Multi-decadal trajectories of soil chemistry and nutrient availability following cutting vs. burning disturbances in upper Great Lakes forests

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Abstract

What are the successional trajectories and impacts of disturbances on forest soil nutrient availability? Answers remain elusive because the timescale of interest is long and many factors affect soil properties. We address this question on a regionally representative landscape in northern Michigan, U.S.A. Late-successional reference stands aside, most forests on this landscape were clear-cut and burned between 1870-1911; subsequently, stands comprising two chronosequences were either cut and burned again, or cut-only, at multi-decadal intervals. Successional trajectories and disturbance impacts were detectable in A, B, and C horizons, most of all for properties affected by ash deposition (pH and Ca, both of which declined with stand age but were higher in twice-burned stands). A horizon NH_4^+ availability was lower in twice- than once-burned stands and declined with age in both chronosequences. B horizon Fe concentrations increased with age in both chronosequences, but were lower in twice-burned stands, suggesting slower recovery of pedogenesis following more severe disturbance. Unanticipated variation in C horizon texture, distributed across stands, revealed bottom-up influences of parent material on Ca, Mg, K, Al, and cation exchange capacity. Collectively, these results indicate deep, long-lasting disturbance impacts on these soils; future work will assess their influence on other ecosystem properties.

Key words: succession, pedogenesis, ecosystem function, nitrogen, base cations

1. Introduction

Researchers often quantify how forest ecosystem functions change during succession and in response to disturbances. In the Laurentian mixed forest province, spanning the Great Lakes and northeastern North America, broad similarities in climate, vegetation, and history (in terms of glaciation and anthropogenic disturbance) have fostered many studies, all asking some version of the same question. Specifically, how do forests change as they undergo succession, and does the type or severity of the disturbance that re-initiated that succession matter? These questions have been addressed using various ecosystem functions as metrics, including primary production rates (Fahey et al. 2005), nitrogen retention (Goodale et al. 2000), soil microbial processes (Leduc and Rothstein 2007), and soil properties (Roberts and Gilliam 1995).

Disturbance regimes of forests throughout the Great Lakes (Schulte and Mladenoff 2005) and northeastern North America (Foster et al. 1998) were, at an ecoregional level, generally consistent before Euro-American settlement; namely, some combination of wind- and fire-driven gap or stand dynamics across forested landscapes (although the frequencies of these disturbances probably varied widely across the region). Subsequently, forests were impacted by a prolonged period (>150 years) of generally similar westward-moving disturbances: intensive logging, followed variously by more frequent severe fires and, in some areas, farming. This broadly similar disturbance history is more than the basis for current patterns of forest composition and ecosystem functioning across the region; it constrains the designs of studies that attempt to unravel the effects of disturbances themselves, and the successional changes that follow, on ecosystem functions. In particular, longitudinal studies of forest succession are rare because the historic disturbance period began in the distant past, succession is slow to unfold, and forest ecosystem research is young by comparison.

In lieu of longitudinal studies, empirical research in northern forests has often been based on observational comparisons (“snapshots”) of forests with different disturbance histories (Ollinger et al. 2002) or opportunistic chronosequences (Bergeron 2000). One of the most thorough of these works compared chronosequence vs. longitudinal designs for assessing post-logging changes in forest floor mass and organic matter content in Spodosols (Yanai et al. 2000). Those researchers ultimately rejected the quantitative prediction offered by the chronosequence-based assessment (Covington, 1981), arguing that harvest practices changed over time. While intensive individual studies at some of the same sites (e.g., Johnson et al. 1995) and synthetic reviews (Nave et al. 2010) support the pattern originally proposed (Covington, 1981), a larger point regarding chronosequences still stands. Disturbance-recovery chronosequences—in particular those that are assembled opportunistically—fail to control for variation in the nature of the specific disturbances that established new forests of known ages.

In northern Lower Michigan, the University of Michigan Biological Station (UMBS) “Burn Plots” consist of adjacent, 1-ha plots that have, at intervals, been experimentally treated to re-create the original disturbance (clearcut-bole removal-burn) that occurred on the landscape in 1911. Each manipulation has installed a new stand in the otherwise similar matrix of recovering 1911-origin forestland in 1936, 1948, 1954, 1980, 1998, and 2017. The Burn Plots have supported research on soil microhabitat-vegetation interactions (Scheiner and Teeri 1986), ecosystem carbon (C) budgets (Gough et al. 2007), and changes in O horizon mass, thickness, and C content (Schaetzl 1994). That study (Schaetzl 1994) detected the same increase in O horizon mass and C content that has been reported elsewhere, and is one of the studies that supports the generality of this pattern. While still a chronosequence, the consistently applied treatment over time suggests a true trajectory of this ecosystem function (O horizon recovery) over time.

The potential for disturbances to affect soil properties (including plant nutrient availability) addresses an important aspect of ecosystem functioning, and is a topic of interest to long-term ecosystem research. Many studies of historically cut and burned forests across the Great Lakes and northeastern North America have focused on nitrogen (N) because it is a plant-limiting nutrient (Smithwick et al. 2005). Studies of old-growth vs. mature (historically logged or burned) northern hardwood forests in the U.S. northeast (Goodale and Aber 2001) and upper Great Lakes (Fisk et al. 2002) report differing results in terms of which soil N transformations are responsive to disturbance history or successional status, but converge on a similar theme: disturbances are important, but other factors may exert greater control on soil N cycling. For instance, top-down effects of climate change (Campbell et al. 2009), atmospheric deposition (Goodale et al. 2000), invasive (Ashton et al. 2005) or native woody plant species (Fujinuma et al. 2005), or bottom-up effects of physiographic factors such as drainage (Zogg and Barnes 1995) or soil texture (Reich et al. 1997) all affect the cycling of plant-limiting nutrients. These factors may act independently of or interact with disturbance and successional dynamics. Furthermore, multiple nutrients may interact to limit plant growth; elements such as calcium (Ca; Baribault et al. 2010) and phosphorous (P; Goswami et al. 2018) also limit forest primary production in this ecoregion. Distinct disturbances (e.g., clearcutting vs. wildfire) produce distinct impacts on multi-decadal patterns of Ca availability in boreal forests of eastern (e.g. Simard et al. 2001) and west-central Canada (e.g. Kishchuk et al. 2015), and longer-term (multi-century) successional changes have also been noted for properties including pH, Ca, Mg, K, and P availability (Brais et al. 1995).

In addition to their importance to vegetation-defined processes, such as plant nutrient limitation, soil properties are indices of another key forest ecosystem function: pedogenesis. Although less often a focus of disturbance research than vegetation-defined metrics, pedogenesis is a forest ecosystem function that is impacted by disturbances including logging (Dymov 2017) and fire (Eckmeier et al. 2007). Among the few studies in North America, Barrett and Schaetzl (1998) described "depodzolization" and slower rates of podzolization processes in "stump prairies" of the upper Great Lakes. In these formerly productive forest ecosystems, clearcutting and severe fires during the historic disturbance period eliminated forest cover, with ecosystem structure and vegetation today defined by stumps, charred snags, and largely graminoid taxa. In keeping with these profound changes in vegetation, organic matter inputs, and energy and water budgets, stump prairie soils exhibit different concentrations and depth distributions of extractable aluminum (Al), iron (Fe), and the organic C with which they complex during translocation to illuvial (B) horizons.

