Effects of tree girdling and herbivore exclusion on soils and microarthropod communities in a temperate deciduous forest

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Abstract

Experimental simulations of forest disturbances can be used to study altered resource availability and changes in soil-related processes, and can potentially lead to a better understanding of the long-term and differential effects for belowground communities. The goal of this study was to examine the effects of tree girdling and herbivore exclusion on soils and mesofauna communities at Black Rock Forest (Cornwall, NY) by the collection of leaf litter and soil arthropods. Girdling had a statistically significant effect on total arthropod abundances in leaf litter and only had a significant effect on mite abundances in soils, where abundances were lower in girdled plots. Herbivore exclusion did not have any significant effects on arthropod abundances in leaf litter or soils. Soil moisture was significantly higher inside exclosures compared to open forest and soil pH was higher in girdled plots compared to control plots. No significant effects of girdling or herbivore exclusion were observed for carbon and nitrogen content. The effect of girdling on microarthropod abundance illustrates some of the important links between aboveground and belowground communities mediated through roots and their surrounding habitat. The decreased abundances six years after girdling are indicative of long-term changes in belowground communities with an aboveground disturbance. The consequences of reduced microarthropod populations in forests will likely have important effects on food web dynamics in forest ecosystems. The lack of effect from herbivore exclusion in microarthropod abundances but some changes in soil properties indicates that long-term changes in the soil environment are likely to be important relative to changes to the belowground communities.

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Introduction

Aboveground disturbances and belowground consequences

Aboveground and belowground communities and processes are not independent of each other yet not all of the links have not been elucidated (Wardle 2006), particularly between aboveground plant communities and soil biota. In order to better understand the relationships between aboveground and belowground communities, many studies have investigated the effects of total removal, change in species composition or other aboveground community alterations on the belowground communities (e.g. Hooper et al. 2000, Wardle et al. 2001, Clapperton et al. 2002, Wardle et al. 2006). These studies report many important changes but little consensus on a consistent pattern explaining the links between the above- and belowground communities. Experimental simulations of forest disturbances, such as widespread tree death and plant removal through herbivory, can be used to study altered resource availability and changes in soil-related processes, and should lead to a better understanding of the long-term and differential effects for belowground communities.

One way to experimentally simulate a pathogen attack in forests is by girdling trees, a technique that severs the phloem and, in some cases, the xylem of the tree by cutting through the bark and leaving the rest of the tree otherwise intact (Levy-Varon et al. 2012). Girdling can cause changes in foliage, flowering and fruiting, rooting, sprouting, xylem-phloem dynamics and longevity of a tree (Noel 1970) as well as effects on biogeochemical and nutrient cycling (Edwards & Ross-Todd 1979). After a tree is girdled, roots can temporarily survive and maintain some passage of water and nutrients through the tree. Root respiration and fungi continue to consume carbohydrate reserves in roots (Noel 1970, Levy-Varon et al. 2012) resulting in the gradual depletion of these reserves and resulting in large carbon and nutrient losses (Edwards & Ross-Todd 1979).

Herbivory by browsing mammals affects plant communities in forests both by removal of plant material and through the selective grazing of the more palatable plants in the community (Wardle et al. 2001). Aboveground herbivory can thereby directly influence total resource availability, resource quality and carbon allocation (Bardgett & Wardle 2003). Indirectly, herbivory further influences belowground resource allocation by altering the amount of organic matter reaching the soil (Wardle 2006). Many herbivory studies that use fenced exclosures to explore the effects of herbivore exclusion on soils and soil communities. These studies report

mixed results with both increases and decreases in soil arthropod abundances, which has been attributed to the different feeding strategies and plant responses to herbivory in the various systems (Bardgett & Wardle 2003). The links between herbivores, plants and decomposers need to be better evaluated, particularly in regards to potential feedbacks between the plant and soil communities mediated through the presence or absence of herbivores.

Knowing that herbivore exclusion and tree girdling alter the aboveground plant community and studying the changes to the soils and soil communities can lead to a more complete understanding of the ecosystem consequences of these disturbances. Of particular interest is a greater knowledge of the effects on soil animals, their environment and their feeding patterns in litter and around roots. It is also important to know if these consequences are predictable and have long-term effects in forest ecosystem.

Mesofauna communities and functions

Mesofauna or microarthropods are soil animals that range from approximately 0.10mm to 10mm in body size and that permanently inhabit soil pore spaces. Mites and collembola are the main groups of microarthropods and they play a significant role in decomposition and are often considered significant to site biodiversity (Coleman et al. 2004). Microarthropods can feed on fungi and nematodes and are prey for both macrofauna and some megafauna. Temperate forests can support large communities of microarthropods because of high organic matter concentrations (Coleman et al. 2004). Local microarthropod populations are sensitive to disturbances, generally decreasing with any loss in organic matter (Coleman et al. 2004). Soils and soil biota are influential in the development and success of vegetation in a given environment and are important components of the ecological response to forest disturbances. Soil fauna are one of the major groups of heterotrophs in soils, with complex food web structures and resource use and with species interactions and distributions still needing to be quantified. Their food webs are linked to aboveground systems, but analyzing these links is difficult (Coleman et al. 2004).

