

# Replacement of wildfire by whole-tree harvesting increases nitrification and nitrate movement in jack pine forest soils



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## ABSTRACT

Forest types that were once naturally maintained by stand-replacing wildfires are typically managed with clearcut harvesting; however, we know relatively little about how well clearcutting mimics the effects of stand-replacing wildfire on the availability and cycling of nitrogen (N) in forest soils. We compared net N mineralization, nitrification and  $\text{NO}_3^-$  movement in soils from young (2–9 y) jack pine (*Pinus banksiana*) stands that had been regenerated by either stand-replacing wildfire or clearcut harvesting. We located four pairs of burned and harvested stands that were otherwise similar in age, soil type and geographic location. Net N mineralization, measured both in situ and in the laboratory, was nearly 2 times higher in young stands of clearcut origin compared to stands of wildfire origin. Differences between disturbance types were much more pronounced for net nitrification, which was more than 20 times greater, on average, in clearcut-origin sites. Burned sites rarely exhibited any net nitrification in field incubations, and at nearly 2/3 of the sampling times burned sites exhibited net immobilization of  $\text{NO}_3^-$ . This lack of nitrification occurred despite the fact that we always observed net N mineralization across all of our in-situ incubations in wildfire-origin stands. Finally, we observed nearly four times greater  $\text{NO}_3^-$  movement through the soil profile in clearcut stands, as evidenced by capture on ion-exchange resins at a depth of 25 cm. Together, these results clearly indicate that replacement of wildfire disturbance by clearcut harvesting promotes nitrification and  $\text{NO}_3^-$  movement in jack pine ecosystems of northern Lower Michigan. The exact mechanism underlying this response in our sites remains uncertain; however, it appears that some factor that restricts net nitrification in young stands of wildfire origin is not present in clearcut-origin stands. Our finding of increased nitrification and  $\text{NO}_3^-$  movement in the years following clearcutting could lead to increased losses of N and base cations, and could also favor plant species with greater preference for  $\text{NO}_3^-$  as a N source.

## 1. Introduction

Current thinking in forest management emphasizes emulating the intensity, timing and effects of natural disturbance regimes as a framework for sustaining biodiversity and ecosystem services (Hunter, 1993; Lindenmayer et al., 2006; North and Keeton, 2008). Therefore, an understanding of the effects of natural disturbance on ecosystem structure, composition and function can provide a useful baseline against which to compare the effects of forest management actions (e.g. harvests) (Lindenmayer et al., 2006). Forest types that were once naturally maintained by stand-replacing wildfires are typically managed with clearcut harvesting (McRae et al., 2001; Bergeron, 2004), which can be used to mimic even-aged structure associated with this natural disturbance regime. However, we know relatively little about how well clearcutting mimics the effects of stand-replacing wildfire on the availability and cycling of nitrogen (N) in forest soils (but see

Giardina and Rhoades, 2001; Simard et al., 2001). If clearcut harvesting changes the availability or predominant form of N compared to wildfire, this, in turn, could have impacts on forest productivity and community composition (Kronzucker et al., 1997; Boudsoq et al., 2012; Britto and Kronzucker, 2013) or hydrologic losses of N and other nutrient elements (Van Miegroet and Cole, 1984; Harrison et al., 1996; Jussy et al., 2000; Lundin and Nilsson, 2014).

Stand replacing disturbances have long been known to have profound impacts on the availability, cycling and loss of N from forest ecosystems (e.g. Borman and Likens, 1979; Vitousek et al., 1979). In general, some combination of decreased plant uptake and improved temperature and moisture conditions for decomposition typically results in increased N availability following disturbance. Perhaps of greater importance than overall N availability is the predominant form of N cycled,  $\text{NH}_4^+$  vs  $\text{NO}_3^-$ , following disturbance. This is because production of  $\text{NO}_3^-$  in soil (i.e. nitrification) represents a key

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biogeochemical process with several important ecosystem- and community-level consequences. The nitrification process itself generates acidity and also can produce gaseous emissions of NO and N<sub>2</sub>O (Firestone and Davidson, 1989; Zhang et al., 2015). Once NO<sub>3</sub><sup>-</sup> is generated in soil it can form the substrate for denitrifying bacteria resulting in emissions of N<sub>2</sub>O (a potent greenhouse gas) and N<sub>2</sub> to the atmosphere, even in upland forest soils (Morse et al., 2015). Alternatively, due to its high mobility in soil, NO<sub>3</sub><sup>-</sup> is easily leached, potentially contributing to eutrophication of adjacent aquatic systems and accelerated leaching of base cations (Van Mieghroet and Cole, 1984; Harrison et al., 1996; Jussy et al., 2000; Lundin and Nilsson, 2014). Finally, different plant species often demonstrate strong preferences for NH<sub>4</sub><sup>+</sup> vs NO<sub>3</sub><sup>-</sup>, such that differences in N-form availability following disturbance could have important influences on plant performance and community dynamics (Kronzucker et al., 1997; Boudsocq et al., 2012; Britto and Kronzucker, 2013).

Pioneering work from the 1980s documented marked differences in the response of nitrification to disturbance across different types of forest ecosystems (Robertson, 1982, Vitousek et al., 1982). In a previous study from our lab group (Leduc and Rothstein, 2007) we found that different types of stand-replacing disturbance resulted in very different rates of nitrification by soil samples from a single ecosystem type. In that study, we found that laboratory rates of net nitrification in soils from young jack pine (*Pinus banksiana*) stands of clearcut origin were nearly double those from stands of wildfire origin (149 vs 84 μg NO<sub>3</sub><sup>-</sup>-N g<sup>-1</sup>). Although this finding was intriguing, we do not know if these results from laboratory incubations reflect differences in in-situ rates of nitrification between harvesting and wildfire. We are aware of only two other studies which have directly compared the effects of harvesting vs fire on nitrification, and neither observed a similar pattern of greater nitrification following harvesting. Giardina and Rhoades (2001) found more extractable N in recently clear-cut lodgepole pine (*P. contorta*) stands compared to burned stands, but no significant difference in rates of nitrification. Similarly, Simard et al. (2001) found greater rates of net N mineralization in harvested sites compared to burned sites in boreal forests of Quebec, Canada, but negligible rates of nitrification after either disturbance type. Many studies over the years have focused solely on the effects of fire on soil N dynamics, and these overwhelmingly demonstrate increases in soil NO<sub>3</sub><sup>-</sup> pools in recently burned sites compared to undisturbed controls (see Wan et al., 2001 for a review and meta-analysis). Several studies have focused specifically on the role of charcoal produced by wildfire and found strong evidence that it can stimulate rates of nitrification in both Scandinavian boreal forests (Zackrisson et al., 1996) and montane conifer forests of western North America (DeLuca et al., 2006; Ball et al., 2010). On the other hand, a recent meta-analysis of <sup>15</sup>N pool-dilution studies concluded that wildfires tend to reduce gross production of NO<sub>3</sub><sup>-</sup> within 6 months following burning, with variable effects over longer time scales (Wang et al., 2014).

