MULTITROPHIC IMPACTS OF AN EMERGING INVASIVE PLANT

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By

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ABSTRACT

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The invasion of novel habitats by non-native plant species is a worldwide problem with serious economical and ecological implications. Broad biotic and abiotic filters contribute to the overall invasibility of non-native species. Invasive plants have the ability to rapidly establish themselves and outcompete their native counterparts as result of their relationship with herbivorous arthropods. Because invasive plants displace native plants, reduce overall plant diversity, and alter vegetation structure, this can have cascading effects on insect herbivores, particularly those that rely on one or a few food plants, and arthropod predators. The genus Euonymus (Celastraceae) is comprised of 130 species. *Euonymus alatus* (burning bush) and *Euonymus europaeus* (spindle tree) are two non-natives that have been introduced to North American. Although these species are recognized as invasive in portions of the United States, very little is known about their invasion status, relationship with native herbivores, or community impacts. We sought to fill these gaps with a particular focus on burning bush. We first investigated the distribution of burning bush in Ohio and biotic and abiotic factors that contribute to its success through a citizen science self-reporting protocol. We then examined the relationship of burning bush and spindle tree to herbivorous arthropods through examining field herbivory, success in no-choice bioassays, and analysis of chemical defenses. Finally, we examined the cascading impacts of burning bush and overabundant deer on environmental characteristics and arthropod communities.

Euonymus alatus was present across Ohio but more likely to be successful in locations with greater disturbance and resources. Burning bush and spindle tree are likely experiencing enemy release as both receive significantly less herbivory than a native congener. While both burning bush and spindle tree contained elevated levels of secondary metabolites, a generalist herbivore was able to use spindle tree as a host in no-choice bioassays, suggesting that spindle tree could be evading herbivory through unsuccessful host finding, and both could have novel weapons. Burning bush significantly changed arthropod community composition through alterations in environmental characteristics, and the introduction of white-tailed deer into these interactions more often than not, further intensified these alterations.

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1 DISTRIBUTION AND PREDICTORS OF BURNING BUSH (EUONYMUS ALATUS, (THUNB.) SIEB.: CELASTRACEAE) COLONIZATION AND ESTABLISHMENT IN OHIO

1.1 INTRODUCTION:

The invasion of novel habitats by non-native plant species is a worldwide problem with serious economical and ecological implications (Vitousek et al. 1996). Management of invasive species is estimated to cost over $34 billion a year in the United States (Pimentel et al. 2005). The environmental costs are likely to rise as invasive species alter ecosystem services and displace native species (Dukes & Mooney 2004; D'Antonio & Hobbie 2005). Despite increased global trade and species movement, only a very small proportion of introduced non-native species actually become problematic (Mack et al. 2000). For every ten imported species, only one will colonize the novel environment (appear in the wild; Williamson 1993); of those ten, only one will establish (maintain self-sustaining and growing populations); and of those ten, only one will become invasive (Williamson & Brown 1986). Broad biotic and abiotic filters such as the growth and reproductive traits of non-native species, characteristics of invasion prone ecosystems, and responses of invaded environments all contribute to the overall invasibility of non-native species. These filters and their relative importance in determining invasibility differ between the four stages of invasion (Vermeij 1996; Theoharides & Dukes 2007):

transport, colonization, establishment, and landscape spread. The invasion of a non-native plant into a novel environment depends first on transport (the movement of a non-native from their native range to a suitable novel range). Humans are now the primary dispersers of non-native plants during the transport phase of invasion (Pauchard & Shea 2006). Those species intentionally transported into novel environments, such as those introduced by the nursery trade for ornamental purposes, benefit as their propagules are transported artificially over a long distance, bypassing initial long-distance dispersal barriers (Mack 1995, 2000). Because these plants are crops of the nursery trade, they also undergo climate matching before introduction. They are selected for and sold in areas with climates similar to their native environments greatly increasing their chance of surviving transport (Huenneke 1997; Mack & Lonsdale 2001). Additionally, these plants frequently have physical traits that simultaneously increase their human desirability and invasibility such as attractive foliage, flowers, and abundant seed set. These traits can all act as attractants for pollinators and seed dispersers (birds), further increasing the probability that these species will colonize novel habitats.

After initial transport, only 10% of introduced non-native species will colonize a novel environment. In this stage, populations of non-native invaders must survive the abiotic and biotic filters of the novel environment and achieve positive growth rates at low densities (Chesson 2000; Sakai et al. 2001). Intentionally introduced non-natives are more likely to overcome colonization barriers because of reduced environmental and demographic stochasticity (Mack et al. 2000). These species undergo climate matching before large-scale cultivation and are therefore likely adapted to the local climate of the novel environment, bypassing many abiotic filters. Introduced non-natives with close human associations further overcome much of the demographic stochasticity of invasion. As humans cultivate these plants, they have stable source populations of propagules, which can continually contribute to colonization. Climate matching, along with human association, greatly increases probability that a non-native will escape cultivation and colonize a novel environment (Huenneke 1997; Mack & Lonsdale 2001).

The establishment of self-sustaining populations only occurs for 10% of those species that colonize novel habitats (Williamson & Brown 1986). Biotic filters are particularly important in this stage, as introduced species must outcompete established native communities. Biotic filters will not necessarily prevent transport, germination, and colonization of invaders, but they can affect survival, growth, and reproduction through competition (Theoharides & Dukes 2007). The establishment of an invader is largely dependent upon resource availability – higher resource availability (or open niches) leads to higher invasibility, as there is less competition to prevent invaders from establishing (Davis et al. 2000; Elton 1958). As disturbance disrupts community equilibrium, it leads to higher resource availability and therefore these ecosystems are at higher risk of invasion (Davis et al. 1998; Grime 1974; Grime 1988; Davis et al. 2000; Burke & Grime 1996). This is often the case in secondary forests compared with primary forests. Primary forests contain very few open niches due to high community stability and niche complementarity among resident species (Liang et al. 2015). In these systems, resource availability is low and competition is high, allowing established species to outcompete invaders (Kilmes et al. 2012; Fargione & Tilman 2005). Few primary forests still exist in the eastern United States, however, as forests age, plant communities become more mature leading to fewer open niches and therefore reduced resource availability. In contrast, secondary forests have more open niches, higher resources, and less competition, leading to higher invasibility of these habitats (Fargione & Tilman 2005). Ornamentals, being human associated plants, may experience a positive feedback between high resource availability due to human disturbance as well as high propagule pressure via cultivated source populations.

Burning bush (*Euonymus alatus* (Thunb.) Sieb.; Celastraceae) is an ornamental plant that was introduced from Asia to the United States in 1860 (Dirr 2009, Brand et al. 2012). Burning bush has an extensive native range: from central China and northeastern Asia to the Korea peninsula and Japan (Flora of Asia 2008). It is a deciduous shrub that grows up to 8 ft. tall. The leaves are broad, ovate-elliptic, with an acute apex and are 2-7cm in length and 1-4cm wide. The stems of burning bush have a characteristic "winged" appearance. Adding to its popularity as an ornamental shrub, burning bush has striking red fall color, including attractive red-orange fruits, which remain after many other species have lost foliage. The annual nursery production of this shrub is thought to be at least in the hundreds of thousands (likely millions) and annual sales in Connecticut alone reached $5 million in 2004 (Heffernan 2005). Burning bush is classified as an invasive species in several eastern states (MA, CT, IL, KY, TN, SC, GA, NY; Dirr 2001) and is of growing concern in the Midwest. Although some information is known about the demographics of this plant, very little is known about its ecological impact in novel ecosystems. As an ornamental plant, it is likely that burning bush experienced climate matching for successful transport and cultivation in its novel range. This reduction in abiotic stochasticity could contribute to the colonization of burning bush in novel environments. However, no studies have examined the abiotic climate variables of burning bush invaded habitats. In addition, burning bush has particularly high propagule pressure as it reproduces both sexually and asexually through root sprouts and runners (Dirr 2001). Cultivated individuals produce an average of 3000 seeds per season, with some cultivars producing over 8000 seeds, and germination rates routinely reach 98% (Brand et al 2012, Dirr 2001). Naturally high propagule pressure along with added propagules through human influenced stable source populations is likely to facilitate colonization of burning bush, as overall demographic stochasticity is reduced. This in combination with reduced environmental stochasticity due to climate matching greatly reduces the barriers to colonization of burning bush.

We established a citizen science protocol to first determine the spatial distribution of burning bush in the wild, and to second determine the biotic and abiotic factors that contribute to habitat invasion in Ohio by burning bush during the colonization and establishment phases of invasion. We hypothesized that more disturbed secondary forests would be more heavily invaded by the non-native due to greater resource availability while older, less disturbed “primary forests” would be largely uninvaded. We also hypothesized that proximity to human disturbance would be significantly associated with invaded sites. Additionally, we predicted that invaded sites would have higher precipitation than non-invaded sites.

1.2 METHODS:

The Project Burning Bush citizen science protocol sought to document the presence and/or absence of burning bush in natural areas and the habitat characteristics of these sites (addendum 1). Using the presence and habitat reports, we sought to determine where burning bush was found in the wild in Ohio and to determine biotic and abiotic predictors of invasion. The Project Burning Bush Watch protocol and all supporting documents were disseminated through online outlets such as Facebook, the OIPC listserv (Ohio Invasive Plants Council information dissemination outlet), and individual websites with a message requesting help from citizen scientists, master gardeners, master naturalists, and academics. As word spread of the project, the information was added into the OIPC monthly newsletter as well as the Toledo Naturalist monthly newsletter. This protocol was then redistributed twice a year for the years of 2016 and 2017. The protocol documents included an explanation of the project, a burning bush identification guide, the reporting protocol, and a data sheet. The protocol required participants to report the GPS location of the burning bush. If GPS was unavailable, the participants were asked to record the location of the site in enough detail that we could determine a GPS location at a later date. The protocol sheet included the following example: “Taylorsville MetroPark – one mile north on the orange trail from parking lot CC; on right side of trail approx. 10m off trail”. We strongly suggested that citizen scientists provide photographic evidence of the presence of burning bush. Participants were asked to record habitat variables including dominant plant type, approximate forest age (secondary = less than 50 years in age, primary = greater than 50 years of age), topography, and to estimate the average shrub size and land area covered by the shrub (A = Scattered individuals; B = <

0.25acres; C = 0.25-1 acre; D = > 1 acre). We asked participants to record the proximity of the site to human disturbance such as a trail or an edge habitat. (A = disturbance < 10m away; B = disturbance < 50m away; C = disturbance < 100m away, D = no disturbance). Finally, we asked participants to record the proximity of the site to a past or present homestead (A = homestead < 10m away; B = homestead < 50m away; C = homestead < 100m away, D = no homestead).

Over the three-year implementation of this study, we received a total of 72 individual presence or absence reports. Reports that did not include all of the information required by the protocol were not included in analysis. Reports that were unable to be verified by either photographic evidence or site visits were also removed from statistical analysis. These removed reports, however, were included in the generation of an incidence map. After removing all incomplete reports, we had a total of 36 presence and 20 absence reports.

We utilized site visits and Google Maps to verify the GPS locations provided by the project participants. Using these GPS coordinates and WorldClim (Fick & Hijmans 2017), we extracted 19 climate variables for each of the reported sites. WorldClim is a global database of climate layers with a spatial resolution of 1km^2. The bioclimatic variables included annual mean temperature, mean diurnal range, isothermality, temperature seasonality, max temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter. Before data analysis, the WorldClim environmental variables were tested for correlation to prevent redundant data. We built a correlation matrix including all independent climate variables to aid in model building. For any two independent variables with a correlation coefficient greater than 0.7, the variable spanning the growing season was preferentially selected for inclusion in the models. The climate variables included in analysis were: Mean annual temperature range, mean temperature of the wettest quarter, precipitation of the wettest month, and precipitation of the warmest quarter.

1.2.1 Data Analysis

To construct a map displaying all sites with burning bush present, we used all 55 reports of burning bush presence, regardless of supporting information. All reports used for construction of the map did have an associated GPS coordinates and/or a specific description of the location. GPS coordinates were uploaded into Google Earth. The points were sorted by presence/absence, report type (full or truncated), and by coverage size.

To determine which habitat and environmental variables differed between sites where burning bush was present and absent, we used a combination of hypothesis testing and linear modeling. The proportion of sites belonging to each homestead and human disturbance category was determined for both presence and absence locations. Differences in the frequency of distribution of sites in these categories were assessed using Chi Square analysis. Differences in mean bioclimatic variables between presence and absence locations were assessed using T-tests. Logistic regression (glm, family = binomial) in the lme4 package (Bates et al. 2015) in R was used to determine the variables that most accurately predicted the presence of a burning bush infestation.

We evaluated the importance of the environmental variables in determining the size of the infestation after initial establishment using hypothesis testing and modeling for the presence locations only. Differences in bioclimatic variables between coverage classifications were measured using ANOVA. Pairwise differences in bioclimatic variables between coverage classifications were determined using Tukey's HSD. Ordinal logistic regression in the MASS package (Venables et al. 2002) in R was used to determine the most important variables for predicting the coverage size of an infestation. These methods were repeated for the height classifications at the presence sites.

1.3 RESULTS

1.3.1 Distribution of Burning Bush

Burning bush is present in wild areas throughout the state of Ohio. Absence reports were clustered around metropolitan areas (Map 1.1). However, incidence is least prevalent in the eastern portion of the state (Map 1.1). Size of infestation is relatively evenly distributed throughout the state (Map 1.1). Sites with burning bush present differed from sites without burning bush in almost every metric, including forest type, proximity to a current or abandoned homestead, and proximity to human disturbance (Table 1.1). Locations where burning bush was present showed variation in proximity to a current or abandoned homestead, proximity to human disturbance, shrub height, and infestation coverage (Table 1.2).

Table 1.1: Summarized invasion metrics of 56 citizen scientist reports of burning bush presence or absence in Ohio with all required information reported. Total reports of burning bush presence = 36, total reports of burning bush absence = 20.

Invasion Metric	Burning Bush Presence	Number of sites
Forest Type		
primary (> 50 years old)	Presence	2
	Absence	10
secondary (< 50 years old)	Presence	34
	Absence	10
Proximity to homestead		
(within 100 m)	Presence	25
	Absence	6
(no homestead)	Presence	11
	Absence	14
Proximity to human disturbance		
(within 100 m)	Presence	36
	Absence	20
(no disturbance)	Presence	0
	Absence	0

Table 1.2: Summarized invasion metrics of 36 citizen scientist reports of burning bush presence in Ohio with all required information reported.

Invasion Metric		**Sites (total of 36)**
Proximity to homestead	No homestead	11
	< 10 m	3
	< 50 m	9
	< 100 m	13
Proximity to human disturbance	No disturbance	0
	< 10 m	28
	< 50 m	6
	< 100 m	6
Shrub height	Seedlings	5
	< 1 m	11
	< 2 m	8
	< 3 m	12
Coverage	Scattered individuals	14
	< 0.25 acres	12
	0.25 – 1 acres	2
	> 1 acre	8

1.3.2 Colonization of Burning Bush

Locations where burning bush was present were more likely to be newer secondary growth forests when compared to sites where burning bush was absent (z = 2.649, df = 1, P = 0.003). Ninety-four percent of locations where burning bush was found were secondary or new forest, while 50% of sites where burning bush was absent were older forests (Fig 1.1). Of 11 total old forest sites studied, burning bush was found only twice. 69% of locations where burning bush was present were within 100 meters of a current or abandoned homestead while 30% of locations where it was absent were in the same category (z = 2.216, df = 3, P = 0.008; Fig 1.2). However, there was no significant difference between locations with burning bush present and those without burning bush in proximity to generalized human disturbance (P = 0.55). The mean temperature of the wettest quarter was the only bioclimatic variable that was significantly different between site types. Locations without burning bush had an average temperature of 20.3 ± 0.2 °C SE during the wettest quarter while locations with burning bush averaged 19.3 ± 0.4 °C SE during the same time (t = 2.2174, df = 50.942, P = 0.03). However, sites with burning bush experienced more extreme temperatures within the wettest quarter (Fig 1.3). Although not statistically significant, sites with burning bush had more precipitation during the wettest month (108.1 ± 0.9 mL SE) than the sites where burning bush was absent (105.4 ± 1.9 mL SE, t = -1.7612, df = 32.946, P = 0.08). Although there were many significant models (Table 1.3), the logistic model that best predicted presence or absence of burning bush included proximity to homestead, forest type, and precipitation of the wettest month (AIC = 62.134, F = 4.98, P = 0.0001; Table 1.4).

1.3.3 Establishment and Population Expansion

Of the sites where burning bush was present, 41.7% of the populations reported consisted of scattered individual plants, 30.1% were less than 0.25 acres in size, 5.6% were between 0.25 and 1 acre, and 22.2% were greater than 1 acre in size. After initial colonization, the population size (in area) of burning bush in a given area was best predicted by the proximity to human disturbance and the precipitation during the warmest quarter of the year (AIC = 80.46, P = 0.0004; Table 1.5). However, the precipitation of the warmest quarter was only significantly different between coverage classification A (scattered individuals; 283.5 ± 3.2 mL SE) and D (greater than 1 acre; 297.4 ± 2.7 mL

SE; diff = 13.842, df = 3, P = 0.018). Although larger infestations did experience greater precipitation during the wettest quarter, sites supporting smaller infestations experienced a greater range of precipitation during this same time (Fig 1.4). The average height of the burning bush was not significantly correlated to any of the measured environmental variables.

1.4 DISCUSSION

1.4.1 Biotic Filters

In this study, we sought to determine the spatial distribution of burning bush in Ohio as well as determine those biotic and abiotic factors that influence burning bush success in novel environments. Colonization of burning bush was associated with both biotic and abiotic filters. Forest disturbance was highly predictive of burning bush invasion, as locations with burning bush were almost always within secondary forest. Secondary forests have fewer species (Christensen & Peet 1984; Tang et al. 2010) and more open niches resulting in higher resource availability in these habitats. Secondary forests frequently have been shown to have higher soil carbon (Guggenberger & Zech 1999), higher foliar nutrient stocks, and higher magnesium, calcium, and soil labile phosphorous (Johnson et al. 2001), although these effects can be ecosystem specific. The highly significant association of burning bush invasion with a disturbed forest type lends evidence to that theory that higher resource availability increases invasibility (Davis et al. 2000).

Interestingly, absence sites were just as likely to be primary or secondary forests. This could be a sampling effect, as Ohio has very few primary forest fragments. However, secondary forests generally have higher resource availability and are prone to invasion. Dispersal barriers may impede colonization of invaders into vulnerable habitats (Kolar & Lodge 2001; Lloret et al. 2005). This could be the case with burning bush, as presence locations were over twice as likely to be within 100 meters of a current or abandoned homestead. Secondary forests within proximity of a homestead could be particularly vulnerable to burning bush colonization and establishment as burning bush spreads vegetatively and through seeds. As secondary forests generally have high resource availability, root sprouts or seeds dispersed through short distance dispersal methods have a high chance of success in these environments. However, secondary forests lacking burning bush may be protected from invasion due to a lack of propagule pressure. Although there is anecdotal evidence that burning bush seeds can be dispersed long distances by birds and deer, this has not been empirically studied (Rhodes & Block 2002). If long-distance dispersal methods do exist, however, environments not closely associated with burning bush could be at risk of invasion, although the risk of seed success would be higher in secondary forests as resource availability is high. Eleven of our 36 sites where burning bush was present were not associated with a homestead. This may suggest the presence of a long-distance dispersal method (birds, deer). Future studies should examine directly if birds, deer, or other mammals are actively consuming and dispersing burning bush seeds. However, our data suggest that both disturbance (higher resource availability) and high propagule pressure (close to homestead) are needed for successful burning bush colonization in novel habitats (Theoharides & Dukes 2007), as presence and absence sites did not differ in their proximity to generalized disturbance.

Invasive plants may also experience enhanced competitive ability in novel environments due to a lack of herbivores. Native plants are attacked and regulated by both specialist and generalist herbivores while invasives suffer only to the generalists, if at all as their specialist enemies are unlikely to be endemic (Keane and Crawley 2002). In the absence of range-typical levels of herbivory and disease, invasive species are able to grow and reproduce unchecked and out compete natives (Williamson and Fitter 1996). Thus, invasives in their nonnative range may increase in both distribution and abundance compared to natives in similar niches due to enhanced competitive ability. As burning bush was introduced from Asia, it is likely that this species receives less herbivory than natives through enemy release (Williamson and Fitter 1996; Keane and Crawley 2002). Novel weapons (novel secondary defense compounds; Callaway and Ridenour 2004) could also contribute to the success of burning bush as it has been shown to contain high levels of alkaloids and terpenoids (Zhu et al. 2012). Although the contribution of herbivores to the invasiveness of burning bush was not addressed in this study, it was examined in 2016 and 2017 in a companion study (Roberson, chapter 2). In that study, we we examined comparative herbivory rates of three *Euonymus* species (native - eastern wahoo: *Euonymus atropurpureus,* Jacq., Celastraceae; invasive – burning bush and European spindle tree: *Euonymus europaeu*s, Mill., Celastraceae) in the field, the relative success of a native generalist herbivore, fall webworm, on these species, and comparitive foliar concentrations of two groups of major secondary metabolites known to exist in

Euonymus species. We found that burning bush recived substantially less herbivory than the native, eastern wahoo, (less than 2% leaf area removed compared to 17%) and was toxic to a generalist arthropod herbivore while the other two tested *Euonymus* species supported the insect throughout the lifecycle. We attributed this toxicity to high levels of phenolics which reached levels four times higher than those obseved on spindle tree or wahoo. Therefore, it is likely that burning bush is both escaping specialist herbivory through enemy release ((Williamson and Fitter 1996; Keane and Crawley 2002), and escaping generalist herbivory through novel or increased levels of defensive compounds (Callaway and Ridenour 2004). As burning bush is experiencing reduced herbivory in its novel range, the plant can allocate fewer resources for chemical defense and tissue repair. It is then able to funnel excess resources into growth and reproduction, contributing to the rapid colonization, and establishment compared to native congeners leading to an evolutionary increase of competitive ability (EICA; Alpert et al. 2000; Stowe et al. 2000). Lack of herbivores and subsequent reduced need for the production of defense compounds, therefore, likely contributes to the successful colonization (more energy for reproduction leads to higher propagule pressure) and establishment (more energy for growth even in resource constrained environments).

