

Impact of mound-building ants on ecosystem properties create islands of fertility in an alpine
meadow

Student: Sarah Jeanne Wood

Mentor: Aimee Classen

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Introduction

In resource-limited ecosystems, particularly grasslands, plants can form resource pools (Rietkerk et al. 2004) by using their roots to access nutrients from surrounding areas and then concentrate them beneath their crown (Schlesinger et al. 1996). Nutrients and organic material accumulates over time resulting in “islands of fertility” within the plant community that ultimately promotes species performance aboveground and belowground in the ecosystem (Schlesinger et al. 1990). These facilitative interactions via plants’ “islands of fertility” are present in a broad range of ecosystem dynamics, but often have a stronger impact in high stress environments (Holmgren et al. 1997).

Like plants, the influence of ant establishment in ecosystems can greatly alter the distribution of carbon and nutrient on the landscape (Folgarait 1998), especially in resource limited ecosystems. Aboveground, ants can alter plant community composition and productivity (Wardle et al. 2011); while belowground, ants contribute to soil nutrient heterogeneity by concentrating nitrogen, phosphorus, and organic matter within nest areas (Wagner et al. 2003). Ecosystem processes, such as decomposition and mineralization, are also often accelerated within and around ant colonies (Wagner et al. 2003), and upon periodic mound abandonment, resulting decomposition over time incorporates mound organic material into the soil to further increase spatial heterogeneity of soil carbon and nutrient pools (Jurgensen et al. 2008; Kilpelainen et al. 2007). Ants, like plants, can form resource islands that may alter nutrient redistribution and retention in ecosystems long after the colony has died or moved. However, we know less about how long these impacts may persist in an ecosystem and if changes in soil communities and resources lead to long-term shifts in plant communities.

Many comparative studies of soils on and off ant colonies have confirmed that nutrient retention and cycling can be different on and off nests, however we do not know if these differences persist over time and if they lead to changes in the trajectory (i.e., plant communities that form) over time. In this study, we marked and visited over 250 *Formica obscuripes* colonies over two years to investigate how colony presence, activity, and death impact soil microclimate, soil communities, plant communities and nutrient processes that contribute to ecosystem properties in an alpine meadow in central Colorado.

Methods

I. Study site and species:

Our study was conducted within the Almont Triangle (elev. 2720 m) approximately 30 km southeast of the Rocky Mountain Biological Laboratory in Gothic, Gunnison Co., Colorado (38.669583 N, -106.846494 W). Our site is located on a southwestern facing slope, where an arid climate persists with temperatures averaging yearly lows of -9 and highs of 24 °C; rainfall averages 25.4 cm for the months of June and July. Vegetation in the meadow is dominated by *Artemisia tridentata* (sagebrush), *Chrysothamnus* spp. (rabbitbrush), grasses, and herbaceous perennials.

Formica obscuripes, also known as the western thatching ant, is the most common thatching ant of the Western US (Gregg 571). *Formica* construct large, domed nests composed of thick masses of plant debris (primarily twigs and needles), fecal material, excavated soil, and other organic matter. The brood structure of the colony is centered among two or more queens with high numbers of winged males and females in the months of June and July (Cole 31). The number of adult workers per colony may reach as high as 35,000 to 40,000. They prey on

insects, forage on dead insects, consume honeydew (harvested from aphids), and occasionally consume plant tissue (Heikkinen 1999). Over 250 ant colonies averaging 0.75m in aboveground surface area are present in the study site. This high-density ant population has persisted at this site for decades and has become an integral component of many interactions taking place in the system.

II. Sampling scheme and measurements:

In July of 2010, all active *F.obscuripes* colonies at the study site were mapped using a Trimble GEOXT GPS unit and each colony was individually marked with a wooden stake that was fitted with a metal tag. In 2010, 229 colonies were located, marked and mapped at the site. The site was revisited in June of 2011. Each of the 2010 colonies were relocated and their activity was recorded (active, inactive). In addition, all new colonies were mapped using a Trimble GEOXT GPS unit and marked with a wooden stake and metal tag. In 2011, 48 newly formed colonies were identified.

In 2010 and 2011, all marked colonies (active or inactive) were measured for nest surface area in order to track yearly growth. Nest surface area was estimated by measuring the maximum width and its perpendicular intercrossing using a Keson fiberglass 30 m measuring tape.

After each colony was identified and measured, 8 colonies in each of the following groups were randomly selected for further study: (a) colonies greater than a year that were still active, (b) colonies greater than one year that were inactive (abandoned), (c) colonies that were less than a year and active. Each selected colony was paired with a control sample taken 1 m away from the focal colony and in a random direction. If another colony was within the selected 1 m area another direction was selected until there was no overlap with other ant colonies. In total, 48 areas were sampled.

