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The Multi-Trophic Effects of Buckthorn Removal

Amanda Jacobs
Buffalo State College, jacobsal01@buffalostate.edu

Advisor
Dr. Robert Warren II
First Reader
Dr. Robert Warren II
Second Reader
Dr. Daniel Potts
Third Reader
Dr. Christopher Pennuto

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The Multi-Trophic Effects of Buckthorn Removal

By

Amanda L. Jacobs

An Abstract of a Thesis in Great Lakes Ecosystem Science

Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Arts

July 2024

Buffalo State University
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ABSTRACT OF THESIS

European buckthorn (*Rhamnus cathartica*) is a non-native woody plant in North America that often grows in dense, monotypic stands, frequently displacing native plants and reducing species richness of invaded native communities. Given that plants are basal in most food webs, the homogenization of plant communities might be expected to cascade into homogenization at higher trophic levels (Hunter and Price, 1992). I investigated the multi-trophic effects of buckthorn removal at three levels: (1) 'native,' in which there were no buckthorn trees or shrubs, (2) 'buckthorn trees,' in which buckthorn was not removed and grew into spaced mature trees, and (3) 'buckthorn shrubs,' in which buckthorn was removed ten years prior, but grew back as dense, monotypic thickets. I measured plant species richness, pollinator richness and abundance, leaf litter invertebrate richness and abundance, and rodent abundance in each habitat type. Native plots had more than twice the plant taxonomic richness as the buckthorn tree or buckthorn shrub plots. Similarly, the abundance and richness of invertebrate pollinators in the native plots was twice that of the other habitats. The abundance and richness of bees (Apiform) did not differ between the native and buckthorn tree habitats, but Apiforms were almost nonexistent in the buckthorn shrub plots. Leaf litter invertebrate richness did not differ between habitats, but abundance was highest in native plots. The rodent community was dominated by white-footed/deer mice (*Peromyscus)*, and they overwhelmingly were found in the buckthorn shrub plots. Overall, I found that the removal of invasive buckthorn cover increased native abundance and species richness at multiple trophic levels. These results suggest that homogeneity in primary producers cascades into homogeneity in adjacent and non-adjacent trophic levels – starting in both the green (native plants) and brown (leaf litter) food webs – resulting in reduced richness and biomass across the community.

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To be approved by:
Robert J. Warren II, Ph.D.

Christopher Pennuto, Ph.D.
Chair and Professor

Kevin J. Miller, Ed.D.
Dean of the Graduate School

THESIS COMMITTEE

Robert J. Warren II, Ph.D.
Professor of Biology

Daniel Potts, Ph.D.
Professor of Biology

Christopher Pennuto, Ph.D.
Professor of Biology and Chair

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Introduction

Invasive non-native plants often form dense monoculture stands that ‘crowd out’ native plants by reducing access to key resources such as light, space, and water (Aguilera et al., 2010; Broadbent et al., 2018). These invasive plants can hence simplify the community structure of native habitats by reducing or replacing native species, resulting in reduced native species richness, and at larger spatial scales potentially leading to “biotic homogenization” (Ehrenfeld, 2010; Hunter and Price, 1992; Shea, 2002; Vitousek, 1990). A potential mechanism allowing non-native plants such competitive dominance is that some may bring “novel weapons”, such as unique chemical attacks and defenses, against which native species do not have a shared evolutionary history (Batish et al., 2013; Callaway and Aschehoug, 2000; Johnson and Stinchcombe, 2007). Many plants chemically suppress the establishment and growth of other plants (“allelopathy”) by releasing secondary chemical metabolites that can prevent seed germination and/or inhibit tissue growth in competitors (Inderjit et al., 2011). Indeed, many highly invasive plants in North America bring allelochemicals that do not occur in native North American plants (Cappuccino and Arnason, 2006).

As plant competitors with a shared evolutionary and biogeographic history engage in an evolutionary ‘arms race’ between attack and defense, a similar dynamic occurs between plants and herbivores (Batish et al., 2013). Non-native plants bring novel defenses against which native herbivores have not coevolved; resulting in reduced or even nonexistent herbivory (Hallett 2006). For example, native herbivores may lack the ability to detoxify the secondary compounds (which may also act as allelochemicals against plant competitors) that non-native plants bring with invasion (Cappuccino and Arnason, 2006). Furthermore, native herbivores may not recognize non-native plants as potential food, which adds to their competitive advantage against native plants plagued by their own natural enemies (Keane, 2002). The loss of specialist herbivores may also allow non-native invaders to shift biomass allocation from defense to growth and reproduction, further promoting the competitive abilities against native plants (Barney and Whitlow, 2008). As a result, at the community level, the displacement of native plants by non-native plants degrades feeding opportunities for native herbivores by replacing palatable native species with a few, often unpalatable, non-native species (Tallamy and Shropshire, 2009). Given their role as primary producers, reductions in palatable plants cascade into lower richness and abundance across trophic levels (Johnson and Stinchcombe, 2007; Tallamy and Shropshire, 2009). Essentially, then, homogeneity in primary producers can cascade into homogeneity in adjacent and non-adjacent trophic levels, reducing richness and biomass across the community (David et al., 2017; Hunter and Price, 1992).

Non-native plants also can have indirect effects on native plants by altering the local pollinator assemblage. Pollinator microhabitat selection is heavily dependent on temperature and interspecific differences in thermobiology, so cooler temperatures caused by the increased shade of an invasive monotypic shrub can drive decreases in pollinator abundance (Herrera, 1997; Valladares et al., 2016). Removal of a dominant, monoculture-forming invasive plant can result in shifts in pollinator assemblage by opening the canopy to allow light for flowering plants. For example, the removal of the invasive shrub Chinese privet, (*Ligustrum sinense*), resulted in large increases in Apiform abundance and richness due to greater plant richness and increased light (Hanula and Horn, 2011).

European buckthorn, (*Rhamnus cathartica*) is a well-established woody non-native species brought to North America by early European settlers in the 1800s for medicinal and landscaping purposes (Kurylo and Endress, 2012). In its native range, buckthorn usually grows in open areas or forest edges, but in central and eastern North America it readily invades forest understories (Knight et al., 2007; Kurylo et al., 2007). Moreover, in its native range, buckthorn grows singly or in small groups, but in North America it forms monotypic stands unlike its native range (Knight et al., 2007). These buckthorn stands are widespread and dominant, likely the result of the shrubs producing copious amounts of fruit that contain seeds with very high germination rates (Knight et al., 2007; Kurylo and Endress, 2012). Buckthorn phenology also may be advantageous in North America as it gains at least 40% of its biomass while North American native plants, such as gray dogwood (*Cornus racemosa)* are still leafless (Harrington et al., 1989). In contrast, in its European native range, buckthorn phenology does not differ from co-occurring plants (Knight et al., 2007).