1.4.2 Abiotic Filters

Intentionally introduced ornamental plants frequently bypass many abiotic filters to colonization as these species commonly undergo climate matching prior to introduction (Mack 2000). Of the nineteen tested bioclimatic variables from WorldClim, only temperature of the wettest quarter differed between presence and absence sites. Sites with burning bush were one degree cooler on average than sites without burning bush. Although this may not be biologically significant, these sites also experienced more extreme cold events. As disturbance increases available resources, it is possible that within these cold events, burning bush either has higher survival in these periods or is able to outcompete natives for the acquisition of newly available resources following disturbance (Huenneke et al. 1990). Once burning bush colonized an area, more successful establishment (greater size of infestation coverage) was associated with more precipitation in the warmest quarter of the year. As increased moisture has been shown to increase non-native plant success (Burke & Grime 1996; Davis et al. 2000), locations with higher precipitation are able to support larger populations of burning bush. However, the general lack of abiotic climate variables predicting colonization or establishment success supports the assertion that burning bush experiences reduced effects of environmental stochasticity due to climate matching (Huenneke 1997; Mack & Lonsdale 2001).

1.4.3 Biotic and Abiotic Filter Interactions

Although biotic and abiotic factors could contribute to invasibility of a habitat individually, the interaction between biotic and abiotic filters is likely more important in predicting invasion. The generated models predicting colonization (presence/absence) and establishment (coverage of infestation) of burning bush included both biotic and abiotic factors. Burning bush colonization was most successful in secondary forest habitats close to homesteads, suggesting that disturbed habitats with high propagule pressure from stable source populations contributes significantly to colonization

(Williamson 1999; Pauchard & Shea 2006). Establishment, or size of the burning bush invasion, was significantly associated with proximity to generalized human disturbance, not just homestead. This suggests that propagule pressure from external sources is not important in the establishment stage. However, the high resource availability provided by disturbed habitats likely does significantly contribute to successful establishment (Grime 1988; Davis et al. 1998). Despite the importance of disturbance and propagule pressure in the invasion of burning bush, colonization and establishment were more successful in habitats with greater precipitation in seasons with both high and low resource availability. Increased moisture has been shown to increase non-native plant success (Burke & Grime 1996) as invasive plants respond more strongly to abundant resources than native plants (Huenneke et al. 1990). Therefore, interaction of abiotic and biotic environmental factors determines the success of burning bush as an invader in novel environments.

1.4.4 Invasion in a Changing World

Changes in world climate that have accelerated in recent decades have resulted in altered population and community dynamics of native species, including altered geographical ranges and ecosystem function (Walther et al. 2002; Parmesan 2006). These increased disturbances can facilitate colonization of new invaders as well as the establishment and spread of current populations. Abiotic filters in temperate habitats have limited many introduced ornamental plants from warm global regions. Warmer global temperatures could increase the reproductive output of these non-native plants, and therefore invasibility, through longer growing seasons (Walther et al. 2009). In the case of burning bush, colonized sites had a lower average temperature of the wettest quarter suggesting that increased global temperatures may retard reproductive output of already colonized sites. However, as temperatures warm in higher latitudes, burning bush may become more successful in previously prohibitory cold environments. Changes in precipitation regimes are also likely to influence the invasion of non-native plants. Increased precipitation has been implicated in the spread of many non-native plant species (Blumenthal et al. 2008). As burning bush was more successful in colonizing and establishing in sites with higher precipitation, it is likely that in areas of precipitation increases, burning bush will be more successful. Future studies should examine the impact of increased temperature and precipitation on the success and spread of already colonized habitats, the further spread of established populations, and the colonization of previously uninhabitable environments.

1.5 REFERENCES

Alpert P, Bone E, Holzapfel C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3:52–66.

Blumenthal, D. et al. 2008. Increased snow facilitates plant invasion in mixedgrass prairie. New Phytologist 179:440-448

Brand, MH., Lubell, JD., Lehrer, JM. 2012. Fecundity of winged Euonymus cultivars and their ability to invade various natural environments. HortScience 47(8): 1029-1033

Burke, MJW., Grime, JP. 1996. An experimental study of plant community invasibility. Ecology 77: 776-790

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2:436-443.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343-366

Christensen, NL., Peet, RK. 1984. Convergence During Secondary Forest Succession. *Journal of Ecology* 72(1): 25-36

D'Antonio, CM., Hobbie, SE. 2005. Plant species effects on ecosystem processes. Species invasions: insights from ecology, evolution, and biogeography. Sunderland, MA USA: Sinauer Asociates, 65- 84

Davis, MA., Grime, JP., Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528-534

Davis, MA., Wrage, KJ., Reich, PB. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology 86: 652-661

Dirr, M.A. 2001. Winged euonymus is a stalwart shrub for consistent fall color. Nursery Man- agement and Production 17:16–17, 91–95.

Dirr, M.A. 2009. Manual of woody landscape plants. 6th Ed. Stipes Publishing, Champaign, IL.

Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48

Dukes, JS., Mooney, HA., 2004. Disruption of ecosystem processes in western North America by invasive species. Revisita Chilena de Historia Natural 77: 411-437.

Elton, CS. 1958. The ecology of invasions of animals and plants. Methuen, London, UK.

Fargione, JE., Tilman, D. 2005. Diversity decreases invasion via both sampling and complementarity effects. Ecology Letters 8: 604-611

Flora of China Project. 2008. Flora of China, [Online]. In: eFloras.org/ Beijing: Science Press; St. Louis, MO: Missouri Botanical Garden Press (Producers). Available: http://www.efloras.org/flora_page.aspx?flora_id=2 [2009, January 14]

Grime, JP. 1974. Vegetation classification by reference to strategies. Nature 250: 26-231

Grime, JP. 1988. The C-S-R model of primary plant strategies: origins, implications, and tests. Plant evolutionary biology. (eds LD. Gottlieb, SK. Jain), 371-393. Chapman & Hall, London, UK

Guggenberger, G., Zech, W. 1999. Soil organic matter composition under primary forest, pasture, and seconday forest succession, Region Huetar Norte, Costa Rica. Forest Ecology and Management 124(1): 93-104

Heffernan, R. 2005. Invasive plants of value to the green industry not yet banned in Connecticut. Conn. Green Industries Publishing, Botsford, CT.

Huenneke, LF. 1997. Outlook for plant invasions: Interactions with other agents of global change. Assessment and management of plant invasions. New York, NY. USA: Springer-Verlag, 95-1-3.

Huenneke, LF., Hamburg, SP., Kiode, R., Mooney, HA., Vitousek, PM. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71:478-491

Johnson, CM., Vieria, CG., Zarin, DJ., Frizano, J., Johnson, AH. 2001. Carbon and nutrient storage in primary and seconday forests in eastern Amazonia. Forest Ecology and Management 147(2-3): 245-252

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution. 4:164-170. doi: 10.1016/S0169-5347(02)02499-0

Klimes, P., Idigel, C., Rimandai, M., Fayle, T.M., Janda, M., Weiblen, G.D. & Novotny, V. (2012) Why are there more arboreal ant species in primary than secondary forests? Journal of Animal Ecology, 81, 1103–1112.

Kolar, CS., Lodge, DM. 2001. Progress in invasion biology: predicting invaders. Trands in Ecology and Evolution 16: 199-204

Liang, J., Zhou, M., Tobin, PC., McGuire, AD., Reich, PB. 2015. Biodiversity influences plant productivity through niche-efficiency. PNAS 112(18): 5738-5743

Lloret, F., Medail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambson, P., Hulme, PE. 2005. Species attributes and invasion success by alien plants on Mediterranean islands. Journal of Ecology 93: 512-520

Mack, RN. 2000. Cultivation fosters plant neutralization by reducing environmental stochasticity. Biological Invasions 2: 111-122

Mack, RN., Simberloff, D., Lonsdale, WM., Evans, H., Clout, M., Bazzaz, FA. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10: 689-710

Mack, RN., Lonsdale, WM. 2001. Humans as global plant dispersers: Getting more than we bargained for. Bioscience 51: 95-102

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Evolution and Systematics 37: 637-669

Pauchard, A., Shea, K. 2006. Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8: 399-413

Pimental, D., Zuniga, R., Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52: 273-288.

Rhoads, Ann F.; Block, Timothy A. 2002. Invasive species fact sheet: Winged euonymus--(burning-bush, winged wahoo, winged spindle-tree, Japanese spindle-tree), [Online]. In: Delaware River Invasive Plant Partnership. In: The Pennsylvania Flora Project. Philadelphia, PA: The Pennsylvania Flora Project, Botany Department, Morris Arboretum of the University of Pennsylvania (Producer). Available: http://www.paflora.org/Euonymus%20alatus.pdf

Sakai, AK., Allendorf, FW., Holt, JS., Lodge, DM., Molofsky, J., With, KA., Baughman, S., Cabin, RJ., Cohen, JE., Ellstrand, NC., McCauley, DE., O'Neil, P., Parker, IM., Thompson, JN., Weller, SG. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305-332.

Stowe KA, Marquis RJ, Hochwender CG, Simms EL. 2000. The evolutionary ecology of tolerance to consumer damage. Annual Review of Ecology and Systematics 31:565–595.

Tang, JW., Min, C., Zhang, JH. 2010. Litterfall production, decomposition, and nutrient use efficiency varies with tropical forst types in Xishuangbanna, SW China: a 10 year study. Plant and Soil 335(1-2): 271-288

Theoharides, K.A., Dukes, J.S. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist 176: 256-273

Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Vermeij, GJ. 1996. An agenda for invasion biology. Biological Conservation 78: 3-9.

Vitousek, PM., Dantonio CM., Loope, LL., Westbrooks, R. 1996. Biological invasions as global environmental change. American Scientist 84: 468-478

Walther, GR. et al. 2002. Ecological responses to recent climate change. Nature 416: 389-395

Walther, GR. et al. 2009. Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolition 24(12): 686-693

Williamson, M. 1993. Invaders, weeds and the risk from genetically modifies organisms. Experientia 49: 219-224

Williamson, M.H., Brown, K.C. 1986. The analysis and modeling of British invasions. Philosophical Transactions of the Royal Society B314: 505-522

Williamson, M.H., Fritter, A. 1996. The varying success of invaders. Ecology 77(6): 1661-1666

Zhu, JX., Qin, JJ., Chang, RJ., Zeng, Q., Cheng, XR., Zhang, F., Jin, HZ., Zhang, WD. 2012. Chemical Constituents of plants from the genus Euonymus. Chemistry and Biodiversity 9: 1055-1076

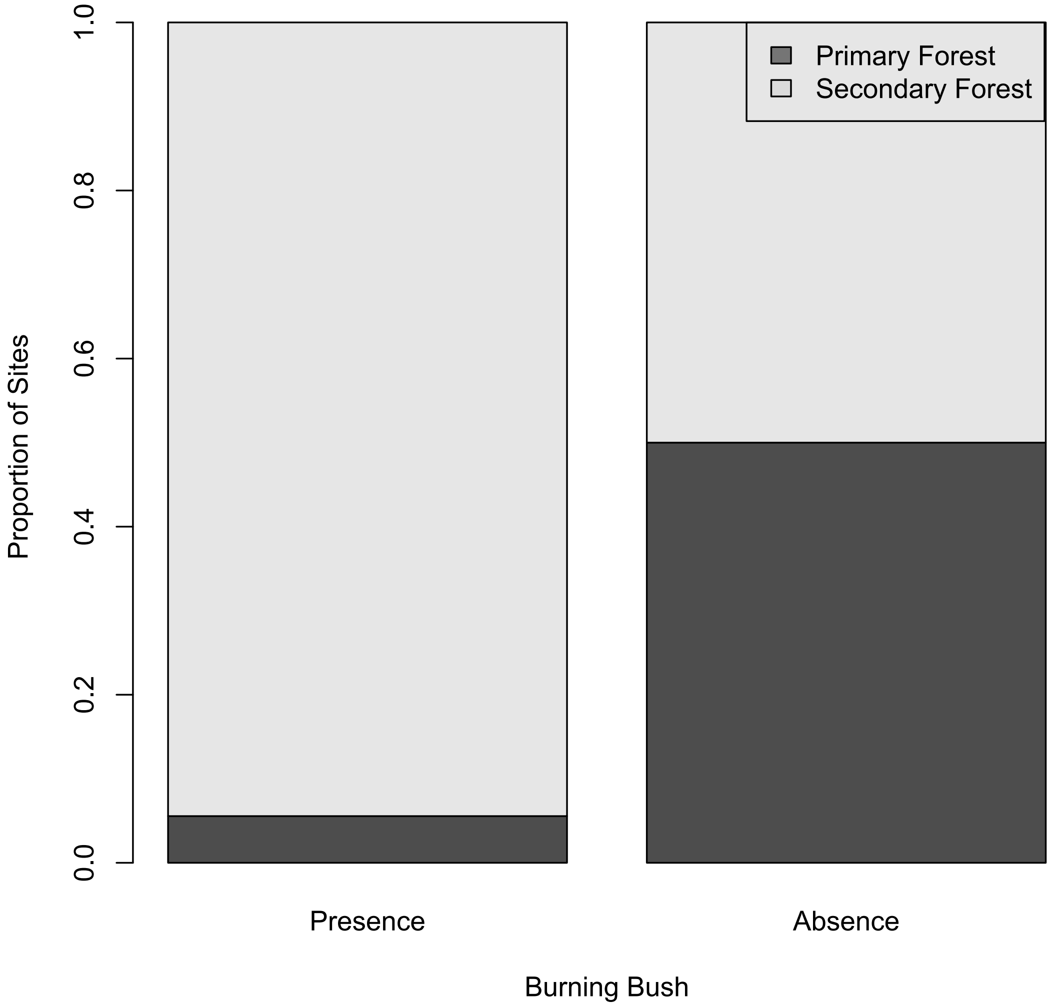


Fig 1.1: Proportion of citizen scientists reported locations within primary (> 50 years old) and secondary (< 50 years old) forests separated by the presence or absence of burning bush. Total of 36 burning bush presence observations and total of 20 reports where burning bush was absent.

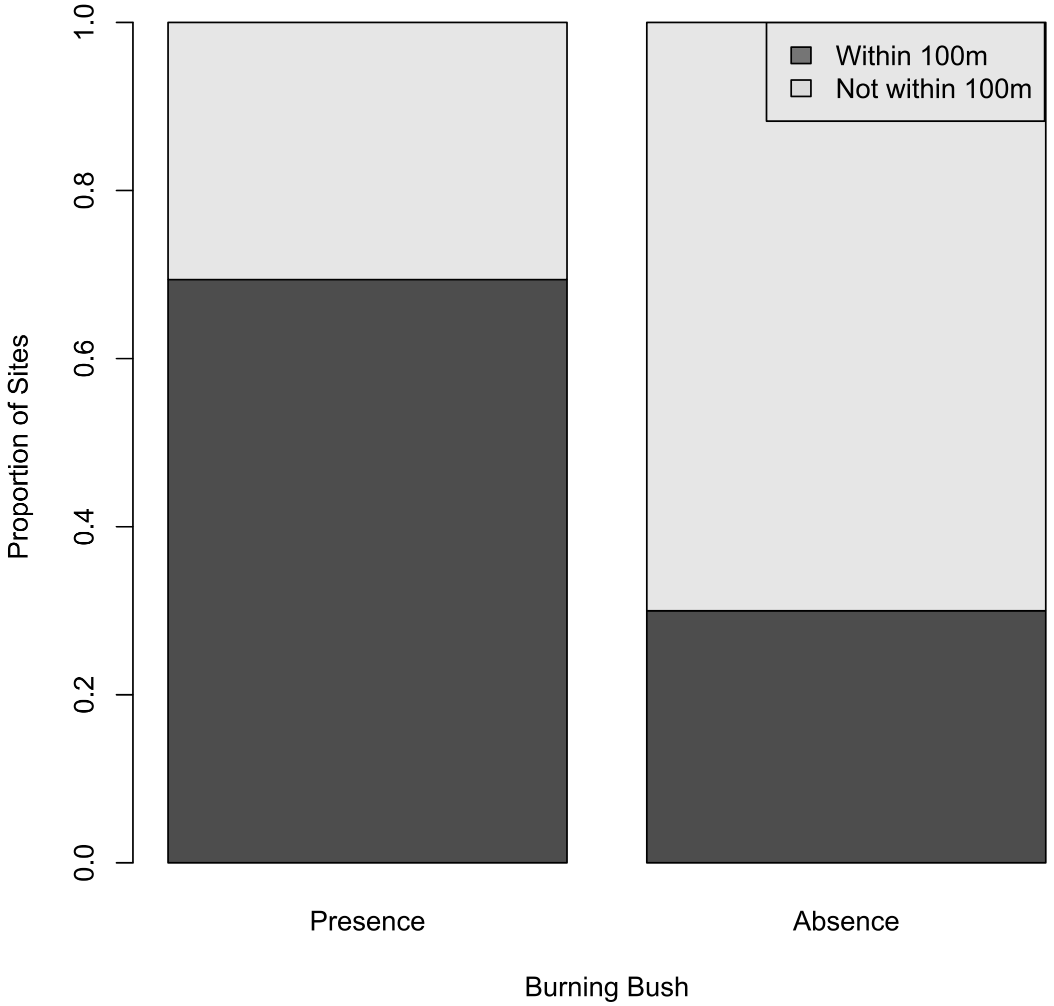


Fig 1.2: Proportion of citizen scientists reported locations within and not within 100m of a current or abandoned homestead separated by the presence or absence of burning bush. Total of 36 burning bush presence observations and total of 20 reports where burning bush was absent.

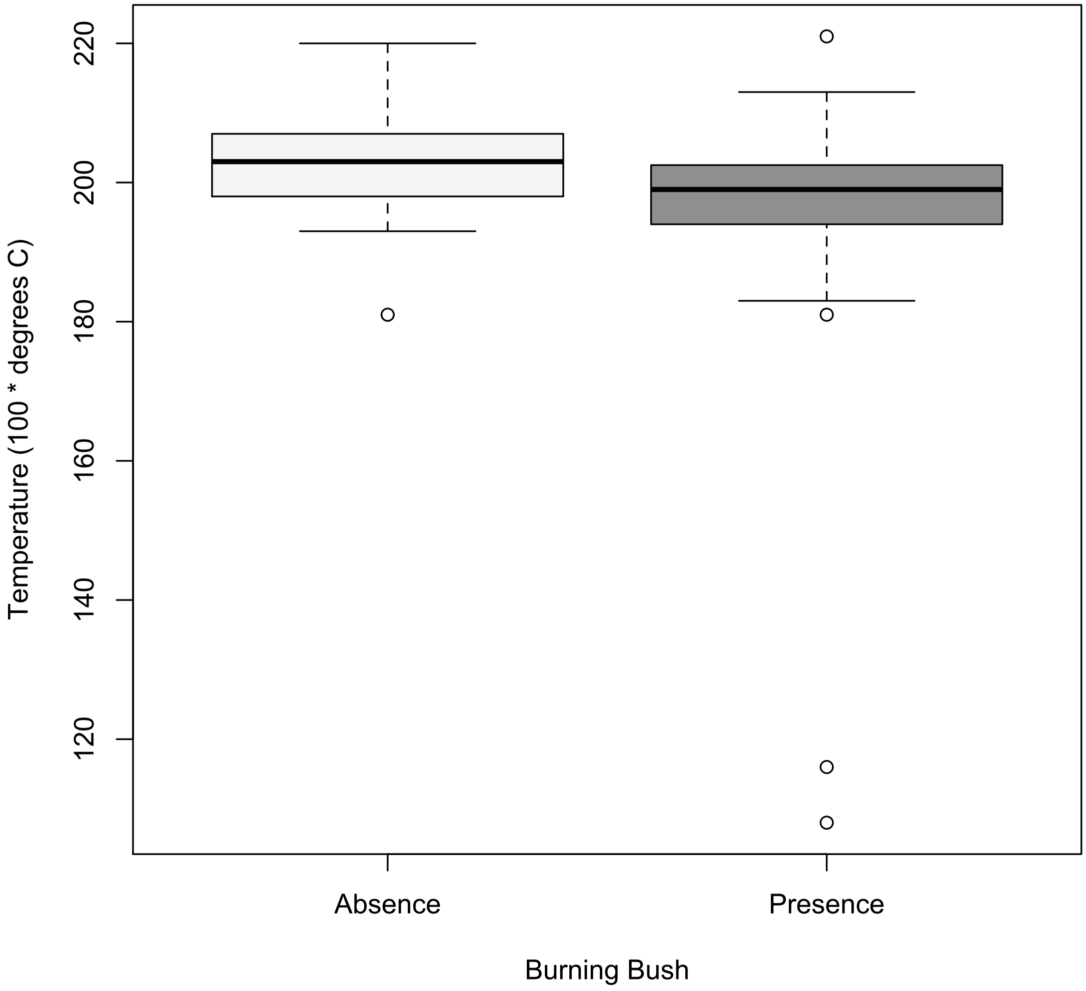


Fig 1.3: Historical temperature of the wettest quarter observed for locations with burning bush present and those with burning bush absent. Temperature measurements were extracted from WorldClim.