Contrasted against the abundance of research on forest vegetation, these scattered examples linking pedogenic soil properties to forest disturbances and succession converge on an important point: there is a substantial need for studies that address disturbance impacts on and successional changes in soil properties. Here, we report the results of a study intended to address one overarching set of questions: which soil depths and properties are most dynamic across stand ages following cut-and-burn disturbances, and do changes in soil properties with stand age differ depending upon disturbance severity? We address these broad questions by testing four specific hypotheses in once- vs. twice-burned chronosequences. First, topsoil properties are most likely to change over time because they are directly impacted by cutting and burning; subsoil and parent material horizons are physically isolated from these disturbances and thus exhibit fewer properties that respond to disturbance or ensuing succession. Second, the soil properties most likely to vary across succession are those which are directly induced by disturbance (e.g., pH and base cations due to ash deposition), indicators of pedogenenic processes disrupted by severe disturbances (e.g., translocation of Al and Fe), or strongly limiting of primary production (e.g., inorganic N). Third, the impact of disturbance on any soil property is to mediate an otherwise predictable successional trajectory, rather than to obviate or reverse it. Fourth, variation in soil properties that is driven by disturbance or succession is not so significant that it obscures variation attributable to differences in initial state factors (e.g., texture) across soils.

2. Methods

2.1 Study Area- This research was conducted at UMBS, in northern Lower Michigan (U.S.; 45.56^{o}, -84.72 ^{o}), where the mean annual temperature is 5.5^{o} and mean annual precipitation is 817 mm (294 cm as snowfall). The UMBS is a ~4,400 ha field station occupying a landscape formed at the end of Laurentian glaciation, between 14,000 and 11,000 years before present (Blewitt and Winters 1995; Lapin and Barnes 1995; Schaetzl et al. 2002). A thorough description of this landscape, its soils and vegetation is available in a paper documenting hierarchical physiographic and soil controls on forest biomass production (Nave et al. 2017). The most extensive major landforms on the landscape are of three types: pitted outwash plains that remained above postglacial lake levels, lower-elevation outwash plains that were inundated by postglacial Lake Algonquin, and moraines (Figure 1; Corner and Albert 1999). Landforms are little modified (e.g, by erosion) since the close of the last glaciation, and bedrock (limestone and shale) is buried beneath >100 m of glacial drift of mixed mineralogy. Regarding soils, the majority of the landscape (and the sites we report here) are on outwash plains, where Entic Haplorthods have formed in the sandy, well-sorted drift. Strata of coarser (e.g., gravel or even cobbles) or finer (loamy) materials occasionally occur within the top 1 m of outwash soil profiles, providing adventitious opportunities to test for the influence of texture on soil properties. These materials are more abundant in the heterogeneous (though still very sandy) till of the less extensive moraine landforms, where Lamellic and Alfic Haplorthods predominate (Soil Survey Staff, 1991). Importantly, the design of the present study (detailed in the following section) limits its inferences primarily to outwash landforms and the Entic Haplorthods that have formed in their sandy parent materials; the forest stands available for study are not distributed across the landscape in a manner that allows a systematic, statistically balanced disentangling of factors such as landform, soil texture or drainage from disturbance and succession.

Current vegetation at UMBS, which is almost completely forested, reflects the broader disturbance history of the upper Great Lakes region. Namely, clearcutting and uncontrolled wildfires in the late 19th and early 20th centuries replaced pre-exploitation forests of *Pinus resinosa* Aiton, *P. strobus* L., *Tsuga Canadensis* (L.) Carriere, and long-lived hardwoods (*Acer saccharum* Marshall, *Fagus grandifolia* Ehrh., *Quercus rubra* L.) with mixed deciduous-conifer forests dominated by early-successional taxa such as *Populus grandidentata* Michx., *Populus tremuloides* Michx., and *Betula papyrifera* Marshall. Across most of UMBS, mixtures of early-successional taxa dominate, though these have been giving way to longer lived hardwoods and conifers since the late 1980s (Gough et al. 2010; Jones et al. 1993). Isolated stands on UMBS property were not clearcut and are dominated by older trees; we report results from 3 of these stands (totaling <200 ha) here, as references for successional stages beyond those encompassed by our experimental design. These three stands include one that was cut and partially burned in

1885, another that regenerated following a stand-replacing fire in 1890, and a third that was very lightly cut (single tree selection) occasionally from the 1890s through the 1940s. These three stands are now uneven-aged; individual tree ages within the first two date as far back as their disturbances, while in the third stand, ages range back into the early 1800s (Nave et al. 2017). As is often the case with stands that are opportunistically studied to represent advanced successional stages (Keeton et al. 2011), these three span a wide range of conditions (i.e., ecosystem types); therefore, their differences from the younger successional (chronosequence) stands on outwash sands cannot be attributed to effects of disturbance alone.

2.2 Experimental design and field data collection- The experimental design of this study centers on a pair of chronosequences differing in establishing disturbance (Figure 1). The first chronosequence, the UMBS "Burn Plots," consists of 6 adjacent, 1 ha stands on a single ecosystem type on a high-level (pitted) outwash plain, in which each stand was experimentally disturbed according to a common protocol in 1936, 1948, 1954, 1980, 1998, or 2017 (the lattermost of these not sampled for the present study). Specifically, each stand was clearcut, all tree boles were removed, and the residues were then burned, in order to re-initiate stand development. The Burn Plots are located in an otherwise essentially homogenous area of forestland that established following this type of disturbance (clearcutting and fire) in 1911, coincident with the broader (landscape- to regional-level) disturbances of the period. Thus, the Burn Plots allow for the study of forest stands ranging in age from 16 to 78 years (at the time of sampling for this study in 2014), which have experienced two clearcuts and two fires. The second chronosequence consists of stands that were clearcut (but not burned) a second time in 1952, 1972, or 1987. Two of these stands (1952- and 1972-origin) are located within the Burn Plots experimental matrix; from these and additional stands (1987- and 1911-origin) on nearby outwash plains (1-3 km from the Burn Plots) we have assembled an opportunistic, complementary chronosequence. Importantly, knowing the 125 ecosystem types classified across the UMBS landscape (Pearsall 1995), and the regional landtype associations into which they nest (Corner and Albert 1999) allows us to ensure the similarity of key physiographic, soil, and biotic factors between the experimental (twice-burned) Burn Plots and the complementary once-burned chronosequence. For a thorough consideration of UMBS' landscape ecosystem types and their long-term plots, readers are referred to Nave et al. (2017).

Soil sampling- In this study, we collected 3 soil profiles in each of 2-3 plots (0.1 ha each) per stand, including the stands in the two chronosequences and the three older reference stands (Figure 1). Plots, which were used for sampling other ecosystem compartments (i.e., biomass) reported elsewhere, were located at random within each stand of known age; they are of no specific interest to the design of this study, which considers each manipulated stand as the experimental unit. Our field sampling, conducted over two days in July 2014, thus yielded 6-9 soil profiles per stand. Each profile was sampled by first removing the intact O and A horizons as a 225 cm^2 monolith, followed by incremental coring (5.2 cm inside diameter steel pipe) of 0-15, 15-30, 30-60, and 60-100 cm depth increments. We used this approach to collect the surface organic (O) and mineral topsoil (A) horizons as genetic horizons, while using depth increments that we had previously empirically calibrated (during a pilot study) to capture the E (0-15), Bs1 (15-30), Bs2 (30-60), and BC (60-100) horizons. In this study, we report most properties of interest for three of these depths, which we refer to as the A (the topsoil genetic horizon), B (15-30 cm depth increment or "subsoil"), and C (60-100 depth increment, which we refer to as the parent material horizon).