Buckthorn invasion is associated with lower herbaceous species richness and cover, particularly in native plants (Knight et al., 2007). The formation a dense buckthorn canopy shades out native competitors and only allows the growth of conspecifics, resulting in a negative relationship between buckthorn basal area and both native seedling density and herbaceous cover (Mascaro and Schnitzer, 2007; Warren et al., 2017). Moreover, buckthorn litter deposition decreases the germination of both woody and herbaceous North American plants, possibly due to the release of novel germination- and growth-inhibiting allelochemicals, such as emodin, that inhibit the germination and survival of competing plants and their associated mycorrhizal mutualists (Pinzone et al., 2018; Warren et al., 2017). Moreover, buckthorn secondary chemicals also deter pathogens and herbivores, potentially giving buckthorn additional competitive advantage as pathogens and herbivores attack their more palatable competitors (Grunzweig et al., 2015; Izhaki, 2002; White et al., 2006).

In addition to containing the allelochemical emodin, buckthorn allocates more nitrogen to its leaves than most co-occurring native plants and, as a result, has relatively accelerated leaf litter decomposition (Heneghan et al., 2006, Heneghan et al. 2002). Buckthorn litter is rapidly colonized by arthropods, possibly because of the higher nitrogen; however, the rapid decomposition appears to rapidly diminish food sources, leading to a collapse in the soil arthropod community (Heneghan et al., 2002). The abundance and species richness of ground arthropods, e.g. ground beetles (Coleoptera: Carabidae) and ants (Hymenoptera: Formicidae) are lower in areas invaded by buckthorn as compared to uninvaded areas (Schuh and Larsen, 2015). The dense, monotypic buckthorn thickets may therefore become an 'ecological trap' for soil fauna as the poor diversity of native plants and rapid decomposition of buckthorn leaf litter limit ground fauna food resources (Heneghan et al., 2002).

The reduction in native plants and the resulting decrease in secondary production in buckthorn stands may, in turn, impact higher trophic levels. For example, carnivorous and omnivorous rodents, such as white-footed (*Peromyscus leocopus*) and deer (*P. maniculatus*) mice, depend on soil arthropods, which may be diminished by buckthorn invasion (Hamilton, 1941; McCay and Storm, 1997). In addition, many rodents avoid non-native plant seeds that contain secondary compounds, such as emodin (Shahid et al., 2009), and *P. leocopus* avoids emodin-containing buckthorn fruit and normally acceptable fruit laced with emodin (Sherburne 1972). For example, in North America both cottontail rabbits (*Sylvilagus spp.*) and beavers (*Castor canadensis*) avoid buckthorn, whereas buckthorn seedlings are frequently damaged by similar herbivores in Europe (Knight et al., 2007).

Assessing the impact of non-native plant invasion plant solely at a plant level may underestimate the greater impacts on the system if the invasion effects cascade through the food web (Carvalheiro et al., 2010). Given that buckthorn invasion may impact several components of woodland communities, my goal was to assess the multi-trophic effects of buckthorn removal on a forest food-web. I did so by investigating the effects of buckthorn removal on local plant, ground arthropod, pollinator, and rodent communities. Given that buckthorn competitively excludes both herbaceous and woody plants through monoculture shading and novel weapon allelopathy, I expected that plant richness would be higher in patches with buckthorn removed. With greater plant richness where buckthorn was removed, I also expected greater pollinator abundance and richness. I also predicted the removal of buckthorn and potential replacement with native leaf litter should support greater arthropod abundance and richness in the leaf litter. Finally, given that most understory rodents are omnivorous, I also expected that rodent abundance will be higher where buckthorn was removed.

Methods

Study Site

Tifft Nature Preserve, located on the shore of Lake Erie in Buffalo, NY, USA, is a post-industrial forest-wetland complex that was converted into a nature preserve in the 1970s. Before industrialization, Tifft was part of an extensive floodplain and wetland complex surrounding the mouth of the Buffalo River. Tifft soils are alkaline, with a pH of 7.6-7.8 with high levels of calcium. Forested areas are dominated by a mature cottonwood (*Populus deltoides*) overstory and a non–native dominated understory, including Japanese knotweed (*Reynoutria japonica*), tree-of-heaven (*Ailunthus altissima)*, and particularly European buckthorn, (*R. cathartica,* Spiering 2009).

In June 2021, I established 18 100 m^2 (10 x 10 m) plots at Tifft, with six in each of three treatments: (1) ‘native’ plots, in which there are no buckthorn trees or shrubs present, and native herbaceous and woody species were actively introduced; (2) ‘buckthorn tree’ plots, from which buckthorn was never removed, containing mature buckthorn trees but no buckthorn understory; and (3) ’buckthorn shrub‘ plots, containing dense, monotypic stands of buckthorn and cultivated native tree species. In shrub plots, buckthorn diameter at breast height (DBH) was lower than 10 cm; once buckthorn DBH is above 10 cm, growth no longer outpaces native plants in North America (Mascaro and Schnitzer, 2011). The buckthorn in the “shrub” plots was mechanically removed in 2008, but subsequently grew back.

Buckthorn DBH and stem counts

Diameter at breast height (DBH) and stem counts of shrub buckthorn (DBH < 10 cm) was measured along a 14m diagonal transect using a caliper. DBH of mature buckthorn trees (DBH ≥ 10cm) was measured with a DBH fabric diameter tape. Diameter at breast height for trees with multiple trunks was calculated by taking the square root of the sum of squares of each individual stem.

Plant community

Herbaceous layer plant species richness was measured in four 0.25 m^2 subplots located 1 m from each corner of each of the 100 m^2 plots. Plants were identified to lowest taxonomic level possible, generally genus, though graminoids were only identified to family (Brown and Elliman, 2020; Del Tredici, 2020; Uva et al., 1997).

Pollinator community

Pollinator abundance and richness was measured using blue vane traps (SpringStar LLC, Woodinville, WA, USA), which consist of a plastic container (15 cm diameter × 15 cm high) with a blue polypropylene screw funnel with two 24 × 13 cm semitransparent blue polypropylene cross vanes of 3 mm thickness. Each trap was suspended approximately 1.2 m from the ground with shepherd's hooks. Each trap was filled with water and a drop of detergent to break the surface tension. Each plot was sampled with a blue vane trap every three weeks, beginning on June 22nd, 2021 and ending August 24th, 2021 with two plots of each treatment sampled per week. Blue vane trapping accounts for the diverse daily schedule and search pattern of different bees, avoiding temporal sampling bias associated with methods like net-sampling (Cane et al., 2000).