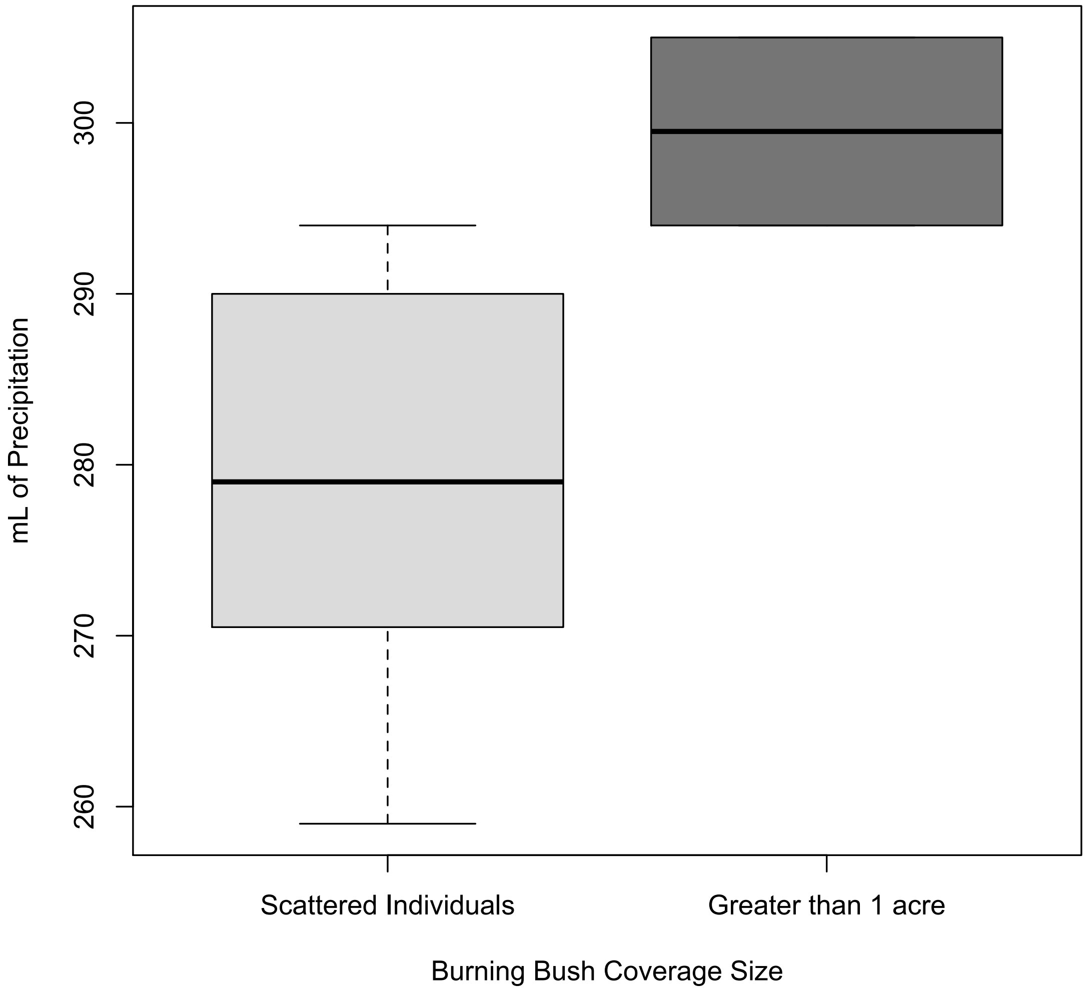
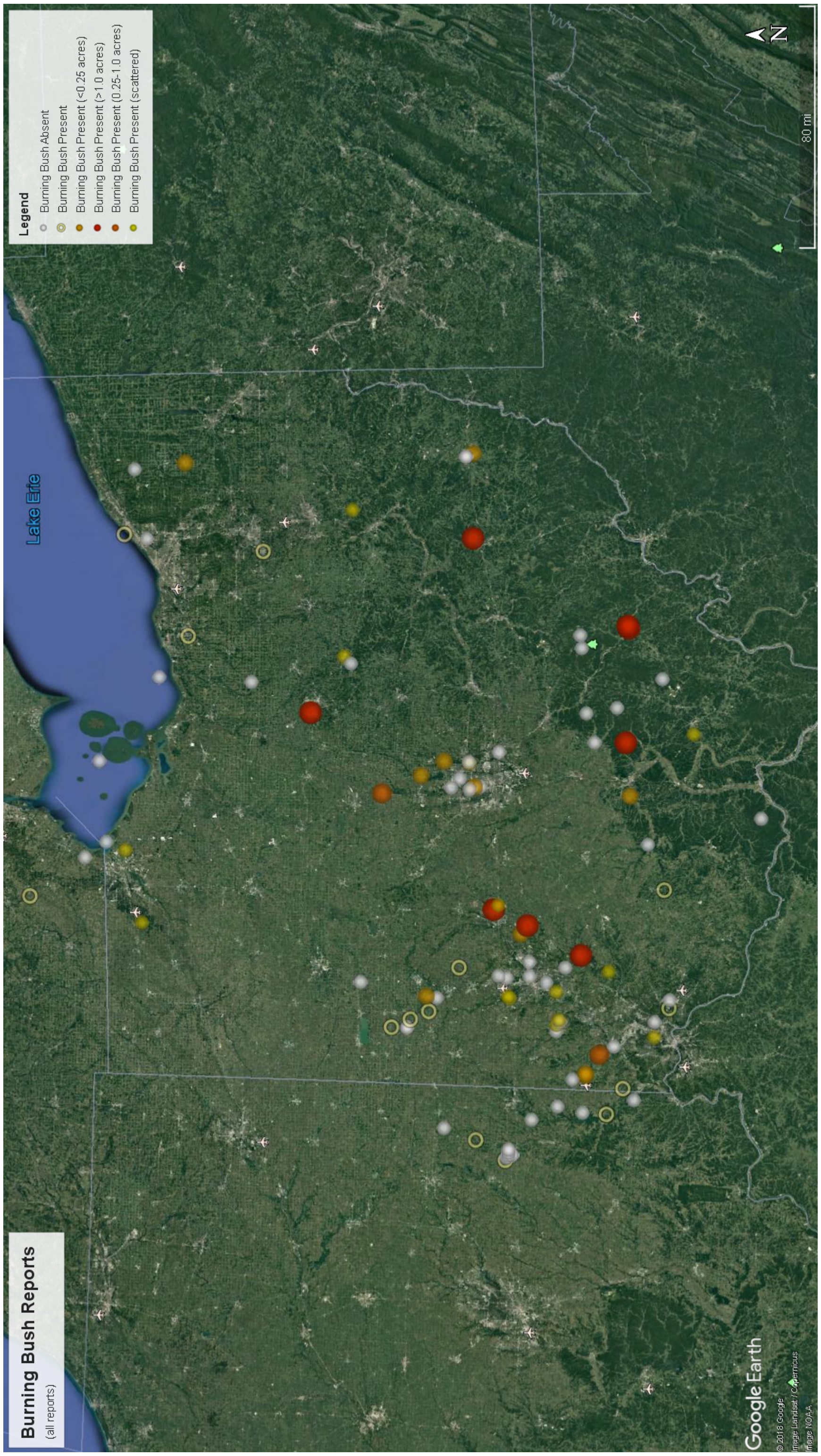


Fig 1.4: Historical precipitation of the warmest quarter observed for locations with burning bush present and separated by size of infestation. "Scattered individual" reports made up 14/36 total citizen science reports of burning bush presence while infestations "Greater than 1 acre" accounted for 8/36 reports. Precipitation measurements were extracted from WorldClim.



Map 1.1: presence and absence of burning bush from all citizen science reports including incomplete reports; coverage size calculated from all complete presence reports

Table 1.3: Significant logistic models to predict burning bush presence in Ohio – Summary of Akaike Information Criterion (AIC) values used to select best-fit models

Significant Models (Independent Variables)	AIC Values	AIC df	F	P(>F)
Home + ForestType + TempAnRange	66.1	51	4.13	0.0008
Home + ForestType + TempAnRange + AvgTempWetQu	65.2	50	3.97	0.0006
Home + ForestType + TempAnRange + PrecWetMo	63.2	50	4.30	0.0002
Home + ForestType + TempAnRange + PrecWarmQu	66.8	50	3.71	0.001
Home + ForestType + TempAnRange + PrecWarmQu + TempAnRange * PrecWarmQu	66.1	49	3.55	0.0008
Home + ForestType + AvgTempWetQu	63.9	51	4.63	0.0003
Home + ForestType + AvgTempWetQu + PrecWetMo	64.0	51	4.17	0.0003
Home + ForestType + AvgTempWetQu + PrecWetMo + AvgTempWetQu * PrecWetMo	65.8	49	3.60	0.007
Home + ForestType + AvgTempWetQu + PrecWarmQu	65.6	50	3.90	0.006
Home + ForestType + AvgTempWetQu + PrecWarmQu + AvgTempWetQu * PrecWarmQu	67.5	49	3.36	0.001
Home + ForestType + PrecWetMo	62.1	51	4.98	0.0001
Home + ForestType + PrecWetMo + PrecWarmQu	62.9	50	4.34	0.0002

Home = Proximity to a current or abandoned homestead, ForestType = primary or secondary forest, TempAnRange = annual temperature range, AvgTempWetQu = mean temperature of the wettest quarter, PrecWetMo = precipitation of the wettest month, PrecWarmQu = precipitation of the warmest quarter; * = interaction between two independent climate variables

Table 1.4: Significance of the individual independent variables within the best-fit logistic model to predict burning bush presence in Ohio – Summary of deviance values, degrees of freedom, and p-values

Model Variables	Deviance	df	P(>Chi)
Home	11.83	3	0.008
Forest Type	8.72	1	0.003
Precipitation of Wettest Month	4.34	1	0.037

Table 1.5: Significant ordered logistic models to predict infestation coverage of burning bush in sites where burning bush was reported in Ohio – Summary of Akaike Information Criterion (AIC) values used to select best-fit models

Significant Models (Independent Variables)	AIC Values	P (>Chi)
Human + TempAnRange	92.1	0.0001
Human + TempAnRange + AvgTempWetQu	93.7	0.0009
Human + TempAnRange + PrecWetMo	93.7	0.0009
Human + TempAnRange + PrecWarmQu	87.9	0.0006
Human + TempAnRange + PrecWarmQu + TempAnRange * PrecWarmQu	86.8	0.0003
Human + AvgTempWetQu	95.6	0.0005
Human + AvgTempWetQu + PrecWetMo	96.9	0.0004
Human + AvgTempWetQu + PrecWetMo + AvgTempWetQu * PrecWetMo	98.0	0.0003
Human + AvgTempWetQu + PrecWarmQu	82.3	0.0001
Human + AvgTempWetQu + PrecWarmQu + AvgTempWetQu * PrecWarmQu	83.3	0.0002
Human + PrecWetMo	95.1	0.0007
Human + PrecWetMo + PrecWarmQu	82.4	0.0004
Human + PrecWetMo + PrecWarmQu	80.5	0.0007

Home = Proximity to a current or abandoned homestead, ForestType = primary or secondary forest, TempAnRange = annual temperature range, AvgTempWetQu = mean temperature of the wettest quarter, PrecWetMo = precipitation of the wettest month, PrecWarmQu = precipitation of the warmest quarter; * = interaction between two independent climate variables

1.6 APPENDIX A

1.6.1 Burning Bush (Euonymus alatus) Watch Protocol

United States Executive Order 13112 defines an invasive species as “an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health.” Invasives have huge impacts, both economically and environmentally. It is estimated that invasive species cost the United State more than $120 billion in damages every year (Pimental et al. 2005)! Most of this cost comes from prevention, detection, rapid response, outreach, and habitat restoration. These invasives cause large-scale environmental impacts in agricultural operations, native fisheries, tourism, outdoor recreation, and the overall health of ecosystems. Invasives alter predation regimes and pressures, degrade the structure of habitats, and compete with native species for resources.

Invasive plant species, in particular, are adaptable, have aggressive growth, and have a high reproductive capacity. These characteristics combined with a lack of natural enemies often leads to outbreak populations. A lot of information is needed to investigate a plant as a potential invasive species including its invasion status (does is maintain populations outside of captivity; where is it located), biological characteristics (does it produce seeds with a high germination rate; does is spread vegetatively), and ecological impacts (does it harm other associated plants or animals). Once a species is listed as invasive, law-makers can use this information to create laws to protect our native ecosystems from these plants!

Burning bush (*Euonymus alatus*) is a very popular ornamental shrub native to Asia that is of growing concern as an invasive species in Ohio. A small amount of information is known about the potentially invasive biological characteristics of burning bush (it produces a high number of seeds, the seed germination rate is high, and it spreads vegetatively through root sprouting). There is no current knowledge of the ecological impacts of burning bush on the forest environment; but researchers at Wright State University are beginning to investigate these impacts.

Burning bush has begun to establish populations outside of planted areas; however, its specific invasive status is unknown. In order to most accurately examine the extent of burning bush invasion, the location and extent of the invasion must be carefully documented. However, because burning bush invasion may be widespread, the researchers are asking for the help of the master naturalists! While out on hikes, camping trips, driving, or any other outdoor experience, please look for burning bush! Tips for identifying burning bush and the documentation protocol are below.

Thank you in advance for your participation and help!

burningbushwatch@gmail.com

1.6.2 Burning Bush (Euonymus alatus) Identification

Burning bush is a deciduous shrub that grows up to 8 ft. tall. The leaves are broad, ovate-elliptic, with an acute apex. They are 2-7cm in length and 1-4cm wide.

The stems of burning bush have a characteristic “winged” appearance, although the “wings” may be less pronounced in shaded individuals.

The most striking characteristic of burning bush is its striking red fall color, which remains after many other species have lost foliage. This makes it very easy to identify during the fall. During this time, the plant also has orange-red fruits.

1.6.3 Burning Bush Reporting Protocol

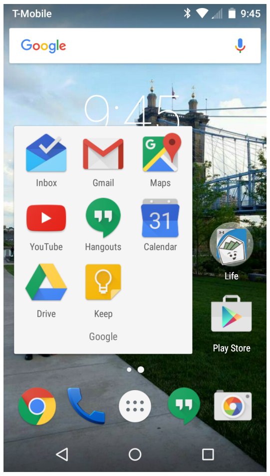
1. Print out the *Burning Bush Watch Data Sheet*

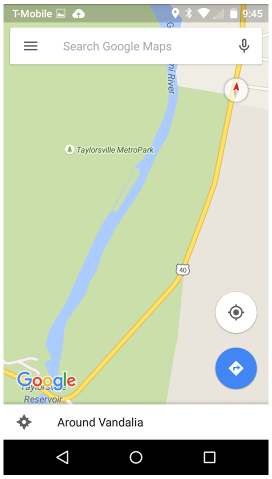
2. Use the burning bush identification guide to locate the shrub.

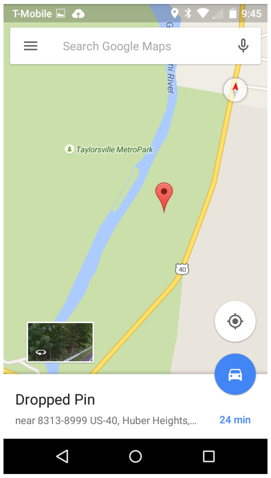
3. Record the observation number (you may find more than one burning bush location on a given observation day)

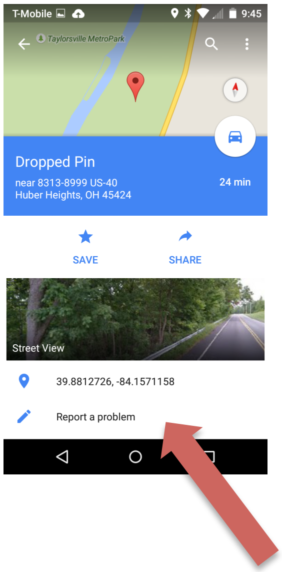
4. Take and record GPS coordinates of the burning bush on the data sheet.

    a. This is very easy using the Google Maps App on Android or iPhone!
        i. Open the app.
        ii. Just press and hold your location on the map.
        iii. On the bottom of your screen, tap the white area that says "Dropped Pin."
        iv. Record the GPS Coordinates on the data sheet.









    b. If you do not have a smart phone, just record the location of the shrub in detail on the data sheet.
        i. For example: "Taylorsville MetroPark – one mile north on the orange trail; on right side of trail approx. 10m off trail"

5. Record a few brief notes about the invaded area: open or forested? Dominant plant species? Flat ground or on hill?

6. Classify the proximity to currently occupied homes or yards/abandoned homesteads where burning bush may have been planted (A = no homestead noted;

B = homestead < 10m away; C = homestead < 50m away; D = homestead < 100m away)

7. Estimate and record the height/ average height of the plant/plants.
    a. It is easy to use your body to help predict height. For example, in the picture below, the shrub is as tall as my mid-thigh. I would estimate the height to be 2ft.

8. Estimate and record the area of land covered by the shrub/shrubs.
    a. For example, in the picture above, I would estimate the area covered to be $1ft^2$.

9. Fill in the electronic data sheet with the data you collected.

10. Email the completed data sheet to burningbushwatch@gmail.com

11. Thank you so much for your help with this project! Please feel free to email with any questions.

2 DAMAGE LEVELS, HERBIVORE PERFORMANCE, AND DEFENSE CHEMISTRY SUGGEST ENEMY RELEASE AND NOVEL WEAPONS FOR INVASIVE EUONYMUS SPECIES

2.1 INTRODUCTION

An invasive plant is a nonnative species that, once introduced to a novel habitat, causes economic or environmental damage or has negative outcomes for human health (NISC; Williamson 1996; Pysek et al. 2006). These species often exist in relatively low densities in their native range but attain destructively high population densities in their novel range (Callaway and Ridenour 2004). Invasive plants have the ability to rapidly establish themselves and outcompete their native counterparts. Many ecological hypotheses that seek to explain invasive success implicate the relationship between herbivorous arthropods and plant defenses as a driver. Because invasive plants displace native plants and reduce overall plant diversity and richness, this can have cascading effects on insect herbivores particularly those that rely on one or a few food plants. When an insect herbivore encounters an invasive plant, there are three possible outcomes, 1) the insect can recognize the invasive and is able to use it as a host, 2) the insect can fail to recognize a suitable host, and 3) the insect can recognize the invasive as a potential host but is unable to succeed on it (Davis & Cipollini 2014). Therefore, a non-native plant could benefit from either a lack of herbivores in the novel environment (enemy release hypothesis), by harboring resistance to herbivores in the novel range (shifting defense, novel weapons), or by failing to be recognized by potential herbivores. Each of these possible outcomes can greatly influence the invasibility of nonnative plants and have cascading impacts for community dynamics. The enemy release hypothesis (ERH) suggests that the proliferation and abundance of introduced species in novel locations is the result of decreased herbivory due to a lack of natural enemies (Williamson and Fitter 1996). Herbivores and pathogens, which regulate plant populations, evolve alongside their native host plants and develop effective methods of overcoming plant defenses. When a plant species is introduced to a new area, it is likely that its specialist enemies are not endemic. Natives, then, are attacked and regulated by both specialist and generalist herbivores while invasives suffer only from generalists, if at all. According to ERH, native generalists impact invasive plants less than native plants, which decreases interspecific competition for the exotic species (Keane and Crawley 2002). In the absence of range-typical levels of herbivory and disease, invasive species are able to grow and reproduce unchecked and out compete natives (Williamson and Fitter 1996). Thus, invasives in their nonnative range increase in both distribution and abundance compared to natives in similar niches. Invasives may benefit from not only a reduction in costly tissue damage but also a decreased need to produce specialist-specific chemical defenses, which allows for the adaptive shift of resource allocation from healing and defense to growth and reproduction. The direct advantage of fewer and less effective enemies coupled with the indirect competitive release advantage allows for these nonnative plant species to become more dominant in their introduced range compared to their native range. The degree to which enemy release contributes to an invasive's success, however, is dependent upon the species and the recipient community (Keane and Crawley 2002). It is possible that upon introduction a nonnative plant species will be attacked by the specialist enemies of a closely related native species. Although nonnative plants may, again, escape herbivory through evasion of these herbivores. Depending on the damage to the introduced species relative to the native species and whether herbivory is sufficient to decrease the fitness of either, the introduced species might still obtain some advantage due to enemy release. Enemy release has been implicated as a driver of the invasion of multiple *Lonicera* species in eastern North America through resistance and escape. In their 2013 study, Lieurance and Cipollini observed that the invasive *Lonicera maackii* received minimal herbivore damage in the field, but was shown to be susceptible to a native honeysuckle specialist in no-choice feeding assays supporting the ERH. However, the closely related *Lonicera japonica* and *Lonicera sempervirens* received low field herbivory and did not support specialist herbivore development, indicating that these species are experiencing ERH through resistance.

Although generalist herbivores may be more likely than specialist herbivores to use invasives as a food source, the novel weapons hypothesis suggests that invasive plants are protected from generalist herbivores through the production of biochemical defenses that are unfamiliar to herbivores within the novel range (Callaway and Ridenour 2004). These biochemical defenses might be especially lethal to native herbivores given that the herbivores have not coevolved with these novel defenses. This has been shown clearly by *Alliaria petiolata* (garlic mustard), a highly invasive understory plant. Garlic mustard contains a secondry metabolite profile that is uniquely distinct from related species native to North America (Barto et al. 2010). These novel weapons have been implicated, not only in low herbivory of this plant in its invaded range (Van Riper et al. 2010), but also to allelopathy of native plants (Cipollini and Cipollini 2016; Sanja 2017) and fungi (Callaway et al. 2008). The novel weapons hypothesis posits that the benefits of possessing novel (perhaps specialized) defenses in reducing herbivory outweigh the costs. Conversely, the shifting defense hypthesis (SDH) assumes that defenses targeting non-present specialists are not worth the costly energy expenditure. SDH suggests that over the course of evolutionary time, invasive plants are able to shift production of chemical defenses away from costly specialist defenses (quantitative, digestibility-reducing defenses) and toward energetically cheap (qualitative) generalist defenses (Doorduin and Vrieling 2011; Müller-Schärer et al. 2004; Poorter and Jong 1999). The simultaneous decrease of quantitative and increase of qualitative defenses is indicative of a highly invasive genotype. Lin and collegues observed this in three geographically separate populations of the invasive *Jacobea vulgaris* (Lin et al. 2015). As the invasion of this plant progressed, the genotypes of these three populations shifted from those prioritizing specialist defenses to those expressing qualitative defenses lending support for shifting defenses. While invaders can shift energy toward one defense type, native plant species, meanwhile, must allocate resources to produce both specialist and generalist defenses. SDH assumes that the combined effort of defending against both specialist and generalist herbivores is more costly to native plants than the singular effort of generalist defense is to invasives, giving invasives a distinct competitive advantage. With fewer resources allocated for chemical defense, the invasive plants are able to funnel excess resources into growth and reproduction, contributing to the rapid colonization and reproduction compared to native congeners, a characteristic of invasive species.

*Euonymus europaeu*s (Mill., Celastraceae), commonly called spindle tree, and *Euonymus alatus* (Thunb., Celastraceae), burning bush, are two nonnative shrubs/sub-canopy trees that are of increasing concern in forests in the eastern United States. Spindle tree, a deciduous sub-canopy tree with a large native range in most of Europe, has been introduced to no fewer than 17 American states, primarily for horticultural purposes (Thomas et al. 2011) (USDA). Burning bush is a common ornamental plant from Asia. It is classified as an invasive species in 8 eastern states (Dirr 2001) and is of growing concern in the Midwest. Both species reproduce sexually with particularly high fecundity and can spread vegetatively through root sprouts (Brand et al. 2012; Fryer 2009; Thomas et al. 2011; Siebal and Bouwma 1998; Hill et al. 2004; Kollmann et al. 1998). As vegetative spread has been implicated as one of the best predictors of invasiveness in woody plants (Reichard & Hamilton 1997), this characteristic may contribute to the invasiveness of these species. Additionally, burning bush and spindle tree may both escape and resist arthropod herbivores as these plants and other related species have been found to contain high levels of alkaloids and phenolics, both secondary compounds used in defense (Thomas et al. 2011; Zhau-hui et al. 2013). These defense compounds can greatly inhibit insect herbivore feeding, adding to their invasive potential, especially if these *Euonymus* species produce higher levels of or novel metabolites relative to other competing plants. The invasive success of these two nonnative species has serious implications for native plants, especially those filling a similar niche, as well as for the ecological communities in which they are a part. *Euonymus atropurpureus* (Jacq., Celastraceae, eastern wahoo) is a deciduous shrub/sub-canopy tree native to the Eastern United States that occupies habitats also invaded by non-native Euonymous species This native congener of burning bush and spindle tree harbors several native insect herbivores including *Ectropis crepuscularia* (Saddleback Looper), *Herpetogramma thestealis* (Pyralid Moth sp.), *Yponomeuta multipunctella* (American Ermine Moth), *Otiorhynchus sulcatus* (Black Vine Weevil), and *Unaspis euonymi* (*Euonymus* Scale) (Knight 1941; Hottes et al. 1931). Due to their close relatedness and the presence of multiple arthropod herbivores, eastern wahoo is an appropriate native congener with which to compare the herbivory rates and herbivore responses on burning bush and spindle tree.

