

Disturbance Decouples Biogeochemical Cycles Across Forests of the Southeastern US

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ABSTRACT

Biogeochemical cycles are inherently linked through the stoichiometric demands of the organisms that cycle the elements. Landscape disturbance can alter element availability and thus the rates of biogeochemical cycling. Nitrification is a fundamental biogeochemical process positively related to plant productivity and nitrogen loss from soils to aquatic systems, and the rate of nitrification is sensitive to both carbon and nitrogen availability. Yet how these controls influence nitrification rates at the landscape scale is not fully elucidated. We, therefore, sampled ten watersheds with different disturbance histories in the southern Appalachian Mountains to examine effects on potential net nitrification rates. Using linear mixed model selection (AIC), we narrowed a broad suite of putative explanatory variables into a set of models that best explained landscape patterns in potential net nitrification. Forest disturbance history determined whether nitrification and nitrogen mineralization were correlated, with the effect apparently medi-

ated by microbially available carbon. Undisturbed forests had higher available carbon, which uncoupled potential net nitrification from potential net nitrogen mineralization. In contrast, disturbed watersheds had lower available carbon, and nitrification rates were strongly correlated to those of nitrogen mineralization. These data suggest that a history of disturbance at the landscape scale reduces soil carbon availability, which increases ammonium availability to nitrifiers at the micro-scale. Landscape-level soil carbon availability then appears to determine the coupling of autotrophic (nitrification) and heterotrophic (nitrogen mineralization) biogeochemical processes, and hence the relationship between carbon and nitrogen cycling in soils.

Key words: autotroph; carbon cycle; competition; disturbance; heterotroph; net nitrification; nitrogen cycle; nitrogen mineralization; scale-dependence; watershed ecology.

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INTRODUCTION

Biogeochemical cycles are linked through organismal demand for stoichiometrically defined amounts of different elements required for growth (McGill and Cole 1981; Schlesinger and others 2011). This coupling of elemental demands likely determines how ecosystems respond to global change (Finzi and others 2011). For example, plant productivity

responses to elevated CO_2 are dependent on the rate at which nitrogen (N) is made available in the soil for plant uptake (Drake and others 2011; Phillips and others 2011). Similarly, N fertilization effects on soil organic matter turnover are dependent on the quality of the constituent carbon (C) compounds (Neff and others 2002). Both C and N cycling processes in soil are affected by disturbances, with the type of land-use change determining the degree of impact to C and N cycles (Guo and Gifford 2002; Murty and others 2002). For example, logging removes aboveground biomass, which subsequently decreases or stops new C inputs (for example, coarse woody debris, leaf litter, root turnover) and plant N uptake. In response, belowground C stocks can then decline (Schlesinger 1986) whereas N export typically increases (Bormann and Likens 1979; Swank and others 2014). Therefore, knowledge of disturbance and land-use history may explain variation in the rates of biogeochemical processes across contemporary landscapes that are caused by changes in the availability of C and N to soil microorganisms.

Soil microbial communities strongly regulate the cycling of C and N in terrestrial ecosystems (van der Heijden and others 2008). Some of the biogeochemical processes involved in these cycles are carried out only by soil microorganisms. One such process is nitrification, where autotrophic microbes (nitrifiers) fix CO_2 through the oxidation of ammonium (NH_4^+) to nitrate (NO_3^-). Nitrification is positively associated with inorganic N availability. The resulting ion, highly mobile NO_3^- , may be taken up by plant roots, leach into aquatic systems, or denitrify to the potent greenhouse gas N_2O (Viviroli and others 2007). Nitrifiers, therefore, play a key functional role in the biogeochemistry of ecosystems and, just like plants, have to compete with heterotrophic soil microbes for inorganic N (Hart and others 1994; Kaye and Hart 1997). The strength of this microbe–microbe N competition is likely strongly dependent on C availability to heterotrophic soil microbes (Verhagen and Laanbroek 1991; Booth and others 2005) because under plentiful C supply the heterotrophs have a high N demand for growth (Hart and others 1994). Therefore, nitrification rates, and hence soil and plant N cycle dynamics, may be inherently coupled to C cycling rates through autotroph–heterotroph NH_4^+ competition in soil microbial communities (Booth and others 2005). However, it is uncertain as to how disturbance history affects nitrification rates across the landscape through influences on soil C and N availability (Booth and others 2006;

Knoepp and others 2014). For example, undisturbed systems might be expected to have tight associations between soil C and N cycling, as evidenced by fast rates of NO_3^- turnover (Stark and Hart 1997) and N assimilation by soil microbes fueled by an abundance of labile C supply (Dijkstra and others 2008). If disturbance decreases C availability to heterotrophic soil microbes, we might then expect an uncoupling of C and N cycling because C-limited heterotrophs have a reduced demand for N (Schimel and Weintraub 2003), thereby facilitating NH_4^+ oxidation by the autotrophic nitrifiers.

We examined how historic disturbance regimes affect potential net nitrification rates in forested landscapes by working across and within ten, experimental watersheds. We appear to be the first to examine patterns and associated controls on net nitrification across pronounced environmental gradients caused by forest disturbance history and watershed topography (for example, ridge vs. riparian habitat) across the same landscape. To do so, we evaluated a broad set of putative explanatory variables that are documented drivers of potential net nitrification rates across landscapes. Despite this extensive assessment of putative explanatory variables, we expected that C and NH_4^+ availability would emerge as dominant controls across the landscape. Previous work in laboratory chemostats (Verhagen and Laanbroek 1991; Verhagen and others 1992) and freshwater systems (Strauss and others 2000; Bernhardt and others 2002; Bernhardt and Likens 2002) demonstrated that nitrifier abundance or activity declines with increasing C availability. Knowing that disturbance can reduce soil C content (Schlesinger 1986), we selected a mixture of four undisturbed and six disturbed watersheds. The six disturbed watersheds were clear-felled (four with no materials removed), and two converted to plantations in the 1950s and 1960s (Appendix 1 in Supplementary material), disturbances that alter soil C content (Knoepp and Swank 1997) and availability (Liao and others 2010).

Lower soil organic C availability should then promote C limitation of heterotrophic microbes, decreasing their demand for NH_4^+ and possibly increasing the availability to nitrifiers (Dijkstra and others 2008). As such, we hypothesized (Hyp. 1) that disturbed watersheds will have lower available soil C and hence higher rates of potential net nitrification because of reduced heterotroph–nitrifier competition. However, soil nitrifiers comprise both ammonia-oxidizing Archaea (AOA) and ammonia-oxidizing bacteria (AOB), with the

former potentially able to outcompete heterotrophic bacteria for NH_4^+ , as demonstrated in marine environments. (Martens-Habbena and others 2009). We, therefore, set up an alternative hypothesis (Hyp. 2) that historical disturbance effects on soil C have minimal influence on potential net nitrification rates. Instead, we expected nitrification would be controlled by a host of edaphic characteristics—such as soil pH, moisture, and texture—that have been identified as controls on net nitrification and that vary across the landscape, independent of disturbance history.

