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Title: Disentangling the long-term effects of disturbance on soil biogeochemistry in a wet tropical forest ecosystem

Running head: legacy of disturbance on soil biogeochemistry

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Abstract

Climate change is increasing the intensity of severe tropical storms and cyclones (also referred to as hurricanes or typhoons), with major implications for tropical forest structure and function. These changes in disturbance regime are likely to play an important role in regulating ecosystem carbon (C) and nutrient dynamics in tropical and subtropical forests. Canopy opening and debris deposition resulting from severe storms have complex and interacting effects on ecosystem biogeochemistry. Disentangling these complex effects will be critical to better understand the long-term implications of climate change on ecosystem C and nutrient dynamics. In this study, we used a well-replicated, long-term (10 y) canopy and debris manipulation experiment in a wet tropical forest to determine the separate and combined effects of canopy opening and debris deposition on soil C and nutrients throughout the soil profile (1 m). Debris deposition alone resulted in higher soil C and N concentrations, both at the surface (0-10 cm) and at depth (50-80 cm). Concentrations of NaOH-organic P also increased significantly in the debris deposition only treatment (20-90 cm depth), as did NaOH-total P (20-50 cm depth). Canopy opening, both with and without debris deposition, significantly increased NaOH-inorganic P concentrations from 70-90 cm depth. Soil iron concentrations were a strong predictor of both C and P patterns throughout the soil profile. Our results demonstrate that both surface- and subsoils have the potential to significantly increase C and nutrient storage a decade after the sudden deposition of disturbance-related organic debris. Our results also show that these effects may be partially offset by rapid decomposition and decreases in litterfall associated with canopy opening. The significant effects of debris deposition on soil C and nutrient concentrations at depth (>50 cm), suggest that deep soils are more dynamic than previously believed, and can serve as sinks of C and nutrients derived from disturbance-induced pulses of organic matter inputs.

Introduction

Climate change is affecting the intensity of severe tropical storms, the most powerful of which are cyclones (also referred to as hurricanes or typhoons), with significant implications for ecosystem processes in near-coastal tropical forests (Knutson *et al.*, 2010, Lugo, 2000, Walsh *et al.*, 2016). These observed and projected changes in disturbance regime are likely to play an important role in regulating ecosystem carbon (C) and nutrient dynamics (Crausbay & Martin, 2016, Dale *et al.*, 2001, Lugo, 2000, Lugo, 2008, Xi, 2015). The major effects of severe storms on ecosystem structure, and feedbacks on multiple ecosystem processes, have been well documented in forests globally (Bellingham *et al.*, 1996, Boose *et al.*, 1994, Burslem *et al.*, 2000, Lin *et al.*, 2011, Lugo, 2008, Shaw, 1983, Tanner *et al.*, 1991, Webb, 1958, Wolfgang, 1985, Xi, 2015). However, the bulk of this research has focused on aboveground dynamics, and much less attention has been given to the effects on belowground processes such as soil C and nutrient cycling (Ostertag *et al.*, 2003, Parrotta & Lodge, 1991, Sanford *et al.*, 1991, Vargas, 2012, Vargas & Allen, 2008). Furthermore, despite the major implications of the belowground effects of severe tropical storms on the global C cycle, the long-term (> 5 y) effects on soil biogeochemistry have only rarely been studied in tropical forests.

Organic matter redistribution is likely to be a major driver of belowground responses to canopy disturbance associated with storm events (Lodge *et al.*, 2014, Sanford *et al.*, 1991, Silver *et al.*, 2014, Turton, 2008, Vargas, 2012). High velocity winds result in a large deposition of biomass from the canopy to the forest floor (Frangi & Lugo, 1991, Horng *et al.*, 1995, Lin *et al.*, 2003, Lodge *et al.*, 1991, Wang *et al.*, 2016, Whigham *et al.*, 1991, Xu *et al.*, 2004). The contribution of green leaves and live branches to total litterfall during these disturbances results in a pulse of C and nutrients to the soil (González *et al.*, 2014, Lin *et al.*, 2002, Lodge *et al.*, 1994, Lodge *et al.*, 1991, Silver *et al.*, 2014, Sullivan *et al.*, 1999). The effects of organic matter redistribution during storms on soil biogeochemistry may be varied and dependent on the time-scale considered (Scatena, 2013, Silver *et al.*, 1996). In the short-term, storm-associated pulses of organic debris can provide labile C, as well as N, phosphorus (P), and other essential nutrients for microbial and root uptake, potentially increasing rates of plant and microbial activity (Lodge *et al.*, 1994, Lodge *et al.*, 1991, Vargas, 2012, Vargas & Allen, 2008). Large inputs of woody debris with high C:N and C:P ratios can simultaneously lead to increased nutrient immobilization by microbial decomposers, which, in addition to leaching losses, results in a transient decrease in nutrient availability (Rice *et al.*, 1997, Zimmerman *et al.*, 1995). Rapid decomposition of storm-related debris may increase rates of ecosystem recovery from disturbance (Beard *et al.*, 2005). Ostertag *et al.* (2003) found that the forest floor mass returned to pre-disturbance levels in less than one year following a hurricane in Puerto Rico. They suggested that the rapid disappearance of leaf litter and associated nutrients was an indicator of a high degree of resilience of tropical forests to severe storms (Beard *et al.*, 2005, Ostertag *et al.*, 2003, Vogt *et al.*, 1996).

Partially decomposed organic materials can be translocated deeper into the soil profile. Most of the research on disturbance effects has been conducted in surface soils (< 50 cm), so little is known about if and how disturbance impacts are propagated through the soil profile (Xu *et al.*, 2004). Over time, a fraction of the C, N, and P in the deposited debris may be transported into the subsoil through a variety of physical and biological pathways (Cotrufo *et al.*, 2015, Leff *et al.*, 2012). The subsoil has the potential to become a major sink for soil C and nutrients derived from the disturbance-induced pulse of organic matter through increasing organ-mineral interactions or accumulating detritus. Thus, the legacy of storms and hurricanes on soil biogeochemistry is likely to occur throughout the entire soil profile, and not just near the surface.

In addition to the pulse of debris, changes in forest structure caused by severe storms can have complex and interacting effects on ecosystem C and nutrient cycling (Shiels *et al.*, 2015, Xi, 2015). For example, canopy opening can alter microclimate conditions (i.e., light, temperature, and humidity; Shiels & González, 2014), reduce litterfall inputs (Beard *et al.*, 2005, Silver *et al.*, 2014), cause fine root mortality (Beard *et al.*, 2005, Silver *et al.*, 1996, Silver & Vogt, 1993), and stimulate decomposition rates at the soil surface (Ostertag *et al.*, 2003). Changes in tree species composition following disturbance (i.e., an increase in light-demanding, low wood density pioneers such as *Cecropia sheberiana*) could alter the quantity and quality of C inputs, and affect subsequent rates of C and nutrient cycling (Shiels *et al.*, 2010). These changes in the quantity and quality of organic matter inputs associated with canopy opening can have major implications for the trajectories of ecosystem recovery, although this may also be a transient response as the pre-disturbance vegetation recovers. At longer time-scales, the recovery of organic matter inputs to pre-disturbance levels (both quantity and quality) may be an important factor in determining legacy effects on soil biogeochemistry (Scatena *et al.*, 1996, Silver *et al.*, 1996).