Collembola, or the springtails, are a globally distributed group, often found in very high densities in soils. They are characterized by a furcula for jumping. Though they were once thought to belong within Insecta, they are currently classified as Entognatha, which with Insecta, composes the Hexapods. Collembola are capable of rapid population growth, therefore are often very responsive to soil disturbances (Coleman et al. 2004). Collembola are considered to be

fungivores, as they feed on fungi on decaying vegetation but there is some evidence that they are "non-specific" feeders or opportunistic feeders when nematodes, plant material and/or feces are readily available (Hopkin 1997, Coleman et al. 2004). Though collembola appear to have little contribution to CO_2 efflux, they have been shown to have an indirect impact on carbon and nitrogen dynamics and plant growth, though possibly indirect (Filser, 2002). Because they feed on fungi, collembola likely help regulate fungal populations and promote the decomposition process in soils (Hopkin 1997). Laboratory studies testing the impact of collembola on soil processes show that enzyme activity, respiration, and rates of nutrient release from leaf litter are increased by the presence of natural densities of collembola (Hopkin 1997). This suggests that the absence of collembola would slow the rates of some decomposition processes.

Mites (Subclass: Acari, Class: Arachnida) are usually the most abundant microarthropods in soils and are also found worldwide. Mites are often separated into four major groups (suborders); Oribatida, Prostigmata, Mesostigmata and Astigmata. Oribatids are fungivores or detritivores whereas mesostigmids are predatory. Prostigmids and Astigmids have varying feeding strategies, are generally less abundant groups (Coleman et al. 2004). Oribatids are usually the most abundant mites in forest soils, and greatly affect organic litter decomposition and nutrient dynamics by grazing on microbial populations and fragmenting plant detritus but their role in the function of forest soils is not fully understood (Evans 1992, Walter & Proctor 2013).

Main questions and hypotheses

Studying the distribution and abundances of these soil arthropods in response to common forest disturbances can lead to a greater understanding of belowground ecological dynamics. Levy-Varon and colleagues (2012) studied the short-term responses of the autotrophic soil CO_2 efflux to oak girdling. They observed a rapid rebound in soil respiration in the three years following girdling (Levy-Varon et al. 2014). Furthermore, Levy-Varon et al. (2012) estimated the autotrophic component of soil respiration at 50%, leaving the remaining 50% for heterotrophic respiration, which is includes the soil mesofauna and their feeding patterns. Though soil respiration rebounded rapidly, the soil organisms may respond differently because of their reliance on fungal communities in the root system and soils and their sensitivity to changes in the quantity and quality of litter. The direct quantification of mesofauna distribution

and abundance should provide valuable new information and insights regarding the effects of disturbance of carbon cycling in forests.

Mites and collembola have been shown to decrease in both abundance and species richness in boreal forests in response to tree girdling because they rely on carbonhydrates from ectomycorrhizal fungi in the root system (Remen et al. 2008 and Malmstrom & Persson 2011). Girdling terminates carbohydrate transport belowground, which eventually starves the roots and limits the soil organisms that rely on these energy sources.

The use of fenced exclosures to exclude large herbivores such as deer often generally increases arthropod abundances inside the exclosures as compared to outside of the exclosures (Baines et al. 1994, Allombert et al. 2005). Similarly, the introduction of browsing mammals has been shown to reduce the abundance of litter-dwelling mesofauna in some cases (e.g. Wardle et al. 2001). Large herbivores remove vegetation and alter carbohydrate exchange between belowground and aboveground plant components and subsequently may reduce the microarthropod communities that rely on the root fungi dependent on the carbohydrates from the plants.

The main questions addressed in this study are: (1) How does the belowground faunal community respond to aboveground alterations like tree girdling and fencing to exclude herbivory by large mammals? (2) Do soil organisms reflect the effects of girdling several years after the main cutting? (3) What are the effects of these alterations on carbon and nitrogen belowground?

I predicted that the total or partial removal of plant material by herbivores as well as the standing girdled trees will affect both the species abundance and composition of the mite and collembola communities, as these aboveground forest disturbances are connected to belowground biotic processes, particularly related to the feeding patterns of the microarthropods. As a result, abundance should be lower in girdled and herbivore-grazed plots compared to control plots and plots where herbivory by large mammals is prevented in both the leaf litter and soil layers. I further predicted that the upper soil layers will have more individuals than the lower soil layers.

Methods

Study site

Black Rock Forest is a 1,550-hectare reserve located in Orange County, New York. Measurements were conducted on the North Slope of Black Rock Mountain (41.45° N, 74.01° W). Soils (Chatfield Rockaway series) are acidic and nutrient poor, composed of clay loams resulting from glacial till (Lorimer 1981). This slope is dominated by mature *Quercus rubra*, *Quercus prinus*, *Quercus velutina*, *Quercus alba*, *Acer rubrum*, *Acer saccharum*, *Betula lenta* and *Nyssa sylvatica*. Soil cores were collected from Swartswood and Mardin soils (SXC, SXD) and from the Rock-Hollis complex (ROD) soils. SXC and SXD soils are very stony, moderately drained soils, composed of loamy till derived mainly from acid sedimentary rock on a moderately steep slope (USDA NRCS Custom soil report 2014). Total annual precipitation for 2013 was 1151.4 mm and for 2014 was 1195.8 mm and mean annual temperature for 2013 was 10.3 °C and 2014 was 9.6 °C.