METHODS

Experimental Design

The study took place at the Coweeta Hydrologic Laboratory, a USDA Forest Service Experimental Forest and National Science Foundation Long-Term Ecological Research (LTER) site located in southwestern, North Carolina ($35^\circ 00' \text{N}$, $83^\circ 30' \text{W}$). The Coweeta basin is 2185 ha, ranging in elevation from 679 to 1592 m, and is composed of multiple sub-watersheds with varying treatment histories. Soils are classified in the Inceptisol or Ultisol orders, with varying physical and chemical properties throughout the basin. Ten sub-watersheds (henceforth referred to as 'watersheds') were selected to represent a range in elevation, aspect, and treatment history, with the latter categorization classified as Undisturbed or Disturbed. In an effort to separate treatment history effects from topographical differences among watersheds, Disturbed and Undisturbed watersheds were identified at both lower and higher elevations, and with both north- and south-facing aspects (Appendix 1 in Supplementary material).

To characterize the spatial variation in putative control and response variables, we established 50 m transects in the upper and lower portion of each watershed. The lower transect was located 20 m upstream from the catchment weir, and the upper transect began at the head of the perennial headwater stream. The transects began 1 m from the stream edge and ran upslope, perpendicular to the slope contour, following the major water flow path to the stream. Plots (5 m radius) were located at 5, 25, and 45 m along each transect to account for variation in soil moisture moving away from the stream bed. Due to the continuous steep slopes (30–90%) up to a watershed boundary, a 50 m transect provided a consistent plot design across the landscape. This sampling design allowed us to capture a snapshot of site properties at three levels

of spatial variation: landscape (watershed), within-watershed (transect), and riparian-upland (plot).

Within each plot, six mineral soil cores (10 cm depth, 8 cm dia.) were taken in a five-point star-design, plus plot center after carefully removing the organic horizon. The organic horizon plays an important role in nutrient availability in forests and O horizon formation is indicative of overall site nutrient cycling rates, with greater Oa horizon mass occurring on sites characterized by low N availability (Perala and Alban 1982; Knoepp and others 2000). However, we concentrated our sampling efforts in the mineral soils because in most southern Appalachian hardwood forests fine tree roots are concentrated in the mineral soils with greater than 60% found in the surface 10 cm (McGinty 1976; Nuckolls and others 2009). Furthermore, within these temperate forests, under both coniferous and hardwood overstory, mineral soils have a greater probability of higher relative net nitrification indices than the surficial O horizon (Lavoie and Bradley 2003). Soils were transported to the lab on ice. Spot measures of soil moisture and temperature to a depth of 12 cm and 10 cm, respectively, were recorded in each plot using a HydroSense probe (Campbell Scientific, Inc., Logan, UT USA) and an electronic thermometer (VWR International, Radnor, PA USA), an approach that resolves relative differences in these variables at the spatial scale of our study (Warren and Bradford 2011).

Soil Analyses

Soil analyses were informed by reviewing the peer-reviewed literature to identify variables reported to be significant controls on potential net nitrification rates in soils. Through this literature assessment, we identified about 20 variables to measure on our study soils (Table 1). Soils within a plot were first homogenized before dividing by mass for analysis of the physical, chemical, and microbial variables we identified. Bulk density of dried soil was calculated on a mass basis (Kramer and others 2012). Briefly, non-sieved soil taken to a known depth was dried for soil content (g soil cm^{-3}) and adjusted for root and stone volume. The soil partitioned for chemical analyses was first passed through a 2-mm sieve. Duplicate subsamples of fresh soil were used to measure field moisture content (105°C for 24 h) and water holding capacity [fully saturated, drain for 2 h, and dried at 105°C for 24 h (Bradford and others 2008a)]. Soil pH was determined in a water solution, 1:1 by volume (Allen 1989). Labile carbon was estimated using a 30-day incubation at 20°C

Table 1. Data Summary Table: Variables Averaged by Watershed Disturbance History

Variable	Disturbed	Undisturbed
Potential net nitrification (mg N g soil ⁻¹ 28 days ⁻¹)	0.011 ± 0.014	0.0013 ± 0.0030
Potential net N mineralization (mg N g soil ⁻¹ 28 days ⁻¹)	0.012 ± 0.013	0.011 ± 0.016
Extractable NO ₃ ⁻ (µg N g soil ⁻¹)	6.6 ± 9.7	0.13 ± 0.46
Extractable NH ₄ ⁺ (µg N g soil ⁻¹)	7.8 ± 3.6	11 ± 8.6
Extractable total N (µg N g soil ⁻¹)	23 ± 18	24 ± 17
Extractable DON (µg N g soil ⁻¹)	8.2 ± 10	13 ± 11
Soil %N	0.27 ± 0.12	0.42 ± 0.29
Net nitrification: net mineralization (ratio, unitless)	0.69 ± 0.58	0.16 ± 0.31
pH (H ⁺ ions)	4.5E-06 ± 2.6E-06	3.0E-05 ± 5.6E-05
Labile C (mg C g dry weight soil ⁻¹)	0.45 ± 0.13	1.0 ± 0.84
Extractable DOC (µg C g soil ⁻¹)	280 ± 78	490 ± 200
Soil %C	4.5 ± 1.5	9.1 ± 7.8
Soil C content (kg C m ⁻²)	3.8 [5.7]	5.0 [7.5]
Soil C:N	17 ± 2.9	21 ± 4.1
Microbial biomass CO ₂ -C (µg C g dry wt soil ⁻¹ h ⁻¹)	2.0 ± 0.53	5.3 ± 6.0
Microbial biomass N (µg N g soil ⁻¹)	65 ± 34	120 ± 88
Microbial biomass C (µg C g soil ⁻¹)	460 ± 150	960 ± 670
% Sand	61 ± 5.8	61 ± 10
% Silt	27 ± 5.3	28 ± 10
% Clay	11 ± 4.3	12 ± 5.3
Textural class	Sandy loam	Sandy loam
Bulk density (g soil cm ⁻³)	0.84 ± 0.23	0.55 ± 0.21
Soil temperature (°C)	21 ± 0.79	21 ± 1.2
Soil moisture (g H ₂ O g soil ⁻¹)	0.33 ± 0.15	0.75 ± 0.96
Soil water holding capacity (g H ₂ O g soil ⁻¹)	0.72 ± 0.21	1.4 ± 1.3
Land conversion	Disturbed	Undisturbed