Disentangling the complex effects of canopy opening and debris deposition in tropical forests is critical to better understand the long-term implications of changing disturbance regimes on ecosystem C and nutrient dynamics. In this study, we used the long-term canopy trimming experiment (CTE) in a wet tropical forest in Puerto Rico (Shiels & González, 2014) to determine the separate and combined effects of canopy opening and debris deposition on soil C and nutrients throughout the soil profile. This design did not mimic all aspects of a severe storm event (e.g. high wind and rainfall and associated sheer stress impacts), but instead was a controlled experiment that facilitated the study of two important impacts common to all severe storm events that would not be possible during an actual storm. We tested the hypothesis that hurricane disturbances (combined canopy opening with debris deposition) have detectable long-term effects on soil organic C and nutrient concentrations, due primarily to the lasting impacts of debris deposition on the soil surface. We predicted that the large debris deposition associated with severe storms would dominate the biogeochemical responses, with greater C and nutrient concentrations than plots with canopy opening only. We also hypothesized that canopy opening alone would lead to long-term declines in soil C and N due to lower litterfall rates (Scatena et al. 1996, Silver et al. 2014), and an increase in soil P, due to lower plant P uptake from a damaged canopy, coupled with higher P retention in soils relative to the C and N released via decomposing litter (Mage & Porder, 2012, Sanford *et al.*, 1991). Finally, we predicted that the effects of debris deposition would lead to long-term C, N, P accumulation through the soil profile, and that when combined with canopy opening this effect would decline due to the higher decomposition rates and lower litterfall inputs associated with canopy disturbance (Ostertag et al. 2003).

Materials and Methods

Study site and experimental design

The study was conducted in the El Verde research area of the Luquillo Experimental Forest (LEF), Puerto Rico, as part of the NSF-sponsored Long Term Ecological Research program (18° 20’ N, 65°49’ W). This area of subtropical wet forest is dominated by the tabonuco forest type, which characterizes most of the lowlands within the LEF (~350 m a.s.l.; Ewel & Whitmore, 1973). Dominant tree species include *Dacryodes excelsa* (Vahl) (Burseraceae), *Sloanea berteriana* (Choisy) (Elaeocarpaceae), and *Manilkara bidentata* ((A.DC)A.Chev) (Sapotaceae), as well as the palm *Prestoea acuminata* (Willdenow) H.E. Moore var. montana (Graham) Henderson and Galeano (Arecaceae). Mean air temperature from 2000 to 2017 was 24 °C, while mean annual precipitation is ~3,500 mm, both exhibiting only slight seasonality (Brown *et al.*, 1983, García-Martinó *et al.*, 1996). Soils are classified as highly weathered Oxisols derived from volcaniclastic sediments, with high clay content (Mage & Porder, 2012, Silver *et al.*, 1994).

Soils were collected from the Canopy Trimming Experiment (CTE), a long-term, ecosystem-scale study aimed at understanding the effects of severe disturbances on forest dynamics by separating the individual and interactive effects of canopy opening and debris deposition (Shiels & González, 2014). The CTE consisted of a randomized complete block design that imposed the following treatments replicated across three blocks: untreated control, canopy opening only, debris deposition only, and a combination of canopy opening and debris deposition. One soil core (2.5 inches in diameter) was collected from each of twelve 30 x 30 m plots, which resulted in three replicates per treatment per depth. Within each block, plots were separated by at least 20 m, and factors such as land-use history (>80% forest cover in 1936), soil type (Zarzal clay series), topography (average slope of 24°), and elevation (340-485 m) were similar across blocks (Shiels *et al.*, 2010).

Treatments were imposed between late 2004 and early 2005, and a range of ecological processes including plant succession, litterfall, and nutrient cycling was followed for nearly a decade afterwards (Shiels & González, 2014). In late 2014, soils were sampled in each plot at 10 cm intervals down to 1 m depth. Immediately after collection, soils were placed in labeled zip-lock bags (double-bagged to retain moisture) and shipped in coolers overnight from Puerto Rico to UC Berkeley for laboratory analyses.

Laboratory procedures

We measured soil pH in a 1:1 soil to water slurry, as well as gravimetric soil moisture by oven-drying subsamples at 105 °C to a constant weight. Total soil C and N content were measured on a CE Instruments NC 2100 Elemental Analyzer (Rodano, Milano, Italy) on soils that were air-dried and ground. To measure labile (i.e., soluble phosphate) and recalcitrant (i.e., bound to Fe or Al) P pools, we used a modified Hedley fractionation with $NaHCO_3$ and NaOH extractions, respectively (Tiessen & Moir, 1993). Briefly, we sequentially extracted approximately 1.5 g fresh soil with 0.5M $NaHCO_3$ and 0.1M NaOH. Both extracts were analyzed colorimetrically for inorganic P and total P after digestion with acid ammonium persulfate, while organic P was calculated as the difference between total and inorganic P (Murphy & Riley, 1962). We measured Fe species as these have been shown to be an important predictor of both C (Hall and Silver 2015) and P (Chacon et al. 2006) cycling in this ecosystem. Concentrations of reduced and oxidized iron (Fe(II) + Fe(III)) were measured with a 0.5 M HCl extraction and analyzed colorimetrically. Soils were extracted with 0.2 M sodium citrate/0.05M sodium ascorbate solution and analyzed on an inductively coupled plasma atomic emission spectrometer (Perkin-Elmer, USA) for poorly crystalline Fe. We were only able to analyze two treatments for citrate ascorbate-extractable Fe due to limited resources, and thus chose the controls and the opening+debris treatments as being most representative of a natural event.

Soil C density fractionation was used to compare free-light (FLF), occluded-light (OLF), and heavy (HF) fractions in surface and deep soils (0-10 and 50-60 cm, respectively) of the control and debris treatments (Marín-Spiotta *et al.*, 2008). We chose this comparison because the debris deposition only treatment was the only one that showed statistically significant changes in soil C concentrations along the depth profile. Depths were chosen based on statistically significant patterns in the bulk soil C concentration data, with the 50-60 cm depth representing the top of the zone of accumulation in the subsoil. Using a sodium polytungstate solution (1.85 g/cm^3) we separated each fraction from moist soils and determined their mass and C concentration after rising repeatedly with DI water (stopped when density reached 1.0 g/cm^3). Bulk density measurements from the CTE (D.J. Lodge and A. Shiels, *unpublished data*) were used to calculate soil C pools in each fraction.

Statistical analyses

A linear mixed-effects model with treatment and depth as fixed factors, and block as a random factor, was used to test for significant differences in soil moisture, pH, bulk soil C and N concentrations, and P and Fe concentrations. To compare the soil density fractionation data from the control and debris deposition treatments we used students t-tests, while linear and non-linear regressions were used to determine relationships between the measured variables (i.e., C, P, Fe). All analyses were conducted in the open source software, R Studio (Version 1.0.136). Values reported in the text are means plus or minus one standard error. Statistical significance was determined at $p < 0.10$ unless otherwise noted.

Results

Soil moisture and pH

Gravimetric soil moisture decreased significantly with depth across all treatments ($p < 0.0001$; Figure 1a). Mean soil moisture at 0-10 cm was 42.7 ± 1.4 % and decreased linearly to 60 cm. Below this depth (60-100 cm), soil moisture showed little variation, with mean values ranging between 32.5 ± 0.5 and 34.2 ± 0.5 % (Figure 1a). There was no significant treatment effect on soil moisture.

Soil pH also decreased significantly with depth across all treatments ($p < 0.0001$; Figure 1b). Soil pH at 0-10 cm ranged from 4.62 ± 0.17 to 4.89 ± 0.08 (canopy opening only and debris deposition only treatments, respectively), while values at 90-100 cm ranged from 4.97 ± 0.11 to 5.16 ± 0.08 (debris deposition only and control treatments, respectively). There was a significant treatment effect of canopy opening only in surface soils (0-30 cm, $p < 0.05$), which resulted in the lowest pH values measured (< 4.75) and a steeper depth gradient than the other treatments (Figure 1b).

Iron species

The concentration of both HCl- and citrate ascorbate-extractable Fe species decreased significantly with depth across all treatments ($p < 0.001$; Table 1). Soil Fe concentrations decreased linearly from surface soils down to 60 cm, where concentrations stabilized at low values. The sum of HCl-extractable Fe(II) and Fe(III) decreased from 1.7 ± 0.3 mg/g at 0-10 cm (mean across treatments), to less than 0.5 mg/g below 50 cm for all treatments. Similarly, citrate ascorbate-extractable Fe showed strong depth gradients regardless of the treatment, decreasing from 1.9 ± 0.2 mg/g at 0-10 cm and stabilizing around 0.1 mg/g below 60 cm. There were no significant treatment effects on any of the forms of soil Fe measured.