After sampling in the field, we immediately froze each combined O+A horizon monolith in its own 4 mil polyethylene bag (-20°); monoliths remained frozen until being individually thawed and processed over the subsequent 4 months. After sampling, mineral soil increments were immediately placed on cafeteria trays and air-dried at ~25° for 1 week, reaching <2% gravimetric moisture content during that time. Air-dried samples were sieved (2 mm mesh) to isolate pebbles and gravel (>2mm), coarse root (> 2mm diameter), fine root (<2 mm diameter), and fine earth fractions; all fractions were subsequently oven dried (60° for rock, coarse and fine root; 105° for fine earth) before making measurements of mass on each to the nearest 0.01g. We archived all fractions in 4 mil polyethylene bags at room temperature for 3 years before later subsampling for soil chemical analyses. Monoliths of combined O+A horizon material were separated in the lab by first removing fibrous litter (Oi and Oe material) from the top to isolate the A horizon, which was then separated into the same fractions as the other mineral soil increments (rock, coarse and fine root, fine earth). As with mineral soils, we oven-dried O (60°) and A horizon (105°) materials, and archived these in polyethylene bags until later analysis.

Ion-exchange resin bag incubation- We prepared and constructed ion-exchange resin bags (IERBs) using previously published methods (Nave et al. 2011). Briefly, our IERBs were made from 30 mL of Dowex Marathon MR-3 mixed-bed IER beads (Dow Chemical, Midland, MI, USA) in a nylon foot stocking (MacPherson Leather, Seattle, WA, USA), packed into a PVC ring (5 cm diameter, 2 cm height). To deploy each IERB, we placed a square 225 cm^2 O+A horizon monolith template on the surface of the O horizon, cut along 3 sides to ~15 cm depth, and folded the resulting flap of monolith (3-10 cm thick and defined by the bottom of the A horizon) aside to expose the top of the E horizon. We then placed each IERB into a precisely excavated void (removed with a short PVC corer) at the top of the E horizon and folded the flap of O+A horizon back into place. We deployed 5 IERBs per plot on 3 June 2014 and incubated them until 8 September 2014.

2.3 Laboratory processing and analytical procedures- In August 2018, we subsampled 30 g of oven-dried material from each archived A horizon, and 60 g from each B and C horizon. Soils were analyzed according to the Standard Soil Test procedure at the Maine Soil Testing Service (University of Maine; detailed in Hoskins 1997). Briefly, separate, carefully weighed splits of our subsampled, archived soils were analyzed for: 1) per cent mass loss on ignition [LOI; 375°]; 2) soil pH [1:1 mixture of soil and distilled water] and buffer pH [1:1 soil and Mehlich lime buffer], and 3) exchangeable cations. Exchangeable cations were extracted using a modified Morgan extract [pH 4.8 ammonium acetate] and their concentrations in extract solutions quantitated by inductively coupled plasma emission spectrometry-optical emission spectrometry. Exchangeable acidity (ExA) was calculated from water and buffer pH; effective cation exchange capacity (ECEC) was determined by the summation of milliequivalent levels of Ca, K, Mg, Na, and acidity. Analytical variances were computed as 95% confidence intervals from repeated runs of internal reference samples; uncertainties for the analytes we report here are soil pH (0.12 units), buffer pH (0.03 units), loss on ignition (0.4%), K, Ca, and Mg (±8% relative error), and Al and Fe (0.8 ppm). Analytical concentrations (of exchangeable cations) were scaled according to the mass of the extracted subsample, in order to express cation concentrations per unit dry soil mass (mg per kg-1). Our laboratory procedures for IERBs have been published elsewhere (Nave et al. 2011a); briefly, we extracted each IERB with 100 mL of 2 M LiCl, and analyzed the extracts for NH_4-N and NO_3-N concentrations on a SmartChem 200 (Westco Scientific Instruments, Brookfield, CT USA) using EPA 350.1 and EPA 353.2 methods, respectively. To express IERB N concentrations on a consistent basis, we first subtracted the mean field blank extract concentration (n=8 and 1-2 orders of magnitude lower than field-deployed IERBS) from each field-deployed IERB, and then scaled up according to the extract volume, IER mass, and PVC ring area.

2.4 Data analysis- We used inferential statistics to test for statistically significant effects of soil horizon, disturbance history, and stand age (successional stage) on measured soil properties. We performed these tests systematically to address our specific hypotheses related to the soil depths and properties that respond to disturbance or change over succession (namely, hypotheses 1-3). Secondarily, upon finding that C horizon textures differed among profiles without apparent regard to age or disturbance history or successional stage, we were able to address one adventitious hypothesis; namely, our fourth: that soil texture is a significant source of variation in soil properties, independent of disturbance or succession. In all of our statistical analyses, we treated each sample (i.e., a specific horizon from a single profile) as an independent observation, of which there were from 6 to 9 per stand age. Similar to past work (Nave et al. 2017) reporting forest biomass data from some of these plots, we define stand age as the age of the oldest trees in a stand (or the plots that are used to sample that stand). For our paired chronosequence stands, which initiated following clearcutting (or clearcut + fire) disturbances, this is a straightforward definition; for the three late-successional reference stands, this definition is problematic because they are uneven-aged. Nonetheless, we use the term "stand age" throughout this work as a quantitative index for successional stage, which is one of the principal variables we wish to test as a source of variation in soil properties. Importantly, because we lack a complete factorial design, we are unable to perform a complete, multi-variate analysis of variation in soil properties as a function of stand age, disturbance history, and state factors such as landform or landscape ecosystem type. Therefore, the results of our statistical tests represent specifically the sampled stands as the population of interest, and broader inferences of our study should be carefully constrained, e.g., to forests of similar disturbance history with sandy soils on outwash landforms.

Before performing statistical tests, we used transformations to normalize non-normally distributed response parameters. In cases where parameters could not be normalized we used nonparametric tests. For categorical tests of data meeting parametric assumptions, we used ANOVA with Tukey's Honest Significant Difference method for multiple comparisons. To test for significant effects of disturbance history (categorical) and stand age (continuous), we used a multi-variate approach: i.e., dummy variable coding to differentiate observations from once- vs. twice-burned stands, with best subsets regressions to assess the predictive capacity of age and the disturbance dummy variables. After identifying which model had the strongest predictive capacity (in terms of the model adjusted r^2 and C-p statistics, and the t and p values of each predictor variable), we ran simple linear (in cases where age alone predicted variation) or multiple linear (where there was a categorical disturbance effect and a temporal trend) regressions to obtain model r^2 and p values and add best-fit lines to scatterplots. To aid in visual interpretation of temporal patterns and disturbance effects, we averaged the 6-9 observations within each disturbance by age group, and presented the mean ±SE on the scatterplots with best-fit lines. We did not use regression, nor fit lines to any continuously varying properties from old reference stands because these are on fundamentally different ecosystem types than those of our chronosequence stands (all of which are on two outwash ecosystem types). Where we present measures of variance associated with our parametric analyses, we elected to use standard errors because the goal of these tests is to estimate the true value of a soil property of interest, rather than express its variability. In nonparametric analyses, we used the Kruskal-Wallis rank sum test, with Dunn's Method, in order to test for significant differences between median values. In these more conservative tests, applied to data that could not be transformed to meet parametric assumptions, we present variance as the 25th and 75th percentiles. Before beginning any analyses, we set p<0.05 as the threshold for accepting test results as significant.