Experimental design

The North Slope is the site of an established large-scale girdling experiment on *Quercus spp*. The site has been monitored since 2006 and girdling of trees to mimic pathogen attack was implemented in June and July 2008. Trees were notch girdled (Noel 1970) using a chainsaw to penetrate about 5 cm deep to cut the bark, phloem, cambium and xylem at breast height. Trees with DBH <2.54cm were not girdled and any trees alive after first round of girdling were cut up to two more times if necessary in 2009 and 2010. The site was divided into three blocks based on the slope position (lower, middle, upper) and each block was divided randomly into four treatments plots in a way that no adjacent plots had the same treatment: all oaks girdled, half of oaks girdled, all non-oaks girdled and control (Figure 1). Plots were 75x75 m divided into nine 25x25 m subplots (Figure 2). Each plot contained one fenced exclosure designed to exclude large herbivores roughly 10x20 m in size subject to forest conditions.

Soil fauna extraction and soil physical and chemical characterization

Two control plots and two oak girdled plots (control plots: C2 and B4, girdled plots: C1 and B2, Figure 1) were selected for study in 2014 based on soil series consistency and similarity. Pre-existing transects used for long-term plant and soil measurements served as sample points

where each point was randomly a number between one and eight and the first four points where cores could be obtained without substantial debris or rocks were collected (Figure 2). Soils from two locations inside the herbivore exclosures were also collected. Soil cores, collected during the first ten days of July using a 7.5 inch AMS Soil Core Sampler, were separated into two depths, 0-5cm and 5-10cm. Cores collected in the field were either immediately extracted or stored in the refrigerator for two days maximum. Two cores with two sampling depths and a 1ft by 1ft area of leaf litter were taken from each sampling point: one core (two sampling depths) was placed in Berlese funnels for 72 hours and the arthropods were collected in 70% ethanol and one core used for soil analysis. Soil fauna were sorted into major groups (mites, collembola, insects, non-acari arachnids, larvae, and other arthropods) using a dissecting microscope. Leaf litter dry weight was recorded along with soil wet and dry weight to calculate bulk density of each core. pH of soils was recorded in the field using a Kelway soil pH and moisture meter. Carbon and nitrogen for leaf litter and soils in the second set of cores from each site were analyzed by the Washington State University Stable Isotope Lab.

Statistical analysis

Linear mixed effect models were used to determine the effects of girdling and herbivore exclusion on the arthropod communities and soil properties. The fixed effects were the treatment (control vs. girdled) and the forest type with presence or absence of large herbivores (open forest vs. herbivore exclosure) for all results and depth for the soil arthropod analysis. The random effects were plot (four total plots) and sample (within each plot). P-values for comparison of full model and model without effect being considered were determined using ANOVA (analysis of variance). All statistical analyses were performed in R version 3.0.2. (R Core Team 2013)

Results

Collection Summary

More than 5400 arthropods were collected for this study, with more than 5000 in leaf litter and more than 370 in soils (Table 1). In litter, the upper soil layer, and soil and litter combined, mites were relatively the most abundance group, whereas insects were the most relatively abundant group in the lower soil layers (Table 2). Collembola were the least abundant group in all forest floor layers (litter and two soil depths).

Arthropod abundances in leaf litter

The linear mixed model results showed highly significant effects of girdling on the total arthropod abundance in leaf litter ($p = 0.003$), where control plots had many times greater mean total abundance compared to girdled plots (Tables 3 and 7, Figure 4). No significant effect of herbivore exclusion (open forest vs. exclosure plots) was found for mean total abundances. Mite abundance in leaf litter was much greater in the control plots compared to the girdled plots ($p = 0.002$). Non-mite arthropod abundance was also greater in control plots compared to girdled plots. Differences in mean total abundances when comparing open forest to exclosure plots were not significant for mite abundance. There were no significant effects of either girdling or herbivore exclusion on abundance of litter collembola.

The linear mixed model results showed significant effects of girdling in the total arthropod abundance per gram leaf litter ($p = 0.002$) and mite abundance per gram leaf litter ($p = 0.001$); the same patterns as for total abundances in leaf litter not corrected for weight (Tables 4 and 7).

Arthropod abundances in soils

Depth was a significant influence on mite abundance in soils ($p = 0.024$), with lower abundance in deeper soil layers; however depth was not significantly related to the abundances of other groups (Tables 3 and 7, Figure 4). The effect of girdling on mite abundance in soils was significant ($p = 0.05$). There was no significant effect of girdling on mean total arthropod abundance or collembola abundance. There was also no significant effect of herbivore exclusion on the abundances of any group. Collembola abundances were very low and not present in all soils samples and thus, they were not reported in soils results.

