



Soil carbon availability decouples net nitrogen mineralization and net nitrification across United States Long Term Ecological Research sites

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Abstract Autotrophic and heterotrophic organisms require resources in stoichiometrically balanced ratios of carbon (C) to nutrients, the demand for which links organismal and ecosystem-level biogeochemical cycles. In soils, the relative availability of C and nitrogen (N) also defines the strength of competition for ammonium between autotrophic nitrifiers and heterotrophic decomposers, which may influence the coupled dynamics between N mineralization and

nitrification. Here, we use data from the publicly available US National Science Foundation funded Long Term Ecological Research (LTER) network to evaluate the influence of soil C concentration on the relationship between net nitrification and net N mineralization. We found that soil C availability constrains the fraction of mineralized N that is ultimately nitrified across the continental gradient, contributing to reduced rates of nitrification in soils with high C concentrations. Nitrate, which is produced by nitrification, is a highly mobile ion that easily leaches to aquatic ecosystems or denitrifies into the greenhouse gas nitrous oxide (N₂O). Understanding the connection between soil C concentration and

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soil N transformations is thus important for managing potential ecosystem N losses, understanding the biogeochemical constraints of these losses, and accurately representing coupled C-N dynamics in ecosystem models.

Keywords Nitrogen mineralization · Nitrification · Soil carbon · Long Term Ecological Research

Introduction

Autotrophic and heterotrophic organisms require carbon (C) and nutrients in fixed ratios, which links biogeochemical cycles from the organismal to ecosystem levels (Sterner and Elser 2002). These stoichiometric relationships constrain soil organic matter (SOM) turnover and nutrient release (Buchkowski et al. 2019) and control soil greenhouse gas emissions (Baral et al. 2014). The coupled dynamics of C and nitrogen (N), specifically, serve as an indicator of stoichiometric limitations on soil microbial metabolism and help determine terrestrial site fertility. Within soil microbial communities, the relative availability of C and N also defines the strength of competition between heterotrophic decomposers (fungi & bacteria) and autotrophic nitrifiers (bacteria & archaea) for ammonium (Booth et al. 2005; Verhagen and Laanbroek 1991), and the subsequent fate of SOM-derived N. Both heterotrophic microbes and autotrophic

nitrifiers play a critical role in N transformations (Keiser et al. 2016), which subsequently support their own nutrient requirements. The N forms produced by heterotrophs and autotrophs have contrasting fates within the soil: heterotrophically-produced ammonium (NH_4^+) can be sorbed onto soil surfaces (Venterea et al. 2015), taken up by plants, or further transformed, while autotrophically-produced nitrate (NO_3^-) is a highly mobile ion easily taken up by plants, leached from soils to aquatic systems, or denitrified into N_2 or the greenhouse gas nitrous oxide (N_2O) (Viviroli et al. 2007). Therefore, understanding the connection between soil C pools and the amount and forms of available N is important for understanding ecosystem C and N dynamics and the potential for N losses from ecosystems (Vitousek et al. 1982, 1979).

Heterotrophic microbes rely on soil C pools for energy, growth, and maintenance (Soong et al. 2020), and on soil N pools, including ammonium, for protein and amino sugar synthesis and to meet nutritional requirements (Farrell et al. 2014). In contrast, nitrifying bacteria or archaea rely on the ammonium produced by heterotrophic N mineralization as their energy source (Kaye and Hart 1997), and fix carbon dioxide (CO_2) through the oxidation of ammonium to nitrate (nitrification). Competition for ammonium-N between autotrophs and heterotrophs can slow the rate of nitrification and nitrate production (Bernhardt and Likens 2002; Leptin et al. 2021; Vitousek et al. 1982). As heterotrophic N demand is stoichiometrically coupled with soil C availability, increasing soil C concentration, if reflective of available C, should increase competition for ammonium-N between heterotrophs and autotrophs (Bernhardt and Likens 2002; Hart et al. 1994; Verhagen et al. 1992). Heterotrophic N uptake reduces the NH_4^+ available for nitrification and subsequently reduces the fraction of mineralized N that is ultimately nitrified (Fig. 1). In contrast, lower soil C availability may promote C limitation of heterotrophic microbes, decreasing their demand for NH_4^+ and increasing its availability for nitrifiers (Dijkstra et al. 2008; Fig. 1). These dynamics are also observed in freshwater ecosystems, where increasing dissolved organic carbon (DOC) availability is associated with declines in nitrifier abundance and activity (Bernhardt et al. 2002; Bernhardt and Likens 2002). Similarly, in a temperate U.S. forest, increasing soil C availability decoupled the rate of N

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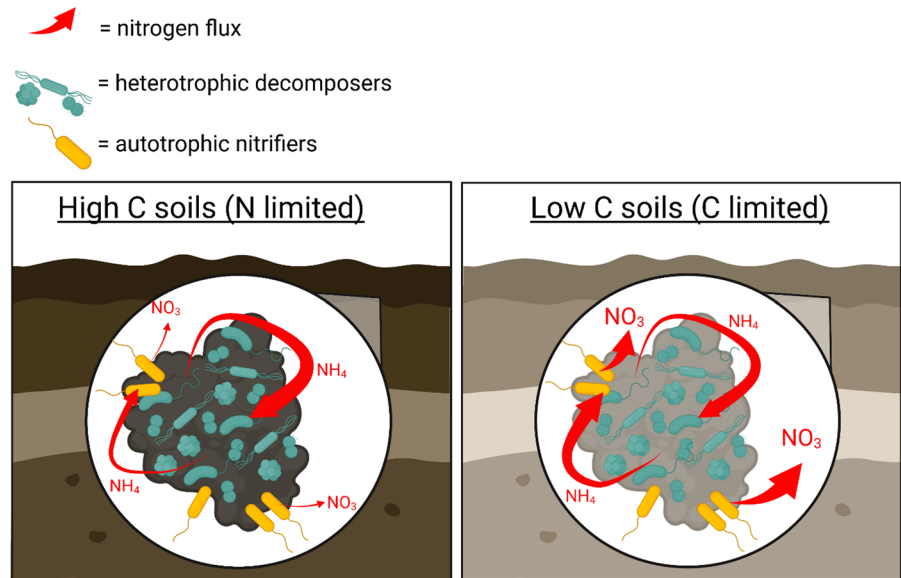
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Fig. 1 Conceptual model of hypothesized differences in microbially-mediated soil N fluxes in high C (N limited) vs. low C (C limited) soils. In high soil C environments, heterotrophic organisms will immobilize more N as NH_4^+ to meet stoichiometric demands, resulting in lower rates of nitrification. In contrast within low soil C environments, more ammonium is available in the soil with greater subsequent rates of nitrification