In this study, we compared herbivory rates of eastern wahoo, burning bush, and spindle tree in the field. We hypothesized that herbivory would be lower on the nonnative plants due to enemy release, novel weapons, and/or shifting defense. We then examined the relative success of a native generalist herbivore, fall webworm, fed leaves of eastern wahoo, burning bush, and spindle tree as well as a natal host, redbud, from which they were collected.We hypothesized that the success of the herbivore would be highest on the natal host, followed by the native, eastern wahoo. In turn, success would be similarly poor on the nonnatives as the herbivore would be unfamiliar with these plants as a food source, likely containing novel weapons. Finally, we examined foliar concentrations of two groups of major secondary metabolites known to exist in *euonymus* species, alkaloids and phenolics. We hypothesized that the nonnative species would have higher levels of these compounds than eastern wahoo, as previous study has detected high levels of these compounds.

2.2 METHODS

2.2.1 Study Sites

Field observations and samplings were conducted at three locations in southwestern and southcentral Ohio due to the sporadic distribution of the species examined in this study. European spindle tree was studied at Shawnee State Park (N 38° 43' 46.01", W 83° 13' 44.36"), which is a 1,095-acre recreational area within the 63,000-acre Shawnee State Forest in Scioto County, Ohio. The terrain consists of erosion-derived hills in a prehistoric raised plain and sits approximately 760 feet above sea level. The study site was located on the south side of the park along an abandoned service road. Burning bush was studied at Glen Helen Nature Preserve (39°47′55″N 83°53′00″W), a 1000-acre privately-owned and managed recreational area located in Greene County, Ohio. The preserve is 980 feet above sea level and the terrain is Wisconsin age glacial drift with limestone-dolomite bedrock. The Little Miami River flows through the preserve (Garner et al. 1978; Bradely & Hickman 2009). Eastern wahoo was studied less than 5 km from the burning bush population on a private property downstream of Glen Helen on the Little Miami River (39°41′49″N 83°55′32″W). Burning bush was also studied in a forested section of Caesar Creek State Park (39°29′07″N 84°03′55″W), which is a 7900-acre park located in Greene, Warren, and Clinton counties in southwestern Ohio. The area was glaciated during the Wisconsin age and the bedrock is Ordovician shale (60%) and limestone-dolomite.

2.2.2 Field Herbivory Measurements

Field herbivory and incidence rates were measured for each plant species in July and September of 2016 and 2017. During each sampling event, we walked through forested areas occupied by each species and haphazardly selected thirty individuals of each species for assessment. On each individual plant, ten mature leaves were chosen haphazardly from each the three lowest branches for a total of thirty leaves per plant. We performed a visual assessment of herbivore damage on each leaf in which damage was categorized on a percentage leaf area removed basis. Damage types included chewed, skeletonized, scraped, and mined leaf tissue. Damage was assigned as 0, 1-5, 5-10, and then in increments of 10% to a maximum of 90-100% for leaf area removed (Fig 2.1). The incidence of damage was calculated as a percentage for each branch as follows: [(# of leaves damaged/# of leaves sampled)*100] (Lieurance and Cipollini, 2012). An average percent leaf area removed and damage incidence was calculated for each plant on each sampling date and used for analysis (n=480).

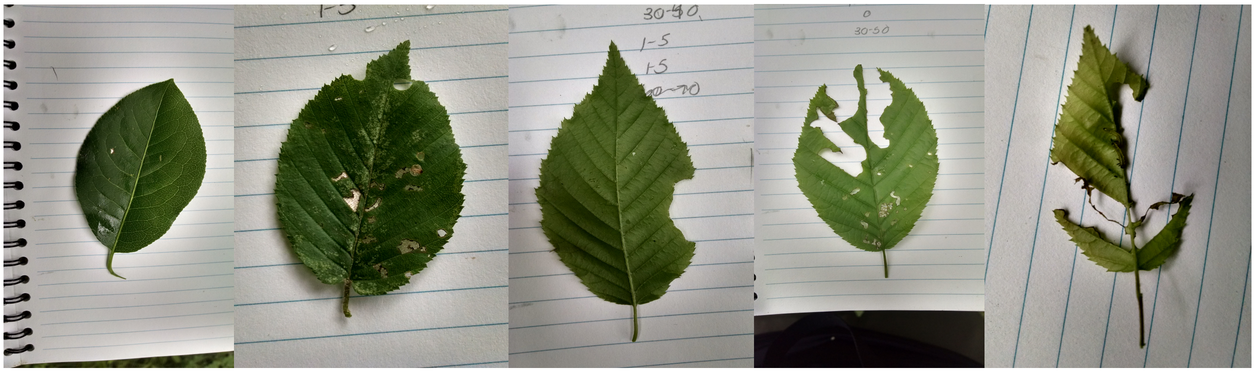


Fig 2.1. Examples of leaves with varying levels of damage – 1-5%, 5-10%, 10-20%, 20-30%, 60-70%

2.2.3 No choice bioassays

Hyphantria cunea (Drury, Erebidae, fall webworm), a generalist foliovore, was used to investigate variation in susceptibility of *Euonymus* species to a generalist herbivore. This lepidopteran is native to North American and can feed upon the leaves of over 630 different plant species (Warren & Tadic 1970). This species has become an invasive pest in Europe and some parts of Asia (Sourakov & Paris 2010). Fall webworm can have one or two generations per year depending upon temperature and humidity (Gordon 1976). It prefers woody species as food and has been known to use the invasive *Lonicera maackii* in the field, a species that is highly chemically defended, (personal observation, Lauren Shewhart and Don Cipollini), suggesting a high likelihood that the herbivore could survive on all studied plant species.

Five fall webworm webs containing early instar larvae were collected from five redbud (Fabaceae: *Cercis canadensis*, Linnaeus) trees in the late summer of 2016 in Yellow Springs, OH. Redbud is a common host of fall webworm in Ohio. Webs were kept in separated plastic containers for transport to the lab. Due to the obligate gregarious feeding behavior of early instar webworms, the no choice bioassays were started as experimental groups. Two webworms from each of the five webs were haphazardly selected, combined, and placed into a bioassay container to form an experimental group. The bioassay containers consisted of 4x6x6cm plastic deli containers with air holes perforating the lid. Each container contained a branch with leaves of one of four focal plant species (red bud, eastern wahoo, spindle tree, burning bush) in a 2.5mL tube filled with DI water. Branches with leaves were collected biweekly from Shawnee, Caesar Creek, and Glen Helen and kept with their cut ends in water at ambient temperature until use. There were three replicate containers of each plant for a total of twelve experimental groups consisting of a total of 120 individuals. Bioassay containers were kept in an incubator at 25°C (16:8 L:D) and rotated daily to minimize microenvironmental effects. Leaves were replaced as it was depleted or dried out. The webworms were reared for eight days until they reached the minimum size to survive individually. Survivorship and mass of each surviving individual was measured every 2-3 days. After eight days, individual no choice bioassays were established. A total of ten individuals that had been reared on each plant species (3 to 4 individuals from each container) were separated into individual bioassay containers. The webworms used in individual bioassays were selected to be representative of the average size of the webworms reared on each plant species (assessed visually). The individual bioassays were run as for the group bioassays, but were kept on a table under grow lights (16:8 L:D.) in an open laboratory at ~25°C. Survivorship and mass of the individual larvae were measured every 2-3 days. Bioassays continued until pupation or death. Time to pupation, pupal weight, and pupation success (proportion of pupae that emerged as adults) were all recorded.

All statistical analyses were performed using R software (Release Version 1.64; R Core Team, 2018). Both burning bush locations were combined for all analyses because there was no difference in the herbivory rates or incidence of herbivory between sites (Tukey's HSD, Avg. Herbivory: difference = 0.0483; P = 0.979; Avg. Inc: difference = 0.0572, P = 0.896). Three-way analysis of variance (ANOVA) was used to test for differences in percent leaf area removal and incidence of damage among plant species (spindle tree, burning bush, eastern wahoo), months, years, and the interactions between these variables. Tukey's honestly significant difference test (HSD) was used to examine pairwise differences in herbivore damage and incidence of damage between all factors. Survivorship, time to pupation, and pupal mass were measured and relative growth rates of larval groups and individual larvae were calculated. Relative growth rate was calculated as $[\ln(\text{mass}_{\text{final day}})-\ln(\text{mass}_{\text{initial}})]/\#$ of days. Individual relative growth rate was calculated between day 8 and day 15 because sample size was most consistent during this period (mortality contributed to a loss of replicates thereafter). ANCOVA was used to examine differences in group growth rate with starting mass as a covariate.. Differences in individual growth rate, time to pupation, and pupal mass of larvae reared on the different plant species were analyzed using ANOVA. Tukey's honest significance difference test (HSD) was used to examine pairwise differences in these metrics across all plant species. Survivorship was analyzed using log-rank Mantel-Haentszel test.

2.2.4 Plant Defense Chemistry

During each September sampling event, leaves were harvested from ten haphazardly selected plants of each species during herbivory data collection. Burning bush leaves were collected only from the Caesar Creek location. After harvesting, the leaves from each plant were placed in plastic bags and placed immediately on dry ice for transport. The leaves were stored at -20°C until analysis.

Total alkaloid content was analyzed using the Dragendorff method of Sreevidya and Mehrotra (2003). All tissue samples were ground by hand using a mortar and pestle kept in an ice bath to reduce sample degradation. The mortar and pestle were cleaned between samples using Alcanox and distilled water, rinsed with acetone, and then triple rinsed with distilled water. Alkaloid extracts were made by incubating 4g of ground leaf tissue in 20mL of 2% acetic acid solution. These extracts were placed in a 60°C water bath for 30 minutes and then incubated at room temperature in the dark for 18 hours. After incubation, 6 mL of each extract were taken and centrifuged at 5,000 rpm for 3 mintues. The supernatants were transferred to small centrifuge tubes, covered, and stored on ice for analysis. Five milliliters of the extract were placed in a new tube, the pH was adjusted to 2-2.5 with dilute HCl, and 2 mL of Dragendorff's reagent (DR) were added. After a five-minute incubation at room temperature, a precipitate formed and the reaction mixture was centrifuged at 5000 rpm for 5 minutes. Complete precipitation was ensured by adding a few additional drops of DR. The supernatant was decanted and the precipitate was washed with 1mL of 100% ethanol and centrifuged. The supernatant was removed and the precipitate was treated with 2mL of a 1% sodium sulfide solution and then centrifuged. The supernatant was decanted and the brownish-black precipitate was dissolved in 2mL of concentrated nitric acid. The solution was then diluted to 10mL with distilled water. One milliliter of the solution was added to 5mL of a 3% thiourea solution. Absorbance was measured at 435 nm in a spectrophotometer and concentrations were determined in relation to a standard curve of bismuth nitrate pentahydrate solution (10mg of Bi(NO3)3*5H2O in 5mL nitric acid diluted to 100mL with distilled water). All plant samples were run in duplicate.

Soluble phenolic content was measured using the Folin method described in Bonello and Pearce (1993). Plant extracts were made by incubating 1g of ground leaf tissue (ground as above) in 1mL of methanol in a microcentrifuge tube at 4°C for 24 hours. After incubation, the samples were tamped down using a micro pestle and 30µL of extract were placed in a clean micro centrifuge tube and centrifuged at 5000 rpm for 5 minutes. Twenty µL of methanol extract were transferred to a clean micro centrifuge tube and placed on ice. Ten µL of the plant extract were added to 75 µL of methanol and 500 µL of distilled water and mixed. Thirty-seven and a half µL of Folin's Phenol Reagent were added and the solution was incubated for three minutes at room temperature. Thirty-seven and a half µL of 1M NaHCO3 were then added, the solution was mixed thoroughly, and the sample was incubated at room temperature for one hour. Absorbance was measured at 725 nm was measured using a spectrophotometer and concentrations were determined in relation to a standard curve of gallic acid. All plant samples were run in duplicate.

Due to sample limitations, both alkaloid and phenolic analysis were performed on five (instead of the usual ten) burning bush plants for 2017. Two-way analysis of variance (ANOVA) was used to test for differences in alkaloid and phenolic concentrations between plant species (spindle tree, burning bush, eastern wahoo) and years. Tukey's honest significance difference test (HSD) was used to examine pairwise differences in leaf chemistry between all factors.

2.3 RESULTS

2.3.1 Field Herbivory

Herbivory rate on eastern wahoo (17.13 ± 2.47% SE) was, on average, over eight times higher than on spindle tree (2.05 ± 0.29% SE) and over ten times higher than on burning bush (1.61 ± 0.25% SE; df = 2, F = 295.5, $P < 0.0001$; Fig 2.1). Tukey's HSD revealed that herbivory rates were significantly different between each pairwise comparison of plant species (EW-ST, $P < 0.0001$; EW-BB, $P < 0.0001$; BB-ST, P = 0.01). Herbivory rates did not differ significantly as the growing season progressed (from July to September: EW, P = 0.16; ST, P = 0.17; BB, P = 0.97; df = 2, F = 8.825) or amongst sampling years (EW, P = 0.99; ST, P = 0.87; BB, P = 0.57; df = 2, F = 3.660) for any plant species. Unsurprisingly, as burning bush and spindle tree experienced low herbivory overall, the range of herbivory on these species (BB: 0-7%; ST: 0-5.1%) was also significantly lower than that of eastern wahoo. As eastern wahoo had a few extremely high cases of herbivory, the median herbivory rate (9.8%) for this species was about two-thirds that of the mean (17.13%)(Fig 2.2).

The incidence of herbivory on eastern wahoo (92.75 ± 2.04% SE) was significantly higher than on both spindle tree (37.56 ± 2.86% SE) and burning bush (26.67 ± 2.18% SE; df = 2, F = 267.42; Fig 2.3). Tukey's HSD revealed that incidence of herbivory was significantly different between each pairwise comparison of plant species (EW-ST, $P < 0.0001$, diff = -1.034; EW-BB, $P < 0.0001$, difference = 1.427; BB-ST, $P < 0.0001$, difference = 0.393). This indicated that both spindle tree and burning bush receive damage on fewer leaves than the native eastern wahoo, and burning bush receives herbivory on fewer leaves than spindle tree. Incidence of herbivory differed significantly as the growing season progressed only for spindle tree (July Avg. = 30.44 ± 2.71% SE, Sept Avg. = 44.71 ± 3.01% SE; difference = 0.457, P = 0.0005). Incidence of herbivory ranged from 0% - 81% leaves showing some level of herbivory on burning bush with spindle tree showing a similar incidence range (0.5% - 78% of leaves showing some level of herbivory). The median incidence rate for these two species was also within 3% of each other (BB: 32%, ST: 35%). Eastern wahoo showed the least drastic range of incidence rates (50% - 100%) although all measured plants showed high levels of incidence (96% median)(Fig 2.3).

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2.3.2 Bioassays

Controlling for starting mass, ANCOVA revealed that group growth rate of larvae was significantly higher on red bud (0.318 ± 0.010g SE, df = 3, F = 38.76, P < 0.0001), the natal host, than on any other plant species. Conversely, larval growth rate on burning bush was significantly lower than on all other plant species (0.116 ± 0.004g SE; diff = BB-EW: 0.131, BB-RB: 0.202, BB-ST: 0.129; P < 0.0001). There was no significant difference in larval growth rate on spindle tree (0.245 ± 0.018g SE) and eastern wahoo (0.247 ± 0.017g SE, difference= -0.002; P = 0.99; Fig 2.4).

Individual growth rate was significantly lower for webworms reared on burning bush (0.000006 ± 0.0148g SE, df = 3, F = 10.32, P < 0.0001) compared to any other plant type.

There was no difference in individual growth rate between red bud (0.0809 ± 0.0100g SE; diff = RB-EW: 0.0008, RB-ST: -0.0081), spindle tree (0.0728 ± 0.0126g SE, diff = ST-EW: -0.007), or eastern wahoo (0.0801 ± 0.0148g SE, $P = 0.99$; Fig 2.4).

Time to pupation was significantly different between plant species (df= 3, $F = 5.678$, $P < 0.01$). No webworms reared on burning bush survived to pupation. Time to pupation was significantly shorter on red bud (19.60 ± 0.60 days SE) and spindle tree (19.57 ± 1.55 days SE; diff = RB-ST: -0.029; $P = 0.99$) than on eastern wahoo (25.56 ± 0.150 days SE; diff = RB-EW: -5.956, ST-EW: -5.984; $P = 0.029$; Fig 2.5). However, there were no significant differences in pupal weight across plant species (RB: 0.204 ± 0.009g SE, ST: 0.162 ± 0.029g SE, EW: 0.150 ± 0.007g, df = 3, $F = 3.0255$, $P = 0.08$; Fig 2.5).

The log-rank Mantel-Haentszel test revealed that survival probabilities of larvae differed between plant species (Chi-sq = 15.9, df = 3, $P = 0.001$; Fig 2.6). All individuals reared on burning bush died before day 40. Those reared on red bud had a 90% chance of surviving to day 40 while that measure dipped to 50% and 60% on spindle tree and eastern wahoo respectively.

2.3.3 Defense Chemistry

Alkaloid concentration was significantly different between all plant species (df = 2, $F = 45.16$, $P < 0.0001$). Burning bush contained no detectable levels of alkaloids for either sampling year while spindle tree leaves contained twice the concentration of alkaloids (0.096 ± 0.009 mg/mL SE) as eastern wahoo leaves (0.042 ± 0.005 mg/mL SE). Tukey's HSD revealed that alkaloid concentration was significantly different between each pairwise comparison of plant species (EW-ST, diff = 0.054, $P < 0.0001$; EW-BB, diff = 0.043, $P < 0.0001$; BB-ST, diff = 0.097, $P < 0.0001$). Alkaloid level differed between sampling years for spindle tree only (diff = -0.042; P = 0.01). In 2016, spindle tree leaves had an average alkaloid concentration of 0.12 ± 0.02 mg/mL SE, about one and a half times the level observed in 2017 (0.075 ± 0.006 mg/mL SE). As mean concentration of alkaloids increased across plant species, so did the variation between sampled individuals. Alkaloid concentration ranged from 0.027mg/mL to 0.181mg/mL in European spindle tree, a difference of 0.154mg/mL. This was two and a half times the range observed in eastern wahoo (0.015 – 0.076 mg/mL; Fig. 2.7).

The concentration of phenolics in burning bush leaves was over four times higher (0.68 ± 0.03 μg/mL SE) than both spindle tree (0.16 ± 0.01 μg/mL SE) and eastern wahoo leaves (0.13 ± 0.01 μg/mL SE; df = 2, F = 247, $P < 0.0001$). Phenolic concentration was significantly higher in BB ($P < 0.0001$) but did not differ between ST and EW (P = 0.38) and did not change across sampling years for any plant species (df = 1, F = 0.344, P = 0.56). The within plant species variation was similar across all plant types (Fig 2.8).

2.4 DISCUSSION

2.4.1 Variation in Herbivory in the Field

We measured field herbivory rates to examine evidence for enemy release of two non-native *Euonymus* plant species in relation to a native congener. Overall, the non-native *Euonymus* species (European Spindle tree and burning bush), in their novel range in southern Ohio are experiencing significantly less herbivore damage than a closely related native shrub (eastern wahoo). There is no consensus in the literature for the amount of tissue damage required for a loss of fitness, due to high species variability, but evidence suggests that 6-12% leaf area removal can reduce woody plant growth and fitness (Crawley 1985; Poorter et al. 2004; Whittaker and Warrington 1985). Eastern wahoo received 17% leaf area removed due to arthropod herbivory and over 92% of leaves showed some level of damage, levels that were substantially higher than herbivory rates on the two invasive species. Spindle tree received about 2% tissue damage on only 38% of leaves while burning bush received 1.6% removed leaf area on 27% of leaves. As each plant species was located at a different geographical site, it could be argued that the observed differences in herbivory could be due to differential herbivore abundance. However, in the summer of 2015, we measured comparative herbivory rates of spindle tree and native musclewood (*Carpinus caroliniana* (Walter): Betulaceae) at Shawnee State Park (the same field site used in this study). We found herbivory rates on spindle tree to be ~2% while herbivory on musclewood was 15% leaf area removed. These data are consistent with the herbivory rates we observed on native and non-native species across southwestern Ohio, suggesting that differences herbivore abundance is not responsible for the observed differences in herbivory. Further, Glen Helen (a burning bush site) and the private property (eastern wahoo) were geographically close, within 5km. It is unlikely that herbivore populations differed between these two sites. Finally, herbivory did not differ significantly between the two sampled burning bush sites. Overall, these low levels of herbivory are similar to the levels observed on *Lonicera maackii,* (Rupr.) Maxim (Amur honeysuckle), one of the most prolific and well-studied invasives in the eastern United States. Lieurance et al. in 2015 showed that honeysuckle receives an average of 2-3% leaf area removed in its invaded range, compared to almost 25% on *Lonicera reticulata*, a native congener. Similar to the conclusions made about honeysuckle, the amount of leaf damage on burning bush and spindle tree is unlikely to lead to a reduction in fitness (Crawley 1985) and these levels of damage are dramatically lower than that received by the native congener. This suggests that these non-natives are benefitting from a lack of herbivore pressure. Additionally, it is likely that these non-native plants are receiving less tissue damage in their novel range than their native range and therefore could invest these energetic savings into growth and reproduction, leading to high invasibility. In its native range, spindle tree loses an average of 25% of its leaf area to herbivory each growing season, one of the highest tissue loss rates of species measured in the lowlands of the British Isles (Thomas et al. 2011). This damage is caused by 27 identified arthropod herbivores, six of which specialize on this species (Thomas et al. 2011). Further, burning bush is likely receiving much lower herbivory rates in invaded areas than in its native range, as it is released from over 25 recorded arthropod herbivores from the native range (Fryer 2009; Ding et al. 2006). Interestingly, two of these specialist herbivores (*Yponometua cagnagelia* and *Pryeria sinica*) have recently been introduced to the Eastern United States and been implicated in the destruction of ornamental plantings of burning bush (Hoebeke, 1987; Bethke 2014). Therefore, it is likely that spindle tree and burning bush are experiencing enemy release and that the lack of arthropod herbivory is contributing to the invasiveness of these species both directly (via release from regulation by herbivores) and indirectly (via reduced growth and fitness of native competitors).