We undertook this study to evaluate if the harvest-induced increases in nitrification rates observed in the laboratory by Leduc and Rothstein (2007) are actually occurring in situ, and if they result in greater NO<sub>3</sub><sup>-</sup> movement through soils following harvesting compared to following wildfire. We hypothesized that in-situ net nitrification would be greater in young stands of clearcut origin compared to young stands of wildfire origin. We further hypothesized that NO<sub>3</sub><sup>-</sup> movement through the soil profile would be greater in clearcut-origin stands compared to wildfire-origin stands.

## 2. Materials and methods

We worked in the same Highplains region of northern Lower Michigan as Leduc and Rothstein (2007), on public-ownership jack pine forests occurring on high-energy outwash landforms with sandy, poorly developed soils (Albert et al., 1995). Jack pine is currently the dominant tree species in this environment as it was prior to European settlement of the region (Comer et al., 1995). Droughty soils combined with highly flammable vegetation resulted in a pre-settlement return interval for stand-replacing fires of ca. 60 y (Cleland et al., 2004). Large wildfires still occur occasionally, but the dominant disturbance regime is now clear-cut harvesting followed by planting of jack pine on a 50-y rotation (MDNR, 2014).

In order to set up our comparative study, we first identified sites where crown fires had burned through large (> 200 ha) areas of jack pine on USDA Forest Service (USDAFS) or Michigan Department of Natural Resources (MDNR) land. These four sites were the Hughes' Lake (HU) fire which burned ca. 2500 hectares in 2006; the Meridian Boundary (ME) fire which burned ca. 3500 hectares in 2010; the Howe's Lake (HO) fire which burned 330 hectares in 2011; and the Little Mack Lake (ML) fire which burned over 600 hectares in 2012. Because the USDAFS and MDNR together harvest and plant over 1500 ha of jack pine each year to provide breeding habitat for the endangered Kirtland's warbler (*Setophaga kirtlandii*), we were able to readily locate nearby sites that had been clearcut within 1 year of each of these wildfires. We used stand inventory data, soil maps and field scouting to identify sampling areas within each disturbance that were as similar as possible in terms of preceding stand conditions, soil properties and topography (Table 1). Paired wildfire and clearcut sites were 1.6 (Hughes' Lake), 3.6 (Meridian Boundary), 1.9 (Howe's Lake) and 2.8 (Little Mack Lake) km apart.

On May 6, 2015 (HU, ME, ML) and May 19, 2015 (HO) we located three random sampling points ca. 30 meters apart along a transect through the middle of each study area, at least 50 meters from any stand boundary. We visited these points again on June 25, August 26 and October 25, 2015. This sampling scheme allowed us to measure in-situ N mineralization, nitrification and NO<sub>3</sub><sup>-</sup> movement over three periods during the 2015 growing season: spring and early summer (May-June), late summer (July-August), and autumn (September-

**Table 1**  
Treatment, stand age, location and soil information for all study sites.

Fire name and treatment	Age in 2015	Lat. (N)	Long. (W)	Soil series	Soil classification
<i>Hughes' Lake (HU)</i>					
Wildfire	9	44°32'15"	84°15'04"	Grayling Sand	Typic Udipsamment
Clearcut	9	44°33'05"	84°15'17"	Grayling Sand	Typic Udipsamment
<i>Meridian (ME)</i>					
Wildfire	5	44°32'19"	84°26'11"	Grayling Sand	Typic Udipsamment
Clearcut	4	44°32'43"	84°23'30"	Grayling Sand	Typic Udipsamment
<i>Howe's Lake (HO)</i>					
Wildfire	4	44°41'37"	84°49'16"	Croswell Sand	Oxyaquic Haplorthod
Clearcut	4	44°41'03"	84°50'22"	Croswell Sand	Oxyaquic Haplorthod
<i>Little Mack Lake (ML)</i>					
Wildfire	3	44°35'22"	84°05'34"	Graycalm Sand	Lamellic Udipsamment
Clearcut	2	44°35'37"	84°03'32"	Grayling Sand	Typic Udipsamment

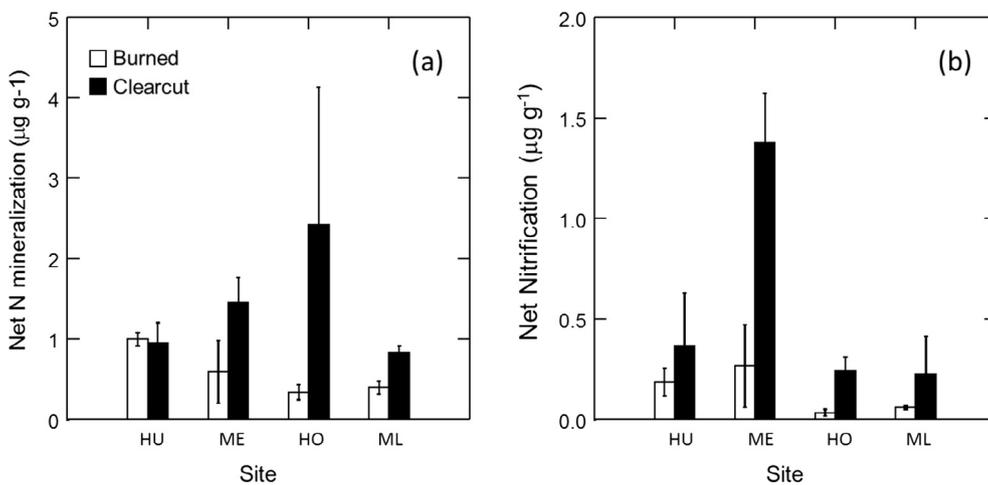


Fig. 1. Mean ( $\pm 1$  SE) rates of net N mineralization (a) and net nitrification (b) from 28-d laboratory incubations of soils from burned vs. clearcut origin stands.

October). We measured N mineralization and nitrification using the buried bag method (Eno, 1960).

