planted deciduous mix (Fig. S2a). American chestnut seedlings were grown from nuts originating in Haun, PA from The American Chestnut Foundation (Asheville, NC). One-year old seedlings of all other species came from a commercial tree nursery (Porcupine Hollow Farm, Central Lake, MI). To mimic natural deciduous forest growth and germination conditions, in fall 2013, we simulated a forest floor (2.2 cm depth) using air-dried and chopped leaves of the four species collected in litter traps from local mature trees. During the experiment, all plants other than the saplings were removed and left on the mesocosm soil surface.

Climate treatments based on low CO₂ emissions scenario model projections for the northeastern United States in the year 2100 (Frumhoff et al. 2007) began in December 2013. Treatments consisted of control, infrared (IR) warming of 2°C above ambient, and snow exclusion at the beginning of winter. Treatments were randomly assigned to mesocosms with four replicates per soil type. For warming treatments, we suspended 4 ceramic IR warming elements (Kimball et al. 2008; Mor Electric Heating, Comstock Park, MI; FTE-1000-240-0-L6-WH-0 240V 1000W), encased in aluminum extrusion reflectors (Mor Electric Heating) and inverted aluminum gutters, around each mesocosm's perimeter on 5 cm diameter galvanized steel posts that were located outside the mesocosm tanks (Fig. 1b). Heaters were hung 1.5 m above the soil surface at a 45° angle to achieve spatially uniform warming (Kimball et al. 2008), which we confirmed through thermal imaging. In IR-warmed and control mesocosms, surface temperatures were measured in the center with a radiometer (as in Rich et al. 2015; Suseela and Dukes 2013; Apogee Instruments, Logan, UT; SI-111) controlled by a CR1000 datalogger (Campbell Scientific, Logan, UT). Radiometers were scanned every 30 s (2014) or 60 s (2015) and used to maintain IR-warmed mesocosms 2°C warmer than their paired control tanks. Surface temperature means were logged every 5 min and used to calculate hourly averages. Non-warmed mesocosms had identical, non-functional heater assemblies to standardize infrastructure effects. To minimize wind interference from December to June, we enclosed mesocosms within 0.6 m tall clear plastic sheeting located around the perimeter (Fig. S2b). We excluded snow by covering mesocosms with tarps during snow events for six weeks following the first snowstorm of the year (Fig. S2b). This began on 14 December 2013 and 9 December 2014 for winters 2013/2014 and 2014/2015, respectively. Prior to initiation of snow exclusion, we allowed two inches of snow to accumulate to maintain consistent albedo across treatments (Groffman et al. 2001b).

Environmental measurements

Soil temperature in each mesocosm was measured at 1, 5, 10, 30, and 60 cm depths using type T thermocouples (Omega Engineering, Inc., Stamford, CT). Temperatures were scanned every 30 s (2014), or 60 s (2015) and 5-minute means were recorded (CR1000 datalogger) and used to calculate hourly averages for analysis.

During the snow-free period, we took weekly soil moisture measurements in the upper 12 cm of soil in each mesocosm in either eight (2014) or six (2015) locations using a FieldScout Time Domain

Reflectometer (TDR) 300 Soil Moisture Meter (Spectrum Technologies, Aurora, IL). We calibrated TDR measurements with gravimetric soil moisture, which was determined by oven drying a soil sample previously measured with the TDR at 60°C to constant mass.

From the first snowfall until snowmelt, we measured soil frost depth weekly, and snow depth three times weekly. Soil frost depth was determined using frost tubes (Iwata et al. 2012), which consisted of tygon tubing filled with 0.03% methylene blue solution inserted into a PVC pipe installed vertically into the soil to 60 cm depth. We measured snow depth weekly using meter sticks affixed to the frost tubes. Area under the curve (AUC; depth vs. date; trapz command in R pracma package version 2.1-4; Borchers 2018) was calculated for snow and soil freezing depths to provide a metric that integrated depth and duration of snow and frost (Durán et al. 2014).

Plant biomass

To account for the impact of between treatment and soil type differences in plant biomass on nutrient losses, we measured total plant biomass in each mesocosm at the end of the experiment in August of 2015. Sapling aboveground stem and leaf material was oven dried at 50°C and weighed. Coarse and fine roots were carefully excavated, oven dried at 50°C and weighed. Total biomass per mesocosm therefore consists of stem, leaf, coarse and fine root mass.

Leachate collection and analyses

During the snow-free period, we measured the water level in each mesocosm weekly by inserting a measurement rod into the center tube (Fig. 1a-b) to the bottom of the leachate drainage area. When leachate reached the top of the drainage area, we extracted it using a pump with attached totalizer to quantify the water volume removed. While pumping, we collected a leachate sample, filtered it using 0.45 µm nylon filters (Fisher Scientific, Hampton, NH, cat. no. 09-719-008) and froze it until analysis.

Leachate samples were analyzed for inorganic N (Ammonium, NH_4^+ , and nitrate-nitrite, $\text{NO}_3^- + \text{NO}_2^-$, hereafter referred to as NO_3^-), phosphate (PO_4^{3-}), dissolved organic C (DOC), total dissolved N (TDN), and cations prone to mobilization following environmental perturbation (Ca, Mg, Al). Nitrate and PO_4^{3-} were quantified colorimetrically using a Lachat QuikChem 8000 flow-injection analyzer (Lachat Instruments, Hach Company, Loveland, CO). Ammonium was quantified using a salicylate method modified from Weatherburn (1967) and analyzed with a Synergy HT Microplate Reader (BioTek Instruments, Winooski, VT). Because ammonium was only a very small percentage of available mineral N (2% in 2014 and 4% in 2015 on average) and was unresponsive to climate treatments and soil type (see Supplementary Results and Table S4), we combined ammonium and nitrate as “total mineral N” for analyses. Dissolved organic C and TDN were measured using a Total Organic C Analyzer (Shimadzu TOC-L with TNM-L, Columbia, MD) by sample combustion followed by infrared gas analysis and chemiluminescence for DOC and TDN, respectively. Lastly, Ca, Mg, and Al were measured by inductively coupled plasma atomic emission spectroscopy (ICP-AES) on an Optima 3000DV (Perkin Elmer, Inc., Boston, MA). For all leached nutrients, we multiplied the concentration by leachate volume to calculate

total losses (flux) on each sampling date. Losses were summed by year to examine each experimental interval.