2.4.2 Variation in resistance in the laboratory

Bioassays using a native generalist herbivore revealed that, although both non-natives received low herbivory rates in the field, the reasons for this might be different. In no-choice bioassays, the natal host, red bud, supported growth and survival rates of the generalist herbivore that were substantially higher than on any other investigated plant species. Spindle tree supported growth and survival of a generalist arthropod herbivore at levels that were similar to the native eastern wahoo, about half that of the natal host. However, spindle tree in the field received very little herbivory. Thus, it is likely that North American arthropods are unable to detect spindle tree as a suitable host, either through benign or novel weapons interactions. In its native range, the specialist herbivore *Yponomeyta cagnagella* (Spindle Ermine moth) uses chemical stimuli present in spindle tree leaves to detect their host. Polar compounds isolated from leaves have been shown to stimulate oviposition in a dose dependent manner (Hora et al. 1999). Dulcitol, a sugar-alcohol in the surface of spindle tree leaves, along with other volatile compounds are attractants and feeding stimulants for specialist herbivores (Kooi 1988; Roessingh et al. 2000). Low herbivory rates in the field suggest that herbivores native to North America are unable to detect these same chemicals and are unable recognize spindle tree as a suitable host – a benign interaction. However, low herbivory could result from a novel weapons interaction if spindle tree is actively deterring herbivores through a defense chemical that is unfamiliar to North American herbivores. In their 2013 study, Lieurance and Cipollini reported similar results for *Lonicera maackii.* Herbivory rates in the field were low, ~3%, while an insect herbivore developed well on the plant in no-choice feeding assays, indicating behavioral avoidance of a suitable host (Lieurance & Cipollini 2013). As suggested in their paper, future research should focus on comparing specific polar defense compound profiles of native and non-native *Euonymus* species and their contribution to attraction and feeding stimulation.

Spindle tree contained high levels of alkaloids, not unusual for members of the Celastraceae family, which could actively deter herbivory. Although we did not determine the exact alkaloids present in spindle tree, it is unlikely that these alkaloids are novel weapons, as many members of the Celastraceae family are native to North America and related plant species frequently have similar chemical defenses (Lieurance et al. 2015). However, the level of alkaloids present in this species was almost twice that of eastern wahoo. This could suggest that these non-novel alkaloid weapons are being expressed at novel levels. Further comparisons of alkaloid levels in spindle tree and other related and unrelated native plant species could help to determine if these defense levels are, indeed, novel.

Although burning bush received similarly low levels of field herbivory as spindle tree, it was not a suitable food source to the generalist herbivore in no-choice feeding trials. As fall webworm is a successful generalist herbivore on over 600 plant species (Warren &

Tadic 1970), it is likely that lack of success of this species on burning bush is indicative of the inability of many other arthropod herbivores to use burning bush as a host. Therefore, the observed low field herbivory is likely a result of toxic plant defense compounds in the plant, not a lack of detection in the field. Our study suggests that high levels of phenolics may be responsible for low herbivory as burning bush contained concentrations that were more than five times higher than the native congener. Phenolics are a large class of plant defense compounds characterized by the presence of a phenol group. This group contains lignins, aromatic amino acids, flavonoids, and tannins, which result in reduced food quality, digestibility, and palatability (Boeckler et al. 2011; Barbehenn & Constabel 2011; Salminen & Maarit 2011). It is unlikely, however, that all of these phenolics are novel weapons, as many members of the Celestraceae family are native to North America and likely produce similar phenolic profiles (Lieurance et al 2015). Phenolic profiles, however, are frequently complex such as those observed in *Lonicera maackii* (Cipollini et al. 2008) suggesting the potential for novel weapons. Future studies should examine profiles across *Euonymus* species to determine if burning bush does, in fact, contain novel phenolic compounds. The high expression of phenolics in burning bush could suggest that this species is either expressing novel levels of non-novel compounds and/or has shifted defense mechanisms from specialized responses to a more generalized expression of phenolic defenses in its novel range. This shift from quantitative specialized defenses to qualitative generalized defenses was examined in a recent meta-analysis. The authors found that, in terms of damage by herbivores, invasive plants generally showed decreased expression of resistance mechanisms to specialist herbivores and increased resistance against generalist herbivores in their introduced ranges (Zhang et al. 2018). Future studies should compare phenolic profiles and expression levels between burning bush in its native and novel range to determine if expression levels have shifted in the introduced range, possibly leading to increased fitness and invasibility.

Overall, non-native *Euonymus* species are receiving less herbivory than their native counterparts in their novel range. It is likely that both spindle tree and burning bush are experiencing enemy release as these species receive minimal herbivory but are known to harbor multiple specialist herbivores in their native ranges. The specific mechanisms of resistance, however, are difficult to disentangle. These species could be exhibiting novel weapons and/or shifting defense as spindle tree shows high levels of alkaloids and phenolics while burning bush exhibits very high levels of phenolics. Further study into the specific defense profiles between native/non-native *Euyomymus* species and between non-natives in their historical/novel range would help to elucidate the true mechanism of resistance. However, regardless of the method of resistance, both burning bush and spindle tree experience some benefit through reduced herbivory in their novel range, likely contributing to increased fitness and invasibility.

2.5 REFERENCES

Barbehenn, RV., Constabel, CP. 2011. Tannin in plant-herbivore interactions. Phytochemistry. 72(13): 1551-1565.

Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z. 2009. Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. Annual Review of Ecology Evolution and Systematics 40:1-20. doi: 10.1146/annurev.ecolsys.110308.120242

Barto, E.K., Powell, J.R., Cipollini, D. 2010. How novel are the chemical weapons of garlic mustard in North American forest understories? Biological Invasions 12: 3465-3471

Bethke, J.A. 2014. Insect hot topics: *Euonymus* caterpillars. UC Nursery and Floriculture Alliance. University of California, division of agriculture and natural resources http://ucnfanews.ucanr.edu/Articles/Insect_Hot_Topics/INSECT_HOT_TOPICS__*Euonymus*_caterpillars/

Bishay, DW., Kowalewski, Z., Phillipson, JD. 1973. Investigations of alkaloids of *Euonymus europaeus* L growing in Poland. Phytochemisty 12:693-698.

Boeckler, G.A., Gershenzon, J., Unsicker, SB. 2011. Phenolic glycosides of the Salicaceae and their role as anti-herbivore defenses. Phytochemistry 12(13): 1497-1509

Bonello, P., Pearce, R.B. 1993. Biochemical defense responses in primary roots of Scots pine challenged in vitro with *Cylindrocarpon destructans*. Plant Pathology 42(2): 203-211.

Bradley, R.A., Hickman, W.L. 2009. Spiders (Araneae) of the Glen Helen Nature Preserve, Greene County, OH. The Ohio Journal of Science 109(2): 3-14

Brand, H., Lubell, J.D., Lehrer, J.M. 2012. Fecundity of winged *Euonymus* cultivars and their ability to invade various natural environments. HortScience 47(8): 1029-1033.

Callaway RM, Ridenour WM. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2:436-443. doi: 10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

Callaway, R.M., Cipollini, D., Barto, K., Thelen, G.C., Hallett, S.G., Prati, D., Stinson, K., Klironomos, J. 2008. Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89(4): 1043-1055

Crawley, MJ. 1985. Reduction of oak fecundity by low-density herbivore populations. Nature 314:163-164.

Cipollini, D. Dorning, M. 2008. Direct and indirect effects of conditioned soils and tissue extracts of the invasive shrub, Lonicera maackii, on target plant performance. Castanea 73: 166-176.

Davis, SL., Cipollini, D. 2014. Do mothers always know best? Oviposition mistakes and resulting larval failure of *Pieris virginiensis* on *Alliaria petiolata*, a noevl, toxic host. Biological Invasions 16(9): 1941-1950

Ding, Jianqing; Reardon, Richard; Wu, Yun; Hao, Zheng; Fu, Weidong. 2006. Biological control of invasive plants through collaboration between China and the United States of America: a perspective. Biological Invasions. 8(7): 1439-1450. [71691]

Dirr, M.A. 2001. Winged *euonymus* is a stalwart shrub for consistent fall color. Nursery Management and Production. 17:16-17, 91-95.

Doorduin LJ, Vrieling K. 2011. A review of the phytochemical support for the shifting defense hypothesis. Phytochemistry Reviews 10:99-106. doi: 10.1007/s11101-010-9195-8

Fryer, Janet L. 2009. *Euonymus* alatus. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2015, October 29].

Fung, SY. 1986. Alkaloids and cardenolides in sixteen *Euonymus* taza. Biological and chemical Systematics and Ecology 14:371-373.

Garner DE, Ritchie A, Siegenthaler VL. 1978. Soil Survey of Greene County, OH. US Dept. of Agric. Soil Conservation Service. 105 p.

Gordon, Scott W. 1976. Population studies of the Fall Webworm in Ohio with the development of life tables in relation to temperature. (Masters dissertation, Ohio State University).

Hill, M.O., Preston, C.D., Roy, D.B. 2004. PLANTATT – Attributes of British and Irish plants: status, size, life history, geography, and habitats. Centre for Ecology and Hydrology, Huntingdon, UK.

Hoebeke, B. 1987. Yponomeuta cagnagella (Lepidopters: Yponimeutidae): A palearctic ermine moth in the United States, with notes on its recognition, seasonal history, and habits. Annual Entomological Society of America 80:462-467

Hora, K.H., Roessingh, P., Menken, S.B.J. 2005. Inheritance and plasticity of adult host acceptance in *Yponomeuta* species: implications for host shifts in specialist herbivores. Entomologia Experimentalis et Applicata. 115: 271-281

Hottes, F.C., Frison, T.H. 1931. The plant lice, or Aphiidae, of Illinois. Illinois Natural History Survey Bulletin 19(3)

Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution. 4:164-170. doi: 10.1016/S0169-5347(02)02499-0

Knight, H. H. 1941. The plant bugs, or Miridae, of Illinois. *Bulletin of the Illinois Natural History Survey* 22:1–234

Kollmann, J., Coomes, D.A., White, S.M. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years, and sites. Functional Ecology 12: 683-690

Kooi, R. 1988. *Yponomeuta cagnagella*, a *Euonymus*-feeder. Proceedings Koninklijke Nederlanse Akademie van Wetenschappen, Amsterdam. 91: 223-232

Lieurance, D., Cipollini, D. 2012. Damage levels from arthropod herbivores on *Lonicera maackii* suggest enemy release in its introduced range. Biological Invasions 14: 863-873.

Lieurance, D., Cipollini, D. 2013. Exotic Lonicera species both escape and resist specialist and generalist herbivores in the introduced range in North America. Biological Invasions 15(8): 1713-1724.

Lieurance, D., Chakraborty, S., Whitehead, SR., Powell, JR., Bonello, P., Bowers, MD., Cipollini, D. 2015. Comparitive herbivory rates and secondary metabolite profiles in the leaves of native and non-native Lonicera species. Journal of Chemical Ecology 41(12): 1069-1079.

Lin, T.L., Doorduin, L., Temme, A., Pons, T.L., Lamers, G.E.M., Anten, N.P.R., Vrieling, K. 2015. Enemies lost: parallel evolution in structural defense and tolerance to herbivory of invasive *Jacobaea vulgaris*. Biological Invasion 17: 2339-2355

McCleary FE, Feusner MM, Hamilton, SJ. 1989. Soil survey of Scioto County, Ohio. United States Department of Agriculture: Soil Conservation Service. http://www.nrcs.usda.gov/wps/portal/nrcs/surveylist/soils/survey/state/?stateId=OH

Müller-Schärer H, Schaffner U, Steinger T. 2004. Evolution in invasive plants: implications for biological control. Trends in Ecology and Evolution 8:417-422. doi:10.1016/j.tree.2004.05.010

Ohio Department of Natural Resources, Division of Forestry. Beech (American, Blue). http://forestry.ohiodnr.gov/beech

Poorter H, de Jong R. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. New Phytologist. 413:163-176. doi**:** 10.1046/j.1469-8137.1999.00428.x

Poorter, L, de Plassche, MV, Willems, S, Boot, RGA. 2004. Leaf traits and herbivory rates of tropical tree species differing in successional status. Plant Biology 6:746-745.

Pysek P, Richardson DM, Rejma´nek M, Webster GL, Williamson M, Kirschner J. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxonomy 53(1):131–143.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reichard, S.H., Hamilton, C.W. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology 11(1): 193-203.

Roessingh, P., Hora, K.H., Fung, S.Y., Peltenburg, A., Menken, S.B.J. 2000. Host acceptance behaviour of the small ermine moth *Yponomeuta cagnagella*: larvae and adults use different stimuli. Chemoecology 10: 41-47

Sajna, N. Habitat preference within its native range and allelopathy of garlic mustard *Alliaria petiolata.* Polish Journal of Ecology 65(1): 46-56

Salminen, J-P., Maarit, K. 2011. Chemical ecology of tannins and other phenolics: we need a change in approach. Functional Ecology 25(2): 325-338.

Siebel, H.N., Bouwma, I.M. 1998. The occurance of herbs and woody juveniles in a hardwood floodplain forest in relation to flooding and light. Journal of Vegetation Science 9:623-630

Sourakov, Andrei, and T. Paris. 2010. Fall webworm, hyphantria cunea (Drury) (Insecta: Lepiodopetar: Arctiidae: Arctiinae). *IFAS Extension University of Florida*.

Sreevidya, N., Mehrotra, S. 2003. Spectrophotometric methods for estimation of alkaloids perceptible with Dragendorff's reagent in plant materials. Journal of AOAC International. 86(6): 1124-1127

Thomas PA, El-Barghathi M, Polwart A. 2011. Biological Flora of the British Isles. J Ecol 99:345-365. doi: 10.1111/j.1365-2745.2010.01760.x

United States Department of Agriculture, National Agricultural Library: National Invasive Species Information Center. Executive order 13112 (2005). https://www.invasivespeciesinfo.gov/laws/execorder.shtml

United States Department of Agriculture, Natural Resources Conservation Service: Plants Database. Euonymous europaeus L. European spindle tree. http://plants.usda.gov/core/profile?symbol=EUEU7

Van Riper, L.C., Becker, R.L., Skinner, L.C. 2010. Population biology of garlic mustard (*Alliaria petiolata*) in Minnesota hardwood forests. Invasive Plant Science and Management 3:48-59

Warren, L. O. and M. Tadic. 1970. The fall webworm, Hyphantria cunea (Drury). *Arkansas AES Bulletin,* 759: 106.

Whittaker, JB, Warrington, S. 1985. An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) III. Effects on tree growth. Journal of Applied Ecology 22: 797-811.

Williamson M, Fitter A. 1996. The varying success of invaders. Ecology 77:1661-1666. doi: 10.2307/2265769

Zhang, Z., Pan, X., Blumenthal, D., van Kleunen, M., Lui, M., Li, B. 2018. Contrasting effects of specialist and generalist herbivores on resistance evolution in invasive plants. Ecology 99(4): 866-875

Zhau-hui, Y., Zhu-zhen, Z., Xian-qing, H., et al. 2013. Chemical constituents of *Euonymus alatus*. Chemistry of Natural Compounds. 49(2): 340-342.

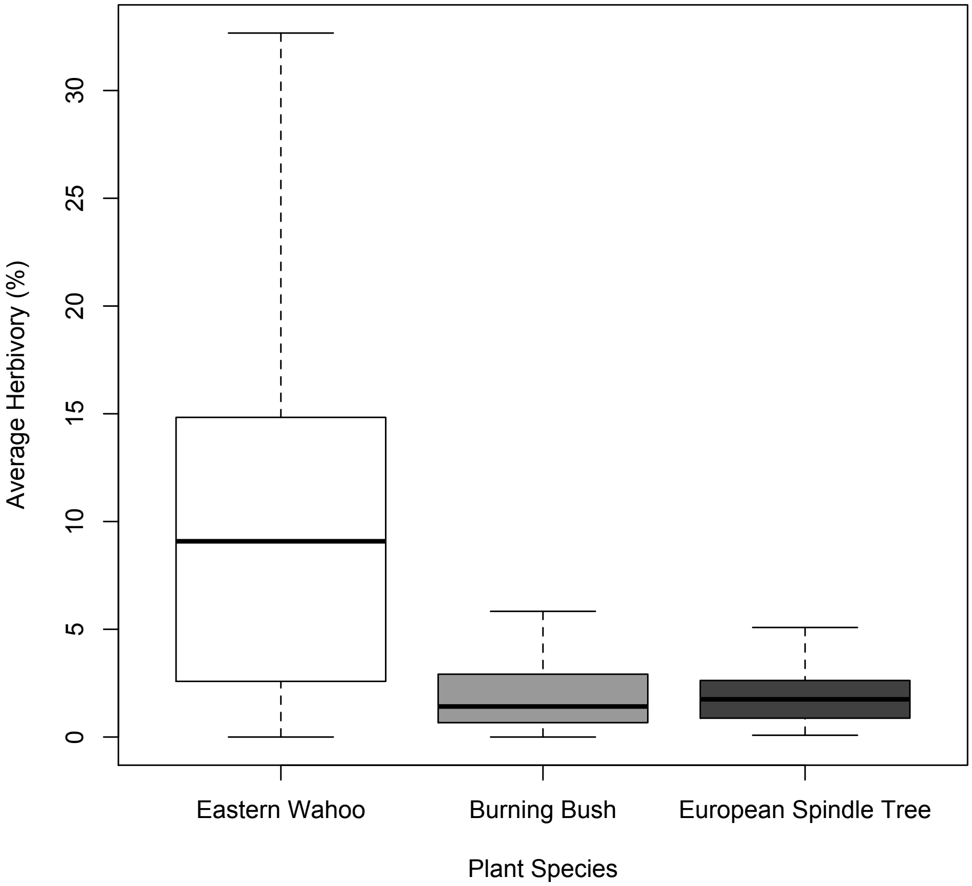

Fig 2.2. Herbivory on eastern wahoo, burning bush and spindle tree. Herbivory was measured on a percent area removed basis. Percent herbivory presented on data pooled for all sampling months and years, and across burning bush sampling sites.

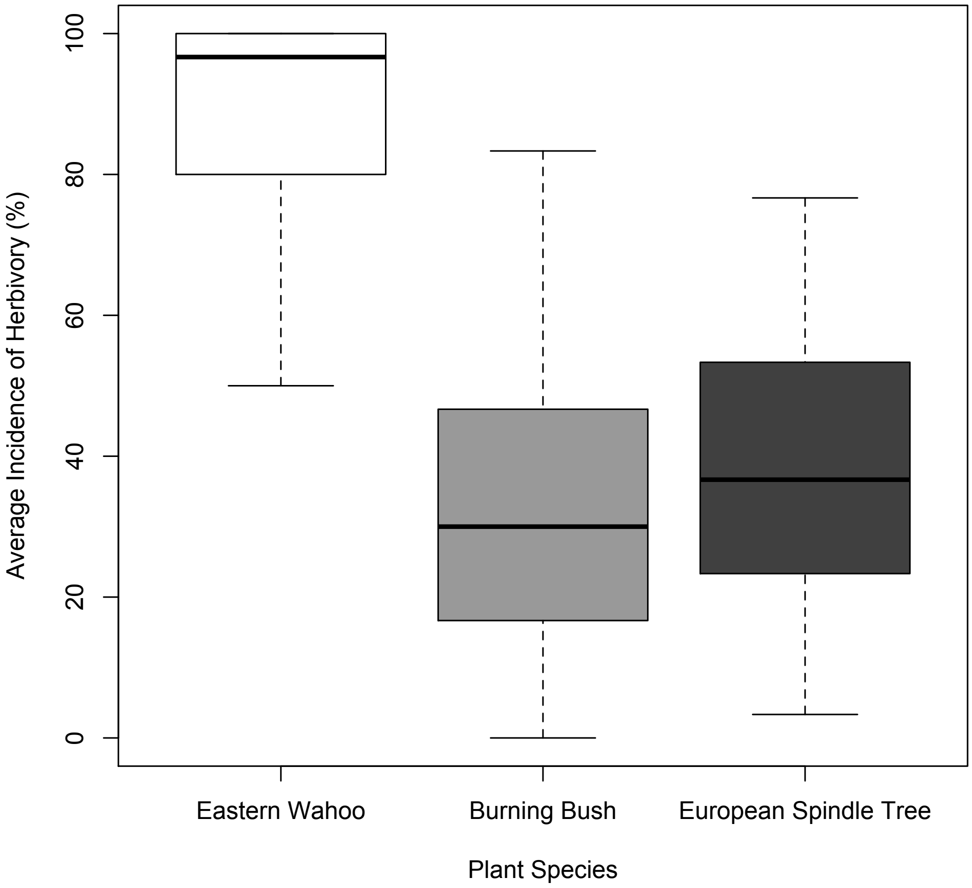

Fig 2.3. Incidence of leaf damage on eastern wahoo, burning bush and spindle tree. Incidence was measured as the percentage of leaves showing some level of herbivory. Incidence of herbivory presented on data pooled for all sampling months and years, and across burning bush sampling sites.