mineralization from that of nitrification (Keiser et al. 2016). These relationships, however, have not been identified across the diverse soil types of terrestrial ecosystems.

An array of abiotic, vegetation, and anthropogenic factors have the potential to disrupt the link between soil C availability and N transformations. Differences in seasonality among ecosystems result in sites with varying precipitation regimes and temperature ranges. Some locations, for example, have distinct dry and wet seasons with cycles of soil drying and rewetting, while others at northerly latitudes or high elevation have freeze/thaw cycles. Limited soil water availability through dry periods or freezing disrupts plant root uptake of N (Campbell et al. 2014; He and Dijkstra 2014) and exudation of labile C substrates used by heterotrophic microbes to mineralize N (Williams and de Vries 2020). Prolonged dry periods or drought and repeated freeze/thaw cycles can also affect the size of the microbial community and thus N transformations, as well as access to substrates and nutrients (Fierer and Schimel 2002; Parker and Schimel 2011). Intrinsic site characteristics, such as soil texture or mineralogy, affect cation exchange capacity (Syers et al. 1970) and soil water retention (Libohova et al. 2018), which, in turn, affect the capacity of a soil to retain ammonium or nitrate. Ecosystem management practices such as fertilizer additions (Poffenbarger et al. 2015) or disruption of soil structure through tilling (Six et al. 1999), as well as N inputs from

atmospheric deposition, which vary in magnitude and composition across the U.S. (NRSP-3 2020), may also skew expected coupled dynamics of C and N. Therefore, changing site conditions that control the availability or microbial access to C and N resources could disrupt the link between soil C and coupled N transformations across regional- and continental-scale gradients. If these or other factors dominate effects on soil C or N availability, soil C and N dynamics may be weak or uncoupled across broad geographic gradients. In addition, total soil C concentration may not accurately reflect microbial soil C availability (Zhou et al. 2020), leading to a weak relationship between total soil C and N dynamics.

We examined whether soil C concentration, as % soil C, influences N mineralization and nitrification coupling across North American ecosystems encompassing a diverse range of climates, vegetation types, and resource availability conditions. Using publicly available archives from terrestrial sites within the US National Science Foundation funded Long-Term Ecological Research (LTER) network, we aggregated data describing net N mineralization and net nitrification rates, as well as total soil C concentration from 2672 independent observations from 14 LTER sites. The large data set allowed us to evaluate how soil C concentration mediates the relationship between N mineralization and nitrification across diverse soil types and climate gradients. We hypothesized that soil

C concentration ultimately controls the fraction of mineralized N that is nitrified beyond local climatic drivers, whereby high soil C concentration reduces nitrate production.

Methods

Database assembly

This work was initiated for an “All Scientists Meeting” of the U.S. LTER network in September 2019 and was limited to LTER cross-site analysis. As such, we searched public databases associated with all terrestrial North American LTER sites for datasets reporting soil net N mineralization ($\mu\text{g N g dry soil}^{-1} \text{ day}^{-1}$), soil net nitrification ($\mu\text{g N g dry soil}^{-1} \text{ day}^{-1}$), and total soil C concentration (% soil C). Mineralization and nitrification rates were measured using both laboratory incubations (56% of samples) and field-buried bag and core approaches (44% of samples). We targeted net N fluxes rather than gross N transformations because they are widely measured and thus allowed for the development of a dataset encompassing diverse soil types and ecosystems.

In instances when prior studies reported two of the three required components to test our hypotheses, we followed up with individual data contributors to access content absent from the LTER database where possible. This included net nitrification rates when net N mineralization rates were solely available in the public archive. From datasets representing 19,271 soil cores from multiple locations within 14 terrestrial LTER sites (Supplementary Table S1), we assembled site- and core-level metadata. Our dataset included: site latitude and longitude, mean annual temperature (MAT), mean annual precipitation (MAP), altitude, soil type, pH, and total soil N content, where available. We used 30-year (1991–2020) average monthly air temperature data (Arguez et al. 2021) to calculate annual site potential evapotranspiration (PET) using the Thornthwaite model (Thornthwaite 1948) and expressed site water balance as MAP-PET (mm year^{-1}). Data were transformed to common units ($\mu\text{g N g dry soil}^{-1} \text{ day}^{-1}$) and percent soil C.

Statistical analyses

For plots containing soil cores taken over time or multiple sub-plot collections, we calculated a plot-level mean of the N mineralization rates, nitrification rates, and soil C concentrations since these cores were not statistically independent (2672 independent observations in final dataset of 19,271 total observations). We used mixed effects models to evaluate the relationship between soil C concentration (% soil C) and site meteorology (single main effect of MAT, MAP, or water balance; random effect = study). Soil C concentration was log-transformed to approximate normality. Soil pH was not regularly reported with the N cycling data, so it is not considered broadly in the analysis.