Soil samples were taken (0-10 cm) using a X diameter hammer core at each of the selected colonies. Two soil cores were collected on the mound, and two were collected at the paired control. Collected cores were placed in plastic bags and kept on ice until analysis.

III. Soil Chemistry Analysis

Soil moisture and temperature readings were taken between the hours of 12 and 3 pm. Soil moisture samples (0-10 cm) were taken with a HydroSense moisture meter. For each mound, three readings were taken on the mound and three readings were taken 1 m off the mound as the paired control; mean soil moisture was calculated for each colony on each date. Soil temperature readings (0-30 cm) were taken once on each mound, and once 1 m away at the paired control using standard soil thermometer. We allowed for the same space in time between soil moisture and temperature readings. Soil pH was calculated by using five grams of soil, weighed using a Denver Instrument Company scale, and followed with an addition of 10 mL of water. Each vial was shaken every ten minutes for half an hour, and then allowed to settle for one hour. Soil pH was taken with an Oaklon Instruments apparatus. Soil nutrients nitrogen, phosphorus, and potassium were tested using LaMotte Soil N,P,K kit and color coding chart using an n=4 and a total of 24 samples.

IV. Plant community composition:

To study vegetation associated with mound activity, we measured all vascular plant species in a 2 x 2 m² plot surrounding the 24 ant mounds in our study, and in 8 randomly chosen sites without nests. At each ant plot, the mound was the center of the square plot. Sites without nests (controls) were chosen at random by implementing a stop watch method to obtain X and Y map coordinates. If a location was selected that had an ant colony present within 1 m of sampling, another location was chosen. The number of plant species (S), and the plant species

diversity using the Shannon Index (H') was calculated. In total, eighteen different plant species were observed.

IV. Data Analysis

Volumetric soil moisture content was analyzed with a MANOVA of the effect size of moisture on and off colony. Soil temperature was analyzed using a Oneway ANOVA. pH among colonies was statistically tested using a Oneway ANOVA of the effect size and individually. Nutrient availability (N,P,K) was analyzed using a Chi Square test for each nutrient. Plant community composition was panelized using a Oneway ANOVA testing for species evenness and richness among colonies.

Results

Change in colony activity from 2010 to 2011 censuses showed that in one year, 14 % of colonies were abandoned and 24% percent of new colonies emerged resulting in net growth of 10% (Fig.1). Surface area was greatest for active colonies greater than one year and averaged .76 m², followed by abandoned colonies averaging .65 m². Colonies established in 2011 were smallest in surface area averaging .60 m² (Fig. 2). The area of colonies measured in 2010 and 2011 had a growth rate of 12%. The nest size measurements indicate that colonies are readily established, growing rapidly in a short amount of time, and eventually slowing and shrinking after reaching capacity.

Our results indicate that volumetric soil moisture content was impacted by both time ($F=67.6$, $P<.001$) and colony age ($F=1.8$, $P<.001$) (Fig 3a). Abandoned nests showed significantly higher moisture content from colonies exhibiting activity. Soil moisture taken both on and off colony decreased over time, however off colony moisture exhibited much more stark contrast and variability over time, while on colony soil moisture depreciated only slightly

indicating the ants ability to stabilize and retain moisture conditions within the nest. Soil temperature was significantly higher among active colonies, regardless of age, compared to temperatures of abandoned nests or off colony areas ($F=28.28$, $P<.0001$)(Fig 3b).

Soil pH did not show significance among ant colony ages when analyzed with a standard effect of size ANOVA ($F=1.86$, $P=.17$). When each colony and its control were treated as individuals (no effect size), a significant difference among the activity of colonies resulted with on colony, abandoned nests significantly different from all other sites ($F=6.07$, $.0003$) (Fig 4a). Abandoned nests had significantly lower pH than active colonies and off-colony soils. Regardless

Nutrient availability among colonies varied significantly with age and activity. Available nitrogen was significantly higher on active nests than inactive or off colony areas ($\text{ChiSquare}=29.1$, $P=.0012$) (Fig 4b). Available phosphorus was significantly higher on colonies that have been active for greater than year ($\text{ChiSquare}=45.8$, $P<.001$) (Fig 4c). Similarly, potassium availability was significantly higher on colonies active for greater than one year ($\text{ChiSquare}=31.805$, $P<.001$) (Fig 4d). All abandoned nests had extremely reduced amounts of nutrients compared active colonies, and if did not equal, were nearing nutrient concentrations of non-colony soil.

There were significantly different plant community attributes among colony age and activity. As colonies age, a greater percent coverage of woody species (i.e. sagebrush) and herbaceous species (i.e. rabbitbrush) increases. New established colonies had a high percentage of woody species (40%) prior to ant establishment, suggesting that ants deliberately and strategically choose the site for colonization. Plant species richness increased significantly with age ($F=4.71$, $P=.0008$)(Fig 5a), however, no significant difference was found in plant species

diversity among colonies (Fig 5b). Plant species were not evenly distributed in any of the colonies as particular species dominate the community composition.