Leaf litter invertebrate community

Leaf litter invertebrate abundance and richness were measured in four 0.25 m^2 subplots at each plot by collecting all of the leaf litter and decaying organic matter and any soil that was mixed with decaying organic matter at the litter-soil interface (Edgar, 1992). The leaf litter samples were placed in Berlese-Tullgren funnels under a tungsten appliance bulb for seven days to sample for soil macrofauna. Each plot was sampled three times, once every three weeks, beginning on June 22nd, 2021 and ending August 17th, 2021, with two plots of each treatment sampled per week. Arthropods were identified to order, and Coleopterans identified to family (Bland and Jaques, 1978; Evans, 2014).

Rodent community

Rodents were sampled in all plots once in June and once in July 2021 using Sherman traps (H.B Sherman Inc., Tallahassee, FL, USA.). Four traps were placed 1m from each corner of each of the 100 m^2 plots plot at dusk and checked at dawn (Shahid et al., 2009). The traps were baited with a high-quality seed mixture and freeze-dried mealworms. Captured rodents were transferred to a cloth bag, weighed with a hanging field scale when possible, and identified to genus (Whitaker, 1996) before being released.

Data analysis

I used a generalized linear model (GLM) assuming a Poisson error distribution to evaluate plant richness, leaf litter invertebrate abundance, pollinator abundance and pollinator richness as functions of the plot treatment (native, tree buckthorn, shrub buckthorn). I fit the GLM using an analysis of deviance (ANODEV) approach in the R statistical program (R Core Team 2022). ANODEV is a maximum likelihood approach whereby a GLM model is fit using an analysis of variance model with a chi-square test. Where the data were overdispersed ($\Phi > 2.0$), I assumed quasiPoisson error.

Results

Buckthorn DBH and stem counts

Buckthorn shrub plots had relatively smaller buckthorn DBH measurements (1.60 ± 0.15) and high stem count (59.67 ± 5.90), whereas buckthorn tree plots had relatively high DBH (20.65 ± 3.65) and low stem count (21.33 ± 1.93). There were no buckthorn stems in native plots.

Plant community

Native plots contained a greater number of plant taxa (16.00 ± 2.08) than buckthorn tree plots (6.50 ± 1.89) and buckthorn shrub plots (1.17 ± 0.17; Figure 3a, Table 1).

Pollinator community

Arthropod pollinator abundance was higher in native plots (66.56 ± 4.47) than buckthorn tree (23.67 ± 5.58) plots and buckthorn shrub (15.67±2.82) plots (Table 2, Figure 4a). Native plots contained a higher number of arthropod orders captured in blue vane traps (6.83 ± 0.19) than both buckthorn shrub (2.00 ± 0.16) and buckthorn tree (3.33 ± 0.26) treatments (Figure 4b, Table 3). Apiform (Anthophila: Hymenoptera) abundance was higher in native plots (16.83± 2.42) than buckthorn tree (7.33 ± 2.98) and buckthorn shrub plots (0.06 ± 0.06, Figure 5a, Table 4). Apiform richness was higher in native (2.67 ± 0.19) and buckthorn tree (2.17 ± 0.10) than buckthorn shrub (0.02 ± 0.10) plots.

Leaf litter invertebrate community

Leaf litter invertebrate abundance was highest in native plots (81.27 ± 9.52), with lower richness in buckthorn tree (13.33 ± 2.03) and buckthorn shrub (44.50 ± 2.22, Figure 6b). Order-level richness was similar in native (8.33 ± 0.59), buckthorn tree (8.17 ± 0.64), and buckthorn shrub (9.83 ± 0.55) treatments. Coleopteran abundance in leaf litter was highest in native plots, (9.33 ± 2.44), followed by buckthorn shrub (2.67 ± 0.80), and lowest in buckthorn tree (2.17 ± 0.60, Table 8). A similar number of Coleopteran families were found in native (3.50 ± 0.41), buckthorn tree (1.67 ± 0.19), and buckthorn shrub (3.00 ± 0.49) treatments.

Rodent community

Rodent abundance was highest in buckthorn shrub plots (1.667 ± 0.25) and lower in both buckthorn tree (0.25 ± 0.13) and native (0.25 ± 0.13) plots (Figure 8). All rodents captured were in the genus *Peromyscus,* with the exception of one *Microtus* found in a native plot.

Discussion

I investigated the effects of buckthorn removal on plant, pollinator, leaf litter invertebrate, and rodent communities in a woodland. Abundance and richness increased across almost all levels of trophic organization with buckthorn removal. That is, native plants, pollinators and leaf litter invertebrates generally were greater in abundance and richness where buckthorn was removed, and generally appeared most negatively impacted by dense buckthorn shrub stands. Contrary to my predictions, rodents were most abundant in buckthorn shrubs.

Plant community

Native plant taxonomic richness was twice as high in plots without buckthorn, which is consistent with previous work showing that buckthorn decreases native plant richness (Knight et al., 2007; Mascaro and Schnitzer, 2007; Warren et al., 2017). Four out of six buckthorn shrub plots contained only buckthorn at the ground level. Only three species were able to grow in the presence of dense buckthorn shrubs: two non-native plants (stinging nettle; *Urtica diocia* and colt's foot; *Ranunculus bulbosus*), and one native (enchanter's nightshade; *Circeae canadensis*). Given that two out of these three species are native to Europe, it may be that plants that have a shared native range with buckthorn are better able to coexist. In some cases, non-native invaders appear to facilitate additional non-native invaders ('invasion meldown', Simberloff and Von Holle 1999). The less dense buckthorn tree plots had higher plant species richness than very dense buckthorn shrub plots, likely a result of more light and space, and less allelopathy, with fewer buckthorn plants. Whereas every native plot contained some small buckthorn plants, the native plants appear to inhibit buckthorn in the restored areas. This pattern agrees with other recent work that shows planting native plants is an effective means of reducing and preventing further invasion of buckthorn and other invasive shrubs (Schuster et al., 2022). Buckthorn often establishes after disturbance (Knight et al., 2007; Kurylo et al., 2007), which at Tifft would have been in a post-industrial landscape. Once established it alters conditions in a manner that favors its own growth, perhaps enabled by increased density in its invaded range (Catford et al., 2009; Ehrenfeld, 2010; Jones et al., 1994). With its removal and the establishment of native plant communities, this process appears to have reversed.

Pollinator community

Arthropod pollinator abundance was much lower in plots with buckthorn, especially the dense buckthorn shrub stands. Indeed, only two Apiforms were captured in the buckthorn shrub plots for the entirety of the study. The lack of native pollinators may stem from the lack of native plants (Tallamy et al., 2021; Tallamy and Shropshire, 2009). European buckthorn inhibits both germination and mycorrhizal mutualists in North American plants (Pinzone et al., 2018), reducing floral resources for pollinators like Apiforms. Moreover, the disturbance of the monotypic buckthorn stands increases irradiance. The removal of another member of Rhamnaceae, glossy buckthorn, (*Frangula alnus*, formerly known as *Rhamnus frangula*), corresponded with rapid recolonization by generalist pollinators, even though plant richness did not immediately recover (Fiedler et al., 2012). Similarly, removal of Chinese privet (*Ligustrum sinense*) led to a large increase in Apiform abundance and two-fold increase in Apiform richness (Hanula and Horn, 2011).