We used model selection to identify the combination of predictors that best explained variation in nitrification rates. We fit a global mixed-effects model relating net nitrification rate to a potential set of predictor variables including net N mineralization rate, soil C concentration (log-transformed), site MAT, site water balance (MAP-PET), and all two-way interactions with N mineralization (N mineralization*Soil C concentration; N mineralization*MAT; N mineralization*water balance) using the *nlme* R package (Pinheiro et al. 2019). MAP was excluded from the model selection due to strong correlation with site water balance (Pearson correlation = 0.86; Table S2). All remaining main effects maintained a variance inflation factor < 1.6 (car R package; Fox & Weisberg 2019) and thus were retained within the global model. Predictors were centered and scaled by their mean and standard deviations, respectively (*scale* function in R). From each LTER site, data were derived from multiple studies run by separate investigators often with different models. Therefore, individual study was included as a random effect. We used the ‘dredge’ function to generate a full set of sub-models containing all combinations of main effects and interactions (MuMIn R package; Nakagawa and Schielzeth 2013).

To separately compare the effect of MAT, MAP, and soil C concentration on the relationship between net N mineralization and nitrification, we fit three separate mixed effects models associating net nitrification rates to either (1) N mineralization*soil C concentration; (2) N mineralization*MAT; (3) N mineralization*water balance [MAP-PET] (R

package nlme; Pinheiro et al. 2017). Soil C concentration was log-transformed to approximate normality, and variables were centered and scaled as described above. Individual study was included as a random effect. The three models allowed us to examine the strength of the individual and interactive effects on net nitrification.

Results

The fourteen terrestrial LTER sites considered in this analysis (and six additional metropolitan sites outside of the LTER Network sampled in association with the Baltimore Ecosystem Study) were distributed across the continental U.S. (Fig. 2a). The 14 sites ranged in MAT from -7.9 to 24.3 °C and 193 to 2289 mm in MAP. The LTER sites spanned 25.8 to 68.6 degrees latitude and a range of ecosystems, including deciduous forest, coniferous forest, grassland, dryland, and tundra (Supplementary

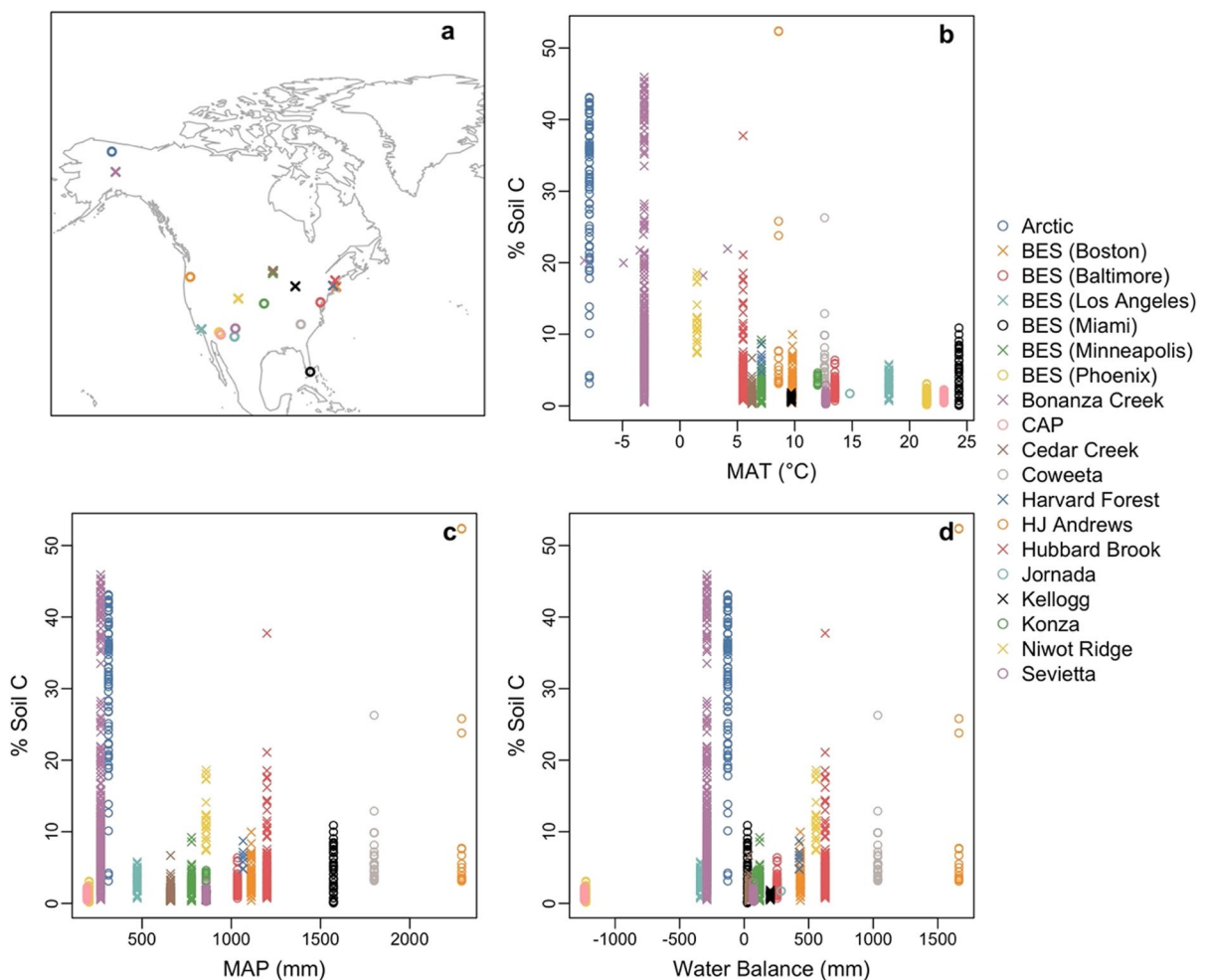


Fig. 2 Site distribution and cross-site meteorological conditions. **A** Distribution of terrestrial LTER sites included in the analysis; **B** Relationship between site MAT and % soil C; **C** relationship between site MAP and soil C concentration; **D** relationship between site water balance (MAP-PET) and soil

C concentration. Soil C concentration was log-transformed to approximate normality in statistical models, but untransformed relationships are shown here. Abbreviations as follows: *BES* Baltimore Ecosystem Study; *CAP* Central Arizona Phoenix

Table 1). Across replicate-averaged samples ($n=2672$), soil C concentration (log-transformed) decreased with MAT ($p<0.001$; Fig. 2b) and increased with MAP ($p<0.001$) and site water balance (MAP-PET; $p<0.001$). Alaskan LTER sites dominated observations with low MAP but high soil C where low temperatures and permafrost presence moderate moisture limitation and slow organic matter decomposition. The soil C-to-N ratio increased significantly with soil C concentration across sites ($p<0.0001$).