On each sampling date, at each point, we collected two adjacent soil cores that were 2.5 cm in diameter and 10 cm deep. One core (initial) was returned to the laboratory on ice, and the second core (final) was placed in a polyethylene bag, reburied in the hole, and incubated in the field until the next sampling date. Upon returning to the laboratory, cores were passed through a 2-mm sieve, picked free of roots, homogenized and a 20-g subsample was extracted with 70 mL of 2 M KCl. Filtered KCl extracts were analyzed colorimetrically for  $\text{NH}_4^+$  using a salicylate-cyanurate assay described by Sinsabaugh et al. (2000) and for  $\text{NO}_3^-$  using a sulfanilamide and N-(1-naphthyl)ethylenediamine dihydrochloride assay following vanadium reduction as described by Doane and Horwath (2003). In cases where  $\text{NO}_3^-$  concentrations in KCl extracts were below the detection limit of our method (ca.  $0.02 \text{ mg NO}_3^- \text{ N L}^{-1}$ ) and came out as negative values, we assigned these a concentration of  $0.01 \text{ mg NO}_3^- \text{ N L}^{-1}$ . Net N mineralization ( $\mu\text{g N g}^{-1} \text{ d}^{-1}$ ) was calculated as the increase in  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N between initial and final (field incubated) cores, whereas net nitrification was calculated as the change in  $\text{NO}_3^-$ -N alone. At the second sample date, we used additional 20-g subsamples of soil to measure rates of potential net N mineralization and nitrification in the laboratory. These were placed into 120-mL polypropylene specimen cups, brought to 20% gravimetric moisture with deionized water, capped and incubated for 28 days at  $20^\circ\text{C}$ . In previous work in these sandy soils we have found this to approximate moisture content at field capacity. At the end of the incubation these soils were extracted and analyzed for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  as described above. Additional subsamples of soils from the second sampling date were pulverized in a ball mill and analyzed for soil organic C, soil organic N and C:N ratio using a Costech ECS 4010 (Costech Analytical Technologies Inc., Valencia, CA).

We also used anion-exchange resin bags to assess the downward movement of  $\text{NO}_3^-$  through soil in the field. Three grams of anion-exchange resin (Sigma-Aldrich, Ambersep® 900, OH- Form, Type I) were sewn into  $6 \times 5 \text{ cm}$ , 86-mesh polyester bags. At each sampling point we used a shovel to expose an ca. 40 cm soil profile. We used a knife to cut a horizontal slit at least 10-cm into the undisturbed pit face at a depth of 25 cm and inserted the resin bag, then refilled the hole. Our assumption here was that water percolating through the resin bag was coming through the undisturbed profile and we took care throughout to minimize disturbance to the exposed pit face. Resin bags were placed in the field beginning on the first sample date in May, and allowed to capture  $\text{NO}_3^-$  undisturbed until the next sample date in June, when we dug out the pits, collected the resin bags and returned them to the lab. At the June and August sampling dates we placed new resin bags, which were collected in August and October, respectively, providing three periods over which resin bags sampled percolating

$\text{NO}_3^-$ : May-June, July-August, and September-October. At each sampling point we took care to ensure that soil disturbance from soil core collection was located well away from where the resin bags were located, and we moved to nearby undisturbed ground at each sampling date. Two of our sites (HU and HO) had been trenched for replanting following harvesting. At these sites we confined our sampling to undisturbed areas between furrows in order to isolate the effects of the clearcutting without any additional effects of soil disturbance associated with trenching. In the laboratory, resin bags were washed free of soil particles using deionized water and then extracted in 35 mL of 2 M NaCl for 1 h in 50-mL centrifuge tubes on a rotisserie shaker. Resin extracts were analyzed for  $\text{NO}_3^-$  colorimetrically as described above. We calculated rates of  $\text{NO}_3^-$  N capture on resin bags for each sampling period ( $\mu\text{g N bag}^{-1} \text{ d}^{-1}$ ), and then calculated cumulative  $\text{NO}_3^-$  N capture ( $\mu\text{g N bag}^{-1}$ ) for the entire growing season.

Log-transformed rates of in-situ net N mineralization, nitrification and resin  $\text{NO}_3^-$  capture were analyzed using repeated measures analysis in SAS version 9.3 software (SAS Institute Inc. 2010). Site (HU, ME, HO or ML), treatment (Cut vs Burn), sampling time (June, August or October) and all interactions were included as fixed effects. The time autocorrelation was modelled by setting sampling date as a repeated measure (R-side random effect) with a first order autoregressive (AR1) covariance structure. The choice of covariance structure was guided by goodness of fit and the Bayesian information criteria (Schwarz, 1978). Cumulative rates of net N mineralization, net nitrification, and resin  $\text{NO}_3^-$  capture, and soil C, N and C:N ratio were analyzed as described above, but without the repeated measure of sampling date. In order to investigate the potential effect of time since disturbance on in situ N fluxes we included age included stand age (in years; Table 1) as a covariate in analyses of cumulative N mineralization, net nitrification and resin  $\text{NO}_3^-$  capture. Finally, we used an Analysis of Covariance to assess whether the relationship between net N mineralization and net nitrification differed between clearcut and burned sites. The significance level of all statistical tests was set to  $\alpha = 0.05$ .

### 3. Results

Potential net N mineralization rates from the laboratory incubation were significantly higher ( $P = 0.006$ ) in soils from clearcut sites compared to soils from burned sites (Fig. 1a). There was no overall effect of site on lab N mineralization rate ( $P = 0.608$ ), nor was there a significant interaction between site and treatment ( $P = 0.195$ ). Potential net nitrification rates from the laboratory were also significantly higher ( $P = 0.016$ ) in soils from clearcut sites compared to soils from burned sites (Fig. 1b). There was a significant main effect of site on potential net nitrification ( $P = 0.039$ ) with notably higher rates in soils from the ME site (significantly different from HO and ML), but there was not a