The mean values (±SD) for each measured soil variable averaged by watershed disturbance history (Disturbed and Undisturbed). The average soil carbon content (kg C m⁻²) was calculated using average %C and average bulk density, estimated to a depth of 10 cm as well as 15 cm—the latter to directly compare with the Fraterrigo and others (2005) results (see Discussion). Fraterrigo and others (2005), working within the region, found coupled net nitrification and net N mineralization in both reference and previously logged sites, but had a total soil C content just below 4 kg C m⁻², throughout.

using methods described in Fierer and others (2005) and Bradford and others (2008b). This method provides an estimate of microbially available C resources through repeated CO₂ efflux measurements across 30 days. Labile C is then calculated as the cumulative CO₂ efflux across the 30-day assessment (mg C g dry weight soil⁻¹). Active microbial biomass was estimated through substrate-induced respiration (SIR) (West and Sparling 1986; Bradford and others 2008b). Chloroform fumigation extraction (CFE) was used to measure active and inactive microbial biomass C as well as K₂SO₄-extractable NH₄⁺ and NO₃⁻ concentrations to determine microbial biomass N. We followed CFE methods described by Fierer and Schimel (2003). Samples were run on an Astoria 2 Flow Analyzer (Astoria-Pacific, Clackamas, OR, USA) for N products and a Shimadzu TOC-V (Shimadzu, Maryland, USA) for C. Air-dried, sieved soil was analyzed for texture using the hydrometer method at the University of Connecticut Soil

Nutrient Analysis Laboratory, and run for total C and N concentrations on a Carlo Erba elemental analyzer (CE Elantech, Inc. Lakewood, NJ, USA).

Potential rates of net N mineralization and net nitrification were calculated using laboratory incubations following published protocols (Robertson and others 1999; Fraterrigo and others 2005). Briefly, a sub-set of soil from each plot was passed through a 4-mm sieve in the field, and then about 10 g of this sieved soil was added to a pre-weighed bottle containing 50 mL of 2 M KCl and shaken. These initial N extractions were then returned to the lab to determine NH₄⁺ and NO₃⁻ extract concentrations using an Astoria 2 Auto-Analyzer (Astoria-Pacific, Clackamas, OR, USA). Also on return to the lab each afternoon, around 20 g of the 4-mm sieved soils were added to a jar for incubation at 20°C and covered with plastic wrap to allow air diffusion but prevent drying. Soil water contents were adjusted and maintained at 65% of water holding capacity, and so were favorable for micro-

bial activity (Bradford and others 2008b). After 28 days, 10 g dry weight soil equivalent was extracted with 50 mL of 2 M KCl to analyze NH_4^+ and NO_3^- concentrations. Nitrification was calculated as NO_3^- at 28 days minus initial NO_3^- at time zero; N mineralization equals $\text{NH}_4^- + \text{NO}_3^-$ at 28 days minus $\text{NH}_4^- + \text{NO}_3^-$ at time zero (Goodale and Aber 2001).

Statistical Analyses

First, we ran a univariate regression for each putative controlling variable against potential nitrification for all 60 plots (6 per watershed) combined. All plots were treated as independent replicates. We set the explanatory threshold low ($r^2 \geq 0.05$) to be inclusive of explanatory variables that explained at least some variation or that might interact. We then used model selection with Akaike Information Criterion (AIC) to find a reduced set of the 22 putative variables to form the best statistical model (Kramer and others 2012) to describe net nitrification. This stepwise approach allowed us to narrow the factors within our dataset, and to use linear regression to identify the strongest predictors for nitrification (Cottingham and others 2005). A linear mixed model (LMM) approach was used so that the spatial associations inherent in the study design were accounted for by including watershed and transect as random effects (Bradford and others 2014). Only random effects with a ΔAIC no more than 1 were included in model selection. All variables were tested for collinearity using a variance inflation factor (VIF) test. Those variables, including random effects, with a VIF less than 5 were included in model selection. The fixed effects were permitted to interact as two and three-way interactions. The best model was a composite of the models with a ΔAIC no more than 5. The mixed models were fit using the ‘lme4’ package in the statistical freeware R (R Core Team 2012). Inference from the posterior distributions was run on the best model using a Markov chain Monte Carlo (MCMC) simulation, which allowed for calculation of accurate P values from the LMMs. Based on the initial results (‘Ultimate’ model, see below), observations were split by disturbance history and analyzed as for the full data set. Note that in the full model the only ‘proxy’ variable assessed was disturbance history (0,1). All other variables contained only proximate variables (for example, soil pH and temperature) as opposed to those that serve as a proxy for such direct measures (for example, elevation). Our intention was to identify patterns in the proximate variables that correlated with the potential for high net nitrification rates.

Given observed patterns in our putative controlling variables, we additionally investigated whether topographic position (transect and plot) within a watershed influences nitrification rates. As such, we ran LMMs for the two groups (Undisturbed vs. Disturbed) where watershed identity was a random effect and transect (high or low) and plot (riparian, mid-slope, and upslope) were fixed effects. Based on the resulting influence of labile C (see Results), we ran post hoc LMMs for the two groups (Undisturbed vs. Disturbed) using the same model structure. Additionally, we ran a t-test (for groups with unequal variance) to confirm the difference in labile C between watershed disturbance history (Undisturbed vs. Disturbed).

RESULTS

In regressing potential net nitrification against potential net mineralization, we observed a split in the data whereby those plots from Disturbed watersheds had a strong positive relationship between nitrification and N mineralization, whereas plots from Undisturbed watersheds had no relationship (Figure 1A). Overall, potential net nitrification was an order of magnitude higher (Table 1) in the Disturbed plots ($0.011 \pm 0.014 \text{ mg N g soil}^{-1} \text{ 28 day}^{-1}$; mean \pm SE) than in the Undisturbed ($0.0013 \pm 0.0030 \text{ mg N g soil}^{-1} \text{ 28 day}^{-1}$). In contrast, potential net N mineralization was approximately equivalent (Table 1) between Disturbed and Undisturbed watersheds (0.012 ± 0.013 and $0.011 \pm 0.016 \text{ mg N g soil}^{-1} \text{ 28 day}^{-1}$, mean \pm SE, respectively). Not surprisingly then, the ratio of net nitrification: net mineralization—a frequent expression of nitrifier activity (Hart and others 1994)—differed markedly (albeit not significantly) between the disturbance histories. Specifically, in the Disturbed watersheds the ratio was 0.69 ± 0.58 (mean \pm SE), with a median value of 0.88, and in the Undisturbed watersheds 0.16 ± 0.31 (mean \pm SE), with a median value of zero.