In situ N mineralization and nitrification

In situ net N-mineralization and nitrification were quantified using an intact core method (Durán et al. 2012) during three periods: overwinter (11/16/2014-4/23/2015), spring (4/22/2015-6/3/2015), and summer (6/3/2015-7/6/2015). Two soil cores were collected from each mesocosm, one of which was enclosed in a polyethylene bag and incubated in the soil. The other was sieved to less than 2 mm, subsampled, and extracted with 2 M potassium chloride (KCl) in a 1:10 soil:KCl ratio. Concentrations of NH_4^+ and NO_3^- were quantified using a salicylate method modified from Weatherburn (1967) and the vanadium method of Doane and Horváth (2003), respectively, and analyzed on a Synergy HT Microplate Reader. For each sampling period, potential N mineralization was calculated as the accumulation of total inorganic N ($\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$), and potential net nitrification was calculated as the accumulation of NO_3^- . Ammonium levels were below analytical detection limits, so we only present results for nitrification.

Statistical analyses

All statistical analyses were performed in R (R Core Team 2017). Effects of experimental climate treatment and soil type on surface and soil temperatures and soil moisture were determined using linear mixed effects models in the R nlme package (version 3.1-131; Pinheiro et al. 2017) with mesocosm as a random effect to account for non-independence due to repeated measures (Zuur et al. 2009). Day of year (doy) and a quadratic day of year term (doy^2) were included in the surface and soil temperature models to account for nonlinearity in temperature by day relationships.

Snow and soil freezing AUC, leachate volume, nitrification rates, and leachate loss of C (DOC) and other nutrients (total mineral N, TDN, PO_4^{3-} , Ca, Mg, Al) in response to soil and climate treatments were determined using generalized least squares (gls) models in the R package nlme (Pinheiro et al. 2017). For all carbon and nutrient leachate losses we then included biomass as a covariate in our gls model to determine the degree to which plant biomass was responsible for treatment effects (e.g., via plant nutrient uptake). We also used gls to examine if plant biomass varied by soil or climate treatment. In all cases, significance of model terms (ANOVA: *soil* × *treatment*; ANCOVA: *soil* × *treatment* × *biomass*) was determined with type 3 (partial) Analysis of Deviance models conducted in the R car package (Fox and Weisberg 2011).

For all models, assumptions of constant variance and normality were assessed by inspection of residuals. When necessary, we constructed variance structures for categorical and continuous variables using the varIdent and varPower functions, respectively (nlme package; Pinheiro et al. 2017), and we applied power transformations to non-normal data. Results were considered significant at $p < 0.05$, and R^2 values were calculated with the rsquared command in the piecewiseSEM package in R (Lefcheck 2016). Unless otherwise noted, reported values are means ± standard errors.

Results

Treatment effects

Climate treatments significantly altered mean surface and soil temperatures year-round, and climate treatment and soil both influenced water dynamics (Table S5). Infrared warming increased average surface temperature by $2.04^{\circ}\text{C} \pm 0.001^{\circ}\text{C}$ ($p < 0.0001$, $R^2 = 0.66$) and increased mean soil temperature to a depth of 60 cm ($p < 0.05$; Fig. 1c). Snow exclusion decreased mean soil temperature to a depth of 60 cm ($p < 0.05$; Fig. 1c; Table S3). Soil type did not affect surface or soil temperatures.

In 2014, fine soils held twice the moisture of coarse soils ($p < 0.0001$, $R^2 = 0.16$), a difference that increased to 2.25 times in 2015 ($p < 0.0001$, $R^2 = 0.34$). Although treatment effects were not significant in 2014, both warming and snow exclusion reduced soil moisture by $\sim 20\%$ in 2015 ($p = 0.03$; Table S5).

Annual leachate volume also varied by both soil and climate treatments. In 2014, 10% more leachate was collected from the coarse soils than fine soils ($p = 0.003$) and warming reduced leachate volume by 14% ($p = 0.005$; $R^2 = 0.52$). In 2015, climate treatment effects on leachate volume differed across soils such that on both coarse and fine soils, warming reduced leachate volume by $\sim 20\%$, but snow exclusion only reduced leachate volume on fine soils (by 30% reduction; $p = 0.04$, $R^2 = 0.36$; Table S5).

Warming and snow exclusion significantly altered winter snow and soil freezing dynamics (Fig. 2). Both climate treatments reduced snowpack AUC. Patterns were consistent between years, with the warmed treatment having the smallest snowpack followed by snow exclusion and control mesocosms having the largest snowpack (Fig. 2; Table S5, 2014: $p < 0.0001$, $R^2 = 0.94$; 2015: $p < 0.0001$, $R^2 = 0.94$). In 2014, soil freezing increased under both snow exclusion (by 130%) and warming (by 18%, Fig. 2; Table S5; $p < 0.0001$, $R^2 = 0.89$). In 2015, delayed onset of snowfall followed by below freezing temperatures resulted in deep soil freezing in all mesocosms prior to onset of the snow exclusion treatment (Fig. 2). This reduced differences in soil freezing depth and duration across treatments in 2015, with soil frost AUC $\sim 10\%$ greater in snow exclusion than control (Fig. 2; Table S5; $p = 0.01$, $R^2 = 0.36$).

Finally, fine soils supported 24% more total plant biomass than coarse soils ($p = 0.007$, $R^2 = 0.29$; Fig. S3).

Dissolved carbon and nitrogen losses

The impacts of soil type, climate treatment, and biomass on dissolved organic C (DOC) losses varied by year, although losses were generally higher from coarse than fine soils. In 2014, there were no impacts of treatment or soil on DOC losses unless differences in biomass were accounted for (Table 1). After accounting for biomass impacts, DOC losses in 2014 were slightly higher from coarse than fine soils (30% on average; Table 1; Fig. 3). Furthermore, increasing biomass decreased DOC loss by roughly 50% (Table 1). In 2015, treatment impacts varied by soil type, and only snow exclusion treatments on coarse soils had DOC losses that were different from the control (30% less loss than in the control). Overall,

coarse soils in 2015 lost 36% more DOC than fine soils, but in the snow exclusion treatment losses from coarse and fine soils were similar (Fig. 3). Biomass had no impact on DOC losses in 2015 (Table 1).

Table 1

Analysis of deviance results for 2014 and 2015 models of soil water leachate carbon and nutrients and nitrification as a function of soil × treatment (ANOVA) and as a function of soil × treatment × total plant biomass (ANCOVA). Bold values indicate $p < 0.05$.