Discussion

Our experiment demonstrates that ants have the capability to quickly impact and change both the belowground and aboveground interactions occurring within the nest area. Active nests leave a strong signature on the soil within the nest area, effecting the soil moisture, chemistry, and surrounding plant biota. Recently established nests also demonstrate these same impacts, just in a slightly less degree. However, in some aspects, such as soil moisture, temperature, and pH, newly established nests demonstrated very similar impacts as nests that have been active for a longer duration. This indicates that ants have the capability to rapidly alter belowground dynamics upon colonization. On the contrary, our results indicate that these changes are not long lasting. Inactive nests had significantly different soil moisture, temperature, pH, and nutrient availability as compared to active nests. Inactive nests are already beginning to match soil properties of non-colony soil.

Volumetric soil moisture was elevated upon ant abandonment of the nest. Studies by Wardle et al. found similar results in that ant exclusion significantly elevated gravimetric moisture content. Ant abandonment from nest enables water content to be distributed throughout the soil. Ants are no longer present to sequester water available moisture. Our results show though, that less fluctuation in ant nest soils is present as compare to surrounding soil. This suggests that ants have a capability of maintaining a stabilized microclimate within the nest. While volumetric water content and temperatures were higher in active nests, less variability existed over time than that of inactive nests and non-colony soils, therefore suggesting that ants

possess biological mechanisms that enable them to maintain homeostatic conditions within the nest area.

As colonies age, the impact on soil becomes intensified (Wagner et al. 2004). Our data suggest that ant nest surface area nearly matches that of nests active for a longer duration. Mean surface area for active nests greater than one year was $.62 \text{ m}^2$, and mean nest surface area for new colonies was $.60 \text{ m}^2$. While nest surface area is variable among colonies, these results show that much energy is allotted into nest building and mound construction within the first year. Surface area could perhaps be indicative of other soil chemistry properties, such as nutrient concentration. Nest building eventually stabilizes perhaps when worker number equilibrates (Wagner et al, 2004; Gordon 1992).

Ant colonies enrich nutrient availability in soils. The accumulation of soil nutrients in ant nest soils indicate that nutrient input via ants exceeds that of use and consumptions (Wager et al. 2004). Foraging and harvesting, decomposition facilitation, feces excretion, species death, and microbial recruitment contribute to the collection of nutrients within nest sites. Active nests of greater than one year establishment had far greater amounts of available nitrogen, phosphorus, and potassium (600-800%) than nests that were inactive. Abandoned nests no longer have the facilitation of ants collecting organic materials, or contributing to nutrient advancement, thus match off-colony nest soils relatively quickly upon ant abandonment.

Ants' impact on plant community composition and structure is recognized through patterns in plant cover among colonies and increased species richness among colonies. Ant colonization is recognized as a very frequent small-scale, natural disturbance affecting vegetation patterns (Farji-Brener & Ghermandi 2000) through various direct and indirect associations with plants. Mound construction and maintenance also alters plant community

dynamics via mobilization and bioturbation of various soil horizons and organic material (Farji-Brener & Ghermandi 2000) creating enriched edaphic conditions that enables plant community growth and development, particularly in nutrient limited ecosystems. We found that woody species (i.e. sagebrush) were much more prevalent around ant colonies than off colony, while herbaceous species were more commonly found off colony than surrounding nests. The woody species utilized as prosperous nest locations for several possibilities, such as protection, structural support, or moisture and temperature regulation. Our results also show that ant colonies increase species richness with age, as a significant difference was found among active colonies that have been established for greater than one year and newly established colonies.

Ant colonization has great impacts on soil dynamics which results in changes of microclimate, soil chemistry, and plant community composition. The age of age and activity of ant nests has great implications as to the degree of impact ant colonies have on soil properties and plant composition. Our study showed that these changes on ecosystem processes are implemented very quickly upon ant establishment, but also dissipate relatively quickly upon ant abandonment. The islands of fertility created by ants result in microclimate changes, nutrient accumulation, and plant heterogeneity within the nest soils that could be of widespread significance to the dynamic structuring of biogeochemical cycles in the Almont Triangle.