Leaf litter invertebrate community

Leaf litter invertebrate abundance (but not richness) was lower in plots with buckthorn. This finding is consistent with other studies. For example, removal of buckthorn in the Chicago region altered relative densities of surface-active arthropods, increasing the density of fungivores and decreasing density of non-native isopods (McCary et al., 2015). A larger study with higher taxonomic resolution reported that areas uninvaded by buckthorn had higher leaf litter invertebrate abundance overall and lower Coleopteran species richness and abundance in invaded areas (Schuh and Larsen, 2015). Decreased arthropod abundance may be the result of buckthorn litter's accelerated decomposition rates. Decomposition generated bare patches in buckthorn thickets may drive leaf litter arthropod migration, especially where invasion is extensive and there are not suitable patches of habitat remaining (Heneghan et al., 2002).

Rodent community

Rodent abundance was highest in the buckthorn shrub stands, which was contrary to my prediction that omnivore abundance would decrease with lowered food resources in buckthorn stands. *Peromyscus spp.* prefer well-protected, shrubby microhabitats due to, at least in part, greater predator avoidance in dense vegetation (Kaufman et al., 1983). Buckthorn as a habitat engineer for *Peromyscus* has human implications: *Peromyscus* are the principal hosts responsible for infecting ticks (*Ixodes scapularis)* with the bacteria that causes Lyme disease (*Borrelia burgdorferi;* Gray 1998; Ostfeld, Miller, and Hazler 1996). Increased shade, like that found in buckthorn thickets, causes increased humidity and protects from increased daytime temperature, creating favorable conditions for invertebrate parasites like black-legged ticks (Valladares et al., 2016).

Conclusion

Buckthorn invasion alters food webs, and buckthorn management appears to restore native food webs with increased plant taxonomic richness, leaf litter invertebrate abundance, and insect pollinator abundance and richness. Whereas some non-native plants become naturalized and absorb into native food webs without consequence, a North American food web that contains buckthorn supports fewer leaf litter invertebrates (an important source of secondary production) and fewer pollinators (an important factor in fitness and reproduction of flowering plants). Buckthorn invasion and native biodiversity loss form a self-reinforcing process: disturbance-driven loss of native plants makes space for buckthorn to invade, and invasion of buckthorn excludes native plants that may otherwise return to an area. Buckthorn invasion and subsequent ecosystem engineering is likely enabled by the higher density buckthorn can reach in North America; this may be the result of other mechanisms, such as the novelty of emodin as an allelochemical (Ehrenfeld, 2010; Knight et al., 2007; Warren et al., 2017). This study reinforces previous findings that buckthorn removal and continuous management are effective means of restoring buckthorn degraded woodlands. Although this study focused on European buckthorn, this work can be applied to other invasive plants that are non-native and unpalatable to native herbivores, especially shrubs like glossy buckthorn and Chinese privet. Removal of these invasive monotypic shrubs and subsequent reversal of invasion induced homogeneity are fundamental first steps in the conservation and restoration of natural lands and food webs.

Tables

Table 1. Analysis of deviance table showing estimated differences in species richness of non-woody vegetative flora between treatments, subsampled in 4 0.25m^2 quadrats per 100 m^2 plot.

Treatments	Estimate	St. Error	Z value	Pr	
Buckthorn trees-Native	-0.9008	0.1899	-4.744	<0.00001	***
Native-Buckthorn shrubs	2.3671	0.3486	6.790	<0.00001	***
Buckthorn trees-Buckthorn shrubs	1.4633	0.3698	3.965	0.000198	***

Table 2. Analysis of deviance table showing estimated differences in arthropod pollinator abundance collected via blue vane trap over a seven-day time period, averaged across time (3 samples).

Treatments	Estimate	St. Error	Z value	Pr	
Buckthorn trees-Native	-1.051	0.0983	-10.68	<0.0001	***
Native-Buckthorn shrubs	1.447	0.1146	12.62	<0.0001	***
Buckthorn trees-Buckthorn shrubs	0.3960	0.1334	2.968	0.00816	**

Table 3. Analysis of deviance table showing estimated differences in taxonomic richness (order level) of arthropod pollinators collected via blue vane trap over a seven-day time period, totaled across time (3 samples).

Treatments	Estimate	St. Error	Z value	Pr	
Buckthorn trees-Native	-0.7178	0.2727	-2.632	0.0226	*
Native-Buckthorn shrubs	1.2287	0.3282	3.744	<0.001	***
Buckthorn trees-Buckthorn shrubs	0.5108	0.3651	1.399	0.3374	

Table 4. Analysis of variance table showing estimated differences in Apiform abundance collected via blue vane trap over a seven-day time period, averaged across time (3 samples).

Treatments	Estimate	St. Error	Z value	Pr	
Native-Buckthorn shrubs	5.8260	1.7346	3.359	0.00167	**
Buckthorn trees-Native	-0.7201	0.1644	-4.380	0.0000258	***
Buckthorn trees-Buckthorn shrubs	5.1059	1.7373	2.939	0.00697	**

Table 5. Analysis of deviance table showing estimated differences in leaf litter invertebrate abundance (excluding microarthropods) in leaf litter sampled via Berlese-Tullgren funnel, subsampled in 4 0.25m^2 quadrats per 100 m^2 plot, averaged across time (3 samples).

Treatments	Estimate	St. Error	Z value	Pr	
Native-Buckthorn shrubs	0.6024	0.2304	2.615	0.0231	*
Buckthorn trees-Native	-1.8076	0.3650	-4.953	<0.001	***
Buckthorn trees-Buckthorn shrubs	-1.2052	0.3856	-3.125	0.0047	**

Table 6. Analysis of deviance table showing estimated differences in arthropod richness (excluding microarthropods) in leaf litter sampled via Berlese-Tullgren funnel, subsampled in 4 0.25m^2 quadrats per 100 m^2 plot, totaled across time (3 samples).

Treatments	**Estimate**	**St. Error**	**Z value**	**Pr**
Native-Buckthorn shrubs	-0.1655	0.1922	-0.8610	0.665
Buckthorn trees-Native	-0.0202	0.2010	-0.101	0.994
Buckthorn trees-Buckthorn shrubs	-0.1857	0.1933	-0.961	0.602

Table 7. Five most common Coleopteran families captured via Berlese-Tullgren traps, subsampled in 4 0.25m^2 quadrats per 100 m^2 plot, totaled by treatment.