Soil carbon and nitrogen concentrations

Across all treatments, there was a significant decrease in soil C concentration with depth ($p < 0.0001$; Figure 2a). Mean soil C concentrations across treatments decreased from 5.8 ± 0.3 % at 0-10 cm to 0.6 ± 0.1 % at 90-100 cm. There was a significant treatment effect of debris deposition only on soil C concentrations ($p < 0.05$; Figure 2a), both at the surface (0-10 cm) and at depth (50-80 cm). Notably, soil C concentrations below 60 cm were lower than 1 % for all treatments except debris deposition only, demonstrating the significant treatment effects on subsoil C concentrations. All other treatments (opening+debris and canopy opening only) resulted in trends of increasing soil C across all depths, except deep soils (>80 cm) in the canopy opening only treatment, which showed a trend of lower soil C relative to the control. Including the data from all depths, soil C concentrations were significantly positively correlated with citrate ascorbate-extractable Fe in both control ($R^2 = 0.95$, $p < 0.05$) and canopy opening with debris deposition treatments ($R^2 = 0.85$, $p < 0.05$). Soil C concentrations also showed a significant positive correlation with HCl-extractable Fe ($R^2 = 0.79$, $p < 0.05$).

Soil N concentrations decreased significantly with depth across all treatments ($p < 0.05$; Figure 2b). Mean soil N concentrations ranged from 0.43 ± 0.02 to 0.05 ± 0.01 %, at 0-10 and 90-100 cm, respectively. There was a significant treatment effect of debris deposition only on soil N concentrations from 50-80 cm, where soil N concentrations were particularly low (<0.1 %) and showed a >100% increase in response to the treatment (Figure 2b).

Overall, debris deposition alone signficantly increased soil C and N concentrations by 26 to 142 % and 16 to 123 % (calculated for each 10 cm sampling interval relative to the control treatment), respectively, with the greatest relative increases (i.e., >100 %) occuring deep in the soil profile at 60-70 cm (Table 2).

Soil carbon density fractionation

Analyses of soil C fractions revealed that higher bulk C concentrations in the debris deposition only treatment (0-10 cm depth) was due to greater FLF and HF, although this was only marginally statistically detectable ($p < 0.17$); no change was observed in the OLF (Figure 3b). The increase in FLF C stocks at 0-10 cm likely resulted from an accumulation of particulate organic matter derived from the deposited debris (Table S1), as C concentrations were not significantly different from the control treatment (Figure 3a). Conversely, the trend of increased HF C stock at 0-10 cm in the debris deposition only treatment was likely driven by the significantly higher soil C concentrations of the HF (Figure 3a), as there were no significant differences in the mass of the HF between treatments (Table S1). The greater variability at 50-60 cm depth precluded the detection of statistically significant differences in soil C stocks (Figure 4b). In general, increases in the mass of the free-light and occluded-light fractions tended to be more important than C concentrations, while the opposite was true for the heavy fraction (Table S1).

Soil phosphorus fractionation

There was a significant exponential decline in NaOH-organic P with depth ($p<0.05$; Table 3), which also resulted in a significant decrease in NaOH-total P with depth across all treatments ($p < 0.05$; Table 3). The NaOH-organic P pools was strongly positively correlated with organic C across treatments ($R^2 = 0.94$, $P < 0.01$). Similar to the pattern for soil C, NaOH-organic P was also strongly positively corrleated with citrate ascorabate-extractable Fe ($R^2 = 0.92$, $P < 0.01$) and HCl-extractable Fe ($R^2 = 0.76$, $P < 0.05$).

There was a significant increase in NaOH-organic P in the debris deposition only treatment from 20-90 cm ($p<0.05$; Figure 5b), as well as for NaOH-total P from 20-50 cm ($p<0.05$; Figure 5a). There was also a treatment effect of canopy opening, both with and without debris deposition, which significantly increased NaOH-inorganic P concentrations from 70-90 cm ($p < 0.05$; Figure 5c). Although concentrations of NaOH-organic P made up most of the NaOH-total P found in surface soils, NaOH-inorganic P was of similar magnitude, or greater than NaOH-organic P at depth (i.e., below 80 cm) across all treatments. Overall, both the canopy opening only and debris deposition only treatments had significant effects on NaOH-inorganic P and organic P, respectively, while the combined canopy opening and debris deposition treatment significantly increased NaOH-inorganic P at depth (Figure 5a-c).

Discussion

The impacts of debris deposition

Canopy disturbance and associated debris deposition during severe storm events result in complex and interacting effects on ecosystem biogeochemistry. We hypothesized that debris deposition would be the dominant driver of biogeochemical responses to hurricane disturbance, due to the large direct impact of C and nutrient inputs to the forest floor (Lodge *et al.*, 1994, Lodge *et al.*, 1991, Sanford *et al.*, 1991). We found that the effects of debris deposition significantly increased C, N and P over a decadal time scale. The initial experiment deposited approximately 3 kg C m^{-2} (dry mass) on the soil surface as part of the debris deposition treatments in 2005 (Shiels & González, 2014). In 2015, we measured a significant increase in soil C stocks in response to the debris deposition only treatment amounting to 1.02 ± 0.19 and 1.12 ± 0.71 kg C m^{-2} at 0-10 and 50-60 cm, respectively. There was no significant increase in litterfall in this treatment (first five years only, Silver *et al.*, 2014), thus the greater soil C stocks likely resulted from an increased capacity to sequester C in soil, associated with the transport of dissolved and particulate organic matter from the debris into the subsoil (Cotrufo *et al.*, 2015). This may have been facilitated by an increase in mineral and organic bonding at depth (Vogel *et* *al.*, 2014). Clearly, debris deposition had long-term effects on soil biogeochemistry in this forest, a demonstration of the decadal legacy of hurricane disturbances on wet tropical forests.

Soil density fractionation allowed us to explore the mechanisms behind the significant increases in soil C stocks throughout the soil profile. We found that the FLF was relatively C-rich, while the HF accounted for much of the mass of C in these soils, similar to what has been described in other tropical (Marin Spiotta et al. 2009, Cusack et al. 2010) and temperate (Swanston et al. 2005) forests. In general, the FLF is thought to consist of more labile, and thus less stable materials, while the HF is thought to contain more stabilized organic material (Swanston et al. 2005, but see Schmidt et al. 2011). Ten years following debris deposition, we measured a marginally significant increase in the mass of the FLF and a significant increase in the C concentration of the HF in surface soils. While the increase in HF might be expected given the large initial inputs of C to the soil, the slight increase in the FLF over this time period was surprising given the rapid rates of decomposition in this ecosystem (Parton et al. 2007, Ostertag et al. 2003), and suggests that particulate C may persist in soils for longer than previously believed (Lodge *et al.*, 2016).

Soils at depth (50-60 cm) also showed a trend of increasing FLF and OLF mass, although the magnitude was lower than at the surface where particulate organic matter inputs dominate. Deeper soils were characterized by a low mass of the FLF and OF (<0.1 g), and despite the marked increases of the mass of these fractions, most of the enhancement in soil C stocks at depth could be attributed to the doubling of the C concentration of the HF (0.68 to 1.32 %), which made up more than 98% of the bulk soil mass. The increase in C concentration of this fraction suggests that deep soils were an important sink for the debris-C deposited. This is likely due to the abundance of free sites for C-mineral associations at depth (Coward et al. 2017), further supported by our Fe data. Deep soils may thus serve as a significant hot spot for C sequestration following disturbance in highly weathered tropical forest soils.

Organic P concentrations were significantly higher throughout the soil profile in response to debris deposition only, highlighting the role of soil organic matter as a mediator of the observed responses on soil C and nutrients. Debris deposition alone led to higher NaOH-organic P concentrations throughout the soil profile a decade after the treatments were applied. The observed increase in NaOH-organic P followed a similar pattern to soil C, resulting in a significant correlation between C and P. This suggests that transport of organic matter into the soil profile can also enhance nutrient content at depth. Sanford *et al.* (1991) used the CENTURY model to simulated C and P cycling after repeated hurricanes and predicted greater surface soil P in hurricane-affected forests relative to hurricane-free forests. Our results provide empirical evidence of their modeling results and extends the finding to the subsoil. This reveals a potential role of disturbance events in helping to alleviate P limitation, which often limits biological processes in wet tropical forests (Vitousek *et al.*, 2010).