We next sought to identify the controls that best explained the different relationships between potential net nitrification and net mineralization in the Disturbed versus Undisturbed watersheds. All random effects (watershed and transect) were retained in the best model, revealing strong spatial associations in our data, highlighting the need to account for these dependencies with an LMM framework. After selecting fixed effects from univariate regression analyses, and testing for collinearity, six fixed effects were retained: soil moisture, soil temperature, net N mineralization, disturbance history (0 or 1), microbially available

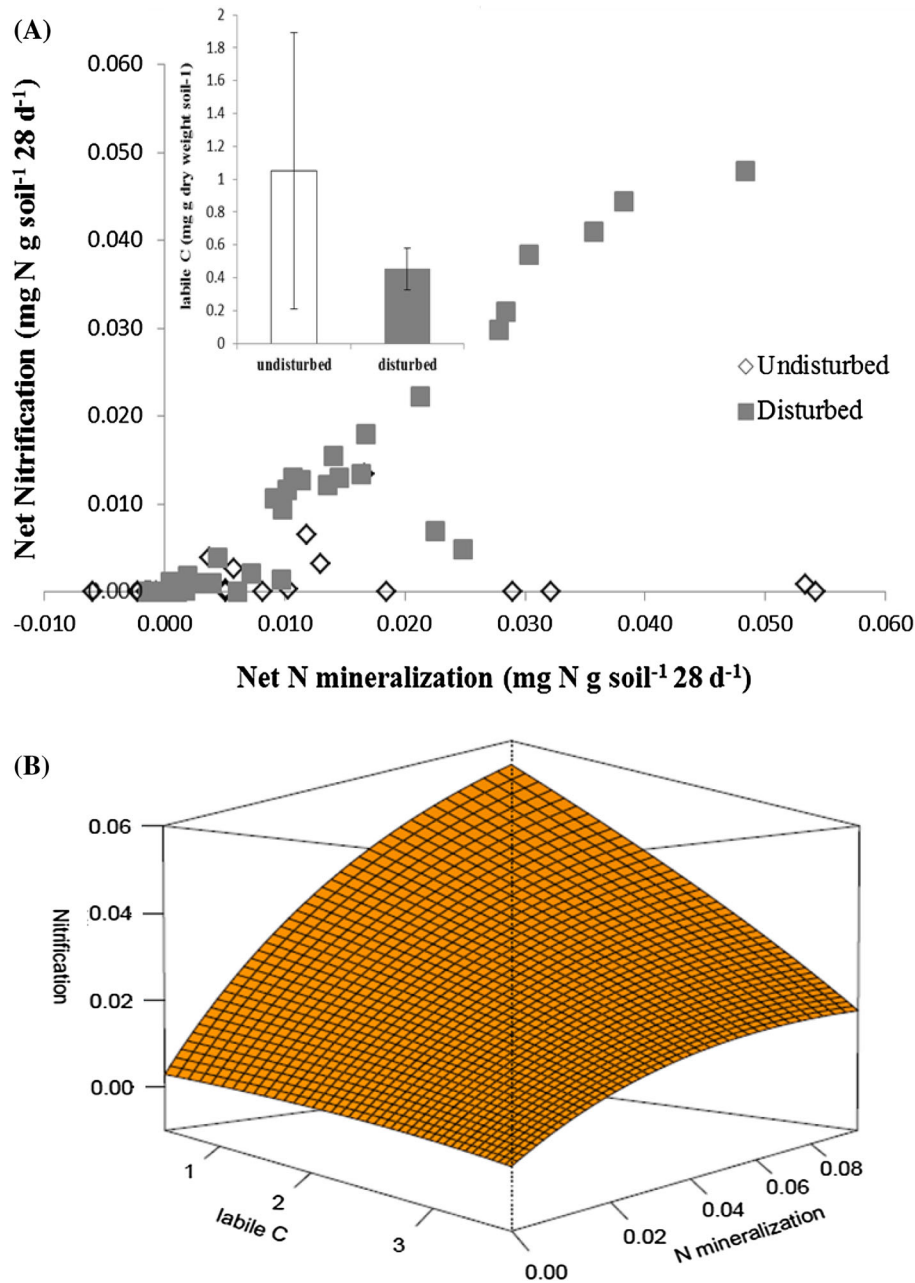


Fig. 1. The results from the full models (60 plots across the ten watersheds) demonstrate the influence on potential net nitrification rates from **(A)** watershed disturbance history and N mineralization, and **(B)** available C and N mineralization. **(A)** The watersheds, and associated plots, are identified as Undisturbed (no known treatment history since 1927) or Disturbed (various treatments—see Appendix 1 in Supplementary material). Plots within disturbed watersheds have a positive, linear relationship between net nitrification (mg N g soil⁻¹ 28 days⁻¹) and net N mineralization (mg N g soil⁻¹ 28 days⁻¹), whereas those in undisturbed watersheds appear to have no relationship. The amount of available C appears to drive the divergent patterns related to disturbance history, with disturbed watersheds having less available C (< 0.8 mg g soil⁻¹) than the undisturbed watersheds (*inset*). **(B)** Visual representation of the interaction between labile C (mg C g soil⁻¹) and net N mineralization (mg N g soil⁻¹ 28 days⁻¹) on net nitrification (mg N g soil⁻¹ 28 days⁻¹). When labile C is lowest, and net N mineralization highest, net nitrification is greatest. Note that the curve is seen from its convex surface, with the peak of the curve showing the highest rate of nitrification and N mineralization, and the lowest availability of labile C.

C, and total extractable inorganic N ($\text{NO}_3^- - \text{N} + \text{NH}_4^+ - \text{N}$). The best-fit (lowest ΔAIC) model for potential net nitrification included net N mineralization, disturbance history, and the interaction between the two, plus the two random effects. This model had an adjusted r^2 of 0.87 (Table 2, 'Ultimate Model'). The interaction between N mineralization and disturbance history was significant ($P < 0.001$), suggesting that the relationship between N mineralization and nitrification depended on past disturbance (as is depicted in Figure 1A).