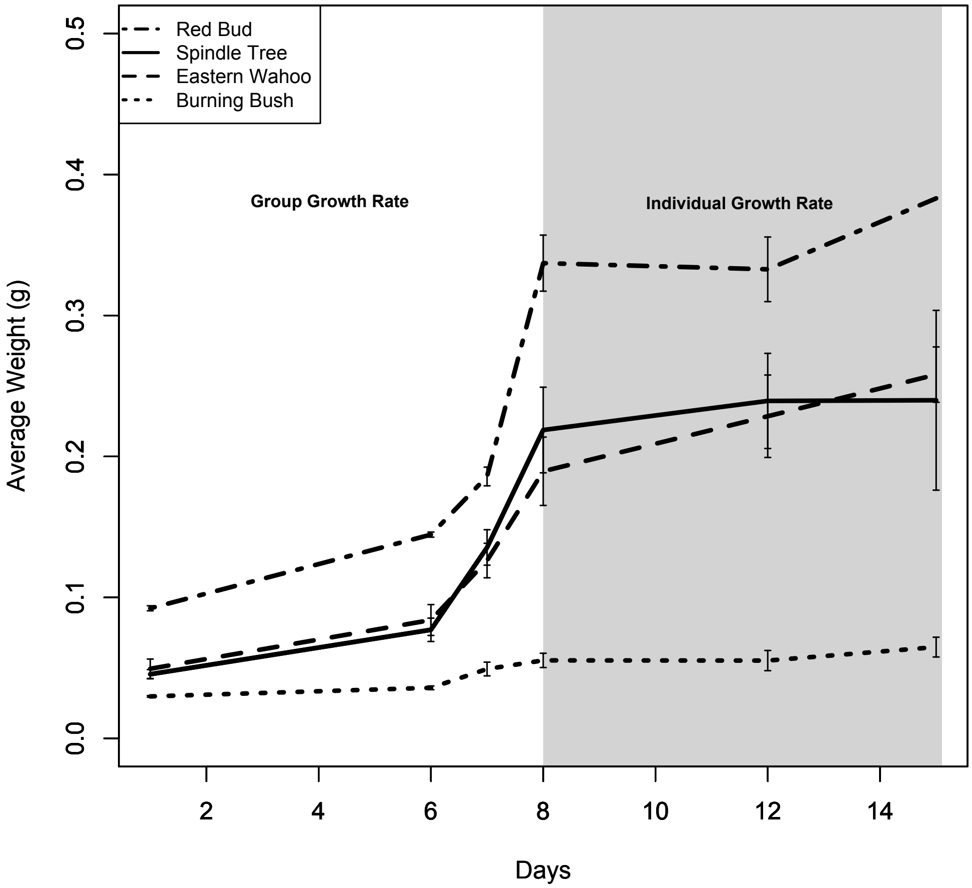

Fig 2.4. Mean change in larval mass of *Hyphantrea cunea,* a generalist herbivore, feeding on two invasive (burning bush, European spindle tree) and two native species (red bud, eastern wahoo). Group growth was averaged among surviving larvae from day 1-8 for each replicate, individual growth rate was measured from day 8-15 for each replicate.

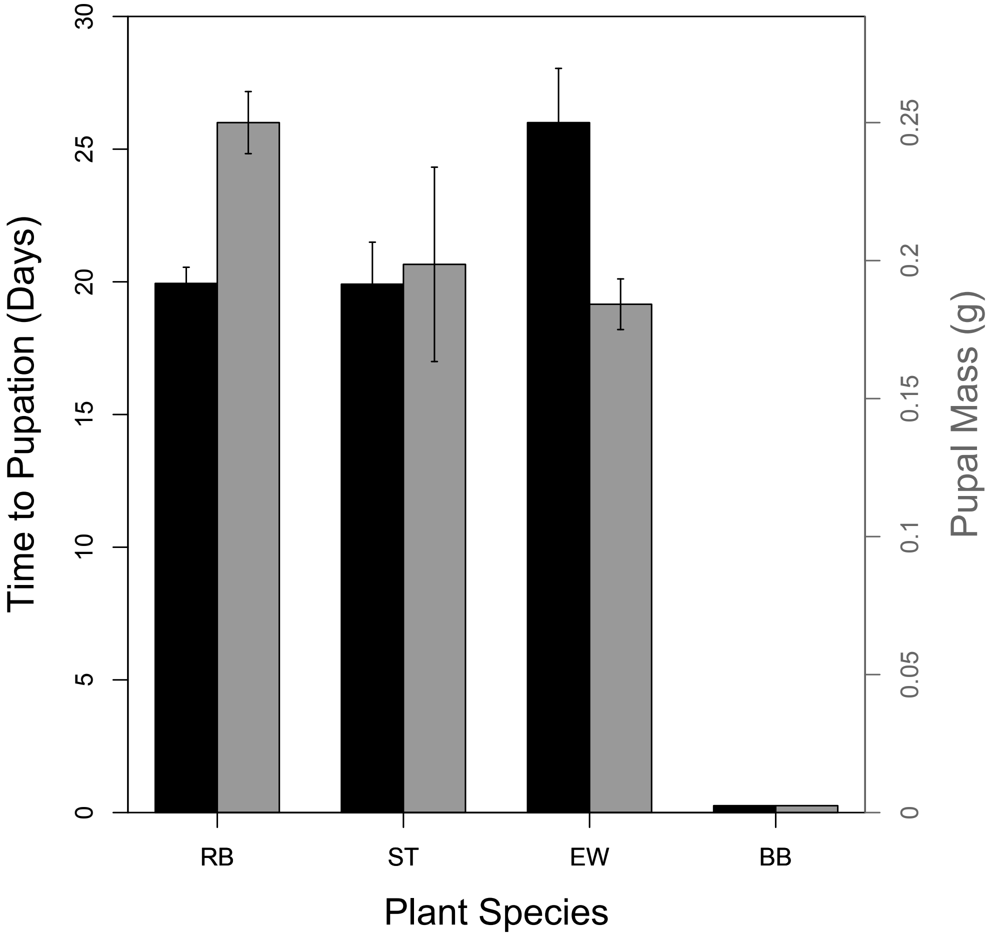

Fig 2.5. Mean ± SE time to pupation (black) and pupal mass (grey) of larval *Hyphantrea cunea,* a generalist herbivore, reared on two invasive (burning bush, European spindle tree) and two native species (red bud, eastern wahoo). Data presented were averaged across replicates.

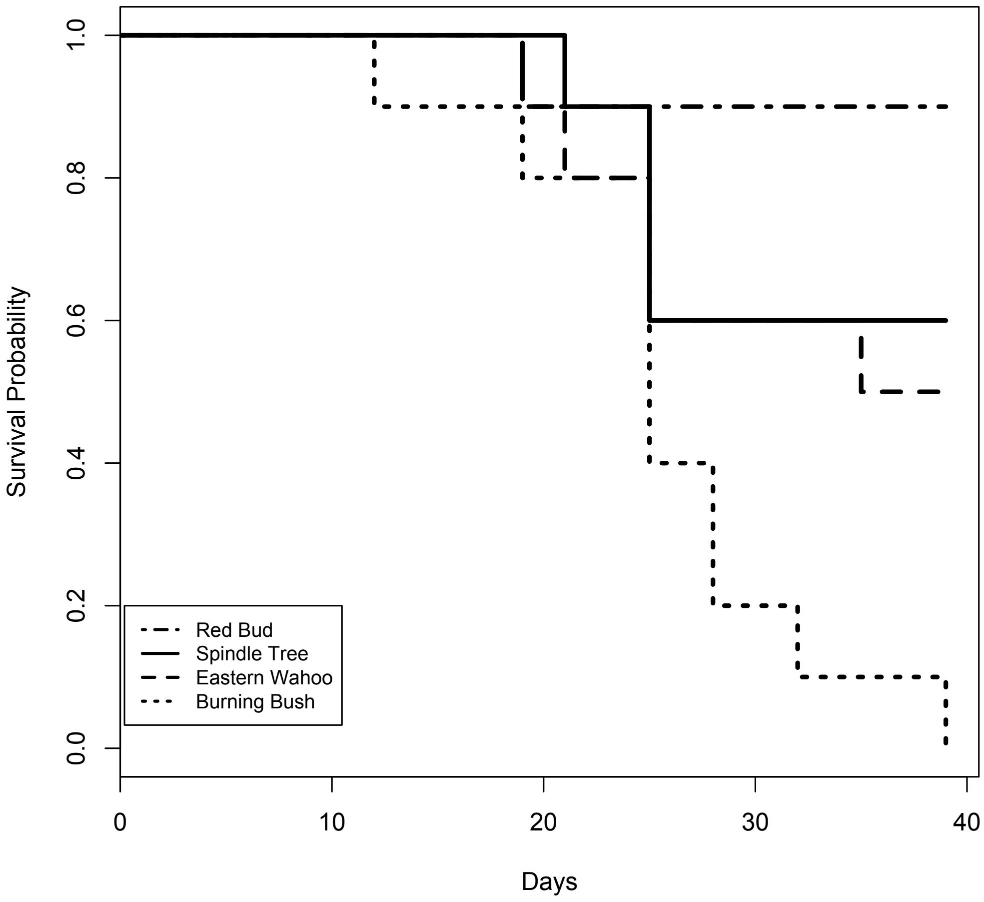

Fig 2.6. Survival probability to pupation for larval *Hyphantrea cunea* reared on two invasive (burning bush, European spindle tree) and two native species (red bud, eastern wahoo). Survival was measured from day 1 until the larvae either reached pupation or expired.

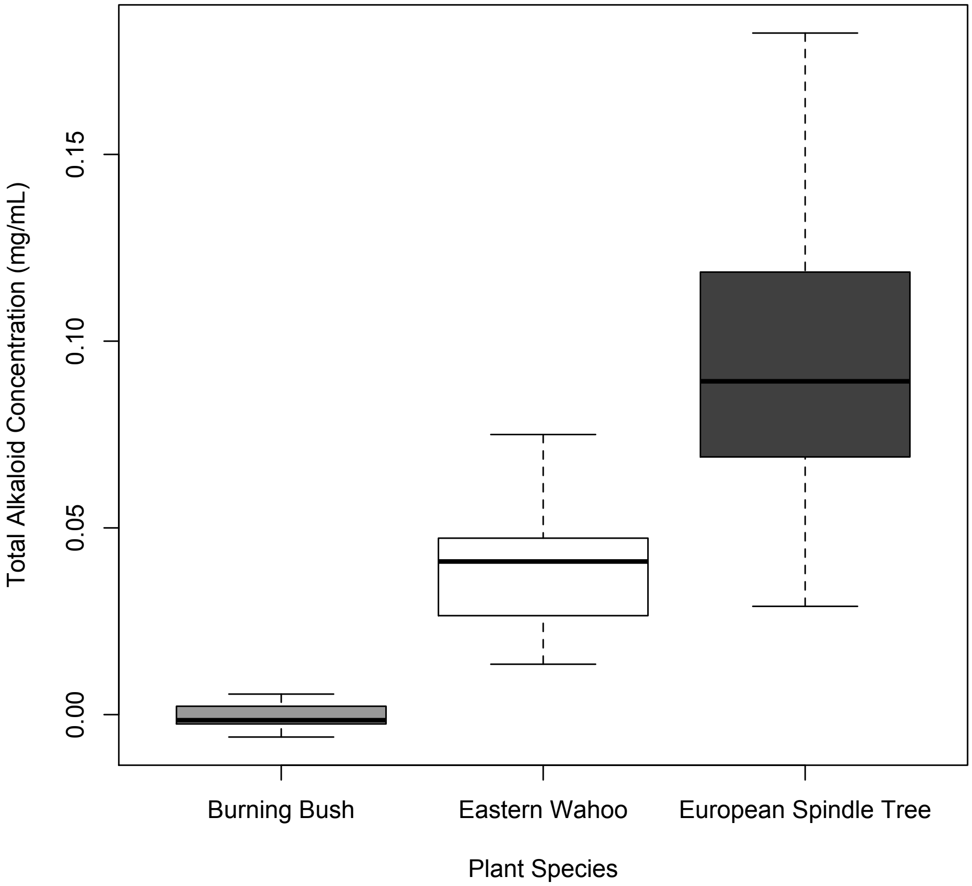

Fig 2.7. Alkaloid concentration in leaf tissue of two invasive (burning bush and European spindle tree) and one native (eastern wahoo) *Euonymus* species. Data presented are averaged amongst replicates and sampling years.

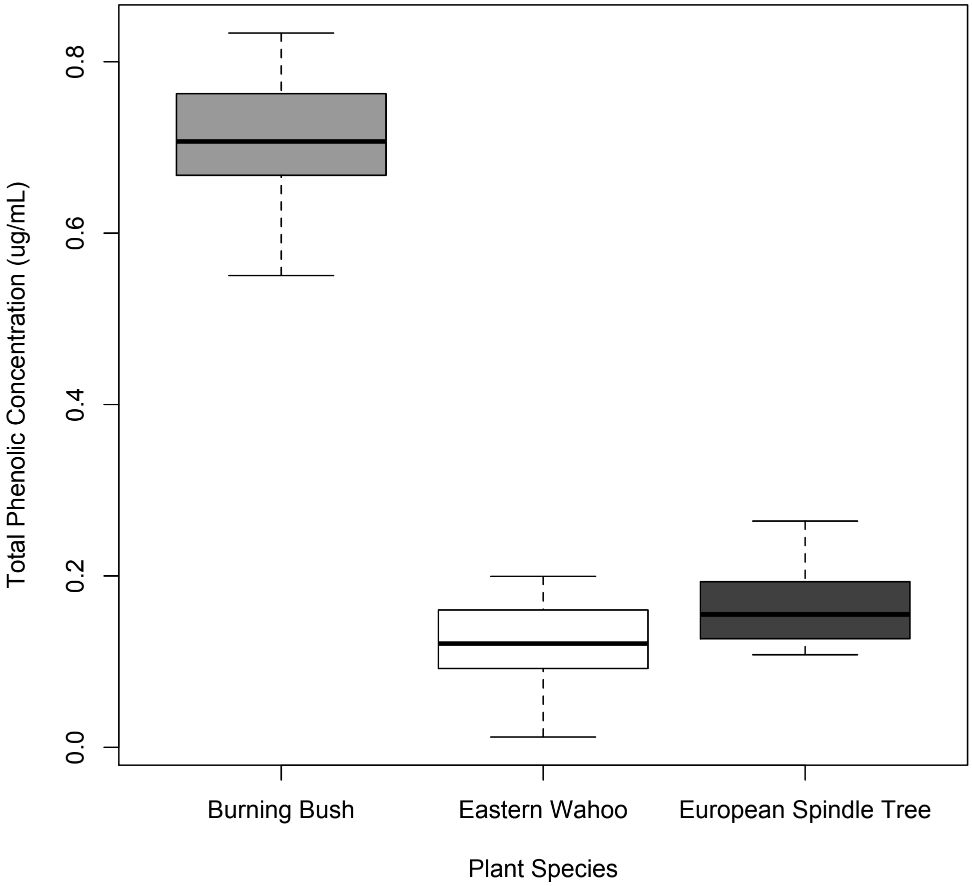

Fig 2.8. Phenolic concentration in leaf tissue of two invasive (burning bush and European spindle tree) and one native (eastern wahoo) *Euonymus* species. Data presented are averaged amongst replicates and sampling years.

3. PLANT INVASION AND DEER OVERABUNDANCE ALTER ARTHROPOD COMMUNITY DYNAMICS THROUGH ALTERATIONS TO VEGETATION STRUCTURE, COVER, AND LITTER DEPTH

3.1 INTRODUCTION

Many exotic plant species are introduced to novel habitats annually either deliberately (i.e. agriculture, forestry, horticulture) or accidentally (i.e. hitchhikers in packing material). Intentionally introduced non-natives are more likely to overcome colonization and establishment barriers because of reduced environmental and demographic stochasticity (Mack et al. 2000). These species undergo climate matching before large-scale cultivation and are therefore more likely adapted to the local climate of the novel environment, bypassing many abiotic filters. Introduced non-natives with close human associations further overcome much of the demographic stochasticity of invasion. As humans cultivate these plants, they have stable source populations of propagules, which can continually contribute to colonization (Huenneke 1997; Mack & Lonsdale 2001; Theoharides & Dukes 2007). This reduced environmental and demographic stochasticity should increase the invasibility of these non-native species, but only a very small proportion of these plants become established and cause negative impacts in their introduced range (Williamson & Fitter 1996). It is this subset of species – “alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health” – that are invasive (United States Executive Order 13112). Invasives have huge impacts, both economically and environmentally. These invaders have the ability to rapidly establish themselves and outcompete their native counterparts due to high fecundity and vegetative spread. Long distance seed dispersal by mammals and birds has also been implicated in regional spread and invasibility of these species (Gorchov 2013; Bartuszevige & Gorchov 2006). Additionally, many ecological hypotheses that seek to explain invader success implicate the relationship between herbivorous arthropods and plant defenses as a driver. The lack of specialist herbivores in the introduced range of these invaders (enemy release hypothesis) allows them to reallocate energy from expensive defense compound synthesis to biomass production leading to further increases in growth and fecundity, increasing invasibility (EICA hypothesis; Keane & Crawley 2002; Blossey & Notzold 1995). Even in the presence of generalist herbivory, invasive plants may shift their defensive chemical composition from specialized defense compounds to “cheaper”, less specialized metabolites leaving more energy for allocation to growth and reproduction (Doorduin & Vrieling 2011).

There are four major ways that invasives have been shown to alter ecosystems (Vitousek 1990) – 1) exotics may differ in their use of resources, therefore altering the resource availability for native species, 2) exotics may alter food web interactions, therefore altering the flow of energy and/or biomass in an ecosystem, 3) exotics may alter disturbance regimes in ecosystems, i.e. erosion, fire., and 4) exotics may cause changes to the physical structure of ecosystems, therefore altering habitat availability and suitability (Crooks 2002). Invasive plants, in particular, are of great concern worldwide because they have large cascading impacts on native ecosystems (Vitousek et al. 1996; Wagner & Van Driesche 2010).

Due to their superior competitive ability in novel habitats, invasive plants can alter native plant composition (Vila et al. 2011), vegetation structure (Crooks 2002), and soil composition (Gratton & Denno 2005) in novel ecosystems. The high fecundity, removal of enemies, increased growth and reproduction, and in many cases extended leaf phenology (Tiley et al. 1996) all contribute to the dominance of invasive plants and subsequent loss of native plant diversity. Plant species composition in these invaded communities shifts in the long term to favor those native species that are resistant to the impacts of the invader (Sharp & Whittaker 2003), leading to an overall reduction in native plant diversity (Vila et al. 2011; Gioria & Osborne 2014). Alteration of plant dominance and composition can lead to distinct changes in the structure of the vegetation. These direct alterations can include changes to percent vegetation cover (Toft et al. 2001), plant height, and plant complexity (Loomis et al. 2014). Changes to vegetation community composition, diversity, and structure can indirectly influence light intensity, temperature, soil moisture, soil nutrients, salinity, pH, and simply the amount of leaf litter (Wolkovich et al. 2009; Gratton & Denno 2005) in an invaded system. Alterations to native plant composition, vegetation structure, and soil and leaf litter composition all contribute to changes in forest ecosystem function and processes.

Because of their diversity, arthropods are simultaneously sensitive to a variety of habitat variables including soil characteristics, plant quality, and vegetation structure (Gratton & Denno 2005; Stewart 2001). Arthropod communities provide a tractable system with which to observe complex community impacts of invasives in a simplified way as arthropods rely on multiple facets of biotic and abiotic habitat quality (Crooks 2002). Increased dominance by invasive plants frequently results in a decrease of native plant diversity (Vila et al. 2011). This can have large impacts on arthropod composition. Arthropod diversity is strongly positively associated with plant species richness (Siemann et al. 1998; Haddad et al. 2001) as many herbivorous species rely on one or a few plant species for food. Some estimates report that at least 90% of insect herbivores are oligophagous (feed only on plants of the same family or even just a few genera) (Bernays & Graham 1988). The impact of invasive plants on arthropods through the reduction in native plant diversity was supported by a meta-analysis by Litt et al. (2014) in which 48% of studies showed a decrease of herbivorous arthropods in invaded environments. Most of these studies imply "direct" impacts of invasive plants on herbivorous arthropods – the inability of these herbivores to feed on these plants due to the production of novel defense compounds (Stireman et al. 2014). Arthropod predator abundance decreased in 44% of studies. Although predators do not directly rely on vegetation for food, invasive plants may indirectly impact predatory arthropods through a reduction of prey (Gratton & Denno 2005).

Invasive plant alteration of vegetation composition can lead to distinct changes in the overall structure of an ecosystem. Direct alterations can include percent vegetation cover

(Toft et al. 2001), plant height, and vegetation complexity (Loomis et al. 2014). Arthropods that depend on vegetation structure, such as web-building spiders, may directly benefit from invasive plant dominance if the plant increases the vertical structure (Loomis et al. 2014). A change in vegetation structure may indirectly impact arthropods through changes in the microclimate, to which arthropods are particularly sensitive (Stewart 2001). This can include changes in light intensity, temperature, soil moisture, soil nutrients, salinity, pH, and simply the amount of leaf litter (Wolkovich et al. 2009; Gratton & Denno 2005). Leaf litter and nutrient changes, in particular, may alter detritivore assemblages, as they rely heavily on the quality of leaf litter (Talley et al. 2012). These changes to the leaf litter may contribute to more favorable microclimates for these taxa because invasive plants have been shown to increase leaf litter (Longcore 2003; Levin et al. 2006). However, increasing invasive plant coverage may negatively impact this group if the plant secretes harmful allelochemicals (Motard et al. 2015). The impacts of invasive plants on arthropods are varying and complex and depend upon both biotic and abiotic changes of an environment (Stireman et al. 2014).

Because of the complex and immense impacts on native flora and fauna, invasive plant removal is a major focus of natural resources agencies in affected areas. However, management strategies can have varying non-target effects on associated plant and arthropod communities (Cipollini et al. 2009) as they alter vegetation structure. The cut/paint method, in which a plant is cut at the base and an herbicide is applied on the stump, results in the complete removal of the plant. This increases light reaching understory plants, which may result in greater herb-layer plant abundance. This strategy also removes much of the vertical complexity in treated sites, resulting in fewer habitats for spiders and arthropods (Cipollini et al. 2009). The basal application method, in which an herbicide is applied around the base of a plant, results in standing dead mass (SDM), leaving structure only. SDM may negatively impact herb-layer vegetation recovery due to the leaching of allelopathic compounds during decomposition (Dorning & Cipollini 2006). Conversely, this management strategy may positively impact arthropods by providing habitat through increased vertical structure. The benefits and drawbacks for each of these management strategies, however, may differ through time as the herb layer develops and/or as the SDM breaks down. Each of these management strategies has the potential to impact associated arthropod and plant communities both directly and indirectly. These impacts are further complicated by the presence of herbivores.