Effects of canopy opening

We hypothesized that canopy opening would decrease soil C and N stocks due to the reduction in litter inputs and the propensity of C and N to be lost during decomposition following disturbance (Vargas and Allen 2012). Contrary to our expectations, there was no significant effect of canopy opening only on soil C and N stocks throughout the soil profile. This is striking given the large decrease in surface litter inputs measured during the first 5-y following the disturbance (Silver et al. 2014). Zhang and Zak (1995) found that litter decomposition rates declined in large gaps relative to smaller openings and intact canopies. Our data suggests that changes in environmental conditions associated with canopy opening, separate from debris deposition, are insufficient to deplete soil C and N stocks at a decadal scale of resolution.

We predicted that soil P pools might increase following canopy opening due to a reduction in P uptake by damaged vegetation and the propensity of Fe- and aluminum (Al)-rich soils to retain P. The canopy opening treatment led to an increase in inorganic P concentration at depth (70-90 cm), a response that was not observed in any other treatment. Canopy opening may have induced an increase in aboveground biomass investment in the recovering vegetation, leading to a decrease in C allocation to deep roots and thus lower P uptake at depth. It is possible that at longer time-scales, after aboveground biomass has fully recovered from canopy opening, belowground C investment by vegetation could again allow for root scavenging of inorganic P at depth, causing concentrations to return to pre-disturbance levels. Canopy opening also led to a significant reduction in soil pH in surface soils (0-30 cm). Forest disturbances that affect the canopy have often been found to increase soil acidity by altering soil moisture, nitrate availability, and nitrification rates, although these effects are often most notable at short time-scales (Silver *et al.*, 1996, Silver & Vogt, 1993). The lasting effects of canopy opening on soil acidity in our study suggests that the recovering vegetation is contributing to the maintenance of this effect, perhaps by increases in root exudation rate of organic acids or changes in the species contributing to litterfall (Shiels *et al.*, 2010).

Combined effects of canopy opening and debris deposition

The goals of this study were to disentangle the effects of canopy opening and debris deposition impacts from hurricane disturbance in a wet tropical forest. As discussed above, debris deposition led to a significant increase in soil C, N, and organic P stocks, while canopy opening alone did not significantly affect C and N, and but increased inorganic P at depth. The combined canopy opening and debris deposition treatment resulted in similar responses of soil C and N, albeit not statistically significant, as the debris deposition only treatment. The long-term reduction in aboveground organic inputs (i.e., litterfall) due to canopy opening may have limited the magnitude of this response. Previous results from the CTE and from studies monitoring the recovery of litterfall following hurricanes have shown that aboveground C inputs take at least 5 years to recover to pre-disturbance level (Scatena *et al.*, 1996, Silver *et al.*, 2014). Our results suggest that a one-time pulse of debris deposition without the effects of canopy opening enhanced C and N pools relative to the control. It is likely that similar processes occurred when debris deposition was coupled with canopy opening, but that reduced litter inputs decreased the amount of C translocated downward. It is interesting that organic P did not show any trend in the canopy opening with debris deposition treatment, suggesting that this fraction could have been exploited by P-limited biota when faced with significant reductions in litterfall nutrient inputs.

Coupled biogeochemical cycles of C, Fe, and P

Our measurements throughout the soil profile and across treatments allowed us to explore relationships between soil C, Fe, and P concentrations, supporting previous work suggesting strong biogeochemical coupling of these elements (Hall *et al.*, 2016, Townsend *et al.*, 2011). The highly weathered soils at our site (i.e., Oxisols) are dominated by Fe and Al oxides, which play a key role in both C and P cycling, especially under fluctuating redox conditions (Chacon *et al.*, 2006). The significant positive correlation between soil C and Fe highlights the role of reactive Fe species in the binding of C to mineral surfaces in the soil—a process that is critical for enhancing rates of soil C sequestration throughout the soil profile (Keiluweit *et al.*, 2016). Moreover, the strong coupling between soil C and Fe was also revealed by the variable responses of soil C to debris deposition across blocks, where the magnitude of the response seemed to be mediated by soil Fe concentrations in each block (i.e., the strongest response of soil C to debris deposition only occurred in the block with the highest soil Fe concentrations). We also found a significant positive correlation between soil C and P, suggesting these elements are bound in soil organic matter whose concentration decreases markedly with depth (as does soil C and P). Although some of these patterns might arise from the vertical distribution of organic matter inputs (i.e., more inputs near the soil surface from litterfall and fine roots), our results highlight the strong biogeochemical coupling of these elements across the landscape and throughout the soil profile.

Implications for disturbance and recovery trajectories

Our results demonstrate that the deposition of organic matter associated with severe storms and hurricanes increased soil C and nutrients over a decade of ecosystem recovery. The increase in soil C and nutrient concentrations at depth (>50 cm) suggest that deep soils are more dynamic than previously believed, and have the potential to serve as sinks of C and nutrients derived from storm-induced pulses of organic matter inputs. However, when coupled with canopy opening, these effects became muted, likely due to the slow recovery of litterfall inputs, enhanced decomposition rates, and resource needs of recovering vegetation. The effects of canopy opening may ultimately limit the amount of C and nutrients transported through the subsoil, decreasing the subsidy, and possibly the resilience of these ecosystems, over the long-term.

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Figure captions:

Figure 1. (a) Depth profiles of gravimetric soil moisture by treatment; (b) Depth profiles of soil pH by treatment (error bars indicate ±1SE; n = 3; $*p<0.05$).

Figure 2. Depth profiles of total soil carbon (a) and nitrogen (b) concentrations by treatment (error bars indicate ±1SE; n = 3; $*p<0.05$).

Figure 3. Surface (0 to 10 cm) soil carbon (C) concentrations (a) and soil C pools (b) by density fraction for control and debris only treatments (FLF, free-light fraction; OLF, occluded-light fraction; HF, heavy fraction; error bars indicate ±1SE; n=3; $*p<0.10$).

Figure 4. Deep (50 to 60 cm) soil carbon (C) concentrations (a) and soil C pools (b) by density fraction for control and debris only treatments (FLF, free-light fraction; OLF, occluded-light fraction; HF, heavy fraction; error bars indicate ±1SE; n=3).

Figure 5. Depth profiles of NaOH-extractable total phosphorus (a), organic phosphorus (b), and inorganic phosphorus (c) (error bars indicate ±1SE; n=3; $*p<0.05$).

Table 1. Mean gravimetric soil moisture, soil pH, soil C and N, and Fe concentrations by soil depth and treatment (n/d = no data; S.E. in parentheses; n=3).

	Gravimetric soil moisture (%)				Soil pH				Soil C (%)				Soil N (%)				Citrate-ascorbate Fe (mg/g)				HCl Fe(II)+Fe(III) (mg/g)			
Soil depth (cm)	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening +Debris	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris
10	42.1 (3.3)	42.7 (1.2)	41.5 (4.2)	44.3 (3.4)	4.89 (0.07)	4.62 (0.17)	4.89 (0.08)	4.88 (0.09)	5.27 (0.65)	5.63 (0.81)	6.72 (0.41)	5.37 (0.27)	0.40 (0.05)	0.40 (0.04)	0.48 (0.04)	0.43 (0.00)	1.89 (0.05)	n/d	n/d	1.97 (0.39)	1.70 (0.48)	1.43 (0.11)	1.35 (0.21)	2.32 (1.23)
20	38.3 (2.0)	40.4 (1.5)	37.5 (3.4)	40.7 (3.0)	5.07 (0.04)	4.77 (0.17)	5.02 (0.06)	4.92 (0.02)	2.83 (0.26)	3.29 (0.73)	3.69 (0.59)	3.04 (0.21)	0.24 (0.02)	0.25 (0.04)	0.28 (0.03)	0.25 (0.00)	1.50 (0.14)	n/d	n/d	1.41 (0.34)	0.95 (0.25)	0.90 (0.23)	1.03 (0.28)	1.91 (1.39)
30	36.8 (1.8)	38.8 (1.5)	36.3 (2.6)	38.6 (2.2)	5.03 (0.04)	4.73 (0.19)	5.03 (0.02)	4.89 (0.04)	2.33 (0.24)	2.51 (0.53)	2.99 (0.67)	2.40 (0.17)	0.19 (0.02)	0.19 (0.03)	0.23 (0.03)	0.20 (0.00)	1.15 (0.17)	n/d	n/d	1.05 (0.37)	0.68 (0.08)	0.73 (0.25)	0.84 (0.36)	0.82 (0.49)
40	35.1 (1.7)	37.0 (2.5)	36.7 (3.4)	36.4 (1.9)	4.99 (0.04)	4.92 (0.19)	4.92 (0.04)	4.97 (0.02)	1.65 (0.29)	1.99 (0.65)	2.64 (0.84)	1.71 (0.26)	0.13 (0.02)	0.14 (0.04)	0.19 (0.05)	0.14 (0.01)	0.84 (0.27)	n/d	n/d	0.56 (0.31)	0.39 (0.12)	0.39 (0.10)	0.59 (0.28)	0.35 (0.19)