Soil properties

Depth had a significant effect on all soil properties measured ($p < 0.0001$) (Tables 5 and 7). Upper soil layer (0-5cm depth) moisture was significantly higher inside exclosures compared to open forest ($p = 0.004$). Lower layer soil moisture tended to be higher in control plots compared to girdled plots but the differences were not statistically significant. Bulk density of

the upper soil layer was greater in open forest plots compared to inside exclosures. Soil pH was not significantly different in girdled plots compared to control plots ($p=0.177$).

Carbon and nitrogen content of litter and soils

Carbon content and nitrogen contents were highest in litter and lowest in deeper soils (5-10cm depth) and all significantly different ($p < 0.0001$) (Tables 6 and 7, Figure 3). No significant effects of girdling or herbivore exclusion were observed. Shallow (0-5cm) and deeper (5-10cm) soil C:N ratios were not significantly different in girdled plots as compared to control plots ($p=0.316$).

Discussion

The belowground microarthropod community was significantly influenced by tree girdling, while soil properties were significantly altered by limiting herbivory. A significant reduction in both total and mite abundance in leaf litter, and for mites in soils, confirms the hypothesis about the effects of girdling on microarthropods. However, herbivore exclusion had no significant effect on any of the litter or soil microarthropod abundances. Soil moisture of the upper soil layer was higher inside the exclosures and this was the only soil property that had an effect from girdling or herbivore exclusion. These results did not confirm the hypotheses that abundance would be lower in girdled and herbivore-grazed plots. Together, these results stress the dynamics complexity of the links between above- and belowground portions of the forested ecosystem.

Surprisingly, collembola abundances were very low in many of the samples collected. Although it was initially expected that they would be comparable to mite abundances, the lack of significant numbers in most plots resulted in them not being included in the soil abundances analyses. There is a possibility that this was due to a sampling error or funnel extraction issues should be considered in additions to the likelihood that disturbance and trophic dynamics lead to the dominance by mites. Regardless, it's interesting to consider the possible ecosystem consequences of low collembola numbers such as reduced fragmentation of soil organic matter and regulation of the soil microbial community (Coleman et al. 2004).

Alterations in the community of mycorrhizal fungi and root death in the girdled plots may be particularly important to both the microarthropod community reported here and the related

soil carbon fluxes reported previously (Levy-Varon et al. 2012). Remen et al. (2008), found decreased abundance in fungivorous mite species shortly after girdling in spruce forests, which was attributed to the dependence of soil fauna on ectomycorrhizal fungi, which decreased post girdling. Schneider et al. (2005) show that mites feed on both mycorrhizal and saprotrophic fungi because they are a high quality food source. Malmstrom and Persson (2011) related mixed results of collembola abundance changes with girdling to root death post-girdling because root and root exudates contribute significantly to nutrition of soil animals. Microarthropod reliance on fungi could explain the long-term low abundance in girdled plots as compared to control plots and illustrates the potential multi-trophic effects of girdling. The small variation in litter quantity and quality (carbon and nitrogen) across all plots indicates that the litter habitat for the arthropods is not different between treatments and can potentially support the same numbers of arthropods. The variation in soil quality between the upper soil layers and the lower soils layers confirms that soil arthropod abundances are usually higher in the upper, most carbon and nitrogen rich layers.

The effect of girdling on microarthropod abundance illustrates some of the important links between aboveground and belowground communities mediated through roots and their surrounding habitat. Aboveground processes can also control the nutrient and physical properties of roots and soil, which themselves may cause changes in arthropod and microbial communities. Six years after girdling, no significant differences in carbon and nitrogen content of soils and litter indicating that the initial disturbance to nutrient availability and cycles had passed. Levy-Varon et al. (2014) noted the importance of time since girdling for soil respiration, showing a rapid rebound. This earlier work illustrates the short-term nature of the perturbation to the carbon cycle in this forest and the establishment of a new cycling pattern in recovery (Levy-Varon et al. 2014). Here, a similar phenomenon for nutrient cycles is suggested, which may have now re-established to near pre-disturbance levels. Furthermore, the observed changes in arthropod abundances are an indication of other, longer-term perturbations to the forest communities resulting from tree girdling.

Despite clear differences in the aboveground response to excluding herbivores, belowground responses were mostly absent. Little variation in soil and litter carbon and nitrogen concentrations, soil properties (except soil moisture) and leaf litter weight was observed. These findings further support the observation that herbivore exclusion is having little to no effect on

litter and soil arthropod communities. Wardle et al. (2001) conclude that the physical effects of browsing such as removal of plants and associated physical disturbances to the soil-plant interface are more likely to have an impact on belowground arthropod communities as compared to changes in vegetation density changes or community-level shifts towards more palatable plants. It is possible that an insufficient time has elapsed since the removal of the herbivores (six years in this study) to allow for a shift in the plant communities that would affect the litter and soil arthropods. Similarly the physical removal of plant material by herbivores may not be leading to significant changes in the belowground community. The only significant difference observed, a higher soil moisture inside the deer exclosures is likely due to the increased plant cover insulating the soils and leaving less soil exposed as compared to the open forest plots. By keeping the soils insulated less evaporation would be expected thereby increasing the soil moisture. In sum, these results suggest that indirect effects of aboveground disturbance resulting from herbivory on belowground chemical and physical properties are minimal.