Var	Year	R ²	Chi-square values						
			Soil	Trt	Soil x Trt	Biomass	Bio x Soil	Bio x Trt	Bio x Soil x Trt
DOC	2014	0.3879	3.7	4.6	3.2				
		0.7277	4.1	4.5	0.2	4.3	3.5	3.7	0.2
	2015	0.5146	8.6	5.5	7.2				
		0.6765	0.9	2.4	2.7	0.0	0.2	3.0	0.9
TDN	2014	0.4150	0.6	2.3	9.0				
		0.6011	0.3	3.0	2.0	0.1	0.4	2.9	1.6
	2015	0.7623	43.4	3.9	12.4				
		0.8668	5.5	2.0	8.2	4.2	2.7	3.9	5.1
TMN	2014	0.6378	1.0	13.1	24.4				
		0.7862	2.0	1.5	9.9	4.0	3.0	2.6	7.2
	2015	0.6531	29.3	1.5	7.2				
		0.9384	34.9	42.9	52.1	44.5	18.8	51.7	56.9
PO ₄	2014	0.3187	5.6	3.0	0.1				
		0.6285	0.0	2.3	6.5	0.4	0.1	2.6	6.9
	2015	0.6450	5.6	3.0	0.1				
		0.7565	1.8	0.5	1.9	0.0	0.5	0.4	1.3
Ca	2014	0.8350	85.2	3.2	2.9				
		0.8972	3.6	0.3	3.2	3.0	0.4	0.5	2.2
	2015	0.9186	181.3	27.7	2.1				
		0.9314	0.7	0.4	0.9	0.2	1.5	0.2	1.4

DOC: dissolved organic C, TDN: total dissolved N, TMN: total mineral N (ammonium plus nitrate), PO₄³⁻: phosphate, Ca: calcium, Mg: magnesium, Al: aluminum, NIT: nitrification rate, Trt: climate treatment, Bio: biomass. W: winter (11/16/2014 - 4/23/2015), Sp: spring (4/22/2015 - 6/3/2015), Su: summer (6/3/2015 - 7/6/2015).

Var	Year	R ²	Chi-square values		
NIT	W 14-15	0.6962	7.71	17.24	16.29
	Sp 2015	0.3604	2.73	7.17	3.86
	Su 2015	0.3444	3.99	3.93	0.82

DOC: dissolved organic C, TDN: total dissolved N, TMN: total mineral N (ammonium plus nitrate), PO₄³⁻: phosphate, Ca: calcium, Mg: magnesium, Al: aluminum, NIT: nitrification rate, Trt: climate treatment, Bio: biomass. W: winter (11/16/2014 - 4/23/2015), Sp: spring (4/22/2015 - 6/3/2015), Su: summer (6/3/2015 - 7/6/2015).

Soil type and climate treatments interacted both years to affect total dissolved N (TDN) losses, even after accounting for differences in biomass (Table 1). In both years, treatments had little impact on coarse soils (no real difference from controls in either year; Fig. 3). In fine soils, warming and snow exclusion increased losses by 75% and 110%, respectively, in 2014 and by 160% and 460% respectively in 2015. Losses from coarse soils were also much larger (~12 times larger) from coarse vs fine soils in 2015, but there was not much difference in losses between soil types in 2014 (Fig. 3). In 2015, but not 2014, TDN losses declined with increasing biomass and accounting for biomass did not change the significance of soil type or its interaction with climate treatments.

Plant available nutrient losses and nitrification

Soil type and climate treatments interacted with biomass to affect total mineral N losses (Table 1, Fig. 4). Regardless of biomass, mineral N loss varied by soil type and climate treatment in both years (soil × treatment interaction, Fig. 4a, c). As observed with TDN, climate treatments had little impact on coarse soils relative to the controls. On fine soils, mineral N loss from warmed and snow exclusion treatments were 140% and 410% greater than controls in 2014, but in 2015, only snow exclusion soils were different than controls, losing 130% more mineral N than controls (Fig. 4a, c). Much like TDN, mineral N loss from coarse soils in 2015 was ~12 times that from fine soils, but losses were similar across soil types in 2014 (Fig. 4a, c). Accounting for differences in biomass revealed significant soil by treatment by biomass interactions in both years (Table 1). Increasing biomass decreased losses from coarse soils in control treatments in both years and warming treatments in 2015; increasing biomass had little or no impact on mineral N losses from fine soils in either year, regardless of treatment (Fig. 4b, d).

The main impact on PO₄³⁻ loss was of soils, with 20% and 60% more loss from fine than coarse soils in 2014 and 2015, respectively. In either year, there was little or no impact of treatment, but in 2014 in control and heated plots, biomass at times reduced losses (in coarse-control and fine-heated; significant soil by treatment by biomass interaction in 2014; Table 1; Fig. 4e-h).

Effects of soil and climate treatments on nitrification rates varied by sampling period. During winter 2014/2015, nitrification rates were 26 times higher in warmed coarse soils compared to other soil-treatment combinations (significant soil × treatment interaction; Fig. 5a). In spring, nitrification in warmed mesocosms was nearly twice that of controls, while snow exclusion and controls had similar nitrification rates (significant treatment effect; Fig. 5b). Finally, in summer, coarse soil nitrification rates were 56% higher than in fine soils, with no significant treatments effects (Table 1; Fig. 5c).

Cation losses

In both years, Ca losses were roughly double from coarse compared to fine soils (Table 1). Treatments had little impact on losses in 2014, but in 2015 warming and snow exclusion both reduced loss by 16% relative to controls. Biomass had no significant impacts on Ca losses (Table 1). Effects of soil and climate treatments on Mg and Al varied across years with no consistent patterns (and biomass for Mg; see Supplementary Results and Table S4).

Discussion

The impacts of warming and snow exclusion varied by soil type. Compared to the fine soil, the coarse soil generally experienced higher losses of C and most nutrients, except PO_4^{3-} . However, it was common for the impact of climate treatments to differ considerably by soil type. For example, on fine soils, snow exclusion elevated N losses, but on coarse soils, snow exclusion had no effect. Furthermore, while high plant biomass was able to mitigate N losses from coarse soils, increasing biomass had little impact on N losses from fine soils. Overall, our results provide experimental evidence that interactions among climate treatments and soil properties are an important factor in determining the magnitude of climate change effects on ecosystem biogeochemistry.