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Figure Legends

Figure 1:

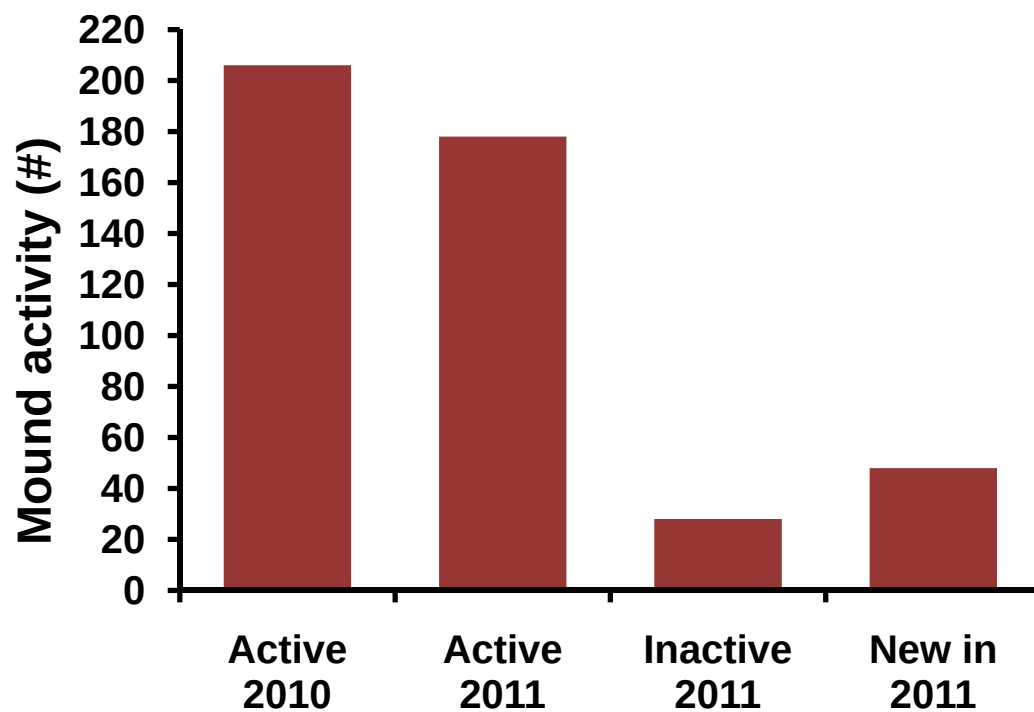


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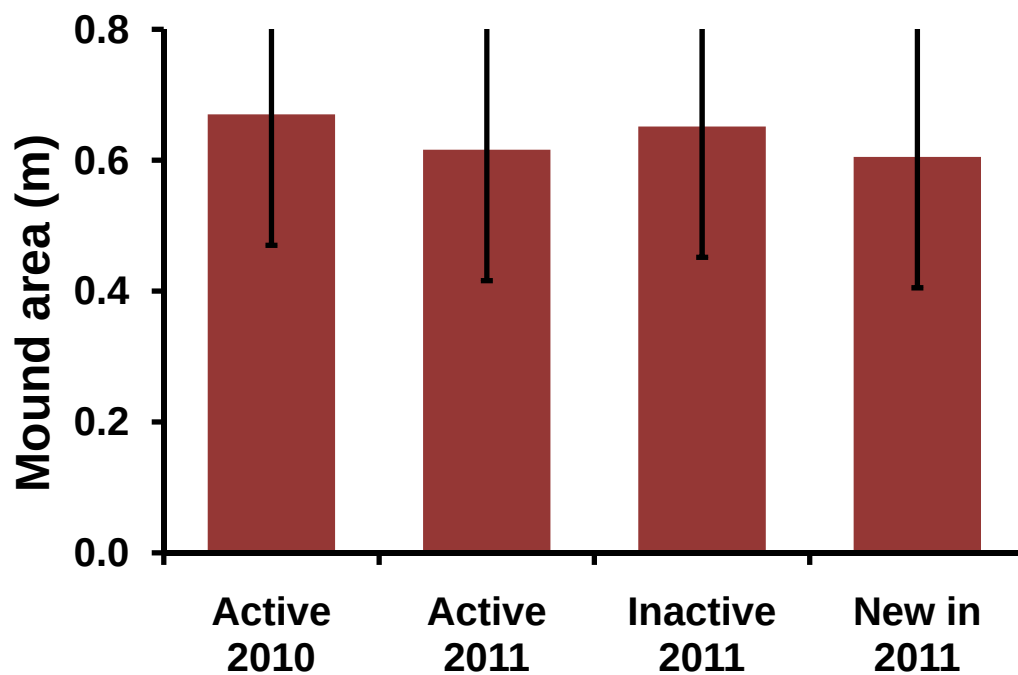
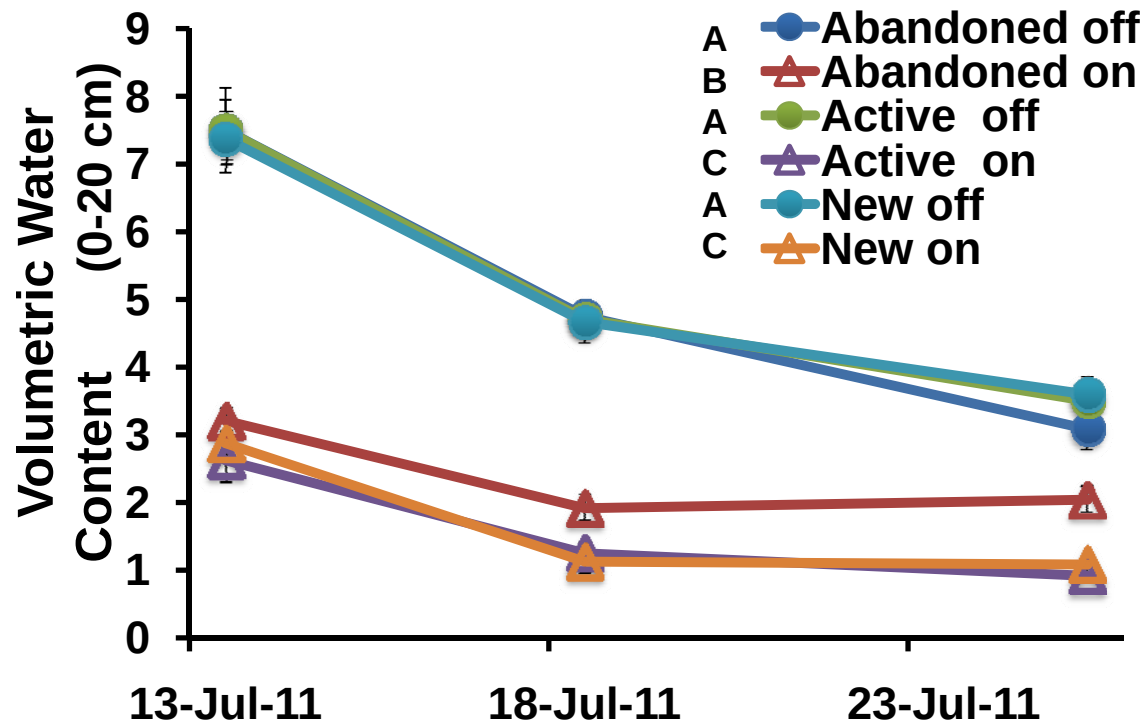