The multiple regression model identified via model selection contained all possible covariates (net N mineralization, MAT, water balance [MAP-PET], and soil C concentration) relating edaphic characteristics and meteorological conditions to soil net nitrification rates. Both the main effects of net N mineralization rate and site water balance, as well as the interactions between net N mineralization and soil C concentration and net N mineralization and site water balance emerged as significant predictors describing net nitrification rates (Table 1). Our subsequent individual

models allowed us to explore these interactions in more detail.

The rate of net nitrification increased with net N mineralization across sites (slope=0.26; $p<0.0001$). When soil C concentration was introduced as an additional main effect with net N mineralization, there was a significant negative interaction between soil C concentration and net N mineralization on nitrification, such that the fraction of mineralized N that was nitrified decreased with increasing soil C concentrations ($p<0.0001$; Table 2a; Fig. 3), as we had hypothesized (Fig. 1). At low soil C concentrations (<5%), there was a positive, linear relationship between N mineralization and nitrification. However, as soil C concentrations increased (>5%), the relationship between N mineralization and nitrification disappeared, showing that increased N mineralization does not always correlate with increased nitrification (Fig. 3). This pattern persisted when we removed all observations from the Arctic tundra, which maintains water-logged permafrost soils (Table S3), and when we considered only the subset of observations in

Table 1 Mixed-effect multiple regression model of net nitrification identified through model selection

	Parameter	Parameter value	Std. Error	P-value
Individual study was included as a random effect	Net N Mineralization	1.619	0.088	<0.0001
	MAT	0.013	0.151	0.932
	Water balance	0.255	0.117	0.030
	% Soil C	-0.185	0.094	0.050
Instances in which $P<0.05$ are italicized	Mineralization* MAT	-0.158	0.140	0.258
	Mineralization* % Soil C	-0.397	0.080	<0.0001
	Mineralization* Water balance	0.769	0.123	<0.0001

Table 2 Results of three mineralization-covariate statistical mixed effects models describing the relationship between net N mineralization and (a) % soil C; (b) site water balance; and

(c) MAT on net nitrification rates (Nitrification~Mineralization+Covariate+Mineralization*Covariate, random effect: LTER site)

	Parameter	Parameter value	Std. Error	P-value
(a)	Mineralization	1.673	0.070	<0.0001
	% Soil C	-0.016	0.094	0.862
	Mineralization * % Soil C	-0.235	0.056	<0.0001
(b)	Mineralization	1.380	0.047	<0.0001
	Water balance	0.184	0.093	0.0449
	Mineralization * Water balance	0.603	0.040	<0.0001
(c)	Mineralization	2.117	0.060	<0.0001
	MAT	0.166	0.133	0.213
	Mineralization * MAT	0.541	0.046	<0.0001

Instances in which $P<0.05$ are italicized

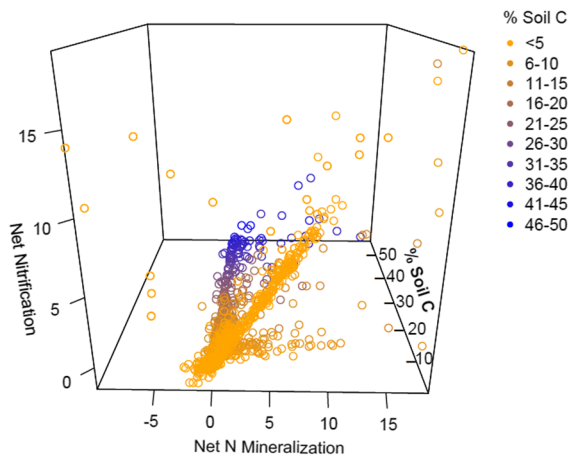


Fig. 3 Relationship between net N mineralization ($\mu\text{g N g soil}^{-1} \text{ day}^{-1}$), net nitrification ($\mu\text{g N g soil}^{-1} \text{ day}^{-1}$), and soil C concentrations (% soil C). Each symbol represents a single observation while the color represents the soil C concentration. At low soil C concentrations, there is a strong, positive relationship between net nitrification and net N mineralization. As soil C increases, the relationship breaks down and net mineralization does not necessarily result in net nitrification

which soil C concentration is $<10\%$ to exclude potentially high organic samples that sustain fluctuating redox conditions or anoxia (86% of observations and spanning all sites; Table S4).

In separate models examining the effects of MAT and then MAP on net nitrification, there were significant positive interactions between net N mineralization rates and site MAP (Table 2b) as well as between net N mineralization and site MAT (Table 2c). This relationship is consistent across the subsets of samples derived from both laboratory (Table S5a) and field (Table S5b) incubations. In contrast to soil C concentration, the fraction of mineralized N that was nitrified increased with both MAT and MAP across sites (Table 2b–c).