3. Results

Across all stands, most measured soil properties differed significantly among the three horizons of interest (Table 1). Soil pH was significantly and successively higher with depth; loss on ignition (LOI- a proxy for organic matter concentration), exchangeable acidity (ExA), and effective cation exchange capacity (ECEC) showed the opposite trend (decreasing values for lower horizons), with all horizons differing significantly from one another. Concentrations of base cations (Ca, Mg, K) were likewise highest in the A, intermediate in the B, and lowest in the C horizon, with all differences significant except B vs C horizon Ca. Exchangeable levels of the hydroxide/organic matter-associating metals (Al and Fe) were significantly higher in B horizons compared to their overlying A or underlying C horizons.

Properties of A and B horizons showed generally more successional variability and were more responsive to disturbance than C horizon properties (Table 2). In C horizons, only one property exhibited a significant successional trend (Ca availability), with four (pH, ExA, exchangeable Ca and Mg) showing significant disturbance effects. In A horizons, 5 of the 9 properties showed significant successional trends and 4 exhibited significant disturbance impacts; in B horizons, 4 properties varied significantly across ages and 5 differed significantly between disturbance categories (once- vs. twice-burned). Notably, some soil properties exhibited significant successional and disturbance-driven patterns nearly universally across all horizons (e.g., pH and exchangeable Ca), while others were specific to only one horizon (i.e., exchangeable Fe in B horizons) or not responsive at all (i.e., exchangeable Al). Inorganic N availability, assessed with IERBs buried immediately beneath the A horizons, showed significant successional trends for NH_4-N (p=0.002) and NO_3-N (p<0.001), although only NH_4-N showed a significant categorical effect of disturbance (p<0.001).

Examining successional trajectories of and disturbance effects on A horizon properties revealed numerous significant patterns in this most superficial portion of the profile (Figure 2). Soil pH and exchangeable Ca declined across stand ages in both chronosequences; however, both of these parameters were significantly higher in twice- than once-burned chronosequence stands at any given stage of successional development. Exchangeable Mg exhibited the same patterns as pH and Ca (declining across stand ages, categorically higher in twice-burned stands). ExA showed opposing patterns in that it increased across stand ages and was higher in once-burned than twice-burned stands. ECEC was not affected by disturbance, but declined significantly across stand ages in both chronosequences. In terms of inorganic N availability, NH_4-N decreased, and NO_3-N increased over time in both chronosequences (Figure 3). However, while NO_3-N availability did not differ for once vs. twice-burned stands, a significant disturbance impact was evident for NH_4-N availability, with significantly lower levels in the twice-burned than once-burned stands across stand ages.

In B horizons, pH and exchangeable Ca showed successional trajectories (declining across stand ages) and disturbance impacts (elevated in twice-burned stands) similar to A horizons (Figure 4). Exchangeable concentrations of other base cations (Mg and K) in B horizons also declined significantly across stand ages, but neither property showed a significant difference between twice- and once-burned stands. In contrast, B horizon exchangeable Fe concentrations increased across stand ages in both chronosequences, with once-burned stands exhibiting consistently, significantly higher concentrations than twice-burned stands. Similarly, ECEC and ExA were significantly higher in once- than twice-burned stands (Table 2).

C horizons possessed only one property that showed significant differences across stand ages and between disturbance groups (exchangeable Ca), although the patterns were consistent with those observed in A and B horizons (Figure 5). Specifically, Ca concentrations declined with stand age in both chronosequences, but levels were significantly higher in the twice-burned stands.

Unlike A and B horizons, which consistently possessed a medium sand matrix regardless where they were collected (paired chronosequence and old reference stands), C horizons of the 87 profiles spanned a range of texture classes. Of these, 47 were (medium) sand, 6 were fine sand, 21were gravelly sand, 10 were loamy sand, and 3 were sandy clay loam. These C horizons with texture classes other than medium sand showed no consistent spatial pattern (e.g., relationship with landtype association or ecosystem type) and their occurrence was likewise not restricted to a particular disturbance group (i.e., one of the chronosequences or the old reference stands). Thus, comparing C horizons from all sampled profiles revealed significant effects of texture on many measured properties, including exchangeable Ca, Mg, K, and Al, and ECEC (Figure 6).

4. Discussion

Overall, our results suggest consistent successional trajectories (differences among stand ages spanning decades) in many properties of the forest soils of our paired chronosequences, with persistent, mediating impacts of disturbances on some of those trajectories. However, there are important differences in the physical and chemical properties of the three horizons we report

(Table 1), as well as which of those horizons and their properties are responsive to disturbance or succession (Table 2). Strictly interpreted, our results do not entirely confirm our first hypothesis: topsoils are indeed successionally dynamic, and sensitive to disturbance, but not more so than subsoils. In fact, 4-5 properties each in A, B, and C horizons showed significant disturbance impacts (many of these consistent), despite the surficial nature of the specific disturbance that contrasts the stands from our two chronosequences: residue-fueled surface fire. While none of the experimental cut+bole removal+burn treatments that established our twice-burned chronosequence monitored soil temperatures, it is unlikely that direct impacts of heating extended below 10-15 cm (Busse et al. 2010). Thus, it appears that physical impacts of fire—e.g., by combustion of organic matter or lethal heating of the soil matrix—is not needed to produce changes in soil properties at considerable depths, ranging from the subsoil (15-30 cm) to the upper parent material (60-100 cm).

Across our paired chronosequences, the soil properties that exhibited the most consistent successional trajectories and disturbance impacts were pH and exchangeable Ca (Table 2). Both parameters declined over time in A and B horizons, and values of each were always higher in the A, B, and C horizons of twice-burned vs. once-burned stands (Figures 2, 4, 5). This consistency confirms our second hypothesis, which predicts fire-induced pH and base cation effects due to ash deposition, while also suggesting physico-chemical mechanisms that explain why once- and twice-burned stands differ in pH and Ca concentration. Namely, direct deposition of harvest residues with high base cation concentrations (including Ca, Mg, and K) onto the soil surface transfers significant quantities of these elements from aboveground biomass to detrital organic matter pools (Bellau et al. 2006). This elevated supply of base cations may be subsequently released slowly by organic matter mineralization and acid solution leaching, as observed in our once-burned chronosequence, or more abruptly as the organic matter is combusted and the cation-rich minerals are left in place as ash (Certini 2005). Subsequently, the very high solubility of Ca in acid soil solution drives the great depth to which elevated pH and dramatically higher Ca levels are observed for our twice-burned chronosequence (Figure 5), and may explain why base cations with greater tendency to adsorb onto secondary mineral surfaces (Mg and K) show less significant disturbance impacts at increasing depths (Adams and Boyle 1979). These differences between individual cation species aside, our results agree with literature reporting that fire-induced increases in base cations are common in this region (Miesel et al. 2012).