Soil and climate treatment impacts on abiotic factors

Climate treatments altered abiotic factors that influence processes related to our hypotheses. Overall, climate treatments had the expected effects: on average, warming raised surface temperatures by 2°C and increased soil temperatures to a depth of 60 cm; snow exclusion decreased soil temperatures to 60 cm, induced deep soil freezing, and reduced snowpack depth. However, between-year variation in winter air temperatures and onset of snowpack resulted in different impacts of the warming treatment between winters. In 2014, warming reduced early winter snowpack, causing soils to freeze deeper than in controls. Conversely, in 2015 warmed mesocosms experienced less soil freezing overall than controls due to faster soil thaw in the spring (Fig. 2). Importantly, late snowpack development in 2015 allowed deep soil freezing in all treatments that persisted under the snowpack (Hardy et al. 2001).

In addition to soil temperature, soil type and climate treatments impacted soil moisture throughout the experiment. Fine soils consistently held twice as much moisture as coarse soils. However, the leachate drained from coarse soils was only 10% higher than from fine soils, likely due to fine soils having higher

plant biomass (Fig. S3) and consequently greater evapotranspiration potential (Kosiba 2017). Finally, both climate treatments resulted in drier soils than controls in the second year.

Coarse textured soils had greater C and nutrient leaching, except for PO_4^{3-}

Cation exchange capacity, clay content, and organic matter content generally correlate with reduced leachate losses. In our study, the coarse soil exceeded the fine soil in each of these metrics (Table S1). Notwithstanding, in all cases with a significant soil effect, except PO_4^{3-} , the coarse soil experienced higher leachate losses. The high fine gravel content of the coarse soil likely reduced its water holding capacity and increased its hydraulic conductivity compared to the fine soil, thereby diminishing its storage capacity for cations and nutrients (Dudley et al. 2008). The nutrients that experienced significant losses across years by soil type were DOC and Ca (higher losses from coarse soils), and PO_4^{3-} (higher losses from fine soils). The effect of soil on losses of all other nutrients varied between years, but in all significant cases, coarse textured soils experienced higher losses (2014: Al; 2015: TDN, mineral N, and Mg).

Contrary to our expectations, the loss of PO_4^{3-} was greater from fine- vs. coarse-textured soils. However, this could be associated with between-soil differences in pH and cation contents. Namely, the fine soil had a lower pH (6.2) than the coarse soil (7.6; Table S1). In soils with $pH < 7$, PO_4^{3-} tends to be available but can be fixed, to some degree, by aluminum (Penn and Camberato 2019). Because aluminum availability in the fine soil was relatively low (Table S1), and aluminum tends to be non-soluble at neutral pH (pH 6-8; Lindsay and Walthall 1996), PO_4^{3-} may have been more easily lost from the fine soil than expected based on its hydraulic conductivity. Conversely, in soils with $pH > 7$, like the coarse soil, P is fixed by Ca (Penn and Camberato 2019), which was very abundant in the coarse soil (Table S1). Thus, the Ca content of the coarse soil may have reduced the susceptibility of PO_4^{3-} to leaching despite that soil's reduced capacity for nutrient storage relative to the fine soil.

Throughout the experiment, one of the largest differences we observed was the change in the magnitude of N loss (mineral N and TDN) across years. Coarse soils lost a similar amount of N in both years, but N loss from fine soils dropped to extremely low levels in 2015, despite no associated decrease in leachate volume, causing a significant soil effect (Fig. 4). Greater N uptake due to the higher plant biomass (24% higher) supported by the fine soil provides one possible explanation for the large reduction in leachate N loss in 2015. However, while increasing plant biomass did reduce mineral N losses in coarse soils in some cases, it had no impact on N losses from fine soils, suggesting that higher plant uptake might not be responsible for this difference. Alternatively, greater nitrification rates were measured on the coarse soil during the 2015 growing season, which could have created a pool of nutrients vulnerable to leaching given the low water holding capacity and larger volume of water leached from that soil.

Warming and snow exclusion did not have strong impacts on C and nutrient loss independent of soil type

Despite consistently altering abiotic conditions in the mesocosms, climate treatment impacts on nutrient losses were inconsistent, and varied interannually (e.g., Ca and Mg). Warming increased springtime net nitrification regardless of soil type, in accordance with prior observations (but see also Barnard et al. 2005; MacDonald et al. 1995). But warming effects varied with soil type in the winter and had no impact on summer nitrification rates. The lack of a summertime response to warming could be explained by the lower soil moisture in that treatment. As we observed, warming treatments tend to dry soils (Xu et al. 2013), which can reduce microbial activity such as nitrification (Liu et al. 2009). Additionally, plant activity dominates terrestrial water movement during the summer (Jasechko et al. 2013). Thus, early spring water availability during plant dormancy combined with elevated temperatures in the warming treatment could explain the ephemeral nature of the nitrification response to warming. Finally, net nitrification did not respond to snow exclusion, unlike previous findings that linked decreased net nitrification to soil freezing (Shibata et al. 2013).

Climate treatments consistently affected C and nutrient responses differently depending on soil type, as observed in wintertime nitrification rates and losses of DOC, TDN, total mineral N, PO_4^{3-} , Mg, and Al during one or both years. This occurred even though climate treatments did not affect the abiotic conditions of the soils differently (Table S5). In all cases, either soil or treatment, but not their interaction, altered soil temperature and moisture, snow, or soil freezing conditions. Additionally, differences in plant biomass across mesocosms did not account for the varying effects of climate treatment by soil type, and accounting for plant biomass at times revealed treatment and biomass interactions with soils (i.e., PO_4^{3-}).

Throughout the experiment, patterns of N loss (TDN and total mineral N) consistently responded to climate treatments differently according to soil type. Across years, snow exclusion elevated N losses from only fine soils. This finding coincides with well-documented increases in NO_3^- loss following soil freezing (Campbell et al. 2014; Mitchell et al. 1996), although with variability (Groffman et al. 2011; Judd et al. 2011). Elevated NO_3^- losses after soil freezing have been attributed to root mortality (Tierney et al. 2001) and decreased root nutrient uptake (Campbell et al. 2014). In both our soil types, differences in plant biomass in the snow exclusion treatment had no impact on mineral N losses (the majority of which was NO_3^- , Fig. 4b and d), suggesting that root uptake in these plots was unable to reduce mineral N losses. Our results therefore indicate that soil differences could additionally account for variability in the NO_3^- leaching response to soil freezing, perhaps due to water content during freezing or thawing events or the type of soil frost (e.g., concrete or granular, Fuss et al. 2016).