Discussion

Using data from across the LTER network, we explored the influence of soil C concentration on the coupling of net N mineralization and net nitrification across a broad range of North American ecosystems. Overall, the pattern conformed with our hypothesis that high soil C concentrations constrain the amount of mineralized N that is ultimately

nitrified. We found that soil C concentration (% soil C) moderated the fraction of mineralized N that was nitrified across diverse soil types and environments. In soils with low C concentration, net nitrification increased with net N mineralization more rapidly than in soils above the cross-site mean C concentration (Fig. 3). This bifurcated pattern matches the role of soil C as gatekeeper over nitrification (Hart et al. 1994) previously identified at a single LTER site, the Coweeta Hydrologic Laboratory in the Appalachian Mountains of southwestern North Carolina (Keiser et al. 2016). At Coweeta, undisturbed forest soils maintained larger soil C concentrations ($9.7 \pm 7.8\% \text{C}$) and nitrification rates were decoupled from net N mineralization rates, whereas the disturbed soils maintained smaller soil C pools ($4.5 \pm 1.5\% \text{C}$) and higher nitrification relative to mineralization (Keiser et al. 2016). Importantly, our study shows that this influence of soil C as a driver of the N mineralization-nitrification relationship extends beyond local scales to operate across a diverse range of ecosystems (deciduous forest, coniferous forest, grassland, desert, tundra) and climates, after accounting for the influence of MAT and MAP (Table 1). Our results demonstrate the broad role of soil C as a mediator of N cycling and as a potential buffer against N loss from terrestrial ecosystems.

Ecological stoichiometry appears to drive the link between soil C concentration and N transformations, despite this analysis employing %C as opposed to a more direct measure of microbially available soil C. Under low soil C concentrations, C limitation should constrain heterotrophic microbial N demand, leaving ammonium available for nitrifying bacteria and archaea. In contrast, high soil C concentrations should induce greater heterotrophic N demand and heighten competition for ammonium between heterotrophs and autotrophs (Booth et al. 2005; Silva et al. 2005), which appears to decouple N mineralization and nitrification (Keiser et al. 2016). The progression or inhibition of net nitrification has been measured in forest soils with low and high C:N ratios, respectively (Midgley and Phillips 2016), despite consistent nitrifier populations (Mushinski et al. 2019). Our results combined with those found previously suggest that the mediating role of soil C on N cycle dynamics is driven by stoichiometric demands by heterotrophs and their ability to outcompete nitrifiers for N

resources. Importantly, our results extend previous single-site-level analyses to show a broader, continental-scale pattern.

While this study highlights broad cross-site patterns, it is unknown how the dominance of ammonia-oxidizing archaea (AOA) versus ammonia-oxidizing bacteria (AOB) and their disparate distribution across ecosystems may alter competitive dynamics with soil heterotrophs. Ammonia-oxidizing archaea, which dominate nitrification in low-N soils and substrates, are strong competitors for ammonium and may out-compete heterotrophic microbes for ammonium, even in high-C environments (Martens-Habbenha et al. 2009; Prosser and Nicol 2012). Therefore, cross-site shifts in the relative abundance of AOA versus AOB may attenuate the influence of soil C on the decoupling of nitrification and mineralization, especially under N-limited conditions.

Our analysis showing the relationship between soil C and N transformations was based on N mineralization incubations in the lab and field, which exclude the role of plants. The presence of N-fixing plants could reduce rates of N mineralization (Hungate et al. 1999) and alter the heterotrophic—autotrophic competition for N irrespective of soil C (Malchair et al. 2010). More broadly, plants compete with nitrifiers for ammonium, and their rates of N uptake vary with MAT and MAP. This plant-nitrifier competition would extend to mycorrhizal associations in forest ecosystems (Phillips et al. 2013), and include mechanisms that further influence soil C. For example, ectomycorrhizal fungi are thought to promote the accumulation of soil C in part by limiting N availability to heterotrophic microbes and slowing decomposition (Averill et al. 2014). In this case, plant and mycorrhizal demand for N also would not only increase the N immobilization potential by heterotrophs via greater soil C but would also drive substrate limitation of nitrifiers directly. Plant-nitrifier competition can further depend on the rhizosphere, which creates hotspots for microbial activity through continuous plant–microbe–soil interactions and exchanges of C and nutrients (Cantarel et al. 2015).

Incubations exclude those root-microbe-soil interactions that could shift our observed N transformation rates at fine scales. Furthermore, these analyses use net, rather than gross, rates of N mineralization and nitrification. Net rates provide a straightforward representation of changes to inorganic N pool sizes,

are commonly measured in field and laboratory studies, and thus observations of them are more widely available than gross transformation measurements. Net fluxes, however, may mask important underlying components of the N mineralization process. For example, in this analysis, we assume that low net nitrate production suggests heterotrophic microbes are outcompeting nitrifiers for N and immobilizing ammonium prior to nitrification. However, nitrate, the product of nitrification, can also be assimilated by heterotrophic microbes to meet their N demand (Laungani and Knops 2012; Laungani et al. 2012), which would also reduce the nitrate pool size and measured net nitrification rate (Hart et al. 1994; Stark and Hart 1997). Gross N mineralization and nitrification rates measured using ^{15}N isotopes can more explicitly track ammonium and nitrate transformations (Elrys et al. 2022). While measurement of gross N transformations could help confirm the underlying mechanism highlighted here, our results and those of others suggest stoichiometric demands and N competition between heterotrophic microbes and autotrophic nitrifiers drives the coupling between soil C and N transformations.

Despite the important role of soil C, site meteorological factors also contribute to the coupling or uncoupling of N mineralization and nitrification across the LTER-wide climate gradient. Soil moisture influences coupled N transformations because it influences aerobic conditions required for N mineralization and nitrification (Robertson and Groffman 2007), the activity and movement of soil microbial communities (Fierer and Schimel 2002) and the movement of the mobile and soluble nitrite ion to prolific nitrite oxidizers (Grundmann et al. 2001; Parker and Schimel 2011; Schimel 2018; Stark and Firestone 1995). Our analysis shows a positive interaction between N mineralization and site water balance (MAP-PET), whereby a larger fraction of mineralized N is nitrified at sites with greater water availability, reinforcing moisture availability as a mediator of coupled N transformations. However, soil moisture is strongly impacted by inherent site characteristics, including soil texture and temperature, which would influence how much water is retained or lost. These site characteristics influence relationships between MAP-PET and nitrification (Fig. S1). For example, the Alaskan arctic tundra and boreal forest soils with the lowest MAP are highly organic,

contributing to the maintenance of water-saturated conditions that limit aerobic activity and contribute to decoupling of net N mineralization and nitrification. Similarly, C-rich soils from HJ Andrews forest, a temperate rainforest in Oregon (MAP=2289 mm) may also experience regular periods of anoxia disrupting inorganic N transformations. Therefore, site water balance, and thus soil moisture, is indicative of coupled N relationships, but mediated by additional site conditions.