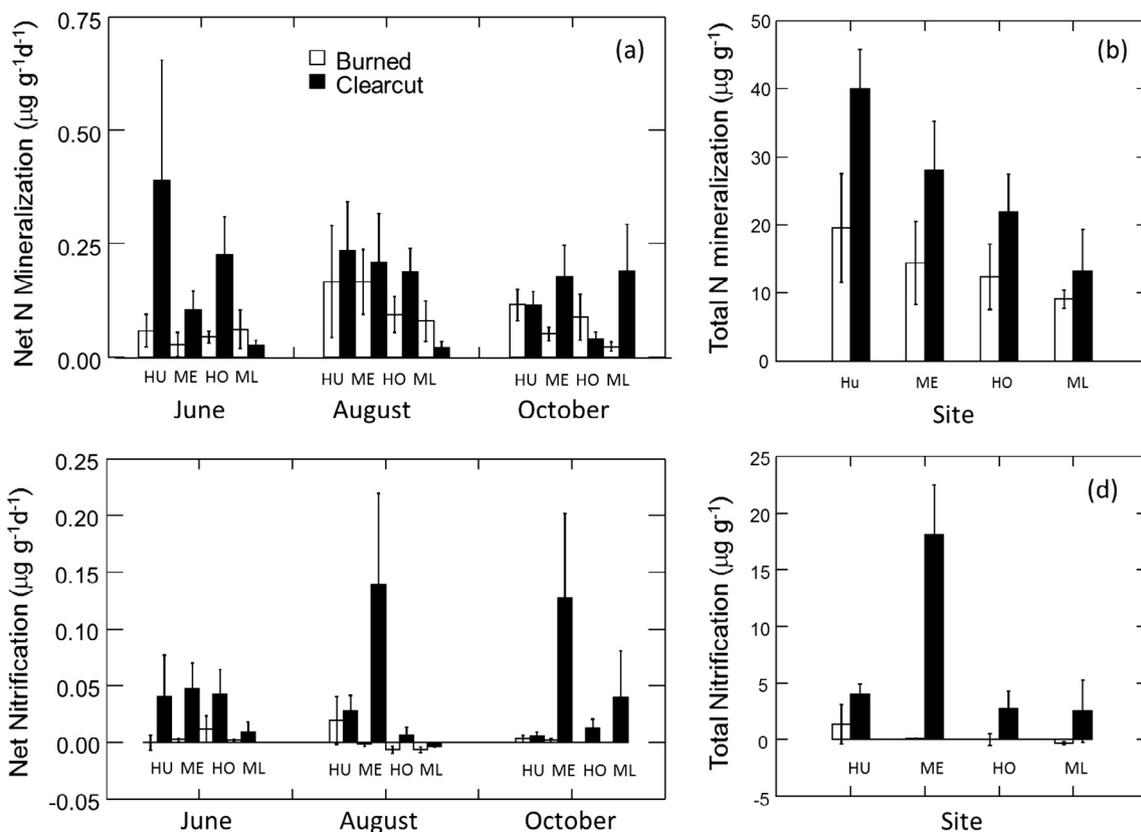


Fig. 2. In-situ net N mineralization (a and b) and net nitrification (c and d) by individual sample date (a and c), and cumulatively for the entire 2015 growing season (b and d). Data are means  $\pm$  1 SE.

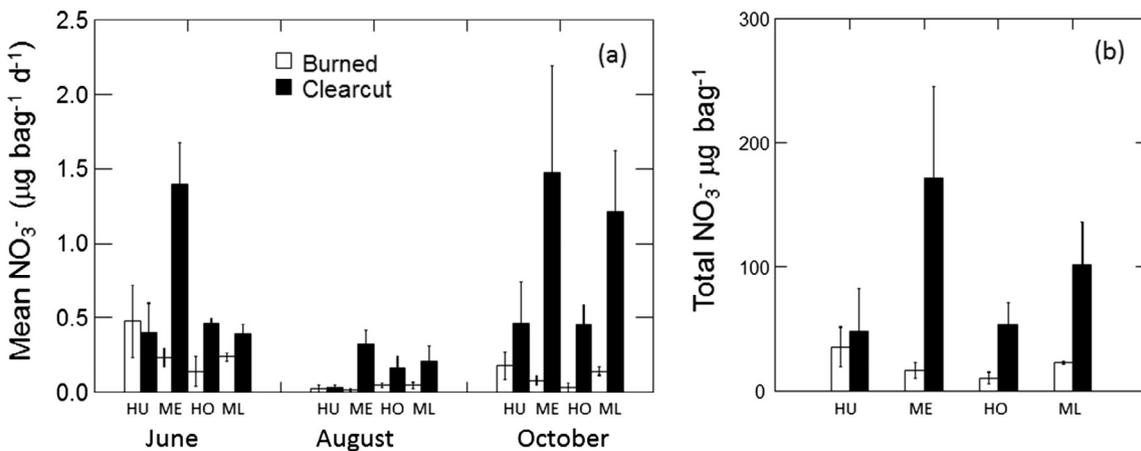


Fig. 3. Mean  $\text{NO}_3^-$  ( $\pm$  1SE) captured by resin bags across individual sampling dates (a) and cumulatively for the 2015 growing season (b) in burned vs. clearcut origin stands.

significant interaction between site and treatment ( $P = 0.260$ ). In-situ rates of net N mineralization are presented for individual sample dates in Fig. 2a, and cumulatively for the entire 2015-growing season in Fig. 2b. Across all individual sample dates rates of in-situ net N mineralization were consistently higher in cut sites compared to burned sites ( $P = 0.020$ ), with a significant effect of site ( $P = 0.043$ ) but no significant site x treatment interaction ( $P = 0.715$ ). Although the overall effect of site was significant, only the HU and ML sites were significantly different from each other ( $P = 0.006$ ). There was not a significant treatment by sampling time interaction ( $P = 0.400$ ). When summed across all individual sampling times, cumulative in-situ N mineralization (Fig. 2b) was significantly greater in clearcut sites compared to burned sites ( $P = 0.027$ ), with no overall effect of site ( $P = 0.112$ ) and no interaction between site and treatment

( $P = 0.791$ ). Cumulative in-situ N mineralization rates tended to decline from older to younger stands ( $P = 0.003$ ; Fig. 2b), a pattern we did not observe in the laboratory (Fig. 1a). Differential effects of clearcutting and wildfire were far more pronounced for in-situ nitrification (Fig. 2c and d) compared to in-situ net N mineralization (Fig. 2a and b). Across all individual sampling dates net nitrification was more than 20 times greater in clearcut sites compared to burned sites ( $P = 0.003$ ). Burned sites rarely exhibited any net nitrification, and at ca. 2/3 of the sampling events burned sites exhibited zero net nitrification ( $\text{NO}_3^-$  below the detection limits in both initial and final samples) or net immobilization of  $\text{NO}_3^-$  (evidenced as negative nitrification rates in Fig. 2c). There were no significant effects of site ( $P = 0.254$ ) or a site by treatment interaction ( $P = 0.639$ ) on in-situ rates of nitrification. Summed across all sampling times, cumulative

net nitrification was markedly higher in clearcut sites compared to burned sites ( $P = 0.001$ ), with no overall effect of site ( $P = 0.075$ ) and no interaction between site and treatment ( $P = 0.359$ ). Only one burned site (HU) exhibited net accumulation of  $\text{NO}_3^-$  over the entire growing season, with the other three exhibiting no accumulation or net immobilization (Fig. 2d). There was no trend of cumulative net nitrification with time since disturbance ( $P = 0.988$ ; Fig. 2d).