Disturbance history is a proxy variable (that is, it does not act directly on nitrifiers) and so we ran models without it to explore which proximate variables accounted for the strong influence of disturbance history. Re-running with the same sub-set of fixed effects (but without disturbance history) revealed that the best-fit model again included not only N mineralization but also microbially available C and the interaction between the two (Table 2, 'Proximate Model'). This model had an adjusted r^2 of 0.75 and a significant net N mineralization by available C interaction

($P < 0.001$). The interaction arose because the potential net nitrification was highest when available C was lowest and net N mineralization was greatest, but when the available C was above about $0.8 \text{ mg C g soil}^{-1}$, increasing N mineralization had very little effect on nitrification (Figure 1B, Appendix 2A in Supplementary material). Notably, there was significantly ($P = 0.002$) less microbially available C in the Disturbed watershed plots, with values in these plots generally falling well below the apparent $0.8 \text{ mg C g soil}^{-1}$ threshold (Figure 1A inset), suggesting that the influence of disturbance history on potential net nitrification rates acts primarily through reductions in microbially available C.

Given the distinct patterning between the Undisturbed and Disturbed watersheds, we further explored the data after sorting by watershed disturbance history to evaluate potential driving variables within each disturbance treatment. The best-fit model for the Undisturbed watersheds had an adjusted r^2 of only 0.38 and included extractable NH_4^+ , total extractable inorganic N, their interac-

Table 2. Coefficients for Factors Explaining Variation in Potential Net Nitrification Rates in Four Distinct Models: Ultimate, Proximate, Undisturbed, and Disturbed

Variables	Coefficient	P value	r^2
<i>Model: ultimate</i>			
Intercept	0.0012 ± 0.0012	0.60	na
N mineralization	0.0096 ± 0.0056	0.93	0.64
disturbance history	-0.0025 ± 0.0026	0.11	0.66
N mineralization by disturbance history	1.024 ± 1.032	0.0001	0.86
<i>Model: proximate</i>			
Intercept	0.0004 ± 0.0004	0.91	na
N mineralization	1.018 ± 0.99	0.0001	0.64
labile C	-0.0017 ± 0.0012	0.72	0.66
N mineralization by labile C	-0.32 ± 0.31	0.001	0.66
<i>Model: undisturbed</i>			
Intercept	-0.0020 ± 0.0019	0.54	na
NH ₄	0.0004 ± 0.0005	0.062	0.074
total N	0.0001 ± 0.0001	0.20	0.047
N mineralization	0.081 ± 0.067	0.41	0.0073
labile C	-0.0017 ± 0.0017	0.17	0.41
NH ₄ by total N	-1.017e-05 ± 0.0000	0.061	0.024
<i>Model: disturbed</i>			
Intercept	0.0017 ± 0.0015	0.73	na
N mineralization	0.26 ± 0.25	0.23	0.88
soil moisture	-0.0048 ± 0.0050	0.68	0.75
N mineralization by soil moisture	1.47 ± 1.52	0.0012	0.94

Coefficients, P , and r^2 values for the minimally adequate linear mixed models explaining soil nitrification potential for both full models (Ultimate and Proximate), the Undisturbed watersheds, and the Disturbed watersheds. Coefficients, their SD, and P values are estimated using an MCMC sampling approach. The r^2 values are also shown for the univariate relationships, but include the model's random effects (watershed and transect). Statistically significant ($P < 0.05$) coefficients are shown in bold. The Ultimate model demonstrates that an interaction between net N mineralization and disturbance history best describes variation in net nitrification across the landscape. When disturbance history is removed (Proximate model), an interaction between net N mineralization and labile C best describes variation in net nitrification. The data were then split by disturbance history (Undisturbed and Disturbed models) to determine what best describes variation in net nitrification when looking at different spatial scales.

tion, N mineralization, available C, and both random effects (Table 2). None of the fixed effects were statistically significant and only two were marginally ($P < 0.1$) significant, including extractable NH_4^+ and its interaction with total extractable inorganic N. Notably, the coefficient for extractable NH_4^+ was positive but the interaction's coefficient was negative. This suggests that the positive effect of NH_4^+ is reduced at higher values of total soil inorganic N, but it is unclear as to why this should be so. Further, the univariate relationships for these variables explained little variation in potential net nitrification rates (Table 2). Notably, albeit not statistically significant, available C was the only variable to explain a substantial proportion of variance (41%) in these data (Table 2), and, as in the full data set, net nitrification was observed only in those plots where there was $< 0.8 \text{ mg C g soil}^{-1}$ (Appendix 2A in Supplementary material).

In contrast, the best-fit model for the Disturbed watershed data had a high adjusted r^2 value (0.92). This model included N mineralization, soil moisture, and the interaction between the two effects (Table 2). The interaction was significant ($P < 0.001$), driven by a decline in potential net nitrification as soil moisture increased at low rates of N mineralization. However, the model predicted that the highest potential net nitrification rates occurred when soil moisture and N mineralization were greatest (Table 2; Figure 2). Available C values in the Disturbed watershed plots were always less

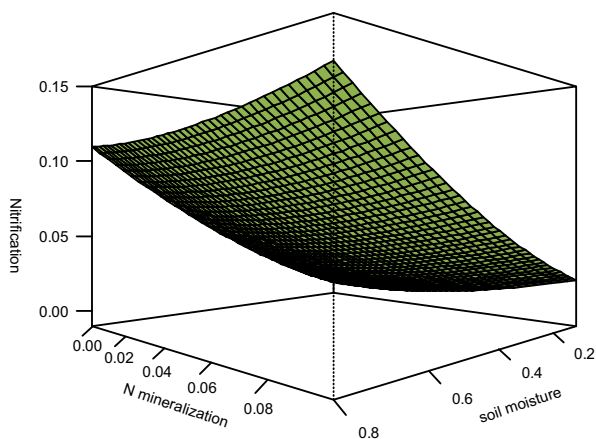


Fig. 2. The relationship between net N mineralization ($\text{mg N g soil}^{-1} 28 \text{ days}^{-1}$) and soil moisture ($\text{g H}_2\text{O g soil}^{-1}$) on potential net nitrification rates ($\text{mg N g soil}^{-1} 28 \text{ days}^{-1}$) in the disturbed watersheds. Note that the curve is seen from its convex surface, with the peak of the curve showing the highest rate of nitrification when N mineralization and moisture are also high, and the lowest point of the curve indicating the lowest nitrification, mineralization, and moisture.

than $0.8 \text{ mg C g soil}^{-1}$ (Appendix 2A in Supplementary material), apparently minimizing the control exerted by this variable, which consequently was not retained in the best model for the Disturbed watersheds.

Whereas potential net nitrification varied according to watershed disturbance history, rates were not influenced by landscape position within watersheds (Appendix 3A in Supplementary material) for either watershed group (Undisturbed vs. Disturbed). However, we examined the influence of potential landscape variation on labile C (Appendix 3B in Supplementary material) due to its influence on potential net nitrification rates. In contrast to net nitrification, variation in labile C did vary by landscape position (high-elevation transect versus low) for the Undisturbed watersheds where labile C was almost twice as large in the upper elevation transect (mean \pm SE: 1.39 ± 0.31 vs. $0.71 \pm 0.08 \text{ mg C g dry weight soil}^{-1}$).