In contrast, temperature exerts control over metabolic activity of soil organisms and thus mineralization of soil C (Alster et al. 2020; Davidson and Janssens 2006). Across our study sites, the relationship between temperature and C turnover is evident through a decrease in soil C concentration as MAT increases (Fig. 2b). Net nitrification also generally increases with MAT, corresponding with both increased metabolic activity and a decrease in soil C concentration at sites with higher temperatures (Fig. S1). Therefore, MAT has potential indirect control over the coupling of N transformations through its influence on soil C availability. Together, temperature and moisture conditions may contribute to the observed variation in the relationship between soil C concentration and the N mineralization-nitrification relationship (Fig. 2). Other site-specific variables, such as land management, the presence of N-fixing plants (Mushinski et al. 2019), or soil mineralogy may contribute to variation noted among sites. For example, soils collected from agricultural experiments at Kellogg Biological Station, located in southwestern Michigan, experienced variable fertilizer inputs, tillage regimes, and cultivation practices, all of which can influence N turnover (Mahal et al. 2019) and microbial biomass (Kim et al. 2020; Nguyen et al. 2016). In light of the importance of temperature and precipitation on coupled N transformations across ecosystems and climates, site-level characteristics need to be examined more closely among sites of similar soil C concentrations to better describe variability in coupled N transformations and the potential cross-scale interactions identified here.

The relationship between soil C and N transformations has important global ramifications for the fate of N. For example, current efforts to increase soil C stocks to offset growing atmospheric CO₂ concentrations may simultaneously reduce nitrification rates. If reduced nitrification rates lead to reductions in N₂O

emissions either due to reduced nitrification itself or a smaller soil nitrate pool accessible for denitrification (Firestone and Davidson 1989; Venterea and Rolston 2000), increasing soil C may be a strategy for reducing concentrations of CO₂ and N₂O, depending on ecosystem and land management (Guenet et al. 2021). At the same time, increasing soil C stocks may further reduce available N for plant uptake because of increased microbial demand for N (Guenet et al. 2021; Yanai et al. 2013), including bioavailable forms of organic N (Daly et al. 2021). Within forested ecosystems or within agroforestry, microbial immobilization of N could increase the rate of progressive N limitation (Groffman et al. 2018) and constrain ongoing increases in forest biomass (Aber and Driscoll 1997). Within agricultural soils, any reduction in nitrification from increased soil C could subsequently reduce soil nitrate losses and improve water quality (Tilman et al. 2002; Zhang et al. 2021). Our results from data collected across North American ecosystems demonstrate that C and N are not simply coupled with each other but can help explain N transformations and availability within and across ecosystems. Coupled C and N interactions can be used to model the influence of N fertilization on SOM decomposition (Neff et al. 2002) and, in turn, soil C storage capacity (Janssens et al. 2010), or to predict greenhouse gas emissions across soils according to N availability and C inputs (Liang et al. 2015). This research advances the use of stoichiometrically based relationships to infer large-scale ecosystem processes. Knowing there is a consistent pattern linking the transformation and availability of inorganic N with soil C across ecosystem types could help refine biogeochemical models and strategies to manage individual ecosystems.

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Data availability All data and code to replicate analyses and figures are available at https://github.com/gill20a/LTER_MicrobialNComp. All data will be permanently archived with the Environmental Data Initiative, DOI will be provided prior to publication.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Aber JD, Driscoll CT (1997) Effects of land use, climate variation, and N deposition on N cycling and C storage in northern hardwood forests. *Global Biogeochem Cycles* 11(4):639–648

Alster CJ, von Fischer JC, Allison SD, Treseder KK (2020) Embracing a new paradigm for temperature sensitivity of soil microbes. *Glob Change Biol* 26(6):3221–3229

Arguez A, Durre I, Applequist S, Vose R, Squires M, Yin X, Heim R, Owen T (2021) NOAA's 1991–2020 climate normal: an overview. *Bull Am Meteorol Soc* 93:1687–1697

Averill C, Turner BL, Finzi AC (2014) Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505(7484):543–545

Baral BR, Kuyper TW, Van Groenigen JW (2014) Liebig's law of the minimum applied to a greenhouse gas: alleviation of P-limitation reduces soil N₂O emission. *Plant Soil* 374(1):539–548

Bernhardt ES, Likens GE (2002) Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. *Ecology* 83(6):1689–1700

Bernhardt ES, Hall JRO, Likens GE (2002) Whole-system estimates of nitrification and nitrate uptake in streams of the Hubbard Brook Experimental Forest. *Ecosystems* 5(5):419–430

Booth MS, Stark JM, Rastetter E (2005) Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecol Monogr* 75(2):139–157

Buchkowski RW, Shaw AN, Sihi D, Smith GR, Keiser AD (2019) Constraining carbon and nutrient flows in soil with ecological stoichiometry. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2019.00382>

Campbell JL, Soggi AM, Templer PH (2014) Increased nitrogen leaching following soil freezing is due to decreased root uptake in a northern hardwood forest. *Glob Change Biol* 20(8):2663–2673

Cantarel AAM, Pommier T, Desclos-Theveniau M, Diquélou S, Dumont M, Grassein F, Kastl E-M, Grigulis K, Lañé P, Lavorel S, Lemauviel-Lavenant S, Personeni E, Schloter M, Poly F (2015) Using plant traits to explain plant–microbe relationships involved in nitrogen acquisition. *Ecology* 96(3):788–799