Overabundance of native species can alter environments in a way that mimics the impacts of invasive plants. White-tailed deer (*Odocoileus virginianus*) populations in North America have increased greatly since pre-colonial times, reaching and maintaining densities above 10/km^2 throughout temperate zones (Bressette et al. 2012). Through selective feeding, deer reduce vegetation cover, change vegetation composition (Rooney 2009), reduce vertical structure (Suominen et al. 2003), and homogenize forest environments (Rooney & Waller 2003; Wiegmann & Waller 2006), all of which may alter microclimates. Reengineering of forest plant communities by deer can alter arthropod assemblages. However, these alterations vary between guilds (e.g., specialist herbivores decrease (Baines et al. 1994), web-building spiders decrease in abundance (Miyashita et al. 2004) and community composition differs (Roberson et al. 2016), active ground beetles and spiders increase (Allombert et al. 2005; Suominen et al 2003)). White-tailed deer have also been shown in to interact with invasive plants. Areas where deer have been excluded support fewer invaders (Webster et al. 2005) as deer reduce native plant diversity, allowing for the establishment of these species. Invaders that establish and are successful in areas with high deer abundance are likely unpalatable, or have a novel chemical defense that reduce herbivory rates (Kalisz et al. 2014). In addition to creating a favorable environment, deer may also assist the spread of invasives by acting as long distance dispersers (Vellend 2002). Because of their potential interactions with invasive spread and success, white-tailed deer management must be considered in an invasive plant species management strategy. Plant management strategies that leave standing dead mass intact have been shown to positively affect herb-layer plant success and reestablishment by guarding these herb-layer plants from herbivory (Gorchov & Trisel 2003; Cipollini et al. 2009). Invasive plant management, especially when the goal is native plant recruitment and ecosystem recovery, needs to encompass many environmental aspects including invasive plant removal and white-tailed deer impacts.

Amur honeysuckle (*Lonicera maackii*, Rupr.) is one of the most prolific and well-studied invasive plant species in the eastern United States. It was introduced to the United States in the 1880s from Asia for use in the ornamental trade (Luken & Thieret 1996). It is a deciduous shrub that reaches maximum heights of approximately 5 m. The leaves are opposite, elliptical to ovate and 5-9cm long and 2-4cm wide. The shrub possesses a multitude of traits that increase its invasibility including extended leaf phenology, high fecundity, and reduced herbivory (Lieurance 2004; Trisel 1997; McEwan et al. 2009;

Lieurance & Cipollini 2011). Sites invaded by honeysuckle show reduced native plant reduces richness, abundance, growth, production, and reproduction (Collier et al. 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2007, 2008; Luken et al. 1997, Miller and Gorchov 2004; Pennington et al. 2010). This invasion and subsequent displacement of native plants alters the structure of understory vegetation (Deering and Vankat 1999; Luken et al. 1997). Due to both direct and indirect mechanisms, honeysuckle significantly alters the arthropod community composition (Conley et al. 2011; McKinney and Goodell 2010; Loomis et al. 2014; Loomis & Cameron 2014; Stireman et al. 2014), although the direction and magnitude of these changes differs between trophic levels.

Burning bush (*Euonymus alatus* (Thunb.) Sieb.; Celastraceae) is an ornamental plant that was introduced from Asia to the United States in 1860 (Dirr 2009, Brand et al. 2012). It is a deciduous shrub that reaches heights up to 3 m. The leaves are broad, ovate-elliptic, with an acute apex and are 2-7cm in length and 1-4cm wide (Dirr 1998). The annual production of this shrub is thought to be at least in the hundreds of thousands (likely millions) and annual sales in Connecticut alone reached $5 million in 2004. Burning bush is classified as an invasive species in eight eastern states (Dirr 2001) and is of growing concern in the Midwest. Burning bush has particularly high propagule pressure as it reproduces both sexually and asexually, both traits routinely associated with invasibility (Dirr 2001; Reichard & Hamilton 1997). Cultivated individuals produce an average of 3000 seeds per season with some cultivars producing over 8000 seeds and germination rates routinely reach 98% (Brand et al 2012, Dirr 2001; Fryer 2009). Once established, burning bush may negatively impact arthropod herbivores as this plant and other related species have been found to contain high levels of alkaloids, phenolics, and terpenoids, secondary compounds used in defense (Thomas et al. 2011; Li et al. 2013; Zhou et al 2014; Roberson chapter 2, 2018). Reductions in arthropod herbivores could indirectly impact arthropod predator communities through an indirect reduction of prey availability. Although of growing concern as an invasive with great potential to negatively alter native plant and arthropod communities, very little is known about the ecology and impacts of burning bush in invaded environments.

In this study, we examined 1) the impact of burning bush and honeysuckle on a variety of environmental characteristics including branch density, litter depth, and vegetation cover compared to a native control. We hypothesized that branch density would be higher in sites containing invasives due to the dominance of the shrubs in invaded sites. However, we hypothesized that litter depth and vegetation cover would be lower for both invaders as these species contain high levels of secondary metabolites that could slow decomposition and these species outcompete native plants. We then examined 2) the impact of burning bush and honeysuckle on total, ground-dwelling, and aerial arthropod assemblages when compared to native plant communities. We hypothesized that the presence of invasive plants would lead to a decrease in arthropod abundance in richness and that these alterations would be most severe for ground-dwelling arthropods due to the likely low ground cover and subsequent reduction of food and habitat in these plots. However, we also hypothesized that burning bush and honeysuckle invasion would lead to an increase of aerial arthropods, especially spiders. The invaders may increase the available habitat for these groups through increased branch density. We also hypothesized, that regardless of habitat or arthropod type, plant invasion would alter the community composition of associated arthropods due to alterations in environmental characteristics. We then 3) determined if the presence of white-tailed deer altered the effect of plant invasion dominant plant species on environmental characteristics and/or the associated arthropod assemblages. We hypothesized that the presence of deer would intensify the impacts on arthropods observed for dominant plant species as deer further reduce vegetation cover and litter depth and can facilitate the dominance of invasive plants. We also hypothesized, that deer would alter the arthropod community due to alterations in environmental characteristics. Finally, we 4) examined if the presence of vertical structure altered the effect of dominant plant species and deer presence on environmental characteristics or the associated arthropod assemblages. We hypothesized that increases in vertical structure would lead to increased aerial arthropods due to increased habitat, but that plots with no structure would support the highest abundance and richness of ground-dwelling arthropods due to increased ground cover regardless of dominant plant type. We predicted that these impacts would be more intense in deer absent plots due to more favorable environmental characteristics.

3.2 METHODS

In summer 2014, we constructed deer exclosures with adjacent open access control plots

Table 3.1: sampling locations. Plots shown are the total and broken down by deer treatment (exclosures, controls)

Site Name	GPS	Burning Bush Plots	Honeysuckle Plots	Native Plots
Caesar Creek	39.540538, 84.007070	10 (5,5)	6 (3,3)	6 (3,3)
Wright State Woods	39.786736, 84.052594	NA	6 (3,3)	6 (3,3)
Taylorsville	39.880257, 84.158186	NA	6 (3,3)	6 (3,3)
Germantown	39.637274, 84.395412	NA	6 (3,3)	6 (3,3)

in four natural areas distributed throughout the Dayton, OH local area: Caesar Creek State Park, Germantown MetroPark, Taylorsville MetroPark, and the Wright State University Woods. Exclosures were 3m X 9m and fenced using 8ft. high plastic mesh fencing. At Caesar Creek, eleven exclosure/control plot pairs were established (five in a burning bush invaded area, three in a honeysuckle invaded area, and three in a native dominated areas), and six exclosures with control plots were established at the other sites (three in honeysuckle invaded areas, three in native dominated areas)(Table 3.1). Native plots were dominated by spicebush (*Lindera benzoin*, L.), paw-paw (*Asimina triloba*, (L.) Dunal), and sugar maple (*Acer saccharum* (Marshall)). All exclosures were built in forest understory and no closer than 50 m to the forest edge to eliminate edge effects. All sites were similarly aged, mature secondary forests. To assess the role of vegetation structure in determining the arthropod community composition in each plot, we established three structure treatments. One third of each plot was designated a control that received no manipulation and had intact plant canopies. The woody vegetation in one third of each plot was removed by cutting it off at the base and painting the stumps with an herbicide (PathFinderII) leaving no structure. The woody vegetation in the remaining third of the plot was killed with a basal bark application of herbicide that left the dead stems standing (structure only; Fig 3.1). We sampled each plot five times during summers of 2015 and 2016 (May-Sept). All plots were again sampled in July of 2017. Plots at Caesar Creek were additionally sampled in September of 2014 and 2017.

Ground dwelling arthropods were sampled using pitfall traps. Pitfall traps were constructed using plastic drink cups dug into the ground so the lip was even with the soil. Traps were filled with ~50mL of a 50/50 mix of water and propylene glycol with a drop of dish washing liquid (Dawn Ultra Original Scent) to break surface tension. A small amount of Bitrex was placed in each pitfall trap to deter small mammals. Three pitfall

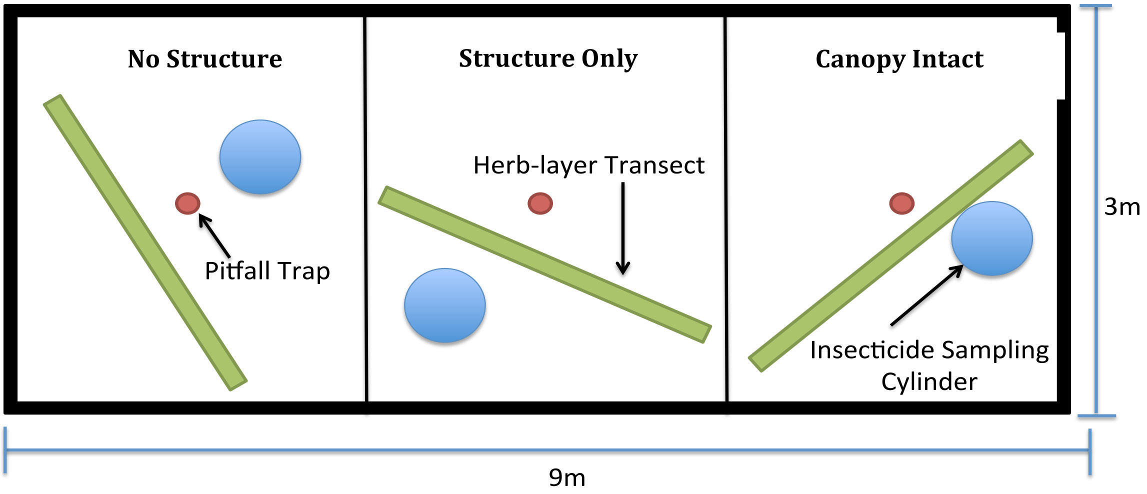

Fig 3.1. Sampling schematic showing one plot with all vegetation structure treatments (No structure, structure only, canopy intact) and all sampling methods (Pitfall, Herb-later transect, Insecticide shrub-dwelling arthropod sampling cylinder)

traps (one in each plant treatment) were deployed in the center of each plot four days before sampling. During sampling, the contents of each pitfall trap were placed in a 100mL-sampling bottle for preservation.

Shrub-dwelling arthropods were sampled using a modified beat sheet method. During each sampling event, a 1m-diameter canvas cloth was placed on the ground below a haphazardly chosen 1m diameter, 2m high sampling cylinder in each plant treatment. An organic insecticide (EssentriaIIC3) was applied using a garden sprayer to all of the vegetation present in the sampling cylinder and the vegetation was lightly shaken to dislodge arthropods. This was repeated in all plant treatments in all plots. All collected arthropods were placed in 70% ethanol for preservation.

During each sampling event, within each establish sampling cylinder, we measured branch density and leaf litter depth. Litter depth was collected from the center of the sampling cylinder using a meter stick and recorded to the nearest 0.5cm. Branch density was measured using a modified point-intersect method. A meter stick was held vertically in the center of each sampling cylinder and slowly moved upward to a total height of 2m. The total number of times that vegetation crossed the transect was recorded as branch density (a proxy for vegetation complexity).

All arthropod specimens were identified in the lab to the lowest possible taxonomic group (family for beetles, genus for spiders, order for all others). During identification, sorted individuals from replicate treatments were combined and dried in an oven at 60C for 24 hours. Samples were then weighed and totoal biomass was recorded to the nearest 0.1mg.

Understory plant sampling was also completed during each sampling event using the point-intersept method outlined in Rooney (2009). In each sampling month, a meter stick was haphazardly placed in each plant treatment plot. Along this 1m transect, every time vegetation crossed the transect, the plant type (forb, graminoid, fern, woody) and length of the tape covered was recorded.

Prey availability for aerial predators was measured at all sites in July 2017 and additionally at Caesar Creek in September 2017 using sticky traps. The traps were constructed using 23cm X 33cm sheets of clear plastic (approximately 0.15mm thick), cut in half, and coated with an adhesive. Traps were hung from vegetation haphazardly in the canopy intact and structure only plant treatment areas of each plot four days before each sampling event. Aerial prey was not sampled in the no structure plots as we did not sample aerial arthropods in these plots. We applied clear plastic film to the adhesive side of the traps at the time of collection for transport. The total number of prey items on each trap was recorded.

Prey availability for ground dwelling predators was calculated for each plot using the total combined abundance of all arthropod orders collected in the pitfall traps excluding coleoptera, hymenoptera, orthoptera, isopoda, and chilopoda. These orders are non-preferred food items for spiders.

3.2.1 Data Analysis

All data were checked for normality using the Shapiro-Wilk test and then natural log transformed to increase normality. Outliers were detected using the "mvoutlier" package in R and removed from analysis.

Total arthropod abundance, order richness, and per individual biomass were averaged across monthly replicates for each plant/deer/vegetation structure treatment. Differences in these values through time, and between vegetation type, vegetation structure, and deer exclusion were determined using split plot repeated measures ANOVA. Dominant plant was the main effect with deer treatment as the first subplot factor and vegetation structure as the second. We explored the effects of site and year and neither factor described any significant differences between any variable. Therefore, these two factors were removed from analysis.

Total community composition was computed using the Bray-Curtis Dissimilarity Index and visualized using non-metric multidimensional scaling (NMDS). These analyses were repeated for ground arthropods, beetles (family level), and spiders (family and genus level) and again for aerial arthropods, beetles (family level), and spiders (family and genus level) separately.

Environmental variables (vegetation percent cover, litter depth, prey availability, and branch density) were combined and averaged across replicates to reduce pseudo-replication. Differences in these values through time, and between vegetation type, vegetation structure, and deer exclusion were determined using split-split plot repeated measures ANOVA. Environmental variable composition was computed using the Bray-Curtis Dissimilarity Index and visualized using non-metric multidimensional scaling (NMDS).

3.3 RESULTS

3.3.1 Total Arthropods

Community Composition

Community composition of total arthropods differed when compared across plant species treatment ($P = 0.001$, $R = 0.776$, Fig 3.2) and by month ($P = 0.001$, $R = 0.1302$; Fig 3.3; Table 3.2).

Abundance

Total arthropod abundance varied between sampling months (df = 4, F = 4.71, P = 0.0097). Abundance peaked in June with an average of 28.4 ± 1.9 arthropods per plot and decreased throughout the season until reaching 12.5 ± 0.7 arthropods per sample in September (Fig 3.4). The range of arthropod abundance was similarly high in May and June and decreased throughout the season reaching a minimum in August. The range of abundance in August was about half that of the peak in June. The interaction between plant species, deer presence, and vegetation structure was significant when assessing total arthropod abundance (df = 2, F = 4.04, P = 0.018, Fig 3.5). For each plant species, the highest arthropod abundance was in plots with deer removed and the vegetation canopy intact. For non-native plant species, when deer were removed, the lowest arthropod abundance was in no structure subplots whereas the lowest abundance for native plots was in structure only subplots. However, the lowest abundance in native plots was still almost twice as high as the lowest abundance in burning bush plots. When deer were present, abundance was highest in structure only subplots, followed by no structure subplots, and then canopy intact subplots regardless of plant species.

Richness

Similar interactions were observed in total arthropod order richness. Again, the interaction of plant species, deer presence, and vegetation structure was significant (df = 2, F = 3.60, P = 0.028, Fig 3.6). When deer were present, richness was highest in structure only subplots, followed by no structure subplots, and then canopy intact subplots regardless of plant species. Although these differences were small, burning bush supported the lowest richness of arthropods regardless of the vegetation structure. For all plant species, the removal of deer increased arthropod order richness regardless of vegetation structure. For both honeysuckle and native plots, canopy intact subplots saw the largest increase of order richness. Richness nominally increased in the other two subplot types. The increase in richness by the removal of deer was even more dramatic in native plots and relied much less on vegetation structure. Richness increased most in canopy intact subplots. Although arthropod order richness increased also in burning bush plots when deer were removed, the largest increase was in no structure plots. However, canopy intact plots also showed a similar increase in richness. Overall, burning bush plots had the lowest order richness regardless of deer or vegetation structure.

Arthropod order richness was significantly affected by the interaction between plant species and sampling month (df = 4, F = 2.55, P = 0.038; Fig 3.7). For all plant species, richness peaked in June, dipped in July, and then increased again in August. The lowest order richness was in September for all plant species. In all months except May, native plots supported higher arthropod richness than either non-native species. Overall, regardless of month, arthropod order richness was approximately two-thirds lower in burning bush plots compared to either honeysuckle or native plots.

The introduction of deer impacts into the plant:month interaction also significantly altered arthropod order richness (df = 4, F = 2.590, P = 0.036; Fig 3.8). In deer present plots, the overall patterns observed in the plant:month interactions held mostly true. All plant species showed relatively high order richness in June and August, and richness decreases in July and September. However, in honeysuckle plots, the highest richness was in May, although this value was only nominally higher than June, and burning bush plots had a richness minimum in July (the previous minimum in September). When deer were removed, richness was higher overall, regardless of plant species. However, richness patterns throughout the sampling season did change. For both honeysuckle and native plots, richness peaked in June and then decreased throughout the remainder of the season to a minimum richness in September. Burning bush plots had peak richness in May and richness decreased throughout the whole sampling season reaching a minimum richness in September. Overall, burning bush plots had the lowest arthropod order richness (1.9 ± 0.2) and native plots had the highest arthropod order richness (2.7 ± 0.2).

Biomass

Average per individual arthropod biomass was significantly different between months (df = 4, F = 4.066, P = 0.003; Fig 3.9) and deer treatments (df = 1, F = 7.325, P = 0.007; Fig 3.10). Biomass started high in May, dipped in June, and continued to increase throughout the season, peaking in September. Arthropods in plots with deer present were, on average, 20% lighter than those in plots with deer excluded. Arthropod biomass varied most dramatically in September, more then 5 times than in June.

3.3.2 Aerial Arthropods

Community Composition

Aerial arthropod composition differed among plant species and month (plant – P = 0.002, R = 0.6991; month – P = 0.009, R = 0.099; Table 3.3).

Richness

Richness of aerial arthropods differed significantly between plant species (df = 1, F = 5.950, P = 0.015; Fig 3.11). Burning bush supported the fewest arthropod orders on average (0.54 ± 0.08 orders), almost 30% fewer than honeysuckle (0.74 ± 0.04 orders) and over 20% fewer than native plots (0.68 ± 0.04). Variation within honeysuckle and native plots was similar, ranging from 0 orders to approximately 2 orders. Richness in burning bush plots, however, varied between 0 and 1.2 orders.

Biomass

The interaction between plant species and deer treatment significantly altered aerial arthropod biomass (df = 1, F = 4.825, P = 0.029; Fig 3.12). In non-native plant plots, aerial arthropod biomass was higher when deer were removed. This was particularly dramatic for burning bush. In native plots, however, arthropod biomass was higher in deer present plots, although only by 8%.

3.3.3 Ground Arthropods

Community Composition

Total ground arthropod community composition differed across plant species and month (plant – P = 0.001, R = 0.800; month – P = 0.018, R = 0.0963; Table 3.4).

Abundance

Ground arthropod abundance differed between dominant plant type (df = 2, F = 4.142, P = 0.016; Fig 3.13) and across sampling months (df = 4, F = 5.918, P = 0.0001; Fig 3.14). Abundance was highest in native plots (17.94 ± 0.86), although the variation in native plots was highest as well. Honeysuckle plots supported less than 5% fewer ground arthropods than native plots (17.08 ± 0.89). However, abundance in burning bush plots was 14% lower than that of native plots (15.44 ± 1.65). Ground arthropod abundance, regardless of plant species, peaked in June (25.65 ± 1.75), decreased throughout the season (July – 16.83 ± 1.03; August – 13.70 ± 0.74), and reached a minimum abundance in September (11.56 ± 0.75).

Richness

Similar to ground arthropod abundance, richness differed between plant species (df = 1, F = 5.950, P = 0.015; Fig 3.15). Plots dominated by native plants supported the highest arthropod richness (2.38 ± 0.05 orders). Honeysuckle plots supported a similar number of orders (2.28 ± 0.04 orders) as native plots. However, richness in burning bush (1.52 ± 0.06 orders) plots was 46% lower than that of native plots. Both honeysuckle and native plots showed similar variation within plots, while variation in burning bush plots was about half that of the others.

Biomass

The interaction of plant species and deer presence significantly impacted ground arthropod biomass (df = 1, F = 4.825, P = 0.029; Fig 3.16). Honeysuckle plots supported arthropods of similar size (individual arthropod mass), regardless of the deer treatment. Ground arthropods in both native and burning bush plots were larger when deer were removed from the system. Arthropods in native plots with deer removed were almost twice the size as those in plots with deer present.

3.3.4 Total Spiders

Community Composition

Total spider community composition differed between plant species and sampling month (both spider family (plant – P = 0.001, R = 0.7879; month – P = 0.002, R = 0.153; Table 3.5) and genus composition (plant – P = 0.001, R = 0.7883; month – P = 0.01, R = 0.121)).

Abundance

Total spider abundance differed between months (df = 4, F = 2.750, P = 0.028; Fig 3.17). Spider abundance was consistent in May and June (2.13 ± 0.17), was highest in July (2.83 ± 0.4), and then decreased in August (2.28 ± 0.21). Abundance decreased heavily in September (1.09 ± 0.14) to less than half of the peak abundance.

Richness

Spider family (df = 2, F = 3.724, P = 0.025; Fig 3.18) and genus (df = 2, F = 4.021, P = 0.013; Fig 3.19) richness both differed significantly between vegetation structure subplots. Richness was the highest in the canopy intact subplots (0.88 ± 0.04 families; 0.71 ± 0.04 genera), slightly lower in the structure only plots (0.78 ± 0.04 families; 0.64 ± 0.04 genera), and lowest in no structure subplots (0.63 ± 0.04 families; 0.43 ± 0.04 genera). Variation within plant treatments largely followed the same pattern.

Genus richness differed significantly between sampling months (df = 4, F = 3.731, P = 0.025; Fig 3.20). Genus richness was highest in June (0.76 ± 0.05 genera) and August (0.83 ± 0.05 genera), twice as high as the minimum richness in September (0.41 ± 0.04 genera). Richness dipped in May (0.53 ± 0.05 genera) and July (0.47 ± 0.04), although not as low as the minimum richness, mirroring the patterns observed in order richness.

3.3.5 Aerial Spiders

Community Composition

Aerial spider community composition differed between plant species and month for spider family (plant – P = 0.001, R = 0.7886; month – P = 0.007, R = 0.1003; Table 3.6).