In Spodosols, pedogenesis involves processes that concentrate Fe/Al-hydroxide-organic matter complexes in illuvial (B) horizons; these include acid solution leaching, *in situ* weathering of primary minerals, and deposition of organic matter (Sanborn et al. 2011). Based upon detailed observational work describing how factors that control pedogenic processes affect morphology, physical and chemical properties in historically burned soils (Barrett and Schaetzl 1998), we hypothesized that indicators of pedogenic processes would show directional successional trajectories (change over time) and sensitivity to disturbance (repeated burning) in our paired chronosequence study. Some of our results support this hypothesis; others neither refute nor confirm it. Congruent with Barrett and Schaetzl (1998), we found higher exchangeable Fe concentrations in B horizons of the less disturbed stands (Figure 4). Elevated Al and Fe concentrations in B horizons (Table 1; *cf.* A and C horizons) indicate our sampling scheme captures the metal-hydroxide-organic matter illuviation typical of Spodosol B horizons, although the lack of a significant disturbance effect on exchangeable Al (Table 2) is in contrast. Notably, Barrett and Schaetzl (1998) performed a wide range of extractions, allowing more detailed insights into functional pools of inorganic and organically bound Fe and Al. Our study reports exchangeable Al and Fe concentrations for only one pool and thus does not advance understanding of soil physico-chemical details; on the other hand, our experimental design does provide an ecosystem-level view of disturbance, pedogenesis, and succession. According to this view, the effect of disturbance is to degrade pedogenic indicators (e.g., diminish B horizon Fe concentrations); when disturbance involves repeated burning, this degradation is more severe and the rate of increase in Fe concentrations during the ensuing 75-100 years is evidently slower. Concurrently, as pedogenesis recovers, so too do other aspects of ecosystem functioning, including forest canopy structure (Scheuermann et al. 2018), C storage (Gough et al. 2007), and the availability of growth-limiting nutrients.

The potential for disturbances to impact soil properties that influence the availability of plant-limiting nutrients is an important area of research on ecosystem functioning (Bae et al. 2015), a core question at this long-term study site (Gough et al. 2007), and the final component of our second hypothesis. Our prediction for this hypothesis derives from research on the twice-burned chronosequence that showed a link between N availability and net primary production (White et al. 2004). Here, we report internally consistent evidence for disturbance impacts on nutrient availability and potential mechanisms for those disturbance impacts. The most critical of these disturbance impacts relate to the availability of NH_4-N, which represents >95% of the *in situ* net N mineralization in the top 30 cm of soils at UMBS, where forest net primary production is N-limited (Nave et al. 2009). The lower IERB NH_4-N availability that we observed in twice-burned stands (Figure 3) has several possible mechanisms, including a lower mineralization rate, lower solubility of, or a more limited availability of cation exchange sites for NH_4^+ in twice-burned soils. These mechanisms are not mutually exclusive- indeed, the higher pH and Ca and lower exchangeable acidity of twice-burned A horizons (Figure 2, Table 2) suggest long-lasting, ashmediated effects on NH_4^+ solubility / mobility in soil solution (Bodi et al. 2014), in addition to the lower ECEC observed in the B horizons of twice-burned stands (Table 2). However, while the proximal soil mechanisms governing NH_4-N availability are important, they may be less important at the ecosystem level than the mechanistic role that N availability plays as a plant-limiting nutrient. In this regard, recent findings from our paired chronosequences revealing lower tree species diversity and leaf area index in the twice-burned than once-burned chronosequence (Scheuermann et al. 2018) demonstrate that disturbance severity influences forest structure through a mechanism of decreased nutrient (in this case N) availability, as proposed by Gough et al. (2007) without the benefit of soil property measurements.

Beneath our third hypothesis—that disturbance impacts are superimposed upon successional trajectories—lies a fundamental question: what controls the timescale of recovery of soil properties, and, in turn, the aspects of ecosystem functioning (e.g., C storage) that they influence? Many of our results support that hypothesis in that both disturbance types (i.e., once-burned and twice-burned chronosequence stands) "set back" soil properties to their highest (or lowest, depending on the property) levels at stand re-initiation, with a subsequent, multi-decadal trajectory of decline (or increase). Concurrently, for many of these properties, including pH, Ca, Fe, and NH_4-N, there is a consistent offset between the trajectories of once-burned and twice-burned stands. In this light, it becomes clear that the specific disturbance—a second residue fire—plays an exacerbating, rather than fundamentally different role in affecting soil properties. Unfortunately, this consistency of impacts between the two chronosequences provides little information for forecasting the duration required for recovery, and because our late-successional reference stands have such fundamental differences in disturbance history and ecosystem type, we cannot confidently consider them to be true end points. In some cases, their properties appear reasonably aligned with the trajectories of our successional chronosequences (e.g., A horizon pH or ExA), while in others there is no direct temporal trend (e.g., B horizon Ca). At best, comparing the trajectories of once- vs. twice-burned stands, we can predict convergence of some properties (e.g., B or C horizon Ca) within ~100 years. At worst, some properties appear to be diverging over time (e.g., B horizon Fe), obviating any attempt to predict (or even define) the term "recovery." Furthermore, one insidious possibility that must be considered is that our chronosequence approach cannot control external, unmeasured factors that have changed over time, which could be playing lurking roles or masking patterns across stand age that we attribute to succession. Perhaps the foremost of these is atmospheric deposition, which has over many decades input significant quantities of constituents such as acidity and N to the soils that we report here. Atmospheric N deposition at UMBS and across the Upper Great Lakes is modest (Nave et al. 2009) by comparison to well-studied areas in the northeastern U.S. (Holland et al. 2005), which has long been a productive area for research on atmospheric deposition impacts on soils (Driscoll et al. 2001) and ecosystems (Aber et al. 2003). But, nearly all atmospheric N inputs at UMBS are input to the soil (rather than retained by the canopy; Nave et al. 2011b), and over the history of elevated atmospheric deposition—which is concurrent with our chronosequences—it is likely that hundreds of kilograms of inorganic N per hectare have been deposited to these N-poor soils. Because essentially all of our measured soil properties include, or are at least sensitive to atmospherically deposited compounds, it is possible that some of the patterns we attribute to stand age are not entirely successional. In the case of N, a reasonable prediction of higher N availability in older chronosequence stands (which have had a longer period to receive N inputs) is supported by the pattern for NH_4-N, but not NO_3-N (Figure 3). In the end, the true effects of non-constant conditions over chronosequence time cannot be tested using the data we present here, but it is likely that atmospheric deposition has interacted with disturbance history to produce (or obscure) some of the patterns we report (Goodale et al. 2000).