Treatment	**Staphylinidae**	**Nitdulidae**	**Curclionidae**	**Carabidae**	**Coccinellidae**
Native	43	5	9	21	8
Buckthorn trees	10	12	3	1	1
Buckthorn shrubs	0	10	12	2	1

Table 8. Analysis of deviance table showing estimated differences in leaf litter coleopteran richness collected via Berlese-Tullgren funnel, subsampled in 4 0.25m^2 quadrats per 100 m^2 plot, totaled across time (3 samples).

Treatments	**Estimate**	**St. Error**	**Z value**	**Pr**	
Native-Buckthorn shrubs	1.2528	0.2853	4.419	0.000024	***
Buckthorn trees-Native	-1.4604	0.3079	-4.744	<0.00001	***
Buckthorn trees-Buckthorn shrubs	-0.2076	0.3734	-0.556	0.841	

Figures

Figure 1. Plots typical of each treatment: a) Native, in which there were no buckthorn trees or shrubs due largely to management and removal; b) buckthorn trees, in which buckthorn was allowed to grow into mature, spaced trees, and c) buckthorn shrubs, in which buckthorn was mechanically removed ten years ago and allowed to grow back, resulting in monotypic buckthorn stands composed of dense shrubbery.

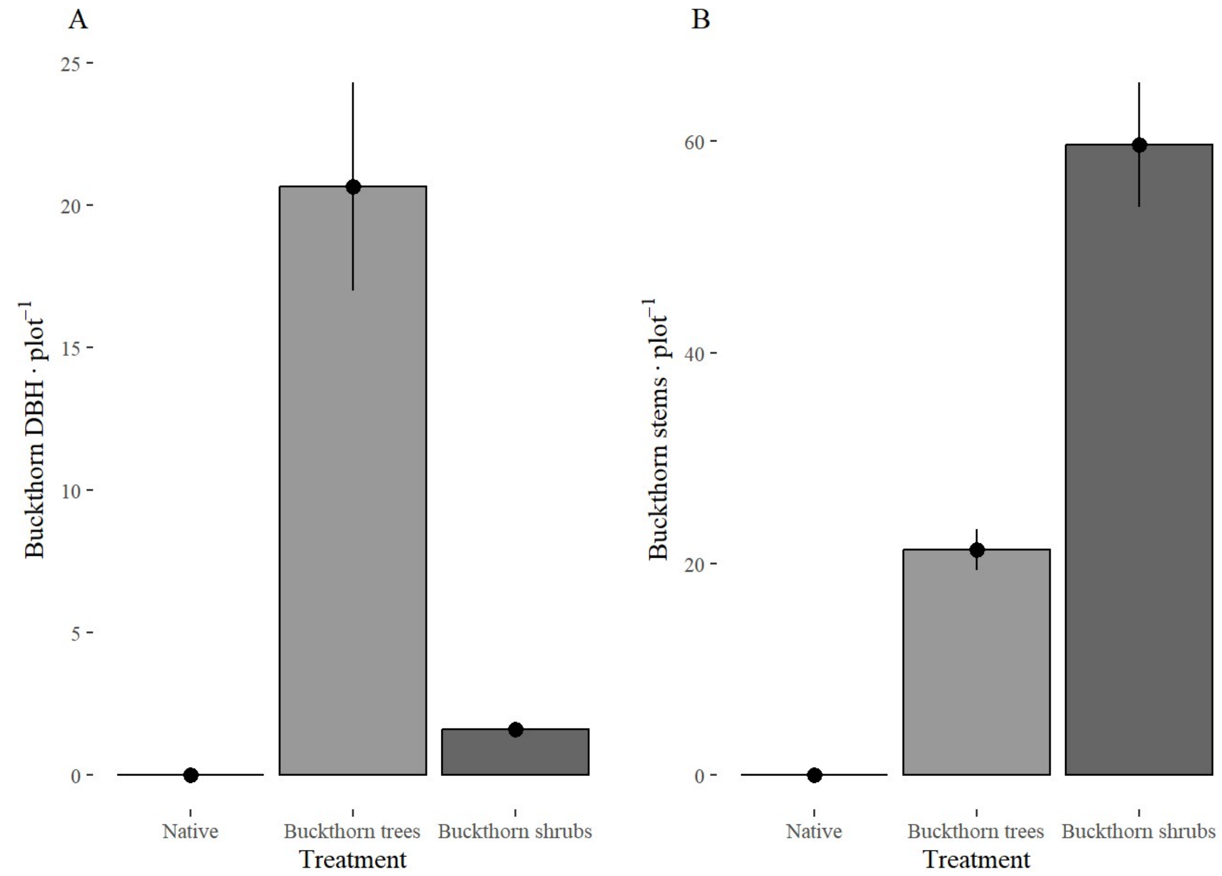

Figure 2. Boxplots showing (a) buckthorn diameter at breast height (DBH) averaged across plot by treatment, and (b) number of stems measured averaged across each plot by treatment.