Figure 3a



3b.

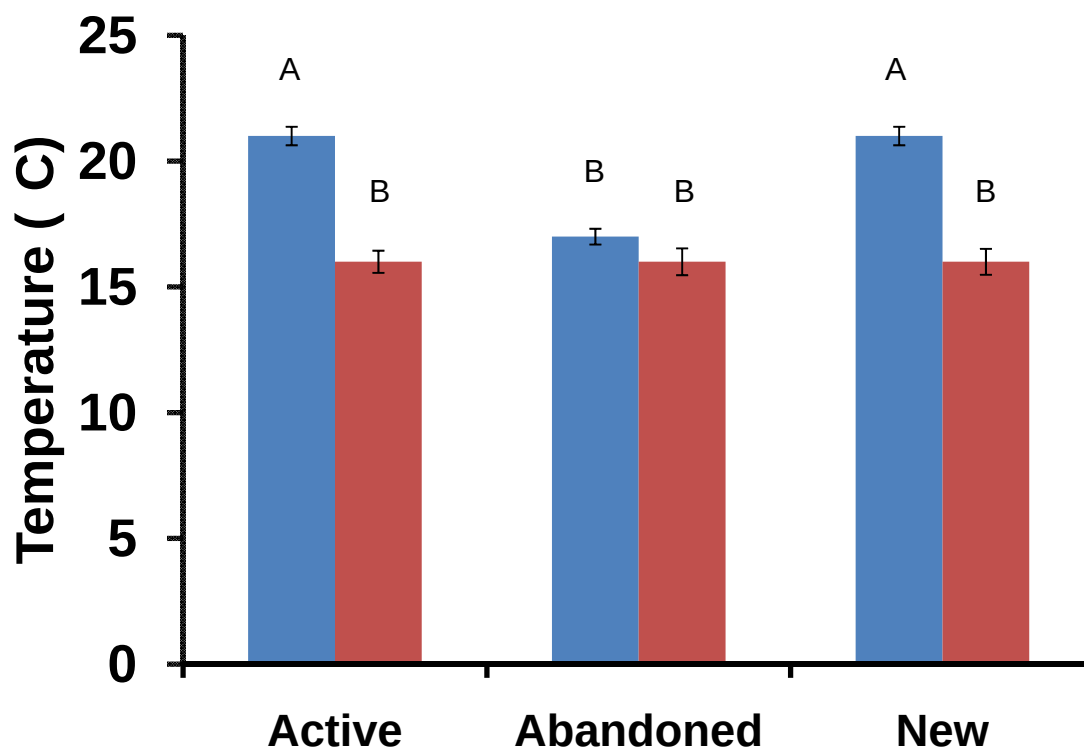
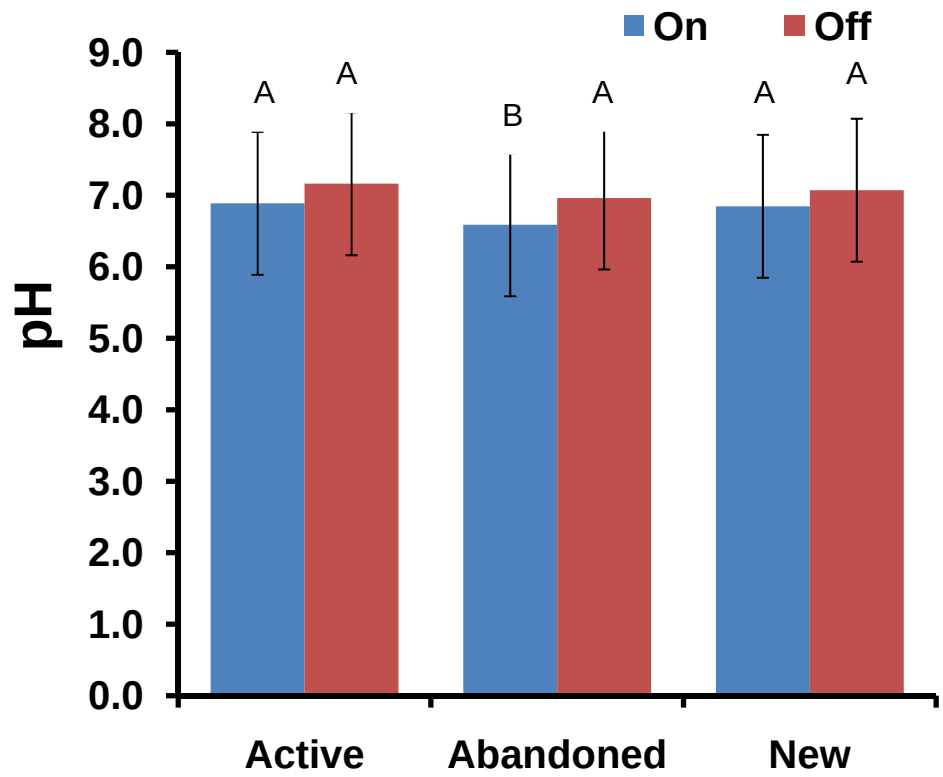
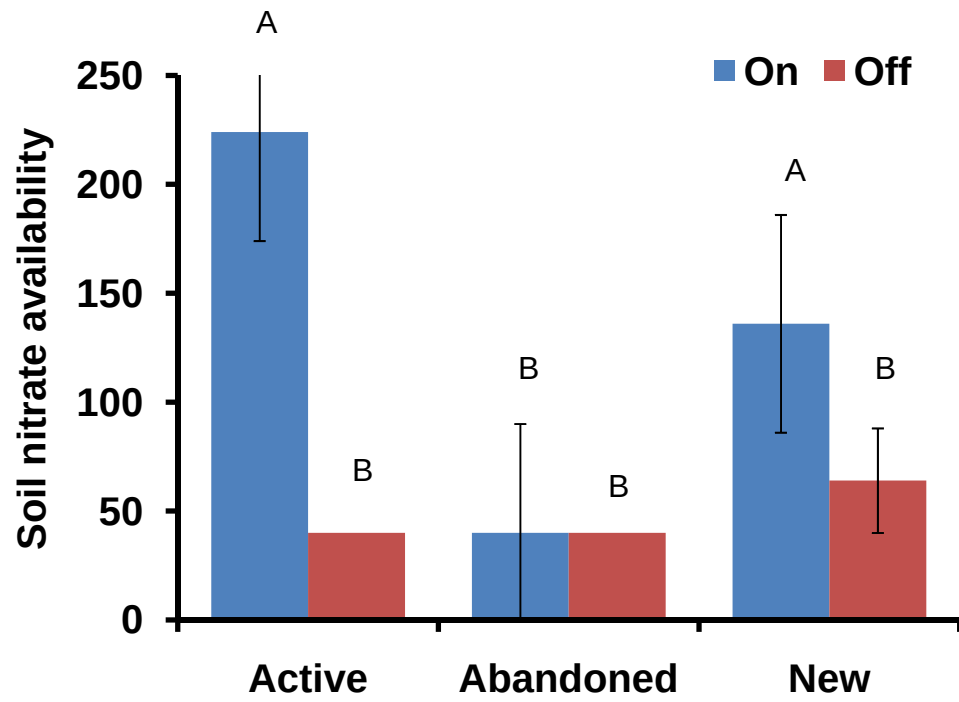