Our final, adventitious hypothesis arose from variation in C horizon textures across the 87 soil profiles that we sampled in this study. To be clear, there is strong similarity in physiographic factors (landform, hydrology) and soil conditions (texture, taxonomy) between our paired chronosequences, as described in the Methods. This similarity is reinforced by the many consistent temporal trends and disturbance impacts that we observed across stands from the once- and twice-burned chronosequence stands, as well as the consistently sandy textures of the A and B horizons of soils from all stands. However, the occurrence of textural variation across C horizons from all stands (both chronosequences and the old reference stands) allowed the opportunity to assess the influence of texture as a bottom-up initial state factor—i.e., one presumably not affected by logging, fire, or century-scale succession—upon soil properties whose variation we interpret in the context of top-down disturbances and temporal dynamics. Here, we report a bottom-up influence of C horizon texture (inherited from parent material) on ECEC and the exchangeable concentrations of four cations (Ca, K, Mg, and Al; Figure 6). The basic interpretation of these differences is straightforward: on an outwash-dominated landscape where medium sand is the typical parent material, concentrations of trace minerals within the dominantly quartz-derived sand increase soil fertility. In turn, the influence of textural variation on specific C horizon properties derives from the landforms where our stands are located, due to their modes of glacial deposition and postglacial modification. Strata of fine sand and gravelly sand are present on postglacial lakebeds, shorelines, and at locations adjacent to wasting ice blocks on pitted outwash, and represent distinct periods of deposition in high- or low-energy moving water (Pearsall 1995). Because the regional Silurian limestone and dolomite bedrock (exposed at the surface ~20 km to the north) is rich in carbonates (of Ca and Mg), many of the glacially transported coarse fragments encountered in gravelly parent materials are calcareous (Adams and Boyle 1982) and thus impart elevated base cation concentrations and levels of ECEC. Loamy sand and sandy clay loam parent materials occur due to direct deposition by ice (as till), ice rafting in glaciofluvial meltwaters, or by wind (Aeolian landforms are present throughout the UMBS landscape). Regardless their mode of deposition, the primary minerals that are the source of these loamy materials are rich in K-feldspar and carbonates that weather to aluminosilicate clays (Hannah and Zahner 1970); indeed, in some instances, these loamy materials are present as pedogenic lamellae (Wurman et al. 1959). Because C horizon textural variation is not distributed across our stands in a way that allows systematic, statistical disentangling of its relative influence (vs. the influence of temporal or disturbance factors) on soil properties, we cannot state which factor is most important, nor under what conditions the relative importance of these factors may change. Nonetheless, these results demonstrate that a significant influence of bottom-up state factors on C horizon properties across our stands can be resolved despite the top-down variation that is driven by disturbance and succession.

Conclusions- Through direct, statistical tests of a twice-burned experimental chronosequence vs. a complementary (observational) once-burned chronosequence, and non-statistical comparisons to old reference stands (>120 years old) across a forest landscape in northern Lower Michigan, we demonstrate consistent successional trajectories of and disturbance impacts on soil properties across 75-100 years of forest succession. Detectable disturbance impacts extended downward through A, B, and C horizons, and were most consistent for properties affected by ash deposition (pH and Ca availability). In A horizons, lower NH_4-N levels in twice-burned than once-burned stands suggest multi-decadal fire effects on the availability of this plant-limiting nutrient. Pedogenesis was set back by stand re-initiating disturbances (more so in the twice-burned chronosequence), as evidenced by lower B horizon exchangeable Fe in twice-burned vs. once-burned stands. Lastly, variation in C horizon texture across all sampled stands revealed bottom-up influences of parent material on cation exchange capacity and the concentrations of cations including Ca, Mg, K, and Al in these deepest portions of the sampled profile. Continued work at this long-term research site will address how successional changes in and disturbance impacts on soil properties affect other aspects of ecosystem function, such as ecosystem C pools and fluxes.

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Table 1. Soil physical and chemical properties for three horizons (n=261 total samples). Values are medians, with 25th and 75th percentiles in parentheses. For each property, superscripts indicate significant differences between depths.

Horizon	pH	Loss on ignition (%)	Exch. Acidity (meq $100g^{-1}$)	ECEC (meq $100g^{-1}$)	Ca (mg kg^{-1})	Mg (mg kg^{-1})	K (mg kg^{-1})	Al (mg kg^{-1})	Fe (mg kg^{-1})
A	4.6 (4.1 - 4.9)^{a}	12 (8.2 - 20.7)^{a}	3.0 (2.0 - 4.1)^{a}	9.1 (7.7 - 10.8)^{a}	861 (584 - 1093)^{a}	126 (106 - 172)^{a}	203 (153 - 262)^{a}	15 (12 - 18)^{a}	4.8 (3.8 - 6.1)^{a}
B	4.8 (4.6 - 5.0)^{b}	0.8 (0.5 - 0.9)^{b}	0.8 (0.5 - 1.2)^{b}	1.1 (0.7 - 1.4)^{b}	28 (14 - 45)^{b}	5.3 (3.9 - 7.9)^{b}	11 (9.3 - 16)^{b}	107 (75 - 130)^{b}	12 (8.9 - 17)^{b}
C	5.5 (5.3 - 5.8)^{c}	0.3 (0.2 - 0.4)^{c}	0.0 (0.0 - 0.0)^{c}	0.1 (0.1 - 0.3)^{c}	12 (8.0 - 50)^{b}	2.6 (1.9 - 7.1)^{c}	6.4 (4.7 - 9.1)^{c}	36 (32 - 45)^{c}	4.2 (3.6 - 5.2)^{a}

Table 2. Overall results of multi-variate analyses testing effects of disturbance severity (D; categorical: once- vs. twice-burned) and successional stage (t; continuous: stand age in years at time of sampling) on soil physico-chemical parameters (pH, loss on ignition, exchangeable acidity, effective cation exchange capacity), exchangeable concentrations of base cations (Ca, Mg, K) and organic matter associating metals (Al, Fe). For each horizon and soil property, *p* values are reported for disturbance severity (D column) and successional stage (t column). Specific significant effects (of D and t) are reported and discussed in the text.

Horizon / Depth	pH		Loss on ignition (%)		Exc. Acidity (meq $100g^{-1}$)		ECEC (meq $100g^{-1}$)		Ca (mg kg^{-1})		Mg (mg kg^{-1})		K (mg kg^{-1})		Al (mg kg^{-1})		Fe (mg kg^{-1})	
	D	t	D	t	D	t	D	t	D	t	D	t	D	t	D	t	D	t
A	<0.001	<0.001	NS	NS	<.001	0.002	NS	0.025	<0.001	<0.001	0.025	0.026	NS	NS	NS	NS	NS	NS
B	<0.001	0.007	0.017	NS	<.001	NS	<0.001	NS	0.010	<0.001	NS	<0.001	NS	0.046	NS	NS	<0.001	0.018
C	<0.001	NS	NS	NS	0.012	NS	NS	NS	<0.001	0.039	<0.001	NS	NS	NS	NS	NS	NS	NS

Figure 1. Inset: Location of the study area in northern Lower Michigan (U.S.). Landscape-level map shows prominent inland lakes, as well as landtype associations, which are differentiated by shading and assigned shorthand names referring to their major landforms. Clusters of points are the plots in which soils were sampled; colors differentiate plots in the once-burned (yellow) vs. twice-burned (red) chronosequence stands, while green points are plots in old, late-successional reference stands.