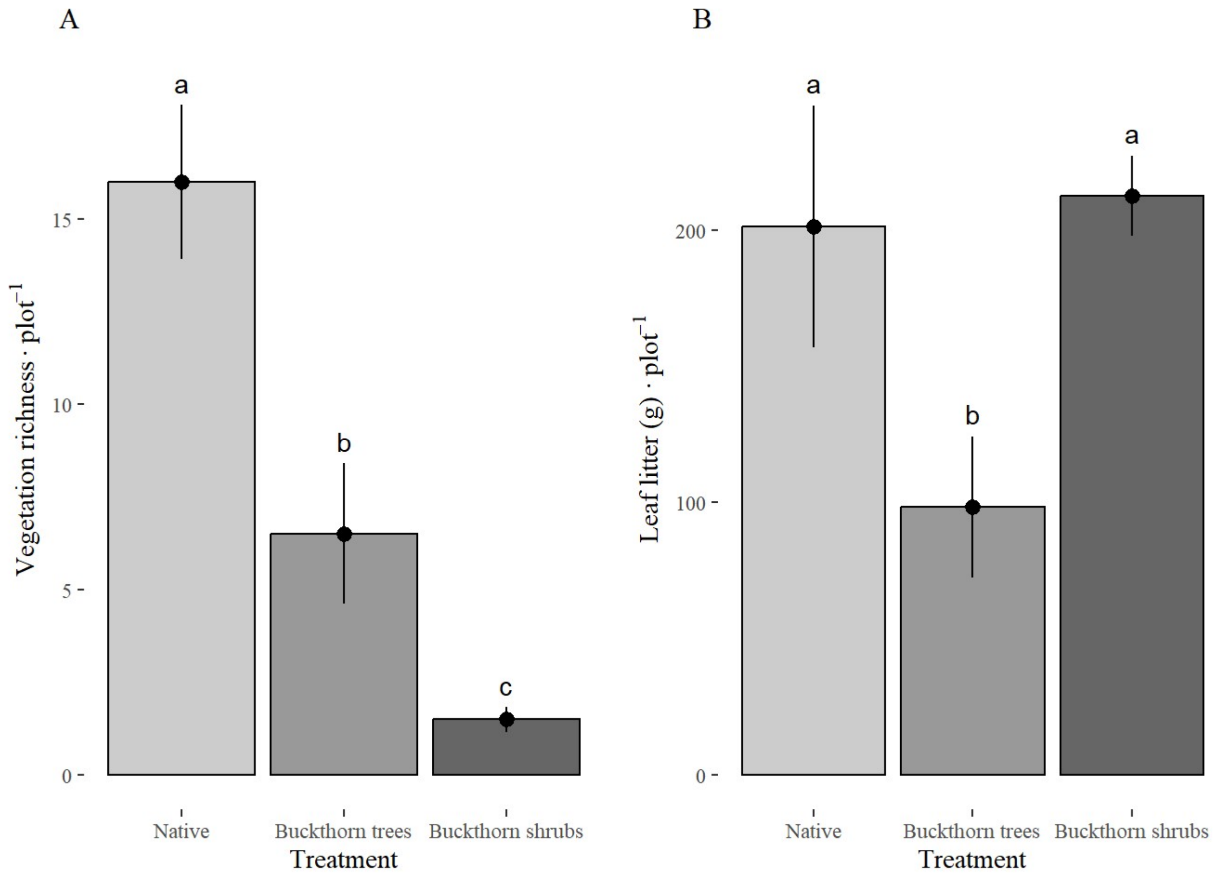

Figure 3. Boxplots showing (a) vegetation taxonomic richness averaged across plot by treatment and (b) dried leaf litter mass (g) averaged across plot and time (3 samples) by treatment. Columns with the same letter do not statistically differ.

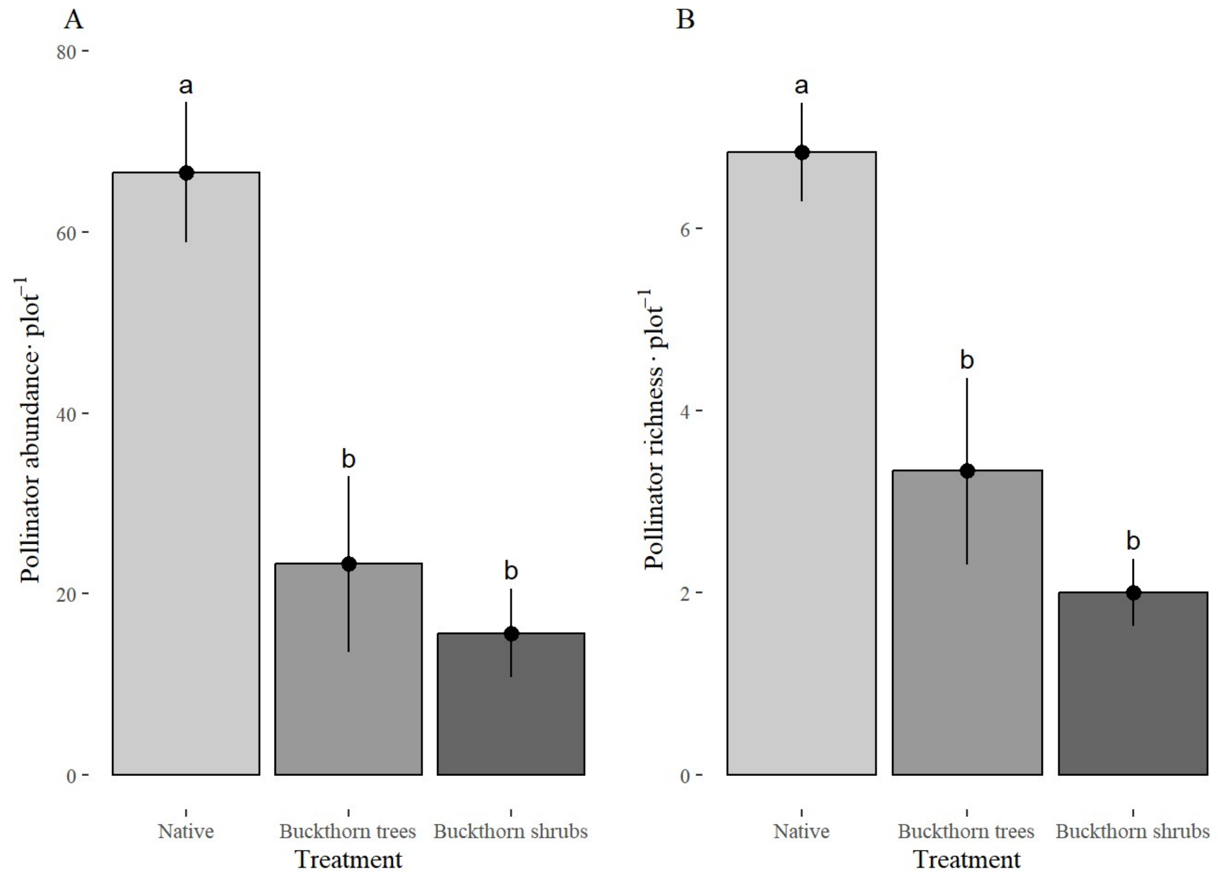

Figure 4. Boxplots showing (a) pollinator abundance averaged across plot and time (3 7-day sampling events per plot) by treatment and (b) pollinator richness (order level) totaled over time and averaged across plot by treatment, collected via blue vane trap.