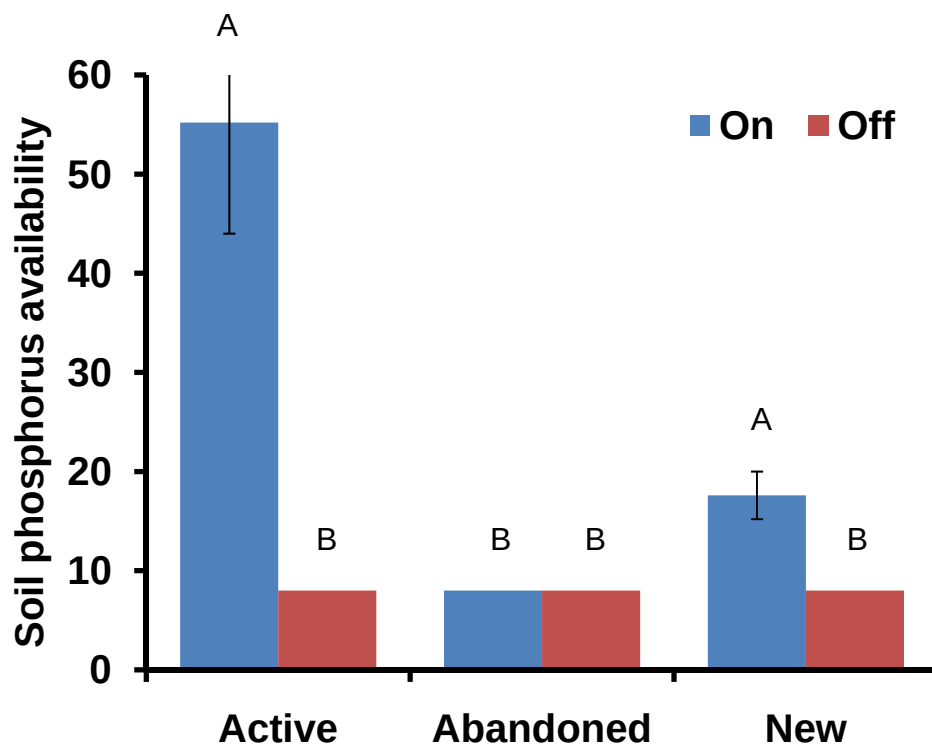
Figure 4a



4b.



4c.



4d.