Resin nitrate capture across individual sample dates (panel a) and summed across the entire 2015 growing season (panel b) are shown in Fig. 3. Across all individual sampling times resin bags captured about four times more  $\text{NO}_3^-$  in clearcut sites compared to burned sites ( $P < 0.001$ ). There was no overall effect of site on resin- $\text{NO}_3^-$  capture ( $P = 0.207$ ); however, there was a significant site by treatment interaction ( $P = 0.046$ ) due to the fact that the treatment effect was muted at the HU site compared to the other three sites. There was a significant interaction between treatment and sampling time ( $P = 0.049$ ), reflecting the fact that resin  $\text{NO}_3^-$  capture was higher in the spring and autumn compared to the drier summer months in clearcut sites, but uniformly low across seasons in burned sites. There was no trend of cumulative resin  $\text{NO}_3^-$  capture with time since disturbance ( $P = 0.421$ ; Fig. 3b).

There were no significant effects of disturbance type on soil organic C ( $P = 0.225$ ), total soil N ( $P = 0.171$ ) or soil C:N ratio ( $P = 0.614$ ) (data not shown), and none of these parameters was significantly correlated with rates of net nitrification (data not shown). Rates of in-situ net N mineralization were a significant predictor of rates of in-situ net nitrification; however, the relationship was significantly different, with a much steeper slope in clearcut compared to burned sites ( $P = 0.022$ ; Fig. 4).

#### 4. Discussion

Prior to European settlement, jack pine forests of northern Lower Michigan were maintained by frequent stand-replacing wildfires which occurred on an estimated 60-y return interval (Cleland et al., 2004). Suppression of fire has extended the modern (1985–2000) fire return interval for this ecosystem to ca. 800 years (Cleland et al., 2004), and instead these systems are managed via clearcut harvesting on a planned 50-y rotation (MDNR, 2014). Concerns have been raised about the failure of this anthropogenic disturbance regime to adequately replicate ecosystem structural features of wildfire disturbance important to

wildlife (Spaulding and Rothstein, 2009; Corace et al., 2010). Herein we demonstrate that replacement of fire by clearcut harvesting results in important functional changes to the ecosystem process of nitrogen cycling.

Results from our laboratory incubations were remarkably consistent with the findings of LeDuc and Rothstein (2007). Although they used a different incubation procedure, they also observed an overall increase in N mineralization in clearcut sites, but a much more pronounced increase in nitrification in recently clearcut sites compared to recently burned sites. It is important to point out that there was no overlap between their study sites and ours; we located four new pairs of clearcut- and wildfire-origin stands that were not studied by LeDuc and Rothstein (2007). Thus, we can say with a high degree of confidence that enhanced nitrification potentials following clearcutting are a real phenomenon in this landscape. We advance their work by also documenting that the pronounced difference in nitrification between clearcuts and wildfires is occurring in situ. In this study, we found a remarkably consistent pattern across all three sets of data: laboratory soil incubation, field soil incubation and in-situ resin  $\text{NO}_3^-$  capture. Together, these data show a clear picture of increasing production and movement of nitrate through soil in young stands of clearcut origin, compared to young stands of wildfire origin.

Although in-situ incubation procedures take place at field temperatures, they still involve isolating a sample of soil, thus disrupting moisture- and root-mediated C and N dynamics. Another potential artefact associated with the buried-bag method, is that severing roots allows  $\text{NH}_4^+$  concentrations to build, which, in turn, could stimulate nitrification rates above what would be seen in undisturbed soil. However, we argue that this makes the almost complete lack of nitrification in wildfire-origin sites more compelling, in that nitrification in this treatment failed to respond to increases in  $\text{NH}_4^+$  substrate. In contrast to our nitrification assays, resin bags captured  $\text{NO}_3^-$  produced from undisturbed soil layers above them and thus provide the most convincing data demonstrating that clearcutting is in fact increasing the production and movement of  $\text{NO}_3^-$  in situ compared to fire (Fig. 3). One potential concern with respect to our resin bag procedure is that soil disturbance associated with installing the resin bags could have influenced our results. We do not believe this is a problem for three reasons. First, we took care to insert the resin bags at least 10 cm into the undisturbed pit face. Second, we would expect preferential flow along the boundary between the disturbed area (hole) and the undisturbed soil, so that there would be minimal movement of water from disturbed soil into the area above the resin bags. Finally, we followed the exact same procedure in burned and clearcut sites, therefore any disturbance effects cannot explain the difference in  $\text{NO}_3^-$  resin capture we observed between treatments.

Closer examination of nitrification results from our in-situ incubations (Fig. 2c) reveals two important observations. The first is that net nitrification is virtually nonexistent in wildfire origin stands (Fig. 2c). Across 36 individual incubations in wildfire sites (4 sites  $\times$  3 dates  $\times$  3 replicates), 26 of these had zero net nitrification or net  $\text{NO}_3^-$  immobilization and only three incubations produced net nitrification rates greater than  $0.01 \mu\text{g g}^{-1} \text{d}^{-1}$ . This lack of nitrification occurred despite the fact that we always observed net N mineralization across all of our in-situ incubations in wildfire origin stands. The second important observation is that in-situ nitrification rates were not raised uniformly in clearcut-origin stands – many in-situ incubations still had net  $\text{NO}_3^-$  immobilization. However, in clearcut sites we observed zero net nitrification or net  $\text{NO}_3^-$  immobilization in far fewer incubations (12 of 36), and where net nitrification occurred it was consistently higher in clearcut stands (18 of 36 incubations produced nitrification rates greater than  $0.01 \mu\text{g g}^{-1} \text{d}^{-1}$ ). Thus it appears that factors constraining nitrate production in soils of wildfire-origin stands are alleviated in clearcut origin stands, although with a fair amount of spatial variability.