Djukic et al. (2013) found soil pH increased 0.2 to 0.7 units in girdled plots compared to control plots one year after girdling. These authors attributed the increase in soil pH to increases in nutrient cations as a result of disturbed absorption post-girdling. Our results show that the increased pH has apparently been maintained from one year post-girdling to six years post girdling. Given with similar magnitude and range of increase in soil pH, the changes observed in this soil property can be considered long-term. Djukic et al. (2013) also observed lower C:N in girdled plots and suggest this is due to an increase in belowground nitrogen and the termination of belowground carbon inputs from the oak trees. Djukic et al.'s (2013) conclusion that changes in the plant community lead to changes in soil chemistry and changes in the soil microbial community composition can now be extended to changes in soil microathropod abundances.

Conclusions and future work

The decreased abundances in one of the major microarthropod groups in girdled plots compared to control plots six years after girdling is indicative of long-term changes in belowground communities resulting from an aboveground plant disturbance. The effects of reducing mesofauna populations in forests will likely have important effects on food web dynamics and results from this study indicate less important effects on nutrient cycling related to carbon and nitrogen. The lack of effect from herbivore exclusion in microarthropod abundances,

despite some changes in soil properties, indicates that long-term changes in the soil environment are likely to be more important compared to changes to the belowground communities.

This was a unique study looking at long-term effects of tree girdling and herbivore exclusion on litter and soil arthropod communities. Long-term effects of girdling are likely due to changes to the roots of girdled trees and their influence on the soil food web. These results suggest the importance of further work at this site should investigate differences in diversity across trophic levels, major microarthropod taxa and other arthropod groups and fungi as well as the effects on plots were all non-oaks were removed to better understand the belowground community changes to tree girdling and herbivore exclusion. A better understanding of the links between above- and belowground communities contributes to a better understanding of the forest ecosystem as a whole and of different response of the major biotic and abiotic components of the ecosystem to possible disturbances in the future.

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Figures

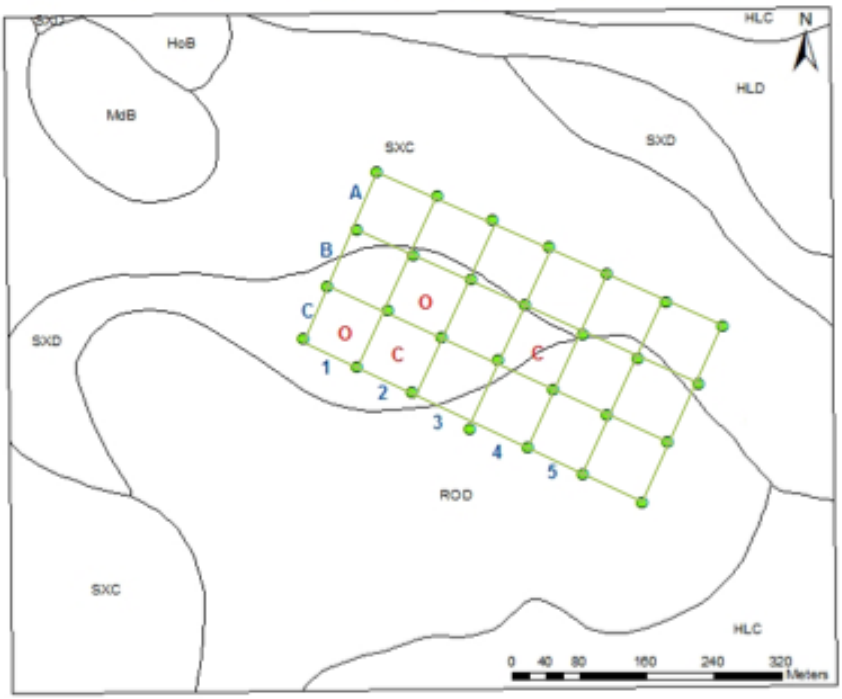


Figure 1: Experimental area on the North Slope of Black Rock Forest outlined by plot corners (green points) and oak-girdled plots sampled are represented by "O" and control plots sampled are represented by "C" with soil series (SXC, SXD: Swartswood and Mardin soils, ROC: Rock-Hollis complex soils)