50	33.6 (1.1)	35.9 (2.6)	35.8 (3.5)	35.2 (1.7)	5.05 (0.02)	4.94 (0.17)	4.96 (0.07)	4.95 (0.07)	1.11 (0.17)	1.66 (0.62)	2.24 (0.86)	1.49 (0.15)	0.08 (0.01)	0.11 (0.03)	0.16 (0.05)	0.12 (0.01)	0.42 (0.11)	n/d	n/d	0.27 (0.13)	0.24 (0.05)	0.23 (0.05)	0.55 (0.24)	0.17 (0.05)
60	32.8 (0.8)	34.2 (1.2)	35.8 (3.6)	33.9 (1.2)	5.09 (0.02)	5.00 (0.17)	4.95 (0.12)	5.05 (0.08)	0.79 (0.09)	1.11 (0.30)	1.80 (0.71)	1.00 (0.18)	0.06 (0.00)	0.07 (0.01)	0.14 (0.04)	0.08 (0.01)	0.26 (0.08)	n/d	n/d	0.16 (0.05)	0.14 (0.02)	0.17 (0.03)	0.47 (0.27)	0.11 (0.02)
70	32.6 (1.5)	32.3 (0.4)	35.1 (3.6)	33.5 (1.9)	5.03 (0.15)	5.02 (0.17)	4.88 (0.03)	4.98 (0.08)	0.62 (0.03)	0.66 (0.20)	1.50 (0.50)	0.81 (0.12)	0.05 (0.01)	0.05 (0.01)	0.11 (0.03)	0.07 (0.00)	0.12 (0.04)	n/d	n/d	0.10 (0.03)	0.11 (0.02)	0.12 (0.01)	0.22 (0.07)	0.10 (0.02)
80	33.4 (1.4)	32.7 (1.5)	33.6 (3.9)	33.2 (1.5)	5.06 (0.04)	4.99 (0.18)	4.99 (0.09)	5.02 (0.05)	0.62 (0.06)	0.48 (0.13)	1.26 (0.38)	0.70 (0.10)	0.05 (0.01)	0.04 (0.01)	0.09 (0.03)	0.06 (0.01)	0.12 (0.03)	n/d	n/d	0.08 (0.02)	0.09 (0.02)	0.13 (0.01)	0.27 (0.10)	0.08 (0.01)
90	33.7 (0.7)	31.2 (0.5)	33.4 (3.8)	32.9 (1.9)	5.20 (0.11)	4.99 (0.25)	4.92 (0.09)	4.95 (0.09)	0.54 (0.08)	0.39 (0.11)	0.81 (0.29)	0.67 (0.19)	0.04 (0.00)	0.03 (0.01)	0.06 (0.02)	0.06 (0.01)	0.08 (0.02)	n/d	n/d	0.09 (0.04)	0.08 (0.01)	0.27 (0.16)	0.13 (0.01)	0.09 (0.01)
100	34.0 (0.8)	32.0 (0.9)	33.1 (3.3)	32.4 (1.9)	5.16 (0.08)	5.14 (0.29)	4.97 (0.11)	5.03 (0.06)	0.52 (0.03)	0.37 (0.07)	0.80 (0.29)	0.61 (0.15)	0.04 (0.00)	0.03 (0.00)	0.06 (0.02)	0.06 (0.01)	0.10 (0.02)	n/d	n/d	0.08 (0.03)	0.08 (0.00)	0.35 (0.25)	0.14 (0.04)	0.08 (0.02)

Table 2. Mean increases in soil C and N between control and debris deposition only treatments by soil depth (S.E. in parentheses; n=3). Bolded values indicate statistically significant differences between treatments ($p<0.05$). *At these depths in Block A (or Block B for soil N at 10 cm), control plots had higher soil C or N than debris deposition only plots.

	Soil Carbon (%)			Soil Nitrogen (%)		
Soil Depth (cm)	Control	Debris only	% Difference	Control	Debris only	% Difference
10	5.27 (0.65)	6.72 (0.41)	**29.8 (9.4)**	0.40 (0.05)	0.48 (0.04)	24.6 (18.5)*
20	2.83 (0.26)	3.69 (0.59)	**28.7 (10.5)**	0.24 (0.02)	0.28 (0.03)	**16.4 (3.3)**
30	2.33 (0.24)	2.99 (0.67)	26.2 (21.4)*	0.19 (0.02)	0.23 (0.03)	19.9 (14.0)
40	1.65 (0.29)	2.64 (0.84)	51.8 (32.3)*	0.13 (0.02)	0.19 (0.05)	**47.8 (22.3)**
50	1.11 (0.17)	2.24 (0.86)	85.7 (53.2)*	0.08 (0.01)	0.16 (0.05)	81.5 (44.6)*
60	0.79 (0.09)	1.80 (0.71)	116.5 (73.8)*	0.06 (0.00)	0.14 (0.04)	120.9 (61.4)*
70	0.62 (0.03)	1.50 (0.50)	142.0 (79.9)*	0.05 (0.01)	0.11 (0.03)	**122.9 (60.0)**
80	0.62 (0.06)	1.26 (0.38)	100.2 (55.7)*	0.05 (0.01)	0.09 (0.03)	73.2 (37.2)
90	0.54 (0.08)	0.81 (0.29)	58.2 (53.3)*	0.04 (0.00)	0.06 (0.02)	42.0 (40.8)*
100	0.52 (0.03)	0.80 (0.29)	58.2 (61.6)*	0.04 (0.00)	0.06 (0.02)	36.9 (39.8)*

	Inorganic $NaHCO_3$ Phosphorus	Organic $NaHCO_3$ Phosphorus	Total $NaHCO_3$ Phosphorus	Inorganic NaOH Phosphorus	Organic NaOH Phosphorus	Total NaOH Phosphorus

Table 3. $NaHCO_3$ and NaOH soil phosphorus fractions by soil depth and treatment (units: μg P/g dry soil; S.E. in parentheses; n=3).