Warming also increased mineral N and TDN losses from fine soils (except for total mineral N in 2015), but not coarse soils. Previous soil warming in temperate forests found no increase in N leaching (Melillo et al. 2011) or soil solution NO_3^- (Sanders-DeMott et al. 2018) under warming conditions despite increased N mineralization (Melillo et al. 2011), a well-documented response to warming (Rustad et al.

2001; Salazar et al. 2020). In those cases, the tight cycling of N between plants and soil accounted for the lack of increased leachate losses despite accelerated N processing under warming (Melillo et al. 2011). Although increasing plant biomass reduced total mineral N losses from coarse soils in 2015 (Fig. 4d), we found no other instances where increasing plant biomass reduced N losses from the warming treatment. These results of increased N loss due to warming from only one soil type show the tightness of nutrient recycling can vary between soils under climate change.

Although elevating temperature increased N losses from our fine soil type, N cycling processes often correlate more with moisture conditions than temperature alone (Beier et al. 2008; Groffman et al. 2009). Nevertheless, overwinter nitrification rates in our study increased under warming on only the drier coarse soils, and over the summer the coarse soils experienced higher nitrification rates than the moister fine soils regardless of climate treatment. In sum, the moister fine soil which supported greater plant biomass had lower rates of summer nitrification and higher leachate N losses under warming, while the drier coarse soil which supported less plant biomass had higher rates of summer nitrification and no response of N loss to warming. These results run counter to expectations based on abiotic moisture and temperature conditions alone, highlighting the role of soil characteristics in mediating biogeochemical losses under climate change.

Plant mitigation of nutrient losses varied by soil type

Finally, plant biomass was able to temper nutrient losses, but the impact of plant biomass often varied by soil type. Increasing biomass reduced DOC and TDN losses independent of soil type and treatment, but only reduced mineral N loss in coarse soils. The impact of soil was more variable for PO_4^{3-} losses, with increasing biomass reducing losses from coarse or fine soils depending on treatment. However, the impact of plant biomass on PO_4^{3-} losses in both cases was relatively small (a reduction of ~ 6-20 mg P) compared to the impact of biomass on mineral N losses (a reduction of ~ 700-1200 mg N). Thus, the ability of plants to mitigate mineral nutrient losses appears to vary with soil texture, often with larger impacts in coarse than fine soils. Although increasing plant biomass is typically effective at reducing nutrient leaching in a range of soils (Bergeron et al. 2011; Lehmann and Schroth 2003), our results suggest that increasing plant biomass may be more effective at reducing leaching losses in soils with low water holding capacity and correspondingly high leaching rates.

Conclusion

Our work provides experimental evidence of the importance of soil properties in modifying the effects of climate change on ecosystem biogeochemistry. Furthermore, our results suggest that soil type can also modify the capacity of plants to mitigate nutrient losses. Our replicated, in-field climate change experiment on two soil types clearly demonstrated that the occurrence and magnitude of biogeochemical losses depends on the interaction of climate treatments with soil type. These results provide further evidence of the need to consider edaphic properties when projecting climate change impacts on future nutrient losses and other ecosystem functions.

Declarations

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Conflicts of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable

Author's contributions All authors conceived of the study, contributed to manuscript review, and approved the final version. SJ PS AK CW GH DW and CA managed the field site and climate treatments, and conducted field measurements. SJ conducted laboratory analyses and prepared the first draft of the manuscript. SJ and CA conducted the statistical analyses.

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Tables

Table 1. Analysis of deviance results for 2014 and 2015 models of soil water leachate carbon and nutrients and nitrification as a function of soil × treatment (ANOVA) and as a function of soil × treatment × total plant biomass (ANCOVA). Bold values indicate $p < 0.05$.

Var	Year	R ²	Chi-square values						
			Soil	Trt	Soil x Trt	Biomass	Bio x Soil	Bio x Trt	Bio x Soil x Trt
DOC	2014	0.3879	3.7	4.6	3.2				
		0.7277	4.1	4.5	0.2	4.3	3.5	3.7	0.2
	2015	0.5146	8.6	5.5	7.2				
		0.6765	0.9	2.4	2.7	0.0	0.2	3.0	0.9
TDN	2014	0.4150	0.6	2.3	9.0				
		0.6011	0.3	3.0	2.0	0.1	0.4	2.9	1.6
	2015	0.7623	43.4	3.9	12.4				
		0.8668	5.5	2.0	8.2	4.2	2.7	3.9	5.1
TMN	2014	0.6378	1.0	13.1	24.4				
		0.7862	2.0	1.5	9.9	4.0	3.0	2.6	7.2
	2015	0.6531	29.3	1.5	7.2				
		0.9384	34.9	42.9	52.1	44.5	18.8	51.7	56.9
PO ₄	2014	0.3187	5.6	3.0	0.1				
		0.6285	0.0	2.3	6.5	0.4	0.1	2.6	6.9
	2015	0.6450	5.6	3.0	0.1				
		0.7565	1.8	0.5	1.9	0.0	0.5	0.4	1.3
Ca	2014	0.8350	85.2	3.2	2.9				
		0.8972	3.6	0.3	3.2	3.0	0.4	0.5	2.2
	2015	0.9186	181.3	27.7	2.1				
		0.9314	0.7	0.4	0.9	0.2	1.5	0.2	1.4

NIT	W 14-15	0.6962	7.71	17.24	16.29
	Sp 2015	0.3604	2.73	7.17	3.86
	Su 2015	0.3444	3.99	3.93	0.82

DOC: dissolved organic C, TDN: total dissolved N, TMN: total mineral N (ammonium plus nitrate), : phosphate, Ca: calcium, Mg: magnesium, Al: aluminum, NIT: nitrification rate, Trt: climate treatment, Bio: biomass. W: winter (11/16/2014 - 4/23/2015), Sp: spring (4/22/2015 - 6/3/2015), Su: summer (6/3/2015 - 7/6/2015).