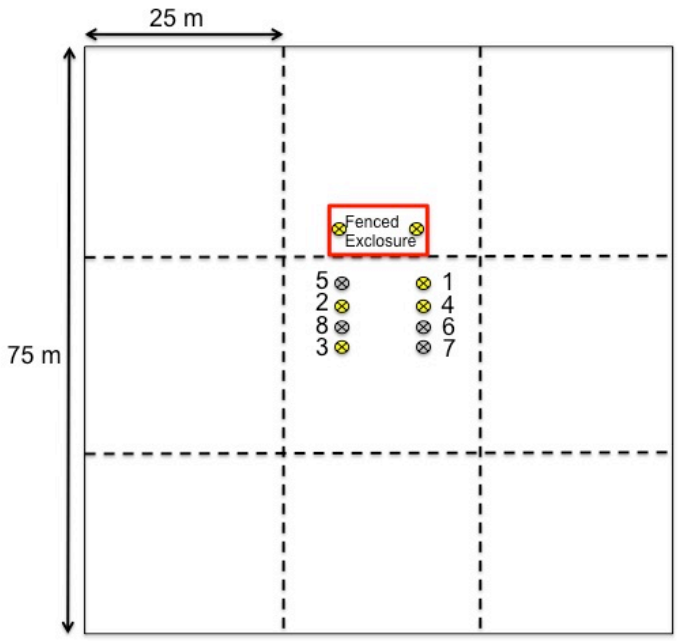


Figure 2: Plot design for girdling experiment with 75 x 75m plots and 25 x 25m subplot and fenced deer exclosure immediately outside of each center subplot. Each central subplot has eight points where long-term plant and soil measurements are collected. Four of theses eight were randomly sampled along with two sampling points inside the exclosure.

Table 1: Total arthropod counts from each layer of forest floor (litter and two soil depths) combined for all samples and treatments

Total Arthropod Counts

	Number of arthropods
Litter	5068
Upper Soil (0-5cm)	190
Lower Soil (5-10cm)	182
Soil Total	372
Litter + Soil	5540

Table 2: Relative abundance (%) of each major arthropod group collected in each layer of forest floor (litter and two soil depths) combined for all samples and treatments

Arthropod Relative Abundances

	Litter	Upper Soil (0-5cm)	Lower Soil (5-10cm)	Soil Total	Litter + Soil
% Mites	89.0	45.8	18.1	32.3	85.1
% Collembola	2.4	8.4	4.9	6.7	2.7
% Insects	7.6	44.7	75.3	59.7	11.1

Table 3: Arthropod abundances (total arthropods, mites and collembola) for leaf litter and soil across all treatments with average (standard error) and sample size

Arthropod Abundances Average (Standard Error)	**Control, Exclosure**	**Control, Open Forest**	**Girdled, Exclosure**	**Girdled, Open Forest**
Litter Arthropods	376.0 (74.07) n=4	327.13 (80.64) n=8	58.50 (8.95) n=4	89.13 (17.27) n=8
Litter Mites	351.50 (69.14) n=4	300.25 (74.80) n=8	41.50 (6.81) n=4	67.25 (16.96) n=8
Litter Collembola	9.05 (6.20) n=4	4.38 (1.55) n=8	3.75 (1.49) n=4	4.38 (1.67) n=8
Soil Arthropods (0-5cm)	14.33 (11.39) n=3	12.00 (3.34) n=8	6.75 (3.20) n=4	3.00 (1.02) n=8
Soil Mites (0-5cm)	5.00 (2.89) n=3	5.63 (2.24) n=8	3.50 (1.94) n=4	1.63 (0.53) n=8
Soil Arthropods (5-10cm)	5.25 (1.44) n=4	16.75 (9.23) n=8	2.25 (0.85) n=4	2.25 (0.94) n=8
Soil Mites (5-10cm)	1.25 (0.48) n=4	2.00 (1.09) n=8	1.75 (1.03) n=4	0.63 (0.38) n=8

Table 4: Leaf litter dry weight and arthropod abundances (total arthropods, mites and collembola) per gram leaf litter across all treatments with average (standard error) and sample size

Abundance per gram litter Average (Standard Error)	**Control, Exclosure**	**Control, Open Forest**	**Girdled, Exclosure**	**Girdled, Open Forest**
Litter Dry Weight (grams)	56.89 (0.19) n=4	53.12 (6.50) n=8	56.23 (8.20) n=4	64.22 (7.60) n=8
Litter Arthropods/gram	6.61 (1.29) n=4	6.38 (1.28) n=8	1.15 (0.28) n=4	1.53 (0.37) n=8
Litter Mites/gram	6.17 (1.20) n=4	5.86 (1.20) n=8	0.81 (0.22) n=4	1.18 (0.35) n=8
Litter Collembola/gram	0.17 (0.11) n=4	0.083 (0.025) n=8	0.064 (0.023) n=4	0.064 (0.024) n=8

Table 5: Soil properties (moisture, bulk density and pH) across all treatments with average (standard error) and sample size

Soil Properties Average (Standard Error)	**Control, Exclosure**	**Control, Open Forest**	**Girdled, Exclosure**	**Girdled, Open Forest**
Soil Moisture 0-5cm (% moisture)	80.09 (6.93) n=4	47.81 (9.51) n=5	65.18 (7.01) n=3	44.01 (4.33) n=6
Soil Moisture 5-10cm (% moisture)	33.80 (2.25) n=4	37.23 (6.39) n=7	33.37 (8.82) n=4	26.19 (2.23) n=8
Soil Bulk Density 0-5cm (g/cm^3)	0.29 (0.031) n=4	0.32 (0.061) n=8	0.28 (0.054) n=4	0.43 (0.081) n=8
Soil Bulk Density 5-10cm (g/cm^3)	0.83 (0.043) n=4	0.81 (0.084) n=8	0.76 (0.083) n=4	0.81 (0.12) n=8
Soil pH	5.93 (0.23) n=4	5.73 (0.21) n=8	6.08 (0.21) n=4	6.23 (0.12) n=8