Soil depth (cm)	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris	Control	Opening only	Debris only	Opening + Debris
10	1.4 (0.0)	1.2 (0.2)	1.5 (0.1)	1.4 (0.1)	5.6 (1.7)	6.9 (1.1)	8.7 (3.2)	6.2 (2.0)	7.0 (1.7)	8.1 (1.2)	10.2 (3.3)	7.5 (2.1)	15.1 (3.1)	15.5 (1.1)	20.2 (2.2)	16.7 (1.8)	57.9 (12.2)	59.0 (9.5)	75.0 (13.1)	60.3 (7.5)	73.0 (15.2)	74.5 (10.7)	95.2 (15.2)	77.0 (9.1)
20	1.2 (0.0)	1.0 (0.0)	1.2 (0.1)	1.1 (0.1)	2.9 (1.7)	3.0 (1.5)	5.8 (2.2)	6.0 (1.6)	4.1 (1.7)	4.1 (1.5)	7.1 (2.2)	7.1 (1.6)	9.3 (1.3)	9.9 (0.1)	12.6 (1.5)	9.7 (0.8)	30.5 (6.4)	33.7 (6.2)	47.3 (6.7)	36.3 (7.7)	39.8 (7.7)	43.6 (6.2)	59.9 (8.0)	46.0 (8.5)
30	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	2.9 (1.6)	3.6 (1.7)	4.6 (1.5)	2.4 (1.7)	4.0 (1.6)	4.7 (1.6)	5.6 (1.6)	3.5 (1.8)	8.4 (0.5)	8.4 (1.0)	12.4 (2.0)	7.8 (0.8)	26.9 (4.3)	24.2 (3.9)	45.8 (8.5)	25.6 (0.7)	35.3 (4.9)	32.6 (3.3)	58.2 (10.3)	33.4 (1.2)
40	1.0 (0.0)	1.0 (0.0)	1.0 (0.1)	1.0 (0.0)	3.4 (0.6)	4.2 (1.8)	4.3 (2.9)	2.9 (1.5)	4.4 (0.6)	5.2 (1.8)	5.3 (2.9)	3.9 (1.5)	7.8 (0.7)	7.5 (1.0)	10.7 (2.1)	7.1 (0.9)	19.4 (3.2)	20.1 (3.7)	32.6 (7.6)	16.7 (2.2)	27.2 (3.0)	27.6 (4.1)	43.4 (9.7)	23.8 (2.4)
50	0.9 (0.0)	1.1 (0.1)	1.0 (0.1)	0.9 (0.0)	2.3 (1.7)	3.4 (1.6)	4.2 (2.2)	3.4 (1.1)	3.2 (1.7)	4.5 (1.6)	5.2 (2.2)	4.4 (1.1)	10.2 (3.1)	9.1 (2.0)	9.1 (1.4)	7.6 (1.6)	20.7 (3.5)	19.1 (3.5)	28.4 (6.5)	13.9 (1.0)	30.8 (2.0)	28.3 (4.2)	37.5 (7.8)	21.5 (1.6)
60	1.0 (0.0)	1.0 (0.1)	1.0 (0.1)	0.9 (0.0)	3.8 (1.9)	2.2 (0.9)	4.3 (2.9)	4.9 (2.2)	4.8 (1.9)	3.2 (1.0)	5.3 (2.9)	5.8 (2.2)	9.3 (2.1)	10.0 (2.1)	9.3 (1.0)	10.2 (3.9)	13.0 (1.8)	15.1 (1.7)	22.9 (4.3)	11.3 (2.0)	22.3 (1.4)	25.0 (1.1)	32.2 (5.2)	21.6 (2.9)
70	0.9 (0.0)	1.0 (0.1)	0.9 (0.1)	0.9 (0.0)	2.3 (1.0)	2.1 (0.9)	4.6 (2.2)	2.3 (1.0)	3.2 (1.0)	3.1 (0.9)	5.6 (2.2)	3.2 (1.0)	9.5 (1.8)	12.2 (3.4)	8.4 (1.5)	10.3 (3.4)	10.2 (3.1)	12.1 (2.2)	22.5 (4.4)	8.9 (0.6)	19.7 (1.9)	24.3 (1.5)	30.9 (5.1)	19.2 (2.8)
80	0.9 (0.0)	1.1 (0.1)	1.0 (0.1)	0.9 (0.0)	1.7 (0.5)	2.6 (0.5)	2.9 (1.7)	1.7 (0.6)	2.6 (0.5)	3.7 (0.6)	3.9 (1.7)	2.6 (0.6)	10.8 (2.2)	15.5 (2.9)	9.5 (1.3)	11.9 (3.5)	10.2 (2.5)	13.3 (0.8)	16.1 (3.2)	8.9 (1.5)	21.0 (2.5)	28.8 (2.1)	25.6 (2.7)	20.8 (2.9)
90	0.9 (0.0)	1.3 (0.2)	1.3 (0.2)	1.0 (0.0)	1.2 (0.5)	2.3 (0.5)	3.7 (2.2)	2.7 (0.7)	2.1 (0.6)	3.6 (0.5)	5.0 (2.0)	3.7 (0.6)	10.7 (1.3)	19.1 (3.8)	9.7 (2.2)	14.7 (4.4)	10.4 (2.8)	13.2 (2.9)	12.1 (3.9)	9.2 (2.5)	21.1 (1.8)	32.3 (2.6)	21.8 (3.0)	23.9 (2.7)
100	1.0 (0.1)	1.2 (0.2)	0.9 (0.1)	1.0 (0.0)	1.1 (0.6)	1.9 (1.0)	2.9 (1.7)	1.7 (0.6)	2.1 (0.6)	3.1 (0.9)	3.9 (1.7)	2.6 (0.6)	12.1 (2.6)	17.1 (3.1)	9.1 (1.9)	16.6 (6.6)	15.1 (6.7)	11.3 (2.7)	11.6 (4.6)	9.7 (2.1)	27.1 (9.2)	28.5 (1.7)	20.7 (5.1)	26.3 (5.3)