Undisturbed forests on acidic soils dominated by hard pines (*Pinus*

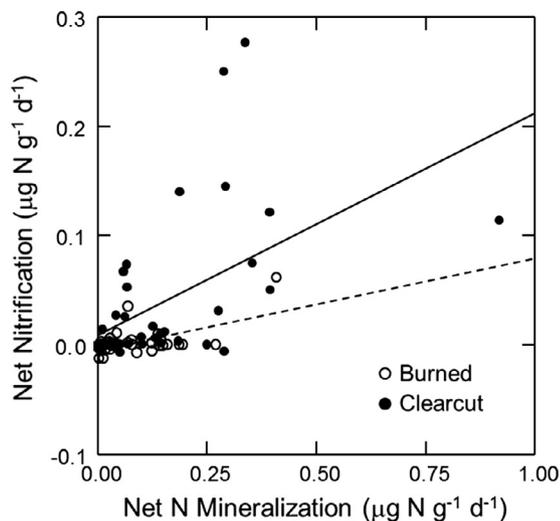


Fig. 4. Relationship between rates of in-situ net N mineralization and in-situ net nitrification across all sampling events. The dashed line represents the best fit linear regression for burned sites (Nitrification =  $0.084 * \text{Nmin} - 0.005$ ;  $R^2 = 0.312$ ;  $P < 0.001$ ) and the solid line represents the best fit linear regression for clearcut sites (Nitrification =  $0.204 * \text{Nmin} + 0.009$ ;  $R^2 = 0.250$ ;  $P = 0.001$ ).

subgenus *Pinus*) and oaks (*Quercus*) have long been known to have very low rates of net nitrification (Gosz, 1981; Vitousek, 1982; Gosz and White, 1986). When disturbed, these systems often exhibit lower rates of nitrification and nitrate loss compared to ecosystems on more neutral soils with more moisture demanding vegetation (Vitousek et al., 1982). Early hypotheses of factors limiting nitrification in hard pine and oak dominated ecosystems focused on low populations of nitrifying microorganisms and the potential influence of allelopathic chemicals in suppressing the activity of nitrifying bacteria (reviewed by Robertson, 1982). However, more recent work has demonstrated that acidic forest soils dominated by hard pines and oaks that exhibit little or no net nitrate accumulation can have active populations of nitrifying microorganisms (De Boer and Kowalchuk, 2001; Isobe et al., 2011; Hu et al., 2014; Levy-Booth et al., 2014) and very high rates of gross nitrification (Stark and Hart, 1997). Instead, the availability of  $\text{NH}_4^+$  substrate is now viewed as the most important driver of net nitrification rates in terrestrial ecosystems, such that net nitrification is thought to only occur where N is available in excess of demand by plants and soil heterotrophs (i.e. Fig. 2 Schimel and Bennett, 2004). For example, in a landscape-scale study of nitrification potentials in New Hampshire, USA, Venterea et al. (2003) found that net N mineralization rate was the single best predictor of nitrification rates, accounting for 37–53% of the total variance.

In our study, we found that net N mineralization rate only explained 25–31% of the variance in net nitrification rates (Fig. 4). Interestingly, we found that net nitrification increased more rapidly in response to increasing net N mineralization in clearcut sites, suggesting that burning in these jack pine forests may have impacted the size or activity of populations of nitrifying microorganisms and reduced their ability to respond to available  $\text{NH}_4^+$ . Research investigating the effects of burning on nitrifying microorganisms using molecular techniques has yielded an unclear picture with some studies showing no effects (Docherty et al., 2012; grassland ecosystem), some negative impacts (Yeager et al., 2005 (mixed conifer forest); Isobe et al., 2009 (tropical rainforest)), some positive effects (Ball et al., 2010; mixed conifer) and others showing differential effects on bacteria vs Archaea (Long et al., 2014; wet sclerophyll forest). Our finding of reduced nitrification in wildfire influenced sites contrasts with a series of studies, which have found that fire-generated charcoal enhances rates of nitrification, presumably by sorbing phenolic compounds that may depress activity of nitrifiers (Zackrisson et al., 1996; DeLuca et al., 2006; Ball et al., 2010).

Regardless of the underlying mechanism, our finding of increased nitrification and  $\text{NO}_3^-$  movement in the years following clearcutting has important implications for the ecology and management of these forests. Ecosystems such as this that are managed using whole-tree harvesting and occur on inherently base-poor parent materials are believed to be susceptible to productivity declines due to base cation depletion (Mann et al., 1988; Johnson et al., 1991; McLaughlin and Phillips, 2006; Zetterberg et al., 2016). The enhanced nitrification and nitrate movement that we have documented herein are likely to exacerbate base cation losses from harvest removals due to the acidity generated in the nitrification process, as well increased co-leaching of base cations as  $\text{NO}_3^-$  percolates through soil (Van Miegroet and Cole, 1984; Harrison et al., 1996; Jussy et al., 2000). Shifts from a predominantly  $\text{NH}_4^+$  dominated N cycle following the natural wildfire disturbance regime, to one in which  $\text{NO}_3^-$  is more prevalent following harvesting, could also affect plant community dynamics due to differences in N-form preference among plant species and functional guilds (Kronzucker et al., 1997; Boudsocq et al., 2012; Britto and Kronzucker, 2013). Most notably, jack pine itself appears to grow poorly with  $\text{NO}_3^-$  as a N source (Lavoie et al., 1992). Land managers and researchers in this area have long noted that the herbaceous plant community arising following clearcutting is very different from that found in wildfire-regenerated stands (Abrams and Dickman, 1982; Houseman, 2002; Probst and Donnerwright, 2003). Of particular concern for land managers is the propensity for dense mats of upland sedge (*Carex pensylvanica*) to

dominate young clearcut sites. While we do not have direct data on the potential role of nitrification in promoting upland sedge dominance, this species is believed to be non-mycorrhizal (Brundrett and Kendrick, 1988; Bauer et al., 2003) and thus would be expected to particularly benefit from an abundance of rapidly diffusing  $\text{NO}_3^-$  compared to slowly diffusing  $\text{NH}_4^+$  (Raven et al., 1992).

In conclusion, laboratory and field results from this study, combined with the independent laboratory results reported by LeDuc and Rothstein (2007), allow us to conclude with a high degree of confidence that replacement of wildfire disturbance by whole-tree harvesting promotes nitrification and  $\text{NO}_3^-$  movement in jack pine ecosystems of northern Lower Michigan. Although the exact mechanism remains uncertain; however, it appears that some factor or factors that restrict net nitrification in young stands of wildfire origin is not present in clearcut-origin stands. Land managers in this region are exploring ways to modify management regimes in order to better emulate the ecological processes associated with wildfire (MDNR, 2014). Alternative approaches to jack pine regeneration such as prescribed burning of logging residues to release seed from serotinous cones, merit investigation to see if they can better emulate the N biogeochemistry associated with a natural disturbance regime.