Table 6: Carbon and nitrogen content for leaf litter and soils across all treatments average (standard error) and sample size

Carbon and Nitrogen Content Average (Standard Error)	**Control, Exclosure**	**Control, Open Forest**	**Girdled, Exclosure**	**Girdled, Open Forest**
Litter %C	46.81 (1.71) n=4	44.90 (0.97) n=8	40.81 (1.68) n=4	43.17 (1.66) n=8
Soil 0-5cm %C	14.46 (1.47) n=4	19.86 (4.57) n=8	19.32 (4.81) n=4	12.41 (2.45) n=8
Soil 5-10cm %C	4.07 (0.59) n=4	7.49 (2.02) n=8	6.07 (2.43) n=4	4.06 (0.63) n=8
Litter %N	1.60 (0.11) n=4	1.41 (0.076) n=8	1.28 (0.077) n=4	1.26 (0.078) n=8
Soil 0-5cm %N	0.57 (0.064) n=4	0.79 (0.19) n=8	0.89 (0.20) n=4	0.62 (0.12) n=8
Soil 5-10cm %N	0.17 (0.024) n=4	0.28 (0.058) n=8	0.27 (0.10) n=4	0.20 (0.026) n=8
Litter C:N	29.67 (1.89) n=4	32.36 (1.51) n=8	32.17 (1.73) n=4	34.73 (1.56) n=8
Soil 0-5cm C:N	25.81 (0.85) n=4	24.49 (1.62) n=8	21.43 (0.71) n=4	19.79 (0.80) n=8
Soil 5-10cm C:N	23.94 (1.16) n=4	23.96 (2.30) n=8	22.18 (0.75) n=4	19.93 (1.05) n=8

Table 7: Linear mixed effects model results for litter and soil arthropods, soil properties arthropod abundance per gram leaf litter with significant p-values from ANOVA highlig bold

Leaf Litter Arthropods

	Effect of Girdling	Effect of Herbivore Exclusion
All arthropods	p = 0.00323	p = 0.880
Mites	p =0.00201	p = 0.819
Collembola	p = 0.386	p = 0.323

Soil Arthropods

	Effect of Girdling	Effect of Herbivore Exclusion	Effect of Depth
Total abundance	p = 0.145	p = 0.874	p = 0.732
Mites	**p = 0.0465**	p = 0.691	**p = 0.0235**
Collembola	p = 0.565	p = 0.755	p = 0.310

Soil Properties

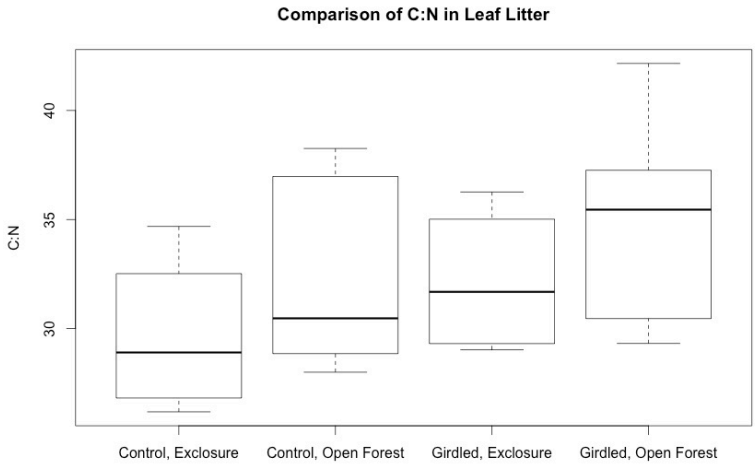
	Effect of Girdling	Effect of Herbivore Exclusion	Effect of Depth
Moisture	p = 0.293	**p = 0.00384**	**p < 0.0001**
Bulk Density	p = 0.745	p = 0.377	**p < 0.0001**
pH	p = 0.177	p = 0.970	**p < 0.0001**
%C	p = 0.255	p = 0.975	**p < 0.0001**
%N	p = 0.265	p = 0.920	**p < 0.0001**
C:N	p = 0.316	p = 0.999	**p < 0.0001**

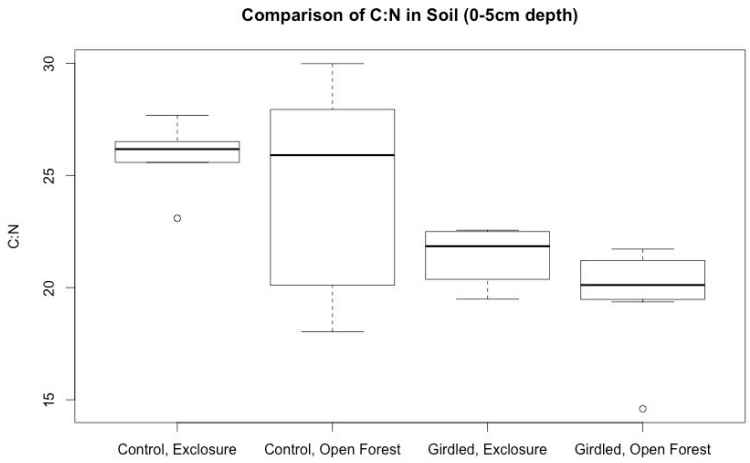
Leaf Litter Dry Weight

	Effect of Girdling	Effect of Herbivore Exclusion
Dry weight (grams)	p = 0.293	p = 0.771