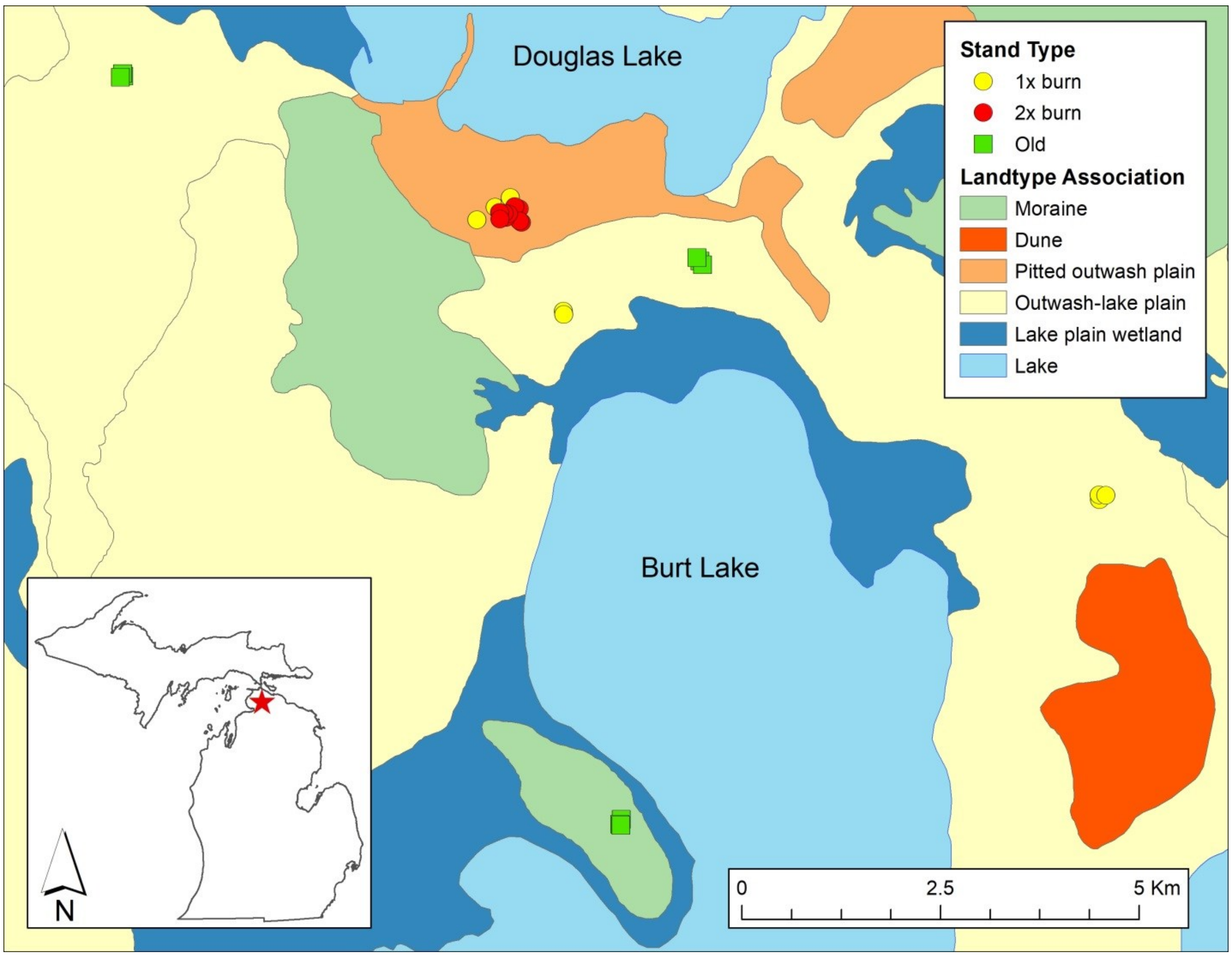

Figure 2. Temporal patterns in and disturbance impacts on A horizon properties for which time was indicated as a significant predictor variable in best subsets regression. Points plotted are means±SE for the 6-9 A horizons per stand age. Old stands are not included in regression tests; they are presented for reference.

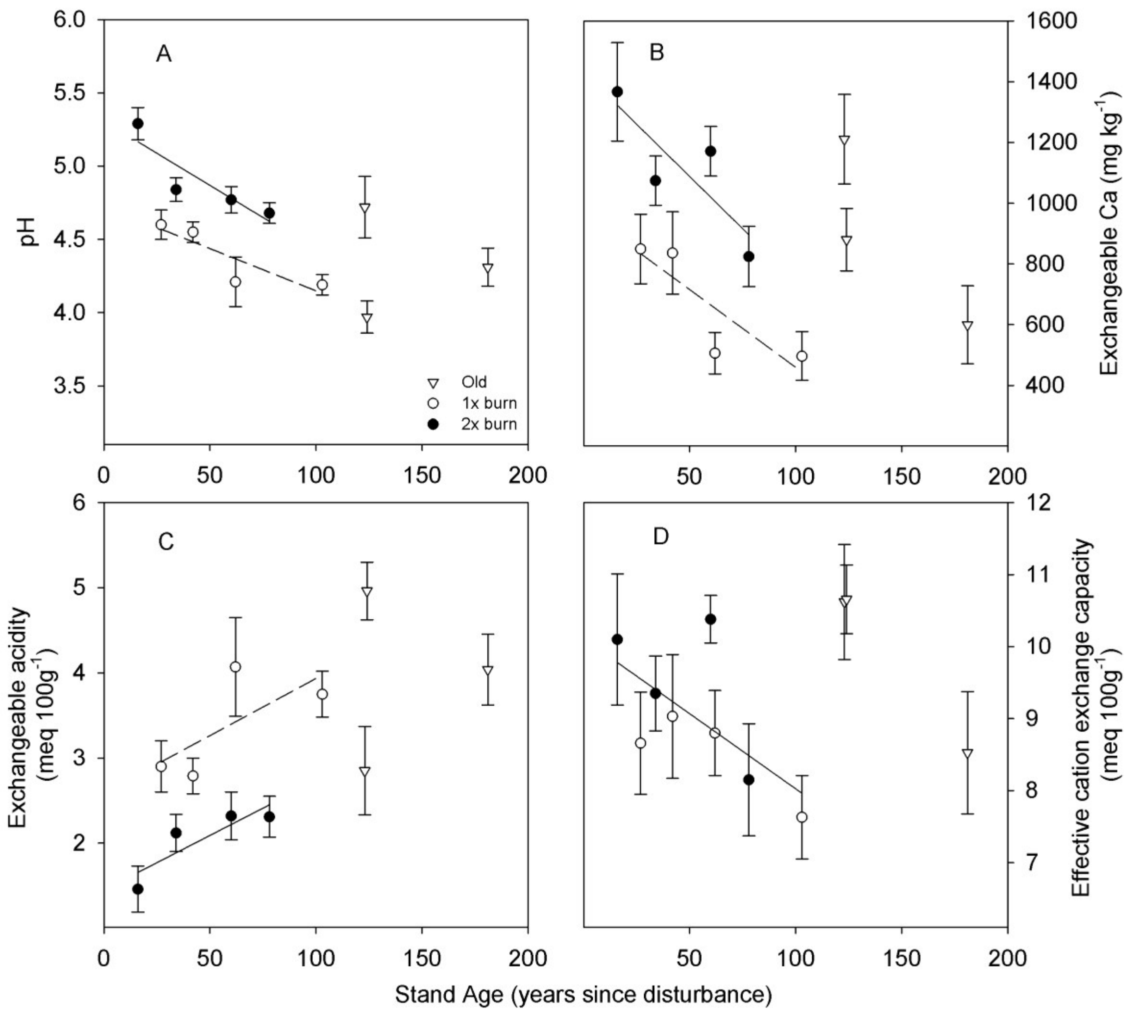

Figure 3. Temporal patterns in and disturbance impacts on IERB NH_4-N and NO_3-N availability. Old stands are not included in regression tests; they are presented for reference. Points plotted are means ±SE for 9-15 IERBs per stand age.