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#### References

- Abrams, M.D., Dickmann, D.I., 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. *Can. J. Botany* 60 (6), 946–954.
- Albert, D.A., 1995. Regional landscape ecosystems of Michigan, Minnesota and Wisconsin: a working map and classification. General Technical Report NC-178. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station.
- Ball, P.N., MacKenzie, M.D., DeLuca, T.H., Montana, W.E., 2010. Wildfire and charcoal enhance nitrification and ammonium-oxidizing bacterial abundance in dry montane forest soils. *J. Environ. Quality* 39 (4), 1243–1253.
- Bauer, C.R., Kellogg, C.H., Bridgman, S.D., Lamberti, G.A., 2003. Mycorrhizal colonization across hydrologic gradients in restored and reference freshwater wetlands. *Wetlands* 23, 961–968.
- Bergeron, Y., 2004. Is regulated even-aged management the right strategy for the Canadian boreal forest? *Forest. Chronicle* 80 (4), 458–462.
- Bormann, F.H., Likens, G.E., 1979. *Pattern and Process in a Forested Ecosystem*. Springer, New York.
- Boudsocq, S., Niboyet, A., Lata, J.C., Raynaud, X., Loeuille, N., Mathieu, J., Blouin, M., Abbadie, L., Barot, S., 2012. Plant preference for ammonium versus nitrate: a neglected determinant of ecosystem functioning? *Am. Nat.* 180, 60–69.
- Britto, D.T., Kronzucker, H.J., 2013. Ecological significance and complexity of N-source preference in plants. *Ann. Botany* 112 (6), 957–963.
- Brundrett, M.C., Kendrick, B., 1988. The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. *Can. J. Botany* 66, 1153–1173.
- Cleland, D.T., Crow, T.R., Saunders, S.C., Dickmann, D.I., Maclean, A.L., Jordan, J.K., Watson, R.L., Sloan, A.M., Brososke, K.D., 2004. Characterizing historical and modern fire regimes in Michigan (USA): a landscape ecosystem approach. *Landscape Ecol.* 19 (3), 311–325.
- Comer, P.J., Albert, D.A., Wells, H.A., Hart, B.L., Raab, J.B., Price, D.L., Kashian, D.M., Corner, R.A., Schuen, D.W., 1995. Michigan's Native Landscape: as Interpreted from the General Land Office Surveys 1816–1856. Michigan Natural Features Inventory, Lansing, MI, 76pp.
- Corace III, R.G., Goebel, P.C., McCormick, D.L., 2010. Kirtland's warbler habitat management and multi-species bird conservation: considerations for planning and management across jack pine (*Pinus banksiana* Lamb.) habitat types. *Nat. Areas J.* 30 (2), 174–190.
- De Boer, W., Kowalchuk, G.A., 2001. Nitrification in acid soils: micro-organisms and mechanisms. *Soil Biol. Biochem.* 33 (7), 853–866.
- DeLuca, T.H., MacKenzie, M.D., Gundale, M.J., Holben, W.E., 2006. Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. *Soil Sci. Soc. Am. J.* 70 (2), 448–453.
- Doane, T.A., Horwath, W.R., 2003. Spectrophotometric determination of nitrate with a