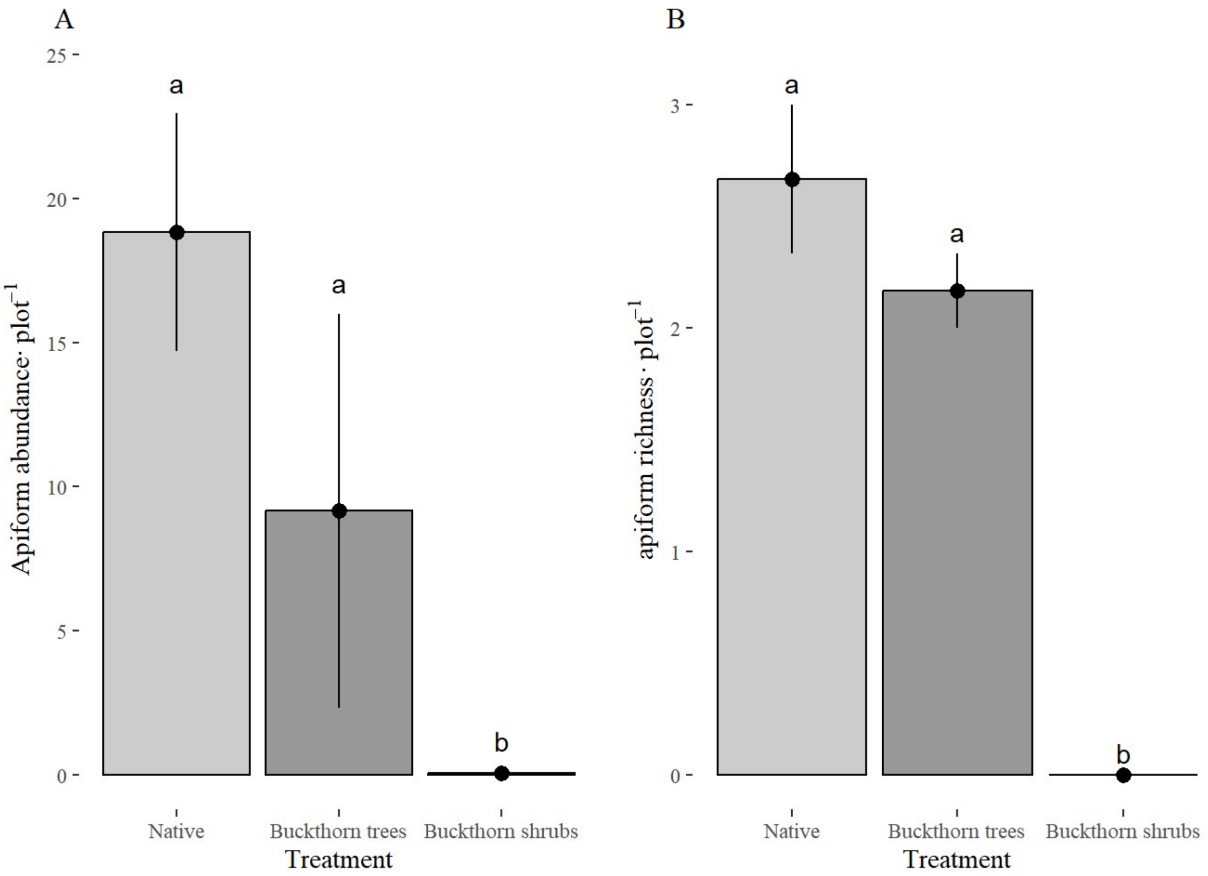

Figure 5. Boxplots showing (a) Apiform abundance averaged across plot and time (3 7-day sampling events per plot) by treatment and (b) Apiform richness (family level) totaled over time and averaged across plot by treatment, collected via blue vane trap.

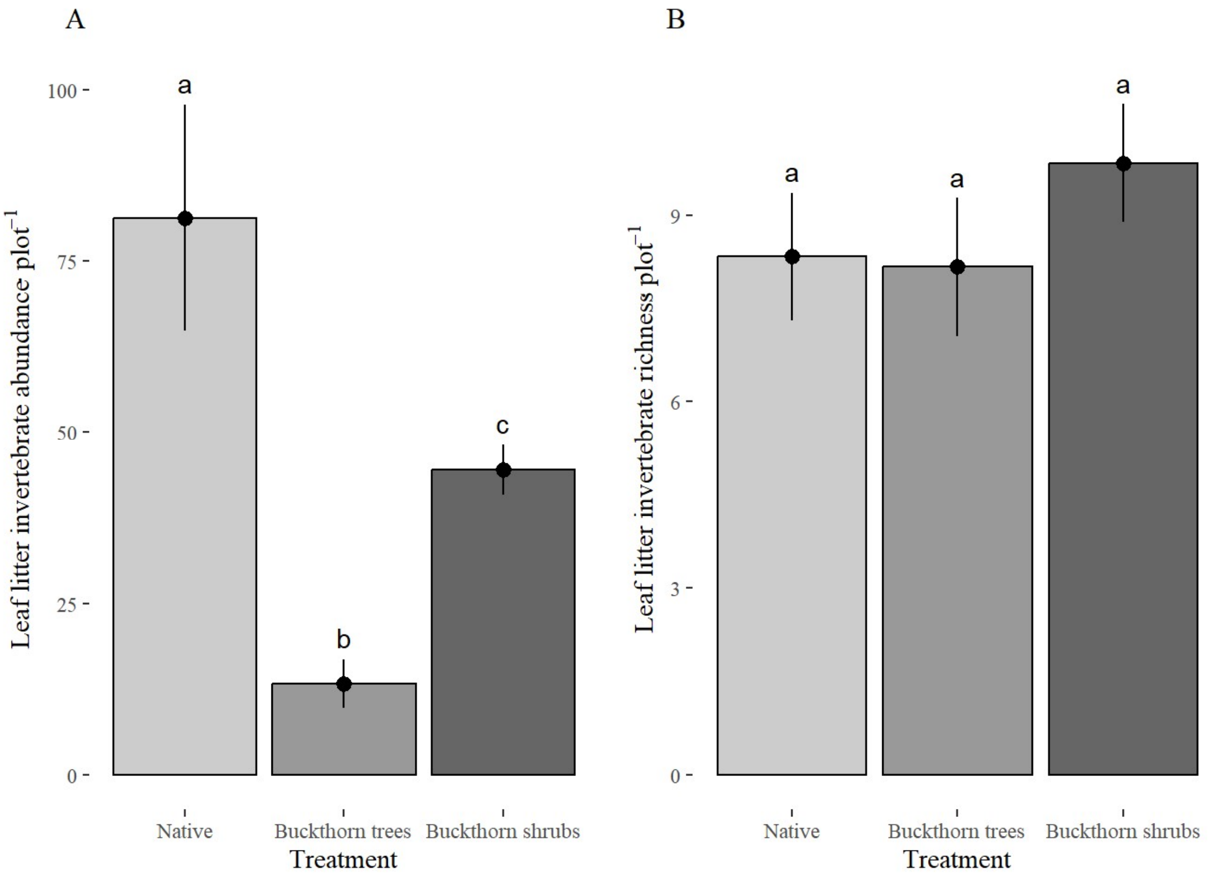

Figure 6. Boxplots showing (a) leaf litter invertebrate abundance averaged across plot and time (3 7-day sampling events per plot) by treatment and (b) leaf litter invertebrate richness (order level) totaled across time and averaged across plot by treatment (3 sampling events per plot, collected in 4 0.25m^2 quadrats per 100 m^2 plot), collected via Berlese-Tullgren funnel.