DISCUSSION

Forest disturbances such as clear-cutting may accelerate net N transformations in the short-term (Murty and others 2002). The legacy effects of these disturbances on soil N transformations are less well understood, but impacts may extend to the long term depending on the site recovery process (Knoepp and others 2014). Our data lend support for our first hypothesis (Hyp. 1) that past disturbance alters soil C availability, apparently shifting the heterotrophic microbial biomass from N- to C-limited, and facilitating higher potential net nitrification rates in stands with historic disturbance. Specifically, where microbially available C is low, heterotrophic N demand is presumably also low, and so mineralized N (NH_4^+) is more available to the autotrophic nitrifiers (Hart and others 1994; Strauss and others 2000; Booth and others 2005; Silva and others 2005). Microbially available C aligned with watershed disturbance history across all scales of investigation. As a consequence, the tight correlation between potential net nitrification and potential net N mineralization observed in the Disturbed watersheds is not observed in the Undisturbed (for > 80 years) watersheds, presumably because the more abundant labile soil C generates a high heterotrophic microbial demand for N. Our findings, therefore, suggest that disturbance history at the landscape scale may act as an ultimate control over the coupling between C and N cycling in soils. This coupling is dictated, potentially, by the ability of microbial heterotrophs to outcompete nitrifiers for NH_4^+ at the micro-scale.

The role of spatial scale in determining controls on potential net nitrification rates was apparent within our study landscape. Specifically, the best explanatory variables for net nitrification differed with the spatial scale of our assessment, either across the whole landscape or restricted only to watershed disturbance history (Table 2). The pronounced scale and context dependence of those variables identified as the best possible controls on net nitrification may help to resolve why net nitrification is linked to many different variables across studies, including pH, N mineralization, and microbial biomass C (Table 1). Our data suggest that C availability to soil heterotrophs is a higher order indirect control on net nitrification rates, and when relaxed (<0.8 mg C g soil⁻¹) other variables (for example, soil moisture) then explain spatial patterns of nitrification.

The influence of scale on the controls of potential net nitrification rates is best highlighted by the strong relationship between net nitrification and net N mineralization in the Disturbed but not Undisturbed watersheds (Figure 1). When potential net nitrification and net N mineralization rates are coupled and available C, and hence presumably heterotrophic NH₄⁺ demands, are low (Disturbed watersheds), net nitrification is driven by an interaction between N mineralization and soil moisture. Ammonium, the product of N mineralization, is the substrate of nitrification whereas soil moisture affects both the activity of the microbial community (Fierer and Schimel 2002) and the movement of ions (Parker and Schimel 2011). For example, soil bacteria and soil solutions are connected through the porous network of the soil profile (Dechesne and others 2007). With adequate soil water content nitrifiers can move towards concentrations of heterotrophs and NH₄⁺, and the highly soluble and mobile NO₂⁻ ion can travel through water-filled pore spaces to prolific NO₂⁻ oxidizers (Stark and Firestone 1995; Grundmann and others 2001). Interestingly, plot (riparian to upslope) was not a significant control over labile C or net nitrification in the Disturbed watersheds where we might have expected soil moisture to vary spatially from the stream edge through to the upslope, and thus, drive plot-level differences. Variation within the Disturbed watersheds (transect) also did not influence nitrification rates or labile C, indicating the possibility of comprehensive land disturbance within a watershed.

Within Undisturbed watersheds four explanatory variables were retained in the best model, but little variance was explained (Table 2). It appears that the primary controls on nitrification in our Undisturbed watersheds remain to be elucidated, but we do highlight that potential net nitrification was

only observed at low availabilities of labile C (Appendix 2 in Supplementary material). This observation again supports the idea that heterotrophic C limitation is a higher order control on net nitrification rates. Notably, availability in labile C did vary between upper and lower regions of the Undisturbed watersheds (that is, between transects). More specifically, the upper transects of our two high-elevation Undisturbed watersheds were associated with the highest values of labile soil C availability that we measured. This within-watershed variation which may imply patchy land clearing events dating to before disturbance history was well recorded at Coweeta; whereby the two upper elevation areas represent the only primary forest within all Undisturbed watersheds having likely been too steep and too high for early land clearing (Flinn and others 2005). Consistent with these observations and our initial literature review identifying a range of potential influences on nitrification rates (Table 1), a broad suite of variables emerge as controls over net nitrification in these watersheds, or when labile C is abundant. These results imply that controls over nitrification depend on the spatial extent of analysis. Therefore, different controls on potential net nitrification rates reported in previous studies may be a product of the spatial scale and associated underlying contexts, including disturbance history.

Fraterrigo and others (2005) worked in watersheds within our same region, but found coupled potential net N mineralization and net nitrification rates in both historically logged and reference sites. The apparent discordance between their results and ours—where we see Undisturbed watersheds associated with uncoupling of the N processes—is resolved if we consider the key role that labile C availability appears to play in coupling net N mineralization with net nitrification (Figure 1; Appendix 2 in Supplementary material, Table 2). In contrast to our study area, the total soil C content for both undisturbed reference and historically logged sites in Fraterrigo and others (2005), collected to a depth of 15 cm, was just below 4 kg C m⁻², and so only about 70% of the mean value for our Disturbed watersheds (when adjusted to the same depth). These low soil C values in both treatments suggest that C availability was low enough in the Fraterrigo and others (2005) study so as not to limit nitrifiers indirectly by driving heterotroph NH₄⁺ demand, matching with what we observed in our Disturbed watersheds. In contrast, our Undisturbed watersheds likely had much higher labile C availability than the reference site in Fraterrigo and others (2005). Specifically, in our watersheds, total soil C showed significant

collinearity with microbially available C ($r^2 = 0.85$, Appendix 2 in Supplementary material), suggesting that it and microbial biomass C (also collinear, Appendix 2 in Supplementary material) were also suitable indicators of C supply to the heterotrophic microbial biomass. If the relationship between total soil C and microbially available C holds between studies, we may expect that only in our Undisturbed sites was labile C availability high enough to promote heterotrophic N demand (Clarholm 1985; Qian and others 1997) to an extent that subsequently reduced NH_4^+ availability for autotrophic nitrifiers (Verhagen and Laanbroek 1991; Verhagen and others 1992; Lovett and Rueth 1999; Strauss and Lamberti 2000; Bernhardt and others 2002). The possibility does exist that other non-measured variables are driving variation in nitrification both locally and across the landscape. However, our work measuring net rates and 20 additional experimental variables suggests that the coupling between N mineralization and nitrification likely depends on the local context in a region—including details of historical disturbance and patterns of recovery—and specifically the impact on C availability to the heterotrophic soil microbial biomass. Our regional comparison (Fraterrigo and others 2005) further suggests a need to explicitly test for the influence of landscape disturbance, both in recent history and over centuries, as an ultimate control over coupled C and N dynamics.