Daly AB, Jilling A, Bowles TM, Buchkowski RW, Frey SD, Kallenbach CM, Keiluweit M, Mooshammer M, Schimel JP, Grandy AS (2021) A holistic framework integrating plant–microbe–mineral regulation of soil bioavailable nitrogen. *Biogeochemistry* 154:211–229. <https://doi.org/10.1007/s10533-021-00793-9>

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440(7081):165–173

Dijkstra P, LaViolette CM, Coyle JS, Doucett RR, Schwartz E, Hart SC, Hungate BA (2008) 15N enrichment as an integrator of the effects of C and N on microbial metabolism and ecosystem function. *Ecol Lett* 11(4):389–397

Elrys AS, Chen Z, Wang J, Uwiragiye Y, Helmy AM, Desoky E-SM, Cheng Y, Zhang J-b, Cai Z-c, Müller C (2022) Global patterns of soil gross immobilization of ammonium and nitrate in terrestrial ecosystems. *Glob Change Biol* 28(14):4472–4488

Farrell M, Prendergast-Miller M, Jones DL, Hill PW, Condron LM (2014) Soil microbial organic nitrogen uptake is regulated by carbon availability. *Soil Biol Biochem* 77:261–267

Fierer N, Schimel JP (2002) Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soil Biol Biochem* 34(6):777–787

Firestone M, Davidson E (1989) Microbiological basis of NO and N₂O production and consumption in soil. *Exch Trace Gases between Terr Ecosyst Atmosphere* 47:7–21

Groffman PM, Driscoll CT, Durán J, Campbell JL, Christenson LM, Fahey TJ, Fisk MC, Fuss C, Likens GE, Lovett G, Rustad L, Templer PH (2018) Nitrogen oligotrophication in northern hardwood forests. *Biogeochemistry* 141(3):523–539

- Grundmann GL, Dechesne A, Bartoli F, Flandrois JP, Chasse JL, Kizungu R (2001) Spatial modeling of nitrifier microhabitats in soil. *Soil Sci Soc Am J* 65(6):1709–1716
- Guenet B, Gabrielle B, Chenu C, Arrouays D, Balesdent J, Bernoux M, Bruni E, Caliman J-P, Cardinael R, Chen S, Ciais P, Desbois D, Fouche J, Frank S, Henault C, Lugato E, Naipal V, Nesme T, Obersteiner M, Pellerin S, Powlson DS, Rasse DP, Rees F, Soussana J-F, Su Y, Tian H, Valin H, Zhou F (2021) Can N₂O emissions offset the benefits from soil organic carbon storage? *Glob Change Biol* 27(2):237–256
- Hart SC, Nason GE, Myrold DD, Perry DA (1994) Dynamics of gross nitrogen transformations in an old-growth forest - the carbon connection. *Ecology* 75(4):880–891
- He M, Dijkstra FA (2014) Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytol* 204(4):924–931
- Hungate BA, Dijkstra P, Johnson DW, Hinkle CR, Drake BG (1999) Elevated CO₂ increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Glob Change Biol* 5(7):781–789
- Ja F, Weisberg S (2019) An R companion to applied regression. Sage, Thousand Oaks
- Janssens IA, Dieleman W, Luysaert S, Subke JA, Reichstein M, Ceulemans R, Ciais P, Dolman AJ, Grace J, Matteucci G, Papale D, Piao SL, Schulze ED, Tang J, Law BE (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nat Geosci* 3(5):315–322
- Kaye JP, Hart SC (1997) Competition for nitrogen between plants and soil microorganisms. *Trends Ecol Evol* 12(4):139–143
- Keiser AD, Knoepf JD, Bradford MA (2016) Disturbance decouples biogeochemical cycles across forests of the Southeastern US. *Ecosystems* 19(1):50–61
- Kim N, Zabaloy MC, Guan K, Villamil MB (2020) Do cover crops benefit soil microbiome? A meta-analysis of current research. *Soil Biol Biochem* 142:107701
- Laungani R, Knops JMH (2012) Microbial immobilization drives nitrogen cycling differences among plant species. *Oikos* 121(11):1840–1848
- Laungani R, Knops JMH, Brassil C (2012) Feedback on plant productivity can be constrained by SOM in N-limited grasslands. *Soil Biol Biochem* 53:1–8
- Leptin A, Whitehead D, Anderson CR, Cameron KC, Lehto NJ (2021) Increased soil nitrogen supply enhances root-derived available soil carbon leading to reduced potential nitrification activity. *Appl Soil Ecol* 159:103842
- Liang LL, Eberwein JR, Allsman LA, Grantz DA, Jenerette GD (2015) Regulation of CO₂ and N₂O fluxes by coupled carbon and nitrogen availability. *Environ Res Lett* 10(3):034008
- Libohova Z, Seybold C, Wysocki D, Wills S, Schoeneberger P, Williams C, Lindbo D, Stott D, Owens PR (2018) Reevaluating the effects of soil organic matter and other properties on available water-holding capacity using the National Cooperative Soil Survey Characterization Database. *J Soil Water Conserv* 73(4):411–421
- Mahal NK, Osterholz WR, Miguez FE, Poffenbarger HJ, Sawyer JE, Oik DC, Archontoulis SV, Castellano MJ (2019) Nitrogen fertilizer suppresses mineralization of soil organic matter in maize agroecosystems. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2019.00059>
- Malchair S, De Boeck HJ, Lemmens CMHM, Merckx R, Nijs I, Ceulemans R, Carnol M (2010) Do climate warming and plant species richness affect potential nitrification, basal respiration and ammonia-oxidizing bacteria in experimental grasslands? *Soil Biol Biochem* 42(11):1944–1951
- Martens-Habbena W, Berube PM, Urakawa H, de la Torre JR, Stahl DA (2009) Ammonia oxidation kinetics determine niche separation of nitrifying archaea and bacteria. *Nature* 461(7266):976–979
- Midgley MG, Phillips RP (2016) Resource stoichiometry and the biogeochemical consequences of nitrogen deposition in a mixed deciduous forest. *Ecology* 97(12):3369–3378
- Mushinski RM, Phillips RP, Payne ZC, Abney RB, Jo I, Fei S, Pusede SE, White JR, Rusch DB, Raff JD (2019) Microbial mechanisms and ecosystem flux estimation for aerobic N₂O emissions from deciduous forest soils. *Proc Natl Acad Sci* 116(6):2138–2145
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- Neff JC, Townsend AR, Gleixner G, Lehman SJ, Turnbull J, Bowman WD (2002) Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature* 419(6910):915–917
- Nguyen DB, Rose MT, Morris SG, van Zwieten L (2016) Impact of glyphosate on soil microbial biomass and respiration: a meta-analysis. *Soil Biol Biochem* 92:50–57
- NRSP-3 (2020) National Atmospheric Deposition Program. In: Office NP (ed). Wisconsin State Laboratory of Hygiene, Madison
- Parker SS, Schimel JP (2011) Soil nitrogen availability and transformations differ between the summer and the growing season in a California grassland. *Appl Soil Ecol* 48(2):185–192
- Phillips RP, Brzostek E, Midgley MG (2013) The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytol* 199(1):41–51
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2017) nlme: Linear and nonlinear mixed effects models. In.. Available at: <http://CRAN.R-project.org/package=nlme>.
- Poffenbarger HJ, Mirsky SB, Weil RR, Kramer M, Spargo JT, Cavigelli MA (2015) Legume proportion, poultry litter, and tillage effects on cover crop decomposition. *Agron J* 107(6):2083–2096
- Prosser JI, Nicol GW (2012) Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. *Trends Microbiol* 20(11):523–531
- Robertson GP, Groffman PM (2007) Nitrogen transformations. In: Paul EA (ed) *Soil microbiology, ecology and biochemistry*, 3rd edn. Academic Press, San Diego, pp 341–364
- Schimel JP (2018) Life in dry soils: effects of drought on soil microbial communities and processes. *Annu Rev Ecol Syst* 49(1):409–432
- Silva RG, Jorgensen EE, Holub SM, Gonsoulin ME (2005) Relationships between culturable soil microbial populations and gross nitrogen transformation processes in a clay loam soil across ecosystems. *Nutr Cycl Agroecosyst* 71(3):259–270