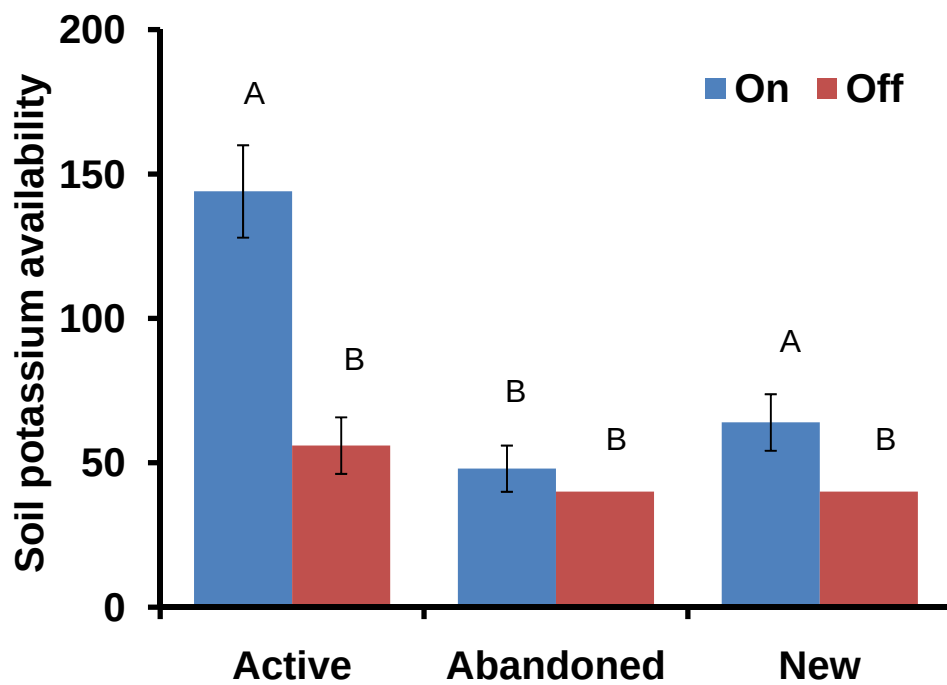
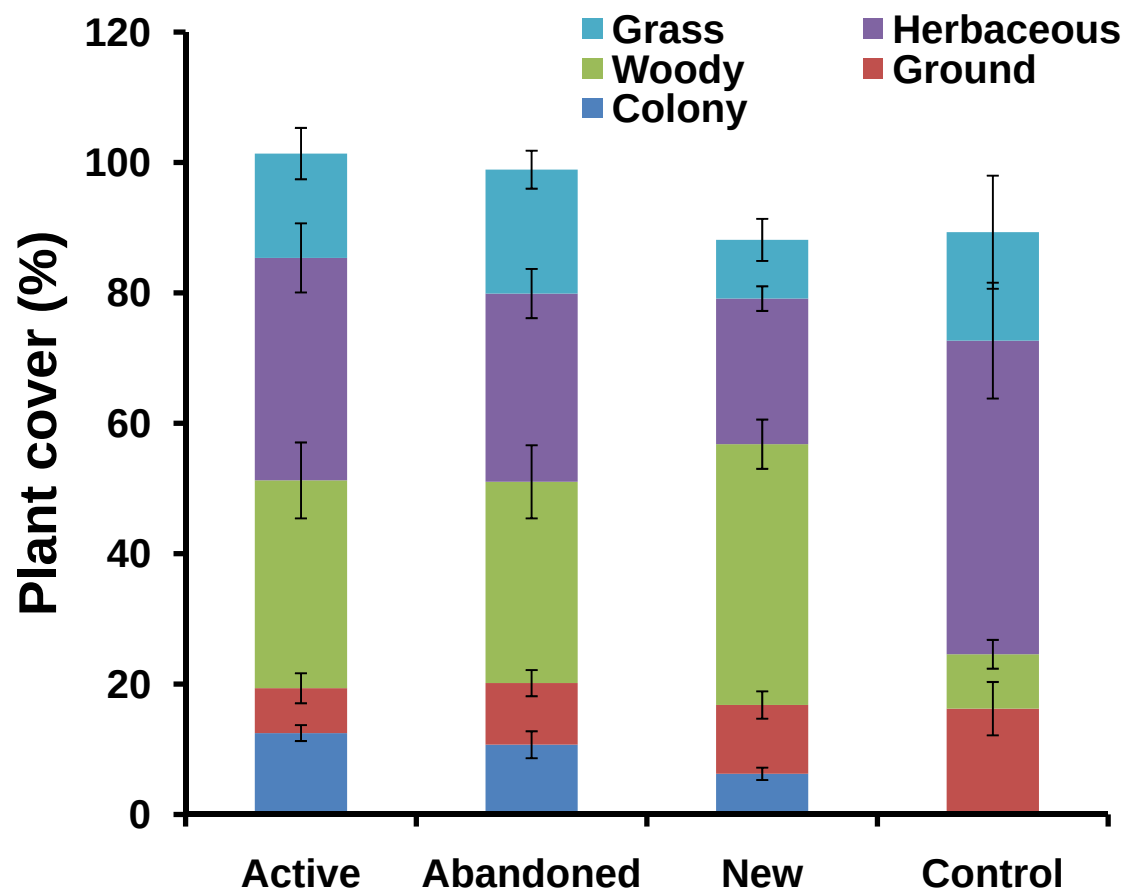