We resolved potential net nitrification rates through lab assays and reasoned that these potentials would be linked to field variables that influenced nitrifier activity. Supporting this assertion, the mean ratio of net nitrification: net mineralization—which is a frequent expression of nitrifier activity (Hart and others 1994)—was four-times lower in the Undisturbed than the Disturbed watersheds. Further, lab potential assays are considered a useful index for assessing available N (Schimel and Bennett 2004), even with the potential to overestimate rates (Knoepp and Swank 1995). Nevertheless, there are limitations to assessments using potential net rates, which may also lead to alternate explanations for our results. In the Undisturbed watersheds where soil C is relatively high, active soil microbial biomass is also high (Appendix 2B in Supplementary material) and, thus, heterotrophic N demand. By measuring net rates we were, therefore, unable to determine whether NO_3^- , the product of nitrification, is immediately assimilated by the heterotrophs (Hart and others 1994; Stark and Hart 1997), or whether the heterotrophs instead assimilate NH_4^+ before nitrification can occur. In contrast, gross nitrifica-

tion measurements may better estimate the fate of these N products (NH_4^+ and NO_3^-) relative to heterotrophic N demand. Therefore, measurements of gross nitrification and N mineralization rates in the field (Hart and others 1994; Schimel and Bennett 2004) are required to substantiate our hypothesis that heterotroph–autotroph competition for NH_4^+ —indirectly determined by C availability to the heterotrophic biomass—is a higher order control on the activities of nitrifiers. Certainly, heterotrophic and autotrophic microbes have different growth and nutrient-capture strategies (Davey and O’Toole 2000; Nunan and others 2003). And even within the nitrifiers, it is thought that ammonia-oxidizing Archaea (AOA) can out-compete ammonia-oxidizing bacteria (AOB) for NH_4^+ , and may even outcompete heterotrophs at low ammonium concentrations (Prosser and Nicol 2012). Field research examining both AOA and AOB as well as other competitors for NH_4^+ , such as roots and mycorrhizae (Hart and others 1994; Bonkowski 2004), is needed to determine the critical NH_4^+ supply rates required by nitrifiers for high activity (Booth and others 2005). This critical supply rate may be dependent upon soil C availability and, therefore, the stoichiometric demands of actively growing heterotrophic bacteria and fungi (Finzi and others 2011).

Our study suggests that variation in labile C availability, which appears to be tied to historic watershed disturbance at the landscape scale, shapes contemporary biogeochemical processes. As such, in disturbed watersheds there is a tight coupling between potential net nitrification and net N mineralization, but in undisturbed watersheds the coupling appears to be between heterotrophic microbial demand for C and N. Although these nutrient transformations and microbial interactions operate at micro-scales, we demonstrate their potential influence over the coupling of biogeochemical processes at the landscape-level.

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REFERENCES

- Allen SE. 1989. Chemical analysis of ecological materials. Oxford: Blackwell Scientific.

- Bernhardt ES, Hall JRO, Likens GE. 2002. Whole-system estimates of nitrification and nitrate uptake in streams of the Hubbard Brook Experimental Forest. *Ecosystems* 5:419–30.
- Bernhardt ES, Likens GE. 2002. Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. *Ecology* 83:1689–700.
- Bonkowski M. 2004. Protozoa and plant growth: the microbial loop in soil revisited. *New Phytologist* 162:617–31.
- Booth MS, Stark JM, Hart SC. 2006. Soil-mixing effects on inorganic nitrogen production and consumption in forest and shrubland soils. *Plant Soil* 289:5–15.
- Booth MS, Stark JM, Rastetter E. 2005. Controls on nitrogen cycling in terrestrial ecosystems: A synthetic analysis of literature data. *Ecol Monogr* 75:139–57.
- Bormann FH, Likens GE. 1979. Catastrophic disturbance and the steady-state in northern hardwood forests. *Am Scientist* 67:660–9.
- Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD. 2008a. Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol Lett* 11:1316–27.
- Bradford MA, Fierer N, Reynolds JF. 2008b. Soil carbon stocks in experimental mesocosms are dependent on the rate of labile carbon, nitrogen and phosphorus inputs to soils. *Funct Ecol* 22:964–74.
- Bradford MA, Warren RJII, Baldrian P, Crowther TW, Maynard DS, Oldfield EE, Wieder WR, Wood SA, King JR. 2014. Climate fails to predict wood decomposition at regional scales. *Nat Clim Change* 4:625–30.
- Clarholm M. 1985. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol Biochem* 17:181–7.
- Cottingham KL, Lennon JT, Brown BL. 2005. Knowing when to draw the line: designing more informative ecological experiments. *Front Ecol Environ* 3:145–52.
- Davey ME, O'Toole GA. 2000. Microbial biofilms: from ecology to molecular genetics. *Microbiol Mol Biol Rev* 64:847–67.
- Dechesne A, Pallud C, Grundmann GL. 2007. Spatial distribution of bacteria at the microscale in soil. In: Franklin RB, Mills AL, Eds. *The spatial distribution of microbes in the environment*. Berlin: Springer. p 87–107.
- Dijkstra P, LaViolette CM, Coyle JS, Doucett RR, Schwartz E, Hart SC, Hungate BA. 2008. 15 N enrichment as an integrator of the effects of C and N on microbial metabolism and ecosystem function. *Ecol Lett* 11:389–97.
- Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML, Moore DJP, Oren R, Palmroth S, Phillips RP, Pippen JS, Pritchard SG, Treseder KK, Schlesinger WH, DeLucia EH, Finzi AC. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO₂. *Ecol Lett* 14:349–57.
- Fierer N, Craine JM, McLauchlan K, Schimel JP. 2005. Litter quality and the temperature sensitivity of decomposition. *Ecology* 86:320–6.
- Fierer N, Schimel JP. 2002. Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soil Biol Biochem* 34:777–87.
- Fierer N, Schimel JP. 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Sc Soc Am J* 67:798–805.
- Finzi AC, Austin AT, Cleland EE, Frey SD, Houlton BZ, Wallenstein MD. 2011. Responses and feedbacks of coupled biogeochemical cycles to climate change: examples from terrestrial ecosystems. *Front Ecol Environ* 9:61–7.
- Flinn KM, Vellend M, Marks PL. 2005. Environmental causes and consequences of forest clearance and agricultural abandonment in central New York, USA. *J Biogeogr* 32:439–52.
- Fraterrigo JM, Turner MG, Pearson SM, Dixon P. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern appalachian forests. *Ecol Monogr* 75:215–30.
- Goodale CL, Aber JD. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecol Appl* 11:253–67.
- 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* 65:1709–16.
- Guo LB, Gifford RM. 2002. Soil carbon stocks and land use change: a meta analysis. *Global Change Biol* 8:345–60.
- Hart SC, Nason GE, Myrold DD, Perry DA. 1994. Dynamics of gross nitrogen transformations in an old-growth forest—the carbon connection. *Ecology* 75:880–91.
- Kaye JP, Hart SC. 1997. Competition for nitrogen between plants and soil microorganisms. *Trends Ecol Evol* 12:139–43.
- Knoepp JD, Coleman DC, Crossley DA, Clark JS. 2000. Biological indices of soil quality: an ecosystem case study of their use. *For Ecol Manag* 138:357–68.
- Knoepp JD, Swank WT. 1995. Comparison of available soil nitrogen assays in control and burned forested sites. *Soil Sci Soc Am J* 59:1750–4.
- Knoepp JD, Swank WT. 1997. Forest management effects on surface soil carbon and nitrogen. *Soil Sci Soc Am J* 61:928–35.
- Knoepp JD, Swank WT, Haines BL. 2014. Long- and short-term changes in nutrient availability following commercial sawlog harvest via cable logging. In: Swank WT, Webster JR, Eds. *Long-term response of a forest watershed ecosystem: clearcutting in the southern Appalachians*. London: Oxford University Press.
- Kramer TD, Warren RJ, Tang YY, Bradford MA. 2012. Grass invasions across a regional gradient are associated with declines in belowground carbon pools. *Ecosystems* 15:1271–82.
- Lavoie M, Bradley RL. 2003. Short-term increases in relative nitrification rates due to trenching in forest floor and mineral soil horizons of different forest types. *Plant Soil* 252:367–84.
- Liao CZ, Luo YQ, Fang CM, Li B. 2010. Ecosystem carbon stock influenced by plantation practice: implications for planting forests as a measure of climate change mitigation. *Plos One* 5(5):e10867.
- Lovett GM, Rueth H. 1999. Soil nitrogen transformations in beech and maple stands along a nitrogen deposition gradient. *Ecol Appl* 9:1330–44.
- 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* 461:976–9.
- McGill WB, Cole CV. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* 26:267–86.
- McGinty DT. 1976. Comparative root and soil dynamics on a white pine watershed and in the hardwood forest in the Coweeta basin. Athens, GA: Institute of Ecology, University of Georgia. p 110.