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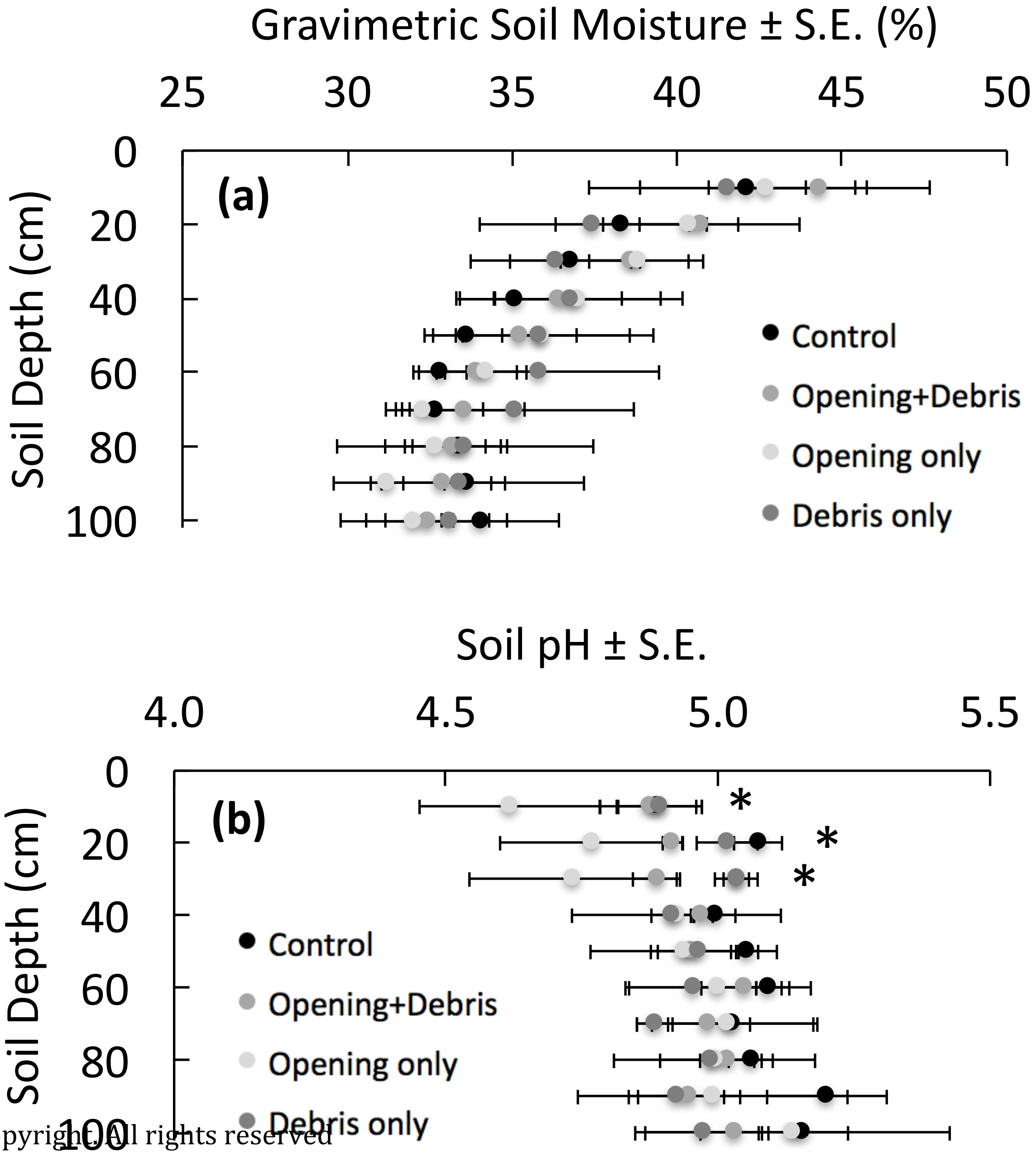
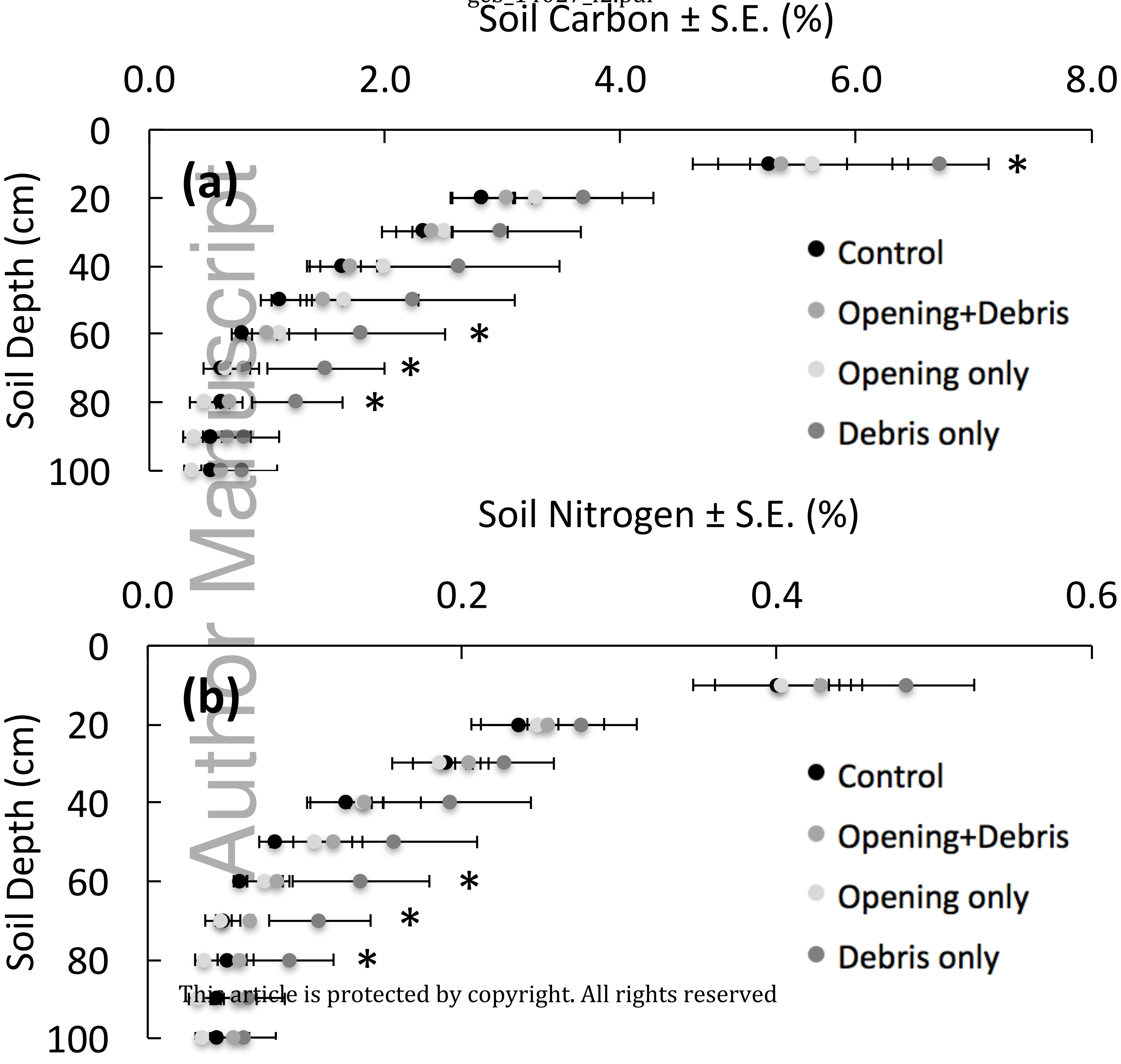
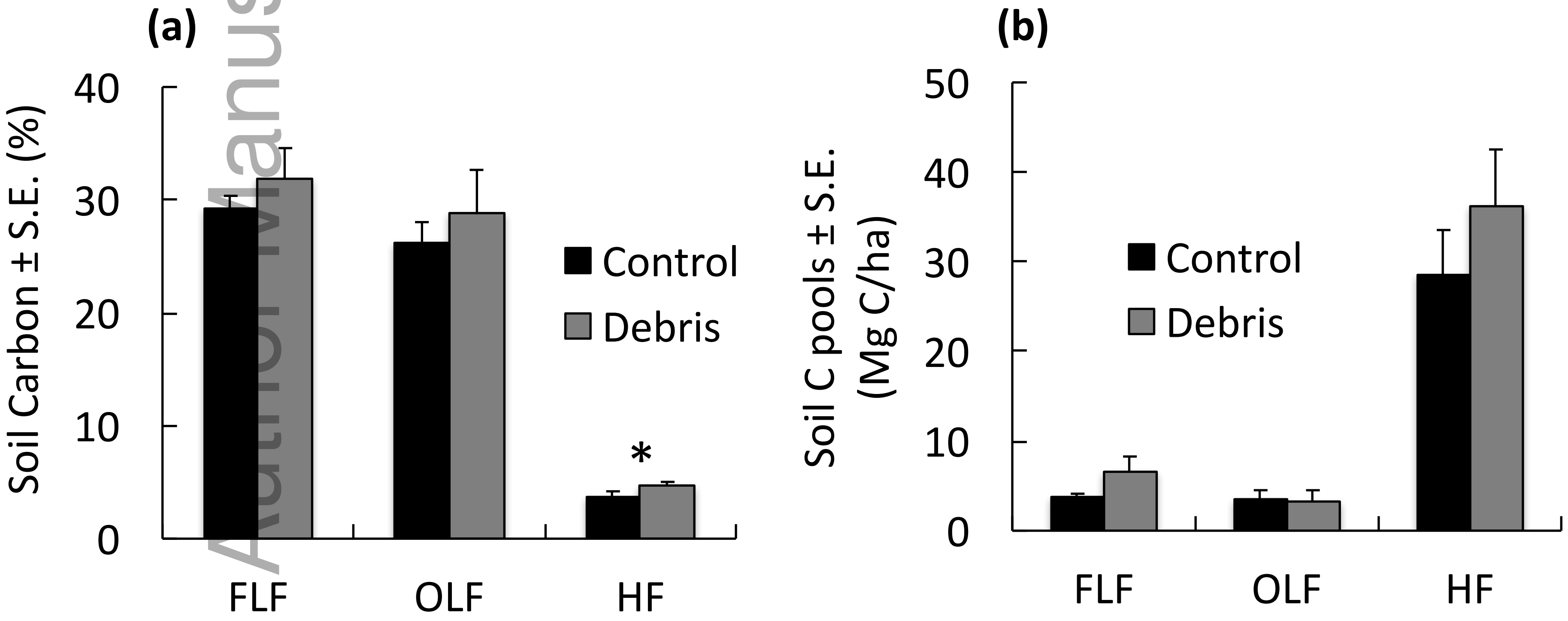
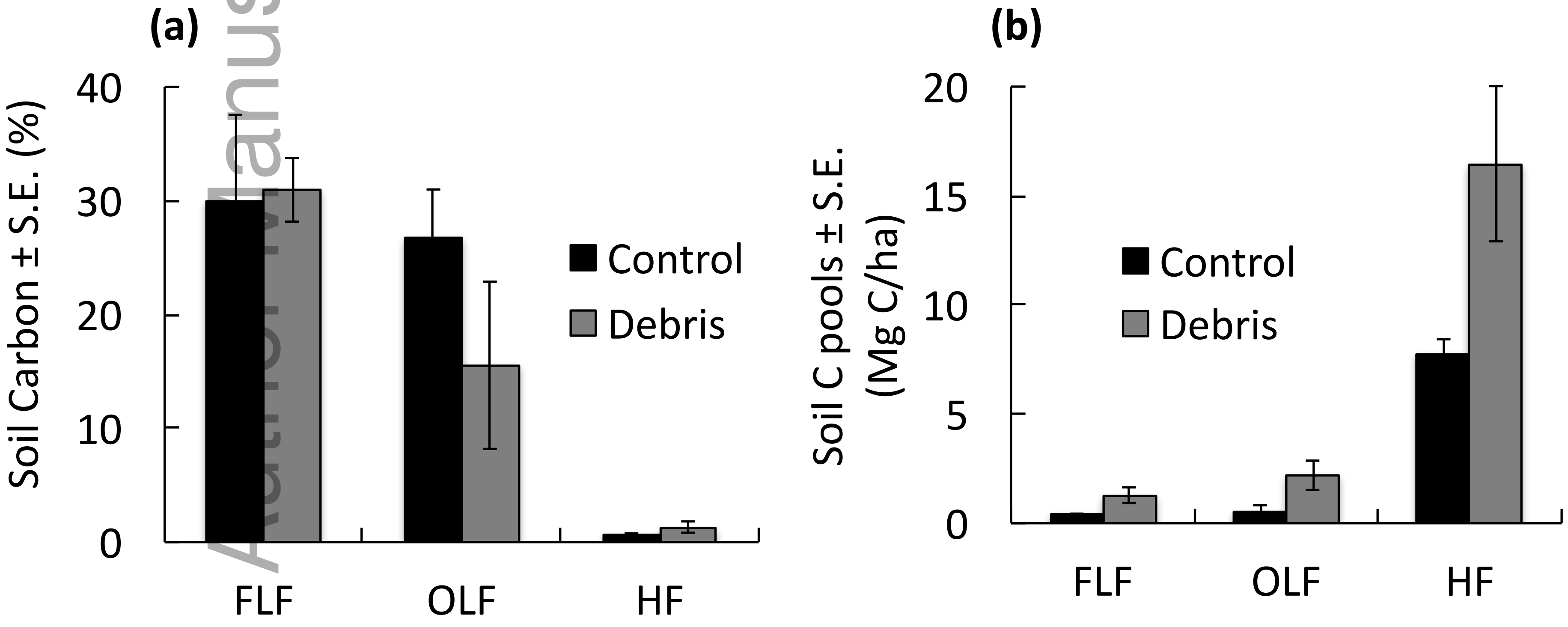
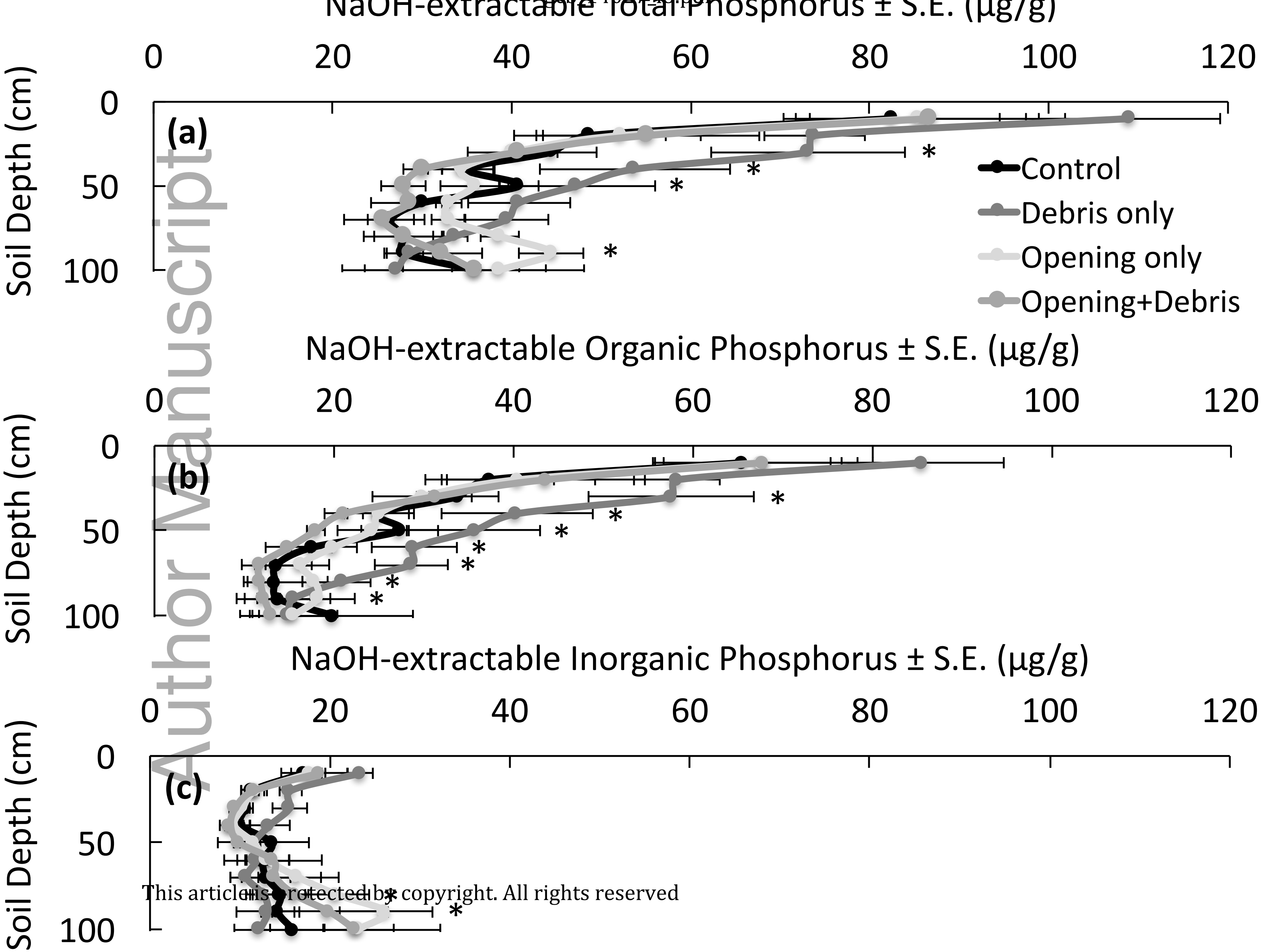



Soil Carbon ± S.E. (%)
0.0
2.0
4.0
6.0
8.0
Soil Depth (cm)
0
20
40
60
80
100
(a)
*
Control
Opening+Debris
Opening only
Debris only
Soil Nitrogen ± S.E. (%)
0.0
0.2
0.4
0.6
(b)


(a)
Soil Carbon ± S.E. (%)
40
30
20
10
0
FLF
OLF
HF
*
Control
Debris
(b)
Soil C pools ± S.E. (Mg C/ha)
50
40
30
20
10
0
FLF
OLF
HF
Control
Debris


(a)
40
30
20
10
0
Soil Carbon ± S.E. (%)
Control
Debris
FLF
OLF
HF
(b)
20
15
10
5
0
Soil C pools ± S.E. (Mg C/ha)
Control
Debris
FLF
OLF
HF


NaOH-extractable Total Phosphorus ± S.E. (µg/g)
0
20
40
60
80
100
120
Soil Depth (cm)
0
50
100
(a)
*
Control
Debris only
Opening only
Opening+Debris
NaOH-extractable Organic Phosphorus ± S.E. (µg/g)
(b)
NaOH-extractable Inorganic Phosphorus ± S.E. (µg/g)
(c)