- Six J, Elliott ET, Paustian K (1999) Aggregate and soil organic matter dynamics under conventional and no-tillage systems. *Soil Sci Soc Am J* 63(5):1350–1358
- Soong JL, Fuchslueger L, Marañon-Jimenez S, Torn MS, Janssens IA, Penuelas J, Richter A (2020) Microbial carbon limitation: the need for integrating microorganisms into our understanding of ecosystem carbon cycling. *Glob Change Biol* 26(4):1953–1961
- Stark JM, Firestone MK (1995) Mechanisms for soil-moisture effects on activity of nitrifying bacteria. *Appl Environ Microbiol* 61(1):218–221
- Stark JM, Hart SC (1997) High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* 385(6611):61–64
- Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey
- Syers JK, Campbell AS, Walker TW (1970) Contribution of organic carbon and clay to cation exchange capacity in a chronosequence of sandy soils. *Plant Soil* 33(1):104–112
- Thornthwaite CW (1948) An approach toward a rational classification of climate. *Geogr Rev* 38(1):55–94
- Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. *Nature* 418(6898):671–677
- Venterea RT, Rolston DE (2000) Mechanisms and kinetics of nitric and nitrous oxide production during nitrification in agricultural soil. *Glob Change Biol* 6(3):303–316
- Venterea RT, Clough TJ, Coulter JA, Breuillin-Sessoms F, Wang P, Sadowsky MJ (2015) Ammonium sorption and ammonia inhibition of nitrite-oxidizing bacteria explain contrasting soil N₂O production. *Sci Rep* 5(1):12153
- Verhagen FJ, Laanbroek HJ (1991) Competition for ammonium between nitrifying and heterotrophic bacteria in dual energy-limited chemostats. *Appl Environ Microbiol* 57(11):3255–3263
- Verhagen FJ, Duyts H, Laanbroek HJ (1992) Competition for ammonium between nitrifying and heterotrophic bacteria in continuously percolated soil columns. *Appl Environ Microbiol* 58(10):3303–3311
- Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA, Todd RL (1979) Nitrate losses from disturbed ecosystems. *Science* 204(4392):469–474
- Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecol Monogr* 52(2):155–177
- Viviroli D, Durr HH, Messerli B, Meybeck M, Weingartner R (2007) Mountains of the world, water towers for humanity: typology, mapping, and global significance. *Water Resour Res.* <https://doi.org/10.1029/2006WR005653>
- Williams A, de Vries FT (2020) Plant root exudation under drought: implications for ecosystem functioning. *New Phytol* 225(5):1899–1905
- Yanai RD, Vadeboncoeur MA, Hamburg SP, Arthur MA, Fuss CB, Groffman PM, Siccama TG, Driscoll CT (2013) From missing source to missing sink: long-term changes in the nitrogen budget of a northern hardwood forest. *Environ Sci Technol* 47(20):11440–11448
- Zhang Y, Pan B, Lam SK, Bai E, Hou P, Chen D (2021) Predicting the ratio of nitrification to immobilization to reflect the potential risk of nitrogen loss worldwide. *Environ Sci Technol* 55(11):7721–7730
- Zhou X, Chen L, Li Y, Xu J, Brookes PC (2020) Abiotic processes dominate soil organic matter mineralization: investigating the regulatory gate hypothesis by inoculating a previously fumigated soil with increasing fresh soil inocula. *Geoderma* 373:114400

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