- Murty D, Kirschbaum MUF, McMurtrie RE, McGilvray H. 2002. Does conversion of forest to agricultural land change soil carbon and nitrogen? a review of the literature. *Global Change Biol* 8:105–23.
- 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* 419:915–17.
- Nuckolls A, Wurzbarger N, Ford C, Hendrick R, Vose J, Kloeppel B. 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: Impacts on the carbon cycle of southern Appalachian forests. *Ecosystems* 12:179–90.
- Nunan N, Wu KJ, Young IM, Crawford JW, Ritz K. 2003. Spatial distribution of bacterial communities and their relationships with the micro-architecture of soil. *Fems Microbiol Ecol* 44:203–15.
- 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* 48:185–92.
- Perala DA, Alban DH. 1982. Rates of forest floor decomposition and nutrient turnover in aspen, pine and spruce stands on two different soils. Res. Pap. NC-227. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experimental Station, 5.
- Phillips RP, Finzi AC, Bernhardt ES. 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO₂ fumigation. *Ecol Lett* 14:187–94.
- Prosser JI, Nicol GW. 2012. Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. *Trends Microbiol* 20:523–31.
- Qian JH, Doran JW, Walters DT. 1997. Maize plant contributions to root zone available carbon and microbial transformations of nitrogen. *Soil Biol Biochem* 29:1451–62.
- R Development Core Team 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robertson GP, Wedin D, Groffman PM, Blair JM, Holland EA, Nadelhoffer KJ, Harris D. 1999. Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil respiration potentials. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P, Eds. *Standard soil methods for long-term ecological research*. New York: Oxford University Press. p 258–71.
- Schimel JP, Bennett J. 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85:591–602.
- Schimel JP, Weintraub MN. 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biol Biochem* 35:549–563.
- Schlesinger W. 1986. Changes in soil carbon storage and associated properties with disturbance and recovery. In: Trabalka J, Reichle D, Eds. *The changing carbon cycle*. New York: Springer. p 194–220.
- Schlesinger WH, Cole JJ, Finzi AC, Holland EA. 2011. Introduction to coupled biogeochemical cycles. *Front Ecol Environ* 9:5–8.
- 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* 71:259–70.
- Stark JM, Firestone MK. 1995. Mechanisms for soil-moisture effects on activity of nitrifying bacteria. *Appl Environ Microbiol* 61:218–21.
- Stark JM, Hart SC. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* 385:61–4.
- Strauss EA, Lamberti AG. 2000. Regulation of nitrification in aquatic sediments by organic carbon. Waco: American Society of Limnology and Oceanography.
- Swank WT, Knoepp JD, Vose JM, Laseter S, Webster JR. 2014. Response and recovery of water yield and timing, stream sediment, abiotic parameters, and stream chemistry following logging. In: Swank WT, Webster JR, Eds. *Long-term response of a forest watershed ecosystem: clearcutting in the southern Appalachians*. London: Oxford University Press.
- van der Heijden MGA, Bardgett RD, van Straalen NM. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol Lett* 11:296–310.
- Verhagen FJ, Duyts H, Laanbroek HJ. 1992. Competition for ammonium between nitrifying and heterotrophic bacteria in continuously percolated soil columns. *Appl Environ Microbiol* 58:3303–11.
- Verhagen FJ, Laanbroek HJ. 1991. Competition for ammonium between nitrifying and heterotrophic bacteria in dual energy-limited chemostats. *Appl Environ Microbiol* 57:3255–63.
- 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* 43(7):W07447.
- Warren RJ, Bradford MA. 2011. The shape of things to come: woodland herb niche contraction begins during recruitment in mesic forest microhabitat. *Proc R Soc B* 278:1390–8.
- West AW, Sparling GP. 1986. Modifications to the substrate-induced respiration method to permit measurement of microbial biomass in soils of differing water contents. *J Microbiol Methods* 5:177–89.