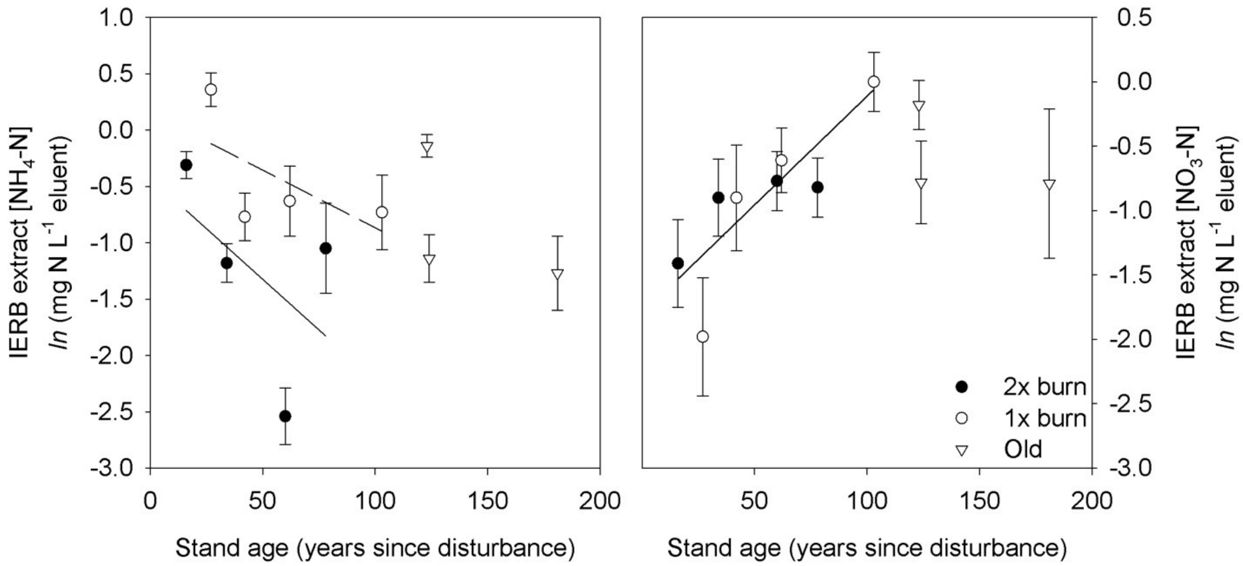

Figure 4. Temporal patterns in and disturbance impacts on B horizon properties for which time was indicated as a significant predictor variable in best subsets regression. Points plotted are means±SE for the 6-9 B horizons per stand age. Old stands are not included in regression tests; they are presented for reference.

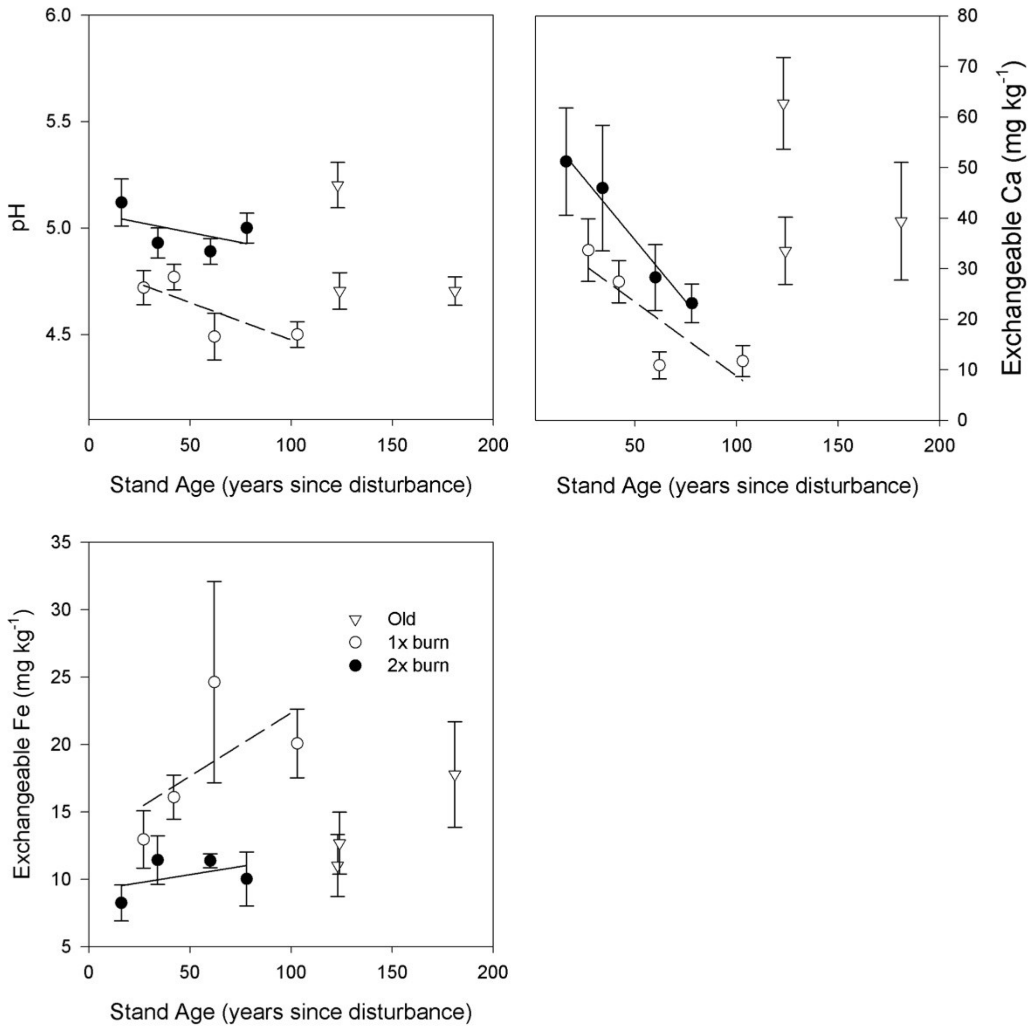

Figure 5. Temporal patterns in and disturbance impacts on exchangeable Ca in C horizons. Points plotted are means±SE for the 6-9 C horizons per stand age. Old stands are not included in regression tests; they are presented for reference.

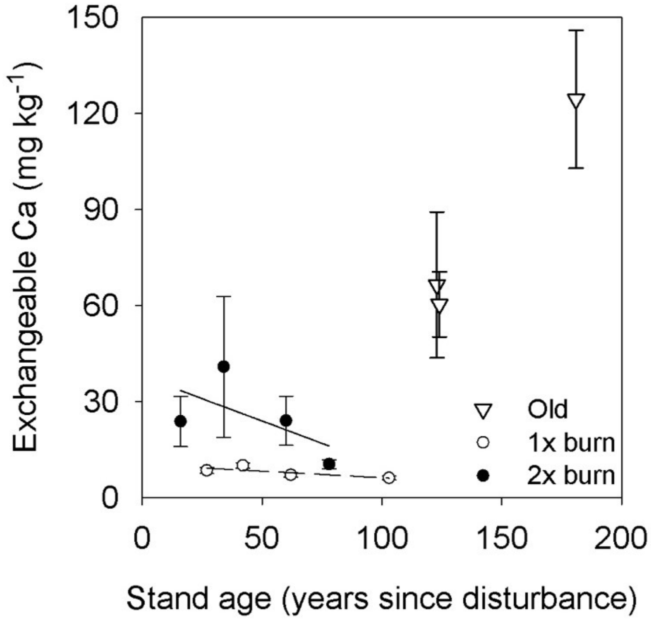

Figure 6. Variation in C horizon properties as a function of texture class. Points plotted are *ln*-transformed means with standard errors. Each analyte shows a significant effect of texture; in the interest of figure clarity, individual multiple comparisons are not shown. Note that units differ among analytes; see Methods (section 2.3) for information about analytical determinations and units of presentation.