Figures

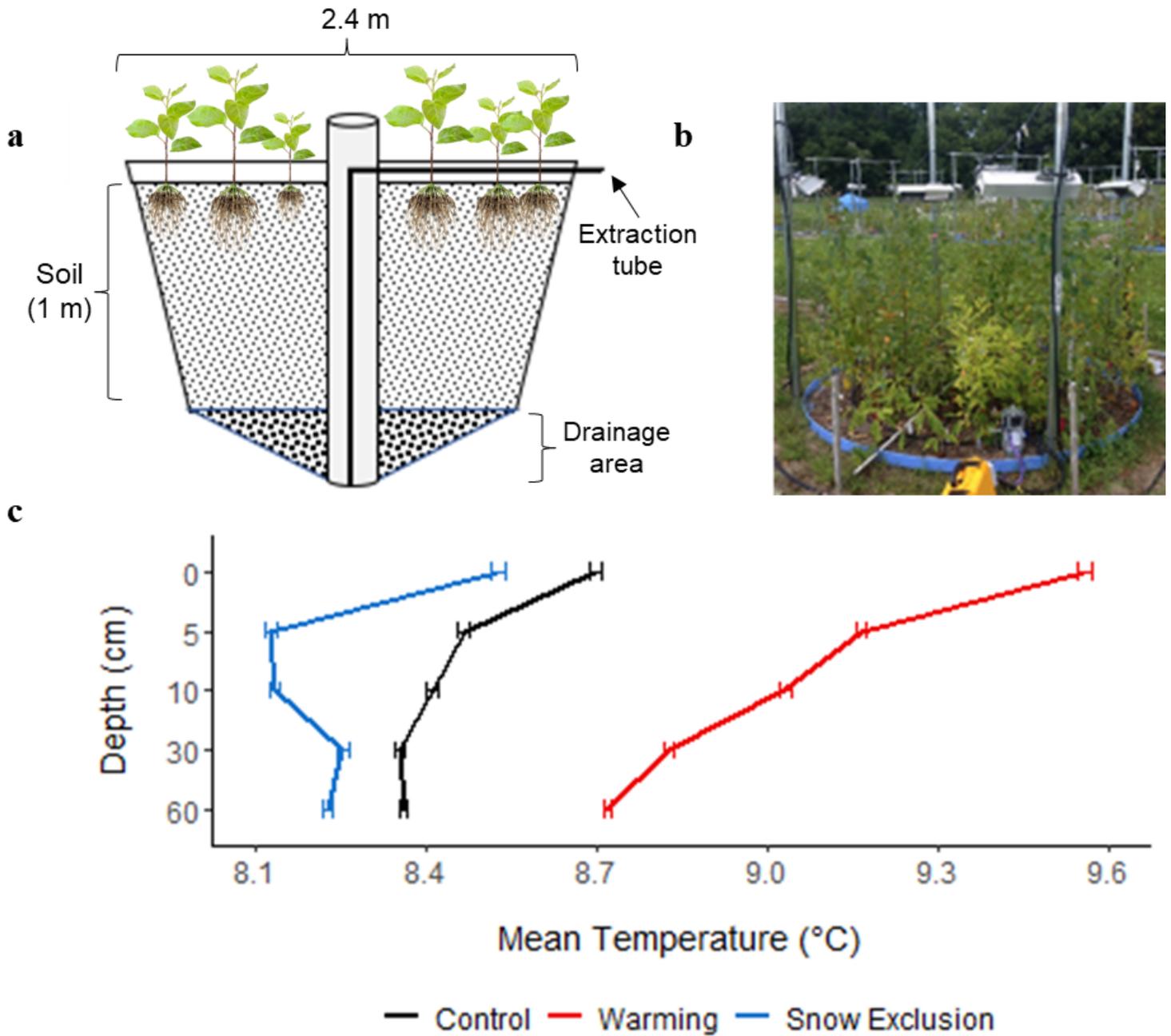


Figure 1

(a) Cross section diagram of in-field forest mesocosms used for the replicated climate change experiment. Coarse fill at the bottom represents gravel in the leachate drainage area. Fine fill represents soil. The two layers were divided by landscape cloth. The top of the soil is even with the surrounding ground level. The dark line entering horizontally and bending 90 degrees through a center tube to the bottom of the mesocosm represents the tubing that allowed leachate removal by pumping. (b) Photo of a mesocosm assigned to the warming treatment with the planted sapling community and infrared heaters on the perimeter. (c) Mean soil temperatures by depth for the three climate treatments for the duration of the experiment. Error bars are ± 1 standard error.