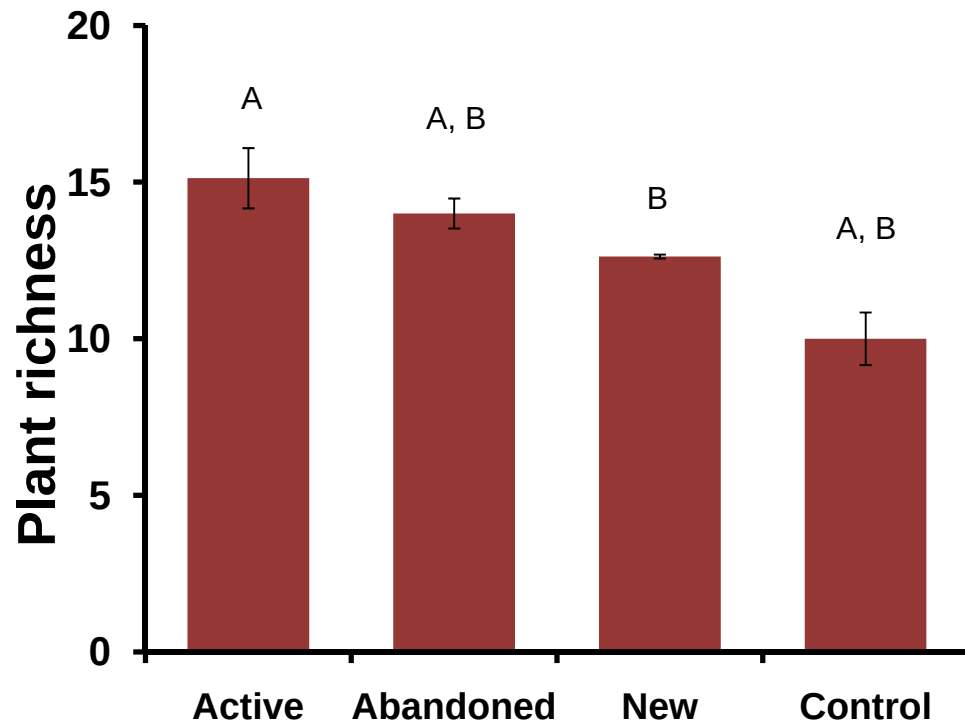


Figure 5a:



5b.



5c.