- single reagent. *Anal. Lett.* 36 (12), 2713–2722.
- Docherty, K.M., Balsler, T.C., Bohannon, B.J., Gutknecht, J.L., 2012. Soil microbial responses to fire and interacting global change factors in a California annual grassland. *Biogeochemistry* 109 (1–3), 63–83.
- Eno, C.F., 1960. Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Sci. Soc. Am. J.* 24 (4), 277–279.
- Firestone, M.K., Davidson, E.A., 1989. Microbiological basis of NO and N<sub>2</sub>O production and consumption in soil. In: *Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*. John Wiley and Sons, New York, pp. 7–21.
- Giardina, C.P., Rhoades, C.C., 2001. Clear cutting and burning affect nitrogen supply, phosphorus fractions and seedling growth in soils from a Wyoming lodgepole pine forest. *For. Ecol. Manage.* 140 (1), 19–28.
- Gosz, J.R., 1981. Nitrogen cycling in coniferous ecosystems. In: Clark, F.E., Rosswall, T. (Eds.), *Terrestrial Nitrogen Cycles*, vol. 33. *Ecological Bulletin*, Stockholm, pp. 405–426.
- Gosz, J.R., White, C.S., 1986. Seasonal and annual variation in nitrogen mineralization and nitrification along an elevational gradient in New Mexico. *Biogeochemistry* 2 (3), 281–297.
- Harrison, R.B., Gessel, S.P., Zabowski, D., Henry, C.L., Xue, D., Cole, D.W., Compton, J.E., 1996. Mechanisms of negative impacts of three forest treatments on nutrient availability. *Soil Sci. Soc. Am. J.* 60 (6), 1622–1628.
- Houseman, G.R., Anderson, R.C., 2002. Effects of jack pine plantation management on barrens flora and potential Kirtland's warbler nest habitat. *Restor. Ecol.* 10 (1), 27–36.
- Hu, H.W., Xu, Z.H., He, J.Z., 2014. Chapter six-ammonia-oxidizing Archaea play a predominant role in acid soil nitrification. *Adv. Agron.* 125, 261–302.
- Hunter, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol. Conserv.* 65 (2), 115–120.
- Isobe, K., Otsuka, S., Sudiana, I., Nurkanto, A., Senoo, K., 2009. Community composition of soil bacteria nearly a decade after a fire in a tropical rainforest in East Kalimantan, Indonesia. *J. General Appl. Microbiol.* 55 (5), 329–337.
- Isobe, K., Koba, K., Otsuka, S., Senoo, K., 2011. Nitrification and nitrifying microbial communities in forest soils. *J. For. Res.* 16 (5), 351.
- Johnson, C.E., Johnson, A.H., Siccama, T.G., 1991. Whole-tree clear-cutting effects on exchangeable cations and soil acidity. *Soil Sci. Soc. Am. J.* 55 (2), 502–508.
- Jussy, J.H., Colin-Belgrand, M., Ranger, J., 2000. Production and root uptake of mineral nitrogen in a chronosequence of Douglas-fir (*Pseudotsuga menziesii*) in the Beaujolais Mountains. *For. Ecol. Manage.* 128 (3), 197–209.
- Kronzucker, H.J., Siddiqi, M.Y., Glass, A.D., 1997. Conifer root discrimination against soil nitrate and the ecology of forest succession. *Nature* 385 (6611), 59.
- Lavoie, N., Vézina, L.P., Margolis, H.A., 1992. Absorption and assimilation of nitrate and ammonium ions by jack pine seedlings. *Tree Physiol.* 11 (2), 171–183.
- LeDuc, S.D., Rothstein, D.E., 2007. Initial recovery of soil carbon and nitrogen pools and dynamics following disturbance in jack pine forests: a comparison of wildfire and clearcut harvesting. *Soil Biol. Biochem.* 39 (11), 2865–2876.
- Levy-Booth, D.J., Prescott, C.E., Grayston, S.J., 2014. Microbial functional genes involved in nitrogen fixation, nitrification and denitrification in forest ecosystems. *Soil Biol. Biochem.* 75, 11–25.
- Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biol. Conserv.* 131 (3), 433–445.
- Long, X.E., Chen, C., Xu, Z., He, J.Z., 2014. Shifts in the abundance and community structure of soil ammonia oxidizers in a wet sclerophyll forest under long-term prescribed burning. *Sci. Total Environ.* 470, 578–586.
- Lundin, L., Nilsson, T., 2014. Initial effects of forest N, Ca, Mg and B large-scale fertilization on surface water chemistry and leaching from a catchment in central Sweden. *For. Ecol. Manage.* 331, 218–226.
- Mann, L.K., Johnson, D.W., West, D.C., Cole, D.W., Hornbeck, J.W., Martin, C.W., Riekerk, H., Smith, C.T., Swank, W.T., Tritton, L.M., Van Lear, D.H., 1988. Effects of whole-tree and stem-only clearcutting on postharvest hydrologic losses, nutrient capital and regrowth. *For. Sci.* 34, 412–428.
- McLaughlin, J.W., Phillips, S.A., 2006. Soil carbon, nitrogen, and base cation cycling 17 years after whole-tree harvesting in a low-elevation red spruce (*Picea rubens*)-balsam fir (*Abies balsamea*) forested watershed in central Maine, USA. *For. Ecol. Manage.* 222 (1), 234–253.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environ. Rev.* 9 (4), 223–260.
- MDNR 2014. *Kirtland's Warbler Breeding Range Conservation Plan*. [https://www.michigan.gov/documents/dnr/Kirtlands\\_Warbler\\_CP\\_457727\\_7.pdf](https://www.michigan.gov/documents/dnr/Kirtlands_Warbler_CP_457727_7.pdf).
- Morse, J.L., Durán, J., Beall, F., Enanga, E.M., Creed, I.F., Fernandez, I., Groffman, P.M., 2015. Soil denitrification fluxes from three northeastern North American forests across a range of nitrogen deposition. *Oecologia* 177, 17–27.
- North, M.P., Keetin, W.S., 2008. Emulating natural disturbance regimes: an emerging approach for sustainable forest management. In: *Patterns and Processes in Forest Landscapes*. Springer, Netherlands, pp. 341–372.
- Probst, J.R., DonnerWright, D., 2003. Fire and shade effects on ground cover structure in Kirtland's Warbler habitat. *Am. Midland Nat.* 149 (2), 320–334.
- Raven, J.A., Wollenweber, B., Handley, L.L., 1992. A comparison of ammonium and nitrate as nitrogen sources for photolithotrophs. *New Phytol.* 121 (1), 19–32.
- Robertson, G.P., 1982. Nitrification in forested ecosystems. *Philos. Trans. R. Soc. B: Biol. Sci.* 296 (1082), 445–457.
- Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85 (3), 591–602.
- Schwarz, G., 1978. Estimating the dimension of a model. *Ann. Stat.* 6, 461–464.
- Simard, D.G., Fyles, J.W., Paré, D., Nguyen, T., 2001. Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. *Can. J. Soil Sci.* 81 (2), 229–237.
- Sinsabaugh, R.L., Reynolds, H., Long, T.M., 2000. Rapid assay for amidohydrolase (urase) activity in environmental samples. *Soil Biol. Biochem.* 32 (14), 2095–2097.
- Spaulding, S.E., Rothstein, D.E., 2009. How well does Kirtland's warbler management emulate the effects of natural disturbance on stand structure in Michigan jack pine forests? *For. Ecol. Manage.* 258 (11), 2609–2618.
- Stark, J.M., Hart, S.C., 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* 385 (6611), 61.
- Van Miegroet, H., Cole, D.W., 1984. The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. *J. Environ. Quality* 13 (4), 586–590.
- Venterea, R.T., Lovett, G.M., Groffman, P.M., Schwarz, P.A., 2003. Landscape patterns of net nitrification in a northern hardwood-conifer forest. *Soil Sci. Soc. Am. J.* 67 (2), 527–539.
- Vitousek, P.M., Gosz, J.R., Grier, C.C., Melillo, J.M., Reiners, W.A., 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecol. Monogr.* 52 (2), 155–177.
- Vitousek, P.M., Gosz, J.R., Grier, C.C., Melillo, J.M., Reiners, W.A., Todd, R.L., 1979. Nitrate losses from disturbed ecosystems. *Science* 204 (4392), 469–474.
- Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecol. Appl.* 11 (5), 1349–1365.
- Wang, Y., Xu, Z., Zhou, Q., 2014. Impact of fire on soil gross nitrogen transformations in forest ecosystems. *J. Soils Sediments* 14 (6), 1030–1040.
- Yeager, C.M., Northup, D.E., Grow, C.C., Barns, S.M., Kuske, C.R., 2005. Changes in nitrogen-fixing and ammonia-oxidizing bacterial communities in soil of a mixed conifer forest after wildfire. *Appl. Environ. Microbiol.* 71 (5), 2713–2722.
- Zackrisson, O., Nilsson, M.C., Wardle, D.A., 1996. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos* 10–19.
- Zetterberg, T., Olsson, B.A., Löfgren, S., Hyvönen, R., Brandtberg, P.O., 2016. Long-term soil calcium depletion after conventional and whole-tree harvest. *For. Ecol. Manage.* 369, 102–115.
- Zhang, J., Müller, C., Cai, Z., 2015. Heterotrophic nitrification of organic N and its contribution to nitrous oxide emissions in soils. *Soil Biol. Biochem.* 84, 199–209.