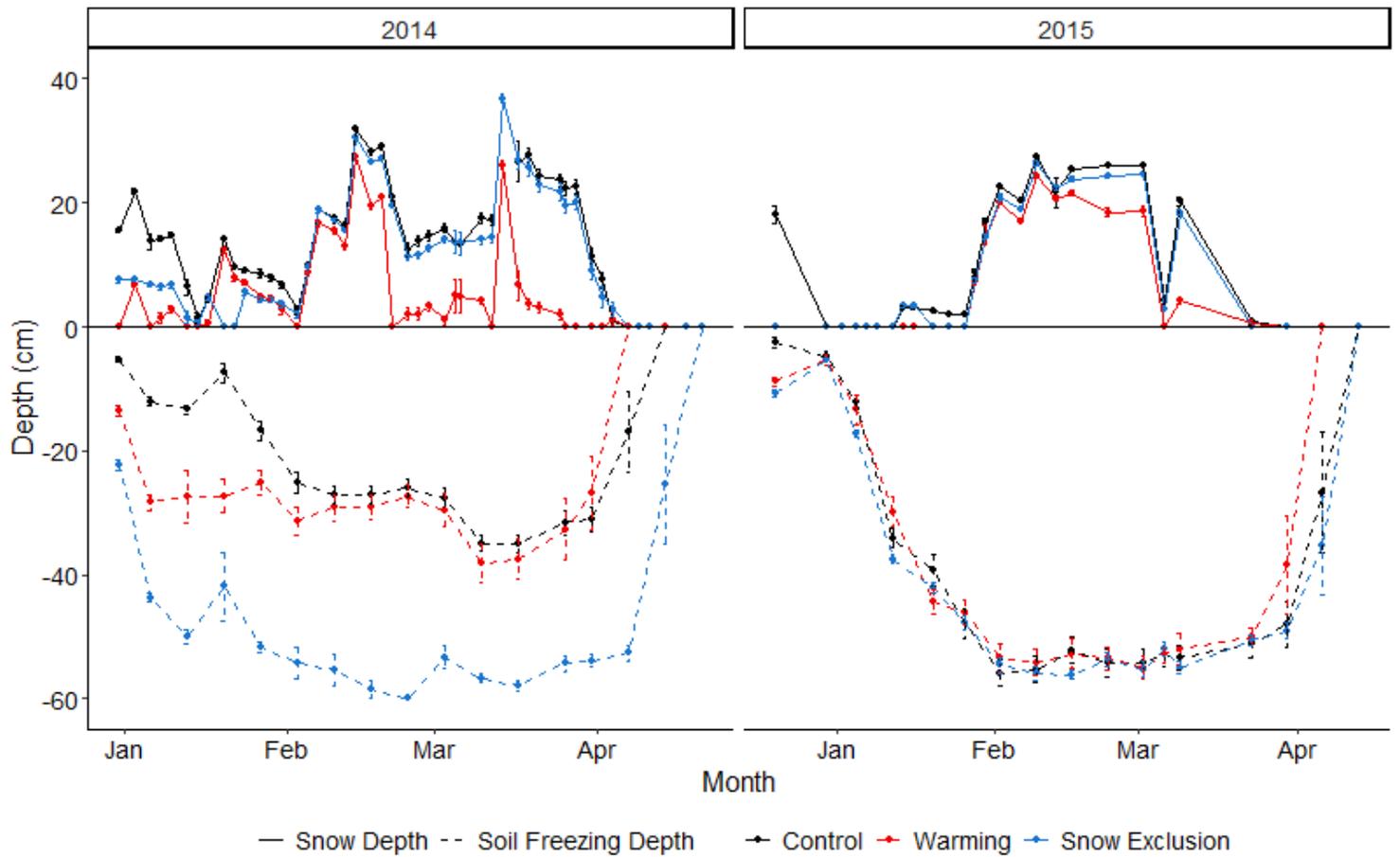


Figure 2

Mean snow and soil freezing depth by climate treatment in 2014 and 2015. Error bars are ± 1 standard error. Values above zero (solid lines) represent snow depth, and values below zero (dashed lines) represent soil freezing depth.

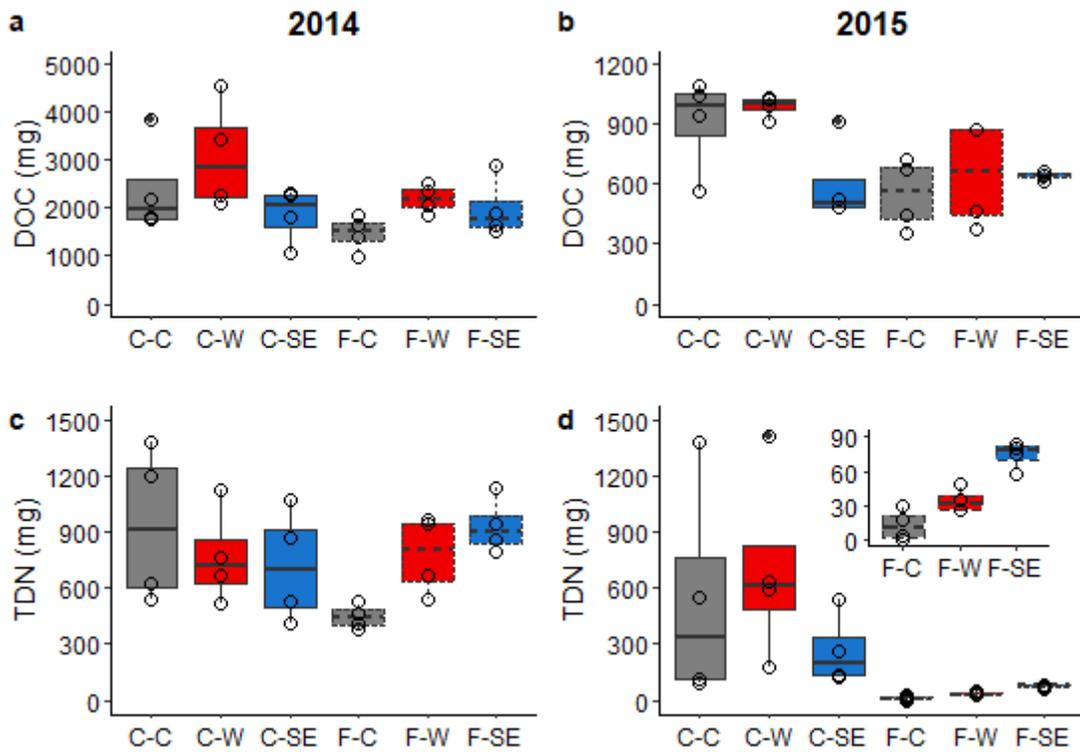


Figure 3

Boxplots for mesocosm leachate loss of (a) 2014 dissolved organic C (DOC), (b) 2015 DOC, (c) 2014 total dissolved nitrogen (TDN), and (d) 2015 TDN. The inset figure in panel d shows the leachate loss of TDN from fine soils that year. X axis codes are soil (C = coarse, solid lines or F = fine, dashed lines) followed by climate treatment (C= control (gray), W = warming (red), SE = snow exclusion (blue)). Note the different y axis limits in the panels. Open circles represent data points and filled circles represent outliers.