Arthropods Abundance per gram Leaf Litter

	Effect of Girdling	Effect of Herbivore Exclusion
All arthropods	**p = 0.00181**	p = 0.933
Mites	**p =0.00100**	p = 0.977
Collembola	p = 0.217	p = 0.296





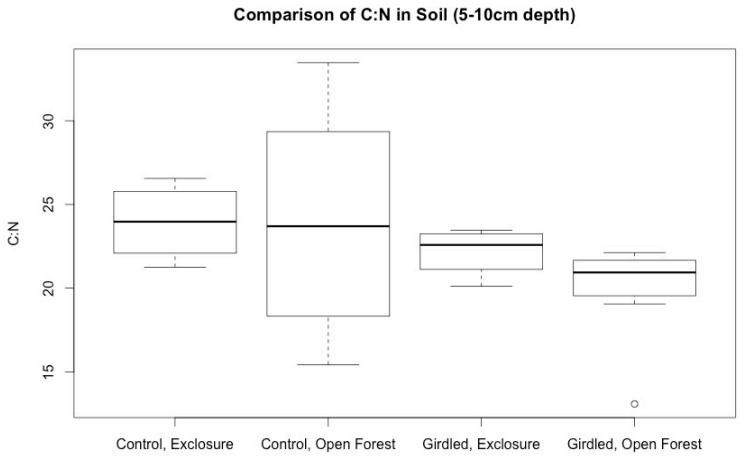


Figure 3: Boxplots for carbon to nitrogen ratio for leaf litter and two soil depths (0-5cm and 5-10cm) across two treatments (girdling and herbivore exclusion)

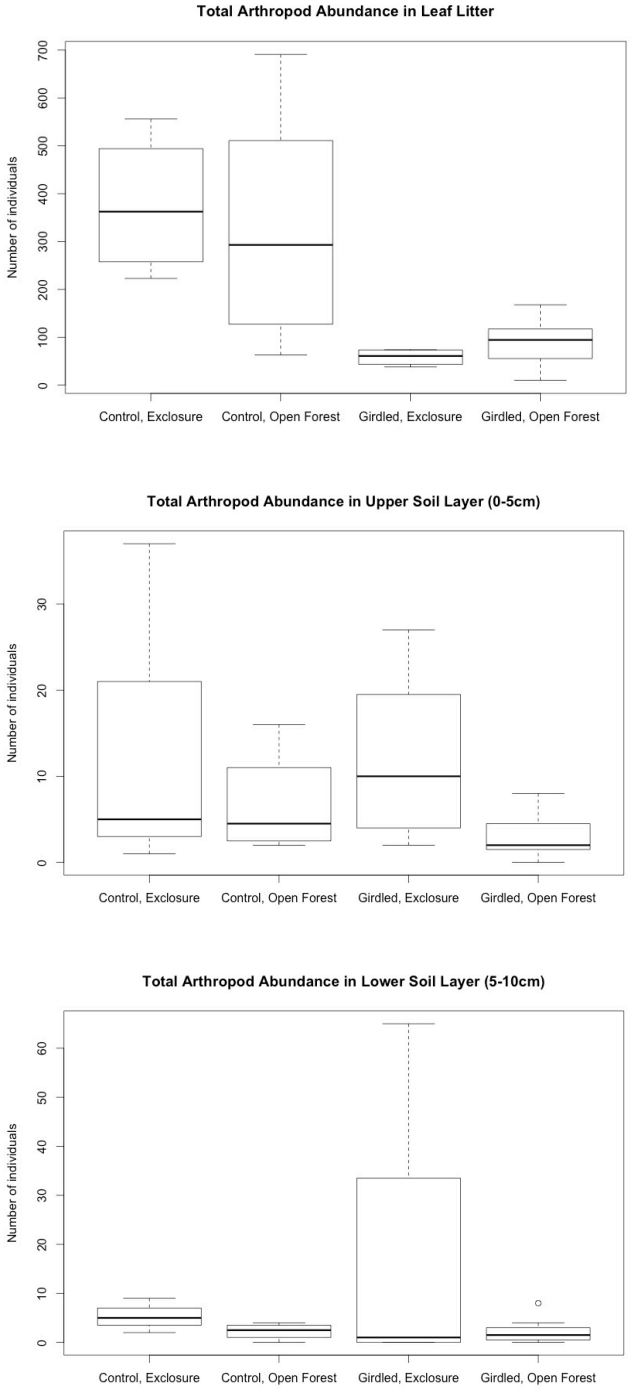


Figure 4: Boxplots for total arthropod abundance for leaf litter and two soil depths (0-5cm and 5-10cm) across all treatments

END