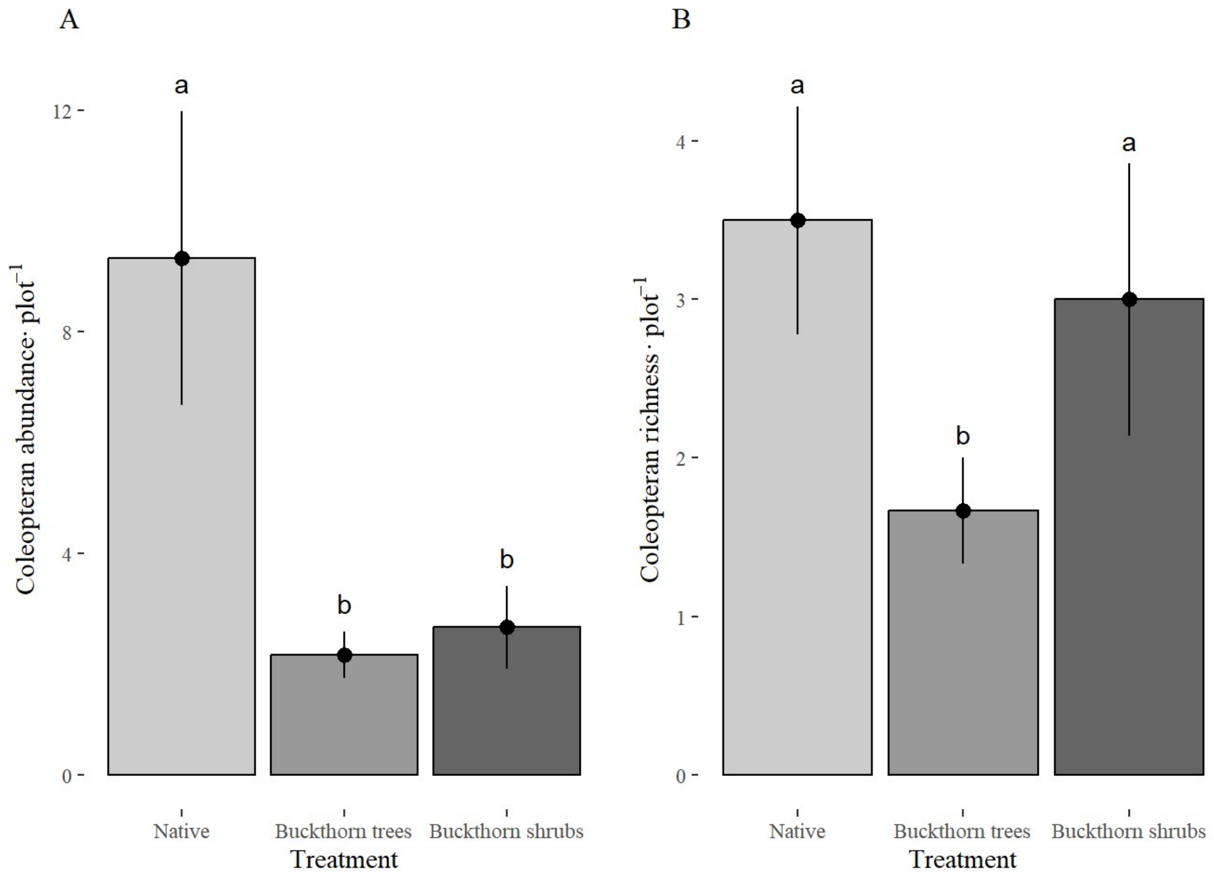

Figure 7. Boxplots showing (a) leaf litter Coleopteran abundance averaged across plot and time (3 7-day sampling events per plot) by treatment and (b) leaf litter Coleopteran richness (family level) totaled over time and averaged across plot by treatment (3 sampling events per plot, collected in 4 0.25m^2 quadrats per 100 m^2 plot), collected via Berlese-Tullgren funnel.

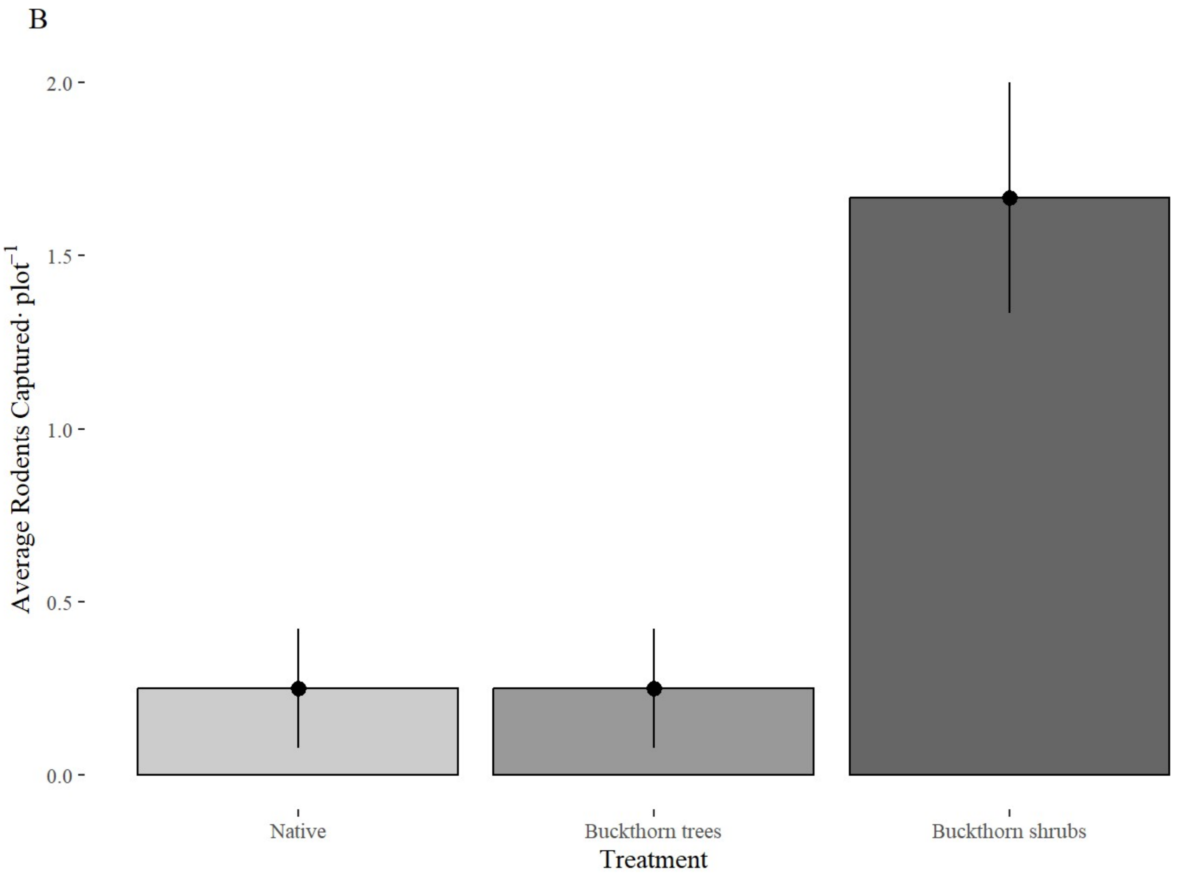

Figure 8. Rodent abundance averaged across time and plot (2 overnight sampling events, 4 traps per plot). All rodents were *Peromyscus,* with the exception of one *Microtus* in a Native plot.

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