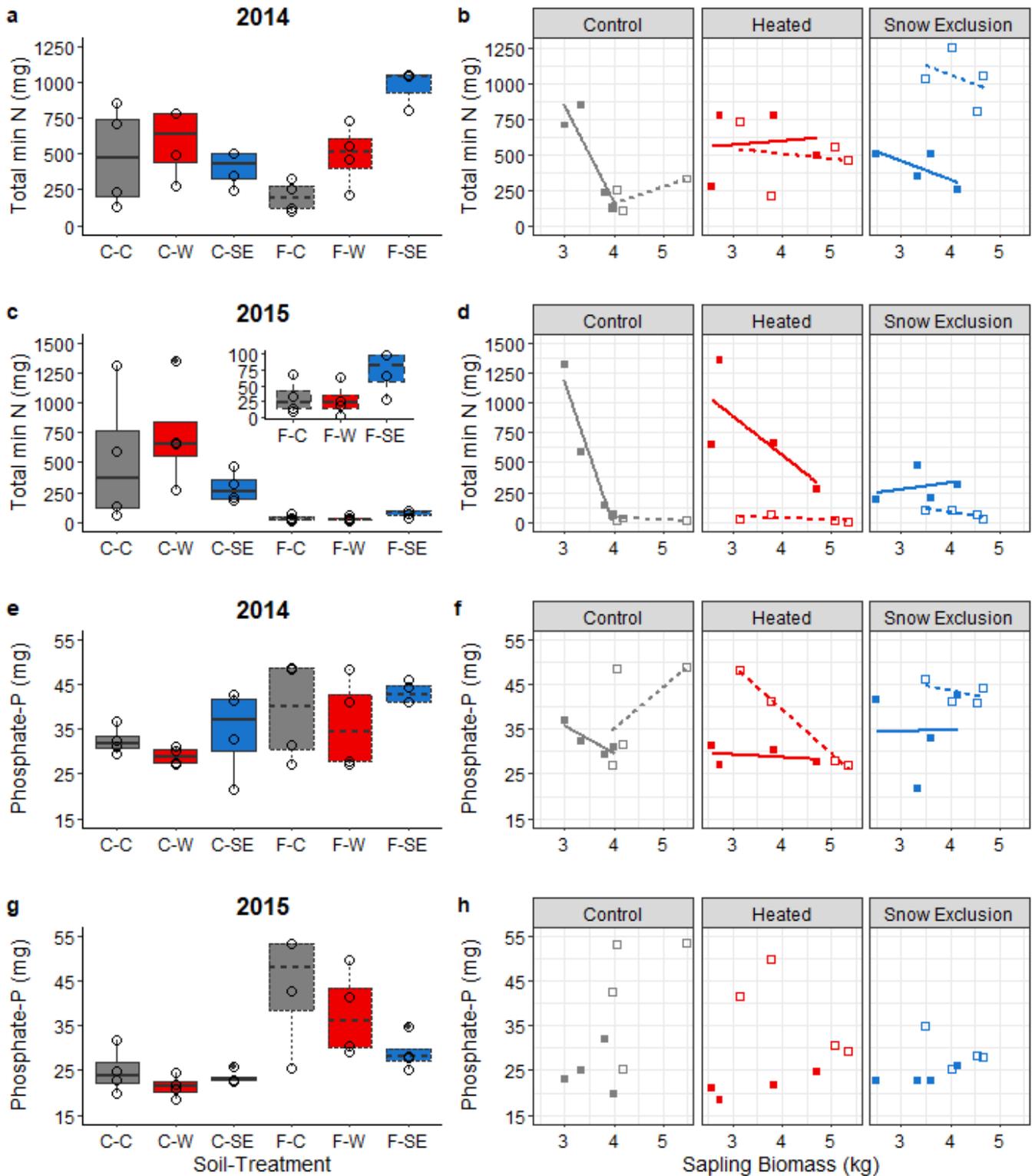


Figure 4

Forest mesocosm leachate loss of total mineral nitrogen (N) and phosphate. Total mineral N loss in 2014 (a) by soil type and treatment and (b) versus biomass; and in 2015 (c) by soil type and treatment and (d) versus biomass. Phosphate leachate loss in 2014 (e) by soil type and treatment and (f) versus biomass; and in 2015 (g) by soil type and treatment and (h) versus biomass. X axis codes are soil (C = coarse, solid lines or F = fine, dashed lines) followed by climate treatment (C = control (gray), W = warming (red), SE =

snow exclusion (blue)). Note the different y axis limits in each panel. In boxplots, open circles represent data points and filled circles represent outliers. In scatterplots, filled points/solid lines are data points from coarse soils and open points/dashed lines are data points from fine soils.

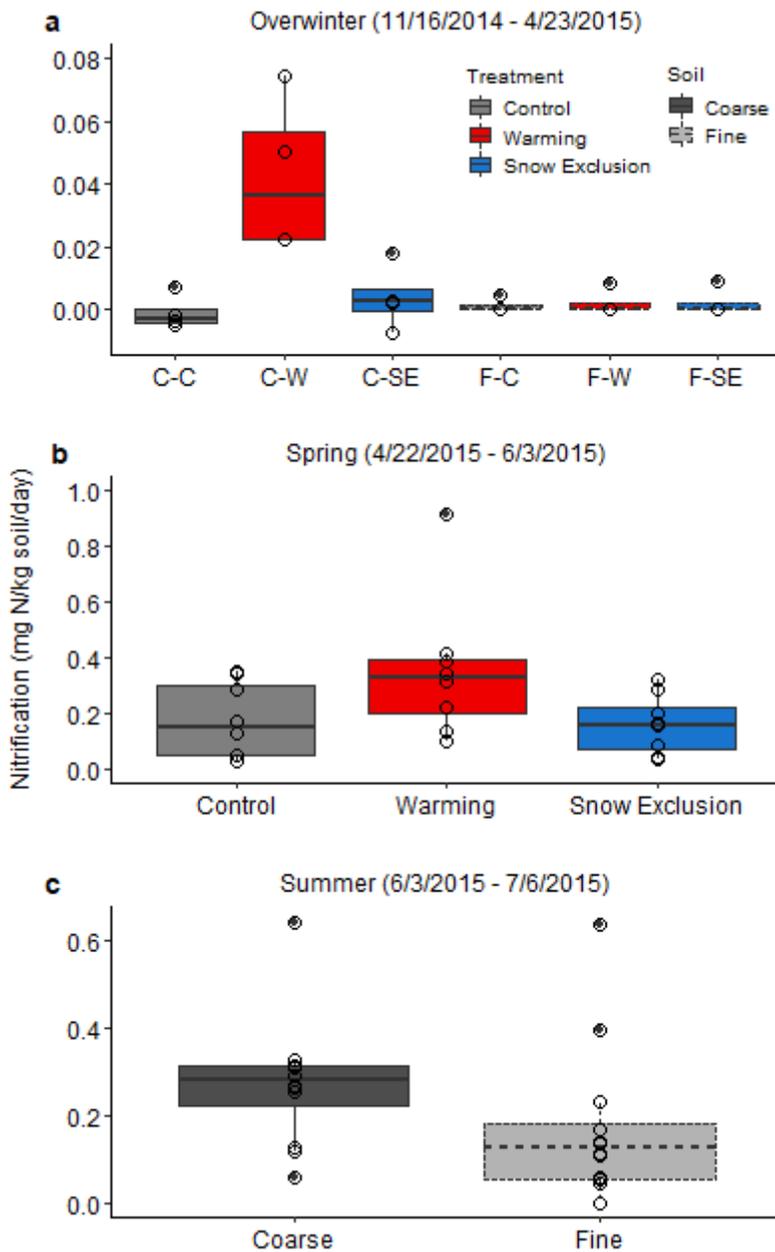


Figure 5

In situ nitrification measured in forest mesocosm soils by season: (a) winter; (b) spring; and (c) summer. Significant model terms (soil, treatment, or soil*treatment) are shown in each panel. X axes are: (a) codes with soil (C = coarse, solid lines or F = fine, dashed lines) followed by climate treatment (C = control (gray), W = warming (red), SE = snow exclusion (blue)); (b) climate treatment; or (c) soil type. Note the different y axis limits in each panel. In boxplots, open circles represent data points and filled circles represent outliers.

Supplementary Files

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