Richness (Family)

Aerial spider family richness varied across sampling months (df = 4, F = 2.654, P = 0.033; Fig 3.21). Family richness was bimodally distributed with peaks in June (0.60 ± 0.06 families) and August (0.68 ± 0.05 families). Richness was within 9% in all other months (May – 0.44 ± 0.04 families; July – 0.45 ± 0.04 families; September – 0.41 ± 0.04 families). However, the range of observed richness was highest in July.

Biomass

Aerial spider biomass differed significantly between vegetation structure subplots (df = 1, F = 7.479, P = 0.0067; Fig 3.22). Spiders in structure only subplots were on average almost twice as large (1.92 ± 0.35 mg) than those in canopy intact subplots (1.03 ± 0.18 mg).

3.3.6 Ground Spiders

Community Composition

Total ground spider community composition differed across plant species and month (plant – P = 0.001, R = 0.813; month – P = 0.02, R = 0.0893; Table 3.7).

Abundance

Ground spider abundance was highest in July (4.14 ± 0.46). Abundance rose steadily by 15% each month from May (May – 2.61 ± 0.22; June – 3.08 ± 0.20) to July, and then decreased quickly (August – 3.12 ± 0.27) until reaching a minimum abundance in September (1.32 ± 0.13; df = 4, F = 4.110, P = 0.0029; Fig 3.23). Abundance in July also showed the highest variation.

Richness (Family)

Richness differed between plant species (df = 2, F = 3.783, P = 0.025; Fig 3.24). Native plots supported the highest ground spider richness (0.78 ± 0.04), 25% higher than burning bush plots (0.59 ± 0.04 families) and 10% higher than honeysuckle plots (0.70 ± 0.03 families).

Richness (Genus)

Ground spider genus richness differed both by month (df = 4, F = 6.188, P = 0.0028), and vegetation structure (df = 2, F = 2.345, P = 0.05). Richness was bimodally distributed with two peaks, one in June (0.76 ± 0.05 genera) and one in August (0.83 ± 0.05). Richness was similar between all remaining months (May – 0.47 ± 0.04 genera; July – 0.45 ± 0.05 genera; September – 0.41 ± 0.04 genera), within 11% of each other. Canopy intact subplots supported the highest genus richness (0.71 ± 0.04 genera), 10% higher than the structure only vegetation structure subplots (0.64 ± 0.04 genera). This percent difference increased to almost 40% when comparing canopy intact to no structure plots (0.43 ± 0.03 genera).

Biomass

Ground spider biomass differed between vegetation subplots (df = 1, F = 7.479, P = 0.0066; Fig 3.25). Ground spiders in subplots with no structure were larger than either of the subplots with structure (17.58 ± 2.24 mg). Spiders in structure only subplots were 12% smaller (15.40 ± 2.13 mg) than those in no structure plots. This difference increased to almost 30% when comparing spiders in no structure and canopy intact subplots (12.62 ± 1.15 mg).

3.3.7 Total Beetles

Community Composition

Total beetle composition differed between dominant plant type and by month (plant – P = 0.001, R = 0.7896; month – P = 0.005, R = 0.1376; Table 3.8).

Abundance

Beetle abundance was significantly different between deer treatments (df = 1, F = 6.958, P = 0.008; Fig 3.26). Although variation was about 30% higher in deer absent plots, abundance was almost 40% lower in plots with deer present at ambient levels (1.78 ± 0.13 beetles) compared to plots with deer removed (2.84 ± 0.21 beetles). Beetle abundance also differed across sampling months (df = 4, F = 9.024 P < 0.0001; Fig 3.27). Abundance was more than twice as high at peak abundance in June (4.16 ± 0.5 beetles) as in May and September (1.74 ± 0.2 beetles), the minima. After abundance peaked in June, it dropped by nearly half in July (2.25 ± 0.19 beetles) and even further in August (1.86 ± 0.19 beetles).

The interaction between deer treatment and month significantly impacted beetle abundance (df = 4, F = 3.005, P = 0.018; Fig 3.28). Regardless of deer treatment, peak beetle abundance still occurred in June. However, when deer were removed, peak abundance doubled. In both deer treatment plots, the overall pattern of beetle abundance across months remains similar to the overall impact of month described above. After peak abundance in June, the number of beetles in subsequent months decreases from July to September. However, in deer removed plots the abundance minimum was in May, and in the deer present plots the minimum was seen in August, instead of September as seen in the total month treatment. Overall, the removal of deer increased beetle abundance regardless of month.

The interaction between plant species, deer treatment, and vegetation structure significantly impacted beetle abundance (df = 2, F = 3.912, P = 0.021; Fig 3.29). In deer present plots, regardless of plant species, canopy intact subplots had the lowest beetle abundance, followed by no structure subplots, and finally structure only plots. With deer removed, beetle abundance increased regardless of vegetation structure for both honeysuckle and native plots. This was most dramatic in native plots where beetle abundance increased by more than two times in canopy intact and no structure subplots. In burning bush plots, beetle abundance only increased in canopy intact subplots. Overall, beetle abundance was highest in native plots – over 1.5 times the abundance of burning bush plots and 20% higher than honeysuckle plots.

Richness

Beetle family richness differed across sampling months (df = 4, F = 7.203, P < 0.0001; Fig 3.30). The pattern of beetle richness mirrored that of overall beetle abundance. Richness began relatively high in May (0.76 ± 0.06 beetle families), reached the highest level in June (0.93 ± 0.06), and then decreased as the sampling season progressed (July – 0.70 ± 0.05; August – 0.59 ± 0.04; September – 0.55 ± 0.03). Variation in richness followed a similar trend.

Biomass

Deer treatment significantly altered average beetle biomass (df = 1, F = 10.888, P = 0.001; Fig 3.31). Beetles in deer present plots were 30% larger (11.09 ± 2.57 mg) than those in deer absent plots (8.51 ± 1.67 mg).

3.3.8 <u>Aerial Beetles</u>

Community Composition

The aerial beetle community did not differ significantly when compared between any main or subplot effect.

Abundance

The interaction between deer treatment and month significantly impacted beetle abundance (df = 4, F = 2.817, P = 0.023; Fig 3.32). Overall, abundance was very similar regardless of the presence of deer. For both deer treatments, abundance peaked in June, fell drastically in July and August, and then rose again in September. Deer present plots had higher abundance in the early sampling months, but deer absent plots maintained higher abundance by the end of the season. Both deer present and absent plots had similarly low abundances in July and August.

Richness (Family)

Aerial beetle family richness differed between sampling months (df = 4, F = 2.836, P = 0.025; Fig 3.33). Similar to aerial beetle abundance, richness was high in May (0.15 ± 0.03 families), peaked in June (0.21 ± 0.03), decreased in July (0.05 ± 0.01) and August (0.05 ± 0.01), and again increased by September (0.16 ± 0.06) to levels similar to the beginning of the season.

3.3.9 <u>Ground Beetles</u>

Community Composition

Beetle community composition differed between plant (P = 0.02, R = 0.452) and month (P = 0.01, R = 0.0989; Table 3.9).

Abundance

Ground beetle abundance differed significantly between plant species (df = 2, F = 3.540, P = 0.0298; Fig 3.34). Native plots, overwhelmingly, supported the highest abundance of ground beetles. This was 1.5 times higher than the abundance supported in burning bush plots, and 35% higher than honeysuckle plots. Abundance also varied by month (df = 4, F = 7.592, P < 0.0001; Fig 3.35). Abundance remained steady in May and June and peaked in July. Abundance decreased by almost 30% in August and remained low in September.

Richness (Family)

Ground beetle family richness also differed across sampling months (df = 4, F = 2.836, P = 0.025; Fig 3.36). Richness saw a steady decline through the sampling season, from the peak in May to the minimum in September. However, richness between the peak in May and minimum in September only differed by 19%.

3.3.10 Environmental Variables

Total Environmental Variable Composition

The composition of environmental variables differed between dominant plant species (P = 0.0001, R = 0.8976; Fig 3.37).

Branch Density

Branch density, our proxy for vegetation complexity, was significantly higher in non-native plant plots compared to native plots (df = 2, F = 26.536, P < 0.0001; Fig 3.38). Vegetation in the burning bush plots was three times denser than that of native plots. Vegetation density was 15% higher in burning bush plots than in honeysuckle plots. Burning bush plots had the highest variation in branch density although variation was similarly high in honeysuckle plots. The range of branch densities was almost 3 times higher in burning bush plots than in native plots.

We did not measure branch density in no structure plots as all shrub layer structure was removed. With these subplots removed from analysis, branch density did differ between the two remaining vegetation structure subplots (df = 1, F = 50.197, P < 0.0001; Fig 3.39). The vegetation in the canopy intact subplots was over twice as dense than structure only plots. Variation in branch density was almost 2.5 times higher in canopy intact plots than in structure only plots.

Litter Depth

Average litter depth differed between plant species (df = 2, F = 4.229, P = 0.04; Fig 3.40) and sampling month (df = 4, F = 5.034, P = 0.0006; Fig 3.41). Overall, native plots had the greatest litter depth (1.84 ± 0.08 cm), followed by honeysuckle (1.40 ± 0.07 cm), and then burning bush (1.17 ± 0.11 cm), and litter depth decreased throughout the sampling season (May – 2.68 ± 0.16 cm; June – 1.88 ± 0.10 cm; July – 1.26 ± 0.07 cm; August – 1.20 ± 0.10 cm; September – 1.11 ± 0.09 cm).

The interaction between plant species and month also significantly impacted litter depth (df = 4, F = 2.803, P = 0.026; Fig 3.42). For all plant species, litter depth was highest in May and decreased in June. Litter depth in burning bush and native continued to decrease throughout the rest of the sampling season. Conversely, honeysuckle plots decreased in July and then increased slightly in August and September. Overall, native plots had deeper litter depth than the two non-native plant plots, which were similar.

Litter depth was affected by the interaction of deer presence and plant species (df = 2, F = 12.009, P = 0.0006; Fig 3.43). In non-native plots, litter was deeper when deer were present. The opposite was true for native plots where litter was deeper in plots with deer removed.

Understory Plant Cover

Vegetation cover was significantly different for plant species (df = 2, F = 10.233, P = 0.002; Fig 3.44), deer treatment (df = 1, F = 14.349, P = 0.0002; Fig 3.45), and vegetation structure (df = 2, F = 10.586, P < 0.0001; Fig 3.46). Understory cover was almost four times higher and 25% higher in native plots (20.23 ± 0.89 cm) compared to burning bush (5.75 ± 0.75 cm) and honeysuckle (15.45 ± 0.75 cm) plots respectively. Deer presence lowered vegetation cover (16.14 ± 0.83 cm compared to 16.61 ± 0.76 cm), although this is likely not biologically significant. In subplots with no structure, average cover was

25% higher (20.65 ± 0.09 cm) than that of canopy intact (14.52 ± 0.9 cm) and structure only (13.95 ± 0.09 cm) subplots.

The interaction between plant species and month significantly contributed to understory vegetation cover (df = 4, F = 3.564, P = 0.008; Fig 3.47). For both invasive plant species, cover peaked in June and decreased throughout the season, reaching a minimum in September. At the start of the season, vegetation cover was less than half of the coverage maximum in burning bush plots. However, in honeysuckle plots, coverage in May was similar to levels reached in June. In native plots, vegetation cover started at the overall highest value in May, decreased throughout the growing season, and then increased again in September. Overall, understory vegetation cover was highest in native. Vegetation cover in the non-native plots was significantly lower than native plots: 75% lower in burning bush plots (6.37 ± 1.38 cm) and 25% lower in honeysuckle plots (16.29 ± 1.61 cm).

Although the changes to vegetation cover in deer treatments were not significant, the interaction between plant species and deer treatment was significant (df = 1, F = 10.700, P = 0.001; Fig 3.48). For both native and burning bush plots, cover was higher when deer were excluded. This pattern was reversed for honeysuckle plots. These differences in vegetation cover between deer treatments, regardless of direction, were larger in non-native plots (burning bush – 40%; honeysuckle – 35%) compared to native plots (15%).

Vegetation cover was significantly impacted by each main effect individually, and the interaction between these three variables was also significant (df = 2, F = 3.298, P = 0.039; Fig 3.49). Overall, regardless of plant species or deer presence, the highest vegetation cover was in the no structure vegetation subplots. For all plant species, in plots with deer absent, there was very little difference between the canopy intact and structure only plots. This was also true for burning bush plots were deer were present. In native plots, where deer were present, cover was lowest in structure only subplots, followed by canopy intact. This pattern was reversed for honeysuckle plots with structure only plots supporting higher cover than canopy intact subplots.

Ground Prey

Ground prey abundance differed significantly by sampling month (df = 4, F = 4.903, P = 0.0007; Fig 3.50). Prey abundance was highest in the first two sampling months (May – 14.44 ± 1.36; June – 17.13 ± 1.35) and decreased by half and remained steady for the remainder of the season (July – 7.79 ± 0.59; August – 7.32 ± 0.50; September – 7.08 ± 0.56). Variation in ground prey abundance followed a similar pattern. The range of observed values was highest in May and decreased throughout the season, reaching a slight uptick in September.

The interaction between plant species, deer treatment, and vegetation structure significantly affected ground prey availability (df = 2, F = 3.208, P = 0.041; Fig 3.51). For all plant species, prey availability was lower where deer were present and there was very little difference between prey levels between the vegetation structure subplots, excluding the structure only subplot in honeysuckle, which was approximately 20% higher than the other vegetation structure treatments. In deer absent plots, for the non-native plant species, prey abundance was similar in the canopy intact and structure only subplots but was significantly lower in no structure subplots. Native plots with deer removed saw an incremental decrease in prey availability from canopy intact plots, to no structure, to structure only plots.

Aerial Prey

Aerial prey differed by deer treatment when separated by plant (df = 1, F = 6.522, P = 0.02; Fig 3.52). For non-native plants, the removal of deer from the plots decreased aerial prey abundance. Prey abundance decreased by 30% in honeysuckle plots and by over 45% in burning bush plots. Conversely, aerial prey increased by 37% in native plots when deer were removed.

3.4 DISCUSSION

3.4.1 Environmental Alterations

In this study we sought to explore the environmental and community changes induced by the invasion of burning bush into novel areas compared to the changes caused by honeysuckle, a common and prolific invader. Overall, both invaders altered many environmental characteristics of their novel habitats compared to nearby uninvaded, native dominated sites; however, by most metrics, burning bush had a greater impact than honeysuckle on most variables. It is worth mentioning that burning bush was sampled only from one site while native and honeysuckle plots were sampled at all four sites introducing the possibility that any affect of burning bush is a site effect, not an effect of plant type. However, there were no site differences for either native dominated or honeysuckle dominated plots. Therefore, we would expect that it is equally likely that burning bush would not experience site effects.

Invasive species frequently alter vegetation complexity, although the direction and magnitude of these interactions depends upon the growth for of the invaders (Loomis et al. 2014; Toft et al. 2001). Plots invaded by honeysuckle showed increased branch density, or vegetation complexity, over native dominated sites in accordance with previous studies. Loomis and others in 2014 found that sites invaded by honeysuckle showed twice the vertical vegetation cover than those uninvaded sites, similar to our observed 2.5 fold increase in honeysuckle plots. However, burning bush plots showed an even more dramatic increase in branch density with invaded plots having three times the branch density of native plots. As both honeysuckle and burning bush are introduced, ornamental shrubs, they have dense branches and foliage and seem to grow in the characteristic “mono-culture” pattern of invasive species (Vila et al. 2011) contributing to increased vertical complexity in invaded areas. Burning bush, in fact, has distinct structural differences when compared to a native shrub, spicebush (one of the dominant species of native plots). In a previous study, we determined that the structure of burning bush is markedly shifted toward thinner, shorter, higher order branches while spice bush contains fewer branches overall and these branches are thicker, longer, and of lower order (Roberson, unpublished data).

Despite greater vertical complexity in invaded plots, litter depth was highest in native dominated sites. This is likely not directly associated with greater leaf biomass contributed by natives, as invasive plants have been documented to contribute positively to forest primary production (Vila et al. 2001; Strayer et al. 2006). Rather, decomposition rates are frequently higher for invasive plants when compared to natives (Liao et al. 2008). Low C:N ratio (Arthur et al. 2012), leaf morphology (Yadav et al. 2005), and early colonization of microbial communities (Arthur et al. 2012) have all been implicated as drivers for this pattern in honeysuckle dominated habitats. Similar, yet more dramatic, patterns were observed for burning bush. Increased rate of decomposition can negatively impact forest floor communities. Leaf litter breakdown provides a food source for decomposers. As decomposition of leaves happens before leaf fall for honeysuckle, this could negatively impact the food availability for these groups in invaded sites. Future studies should examine the impact of leaf nutritional value and morphology as well as the contribution of associated microbial activity on foliar decomposition of this invader.

Perhaps the most dramatic environmental change was the decrease in herb-layer vegetation cover in burning bush invaded areas compared to both native and honeysuckle dominated plots. Cover in burning bush dominated plots was one fourth that of native plots and three times lower than the levels observed in honeysuckle plots. The reduction of herb-layer vegetation cover in invaded plots is likely due to either to greater competitive ability of invasive plants for resources or active reduction in native plant performance through invasive plant allelopathy. Honeysuckle has been shown to directly outcompete native plants for resources, whether through the evolutionary increase of competitive ability facilitated by enemy release or novel weapons (Lieurance & Cipollini 2012; Lieurance et al. 2014) or through beneficial physical and demographic traits such as extended leaf phenology, rapid growth rates, high fecundity, and broad phenotypic plasticity (Lieurance 2004; Luken et al. 1995; Trisel 1997; McEwan et al. 2009). Allelopathy also contributes to the competitive dominance of honeysuckle in novel environments (Cipollini et al 2008; Dorning & Cipollini 2006; McEwan et al. 2009). Therefore, as honeysuckle is a highly competitive, allelopathic invader, it is unsurprising that vegetation cover was lower where honeysuckle was dominant compared to native plant dominated habitats. However, our study provides strong evidence that burning bush may have an even greater negative impact on native understory plant communities. Burning bush has the highest branch density of any plant included in this study. High branch density could suggest high leaf density and high competitive ability for light. Although plant architecture may be contributing to the high competitive ability of burning bush, future studies should examine if allelopathy is also contributing to this pattern.

Although native, overabundant white-tailed deer re-engineer forest ecosystems in ways that mimic the impacts of plant invasion (Rooney 2009; Suominen et al. 2013; Rooney & Waller 2003; Weigmann & Waller 2006). In our study, deer increased the impact of invasive plants in most cases. Deer presence further reduced ground cover in both native and burning bush sites in accordance with the literature as deer reduce vegetation cover (Rooney 2009) through intense and selective feeding. However, in honeysuckle sites, the presence of deer resulted in increased ground cover. Past studies on the interaction between honeysuckle and deer show decreases vegetation cover (Peebles-Spencer et al. 2017. Selective feeding by deer can also lead to local biotic homogenization, or the dominance of a few browse-tolerant species in highly impacted areas (Rooney & Waller 2003; Wiegmann & Waller 2006). The increase in vegetation cover in honeysuckle plots where deer were present could be a result of the increased dominance of browse- and invasion- tolerant species. The reduction of vegetation cover in native plots with ambient deer browsing pressure is likely the reason for reduced litter depth in these plots. Although we did not measure deer herbivory directly, the removal of native shrub foliage through browsing likely contributed to reduced leaf fall and therefore litter. We did observe a marginal increase of leaf litter in invasive plant dominated plots with deer present. However, this increase was only 0.1cm at most and likely was not biologically significant.

As deer reduce vegetation cover, change vegetation composition (Rooney 2009), reduce vertical structure (Suominen et al. 2003), homogenize forest environments (Rooney & Waller 2003; Wiegmann & Waller 2006), and alter microclimates, it logically follows that arthropod communities would be affected. In our study, the presence of deer reduced ground prey regardless of the dominant plant, however, the effects were largest in native plots. Deer reduced vegetation cover and litter depth in these plots, leading to less food and/or habitat for associated ground arthropods. Deer presence resulted in opposite responses of aerial prey abundance for native and non-native plants. In native dominated plots, deer presence reduced aerial prey availability. As deer are more likely browsing on native vegetation than invasive foliage in these plots is likely lower leading to reduced food and/or habitat for native shrub-dwelling arthropods. Conversely, deer presence led to increased aerial prey in invasive dominated plots. Arthropod herbivores do not rely heavily on honeysuckle (Lieurance & Cipollini 2012; Lieurance et al. 2014) or burning bush (Roberson, chapter 2) as food sources, but could use these plants as habitat or for protection. As these species have greater branch density than natives and this is not altered by deer presence, and deer attract flying insects, aerial prey abundance is highest in invasive plots with deer present.

Deer overabundance and non-native plant invasion both have large impacts on native forest characteristics. In this study, we sought to examine how plant structure contributes to and mitigates the negative impacts of these drivers of environmental change. Unsurprisingly, branch density was highest in plots with the canopy left intact, followed by the structure only plots, and then the no structure plots regardless of dominant plant or deer presence as the maintenance of living foliage lead to greater branch density. Herb-layer ground cover, however, was highest in no structure plots. This suggests that the removal of shrubs leads increases available resources for herb layer plants, leading to greater growth. Interestingly, canopy intact and structure only plots resulted in similar levels of vegetation cover, likely through different mechanisms. Canopy intact plots support low levels of herb-layer vegetation likely as a result of low resource availability. The living shrubs compete strongly for resources and shade the understory resulting in slow growth and development of herb-layer vegetation. The structure only plots may still block some light, retarding the growth of understory vegetation. Additionally, honeysuckle is known to be allelopathic (Trisel 1997; Dorning and Cipollini 2006; Cipollini et al. 2008) and thus standing dead stems could continue to leach allelochemicals until they decompose completely, reducing herb layer success. Contrary to previous studies (Gorchov and Trisel 2003; Cipollini et al. 2009), basal application and maintenance of standing dead mass did not confer protection from deer for herb-layer vegetation, as vegetation cover was higher in no structure plots than structure only plots. Future studies should examine the invasion status of vegetation cover as deer may be removing native species and facilitating the invasion of non-natives. It is possible that deer pressure was particularly high in our study sites so intense browsing negated any small protection provided by vegetation structure. The honeysuckle sites were all on either university or park district owned land, which does not allow hunting. This results in high deer densities (Nickell 2004). Conversely, the burning bush sites were on a small parcel of state-owned, hunting allowed land. However, this land is surrounded by thousands of acres of land with no hunting allowed. Therefore, any reduction in deer presence at these sites is likely negated by the abundance of hunting-free land surrounding the property. Vegetation structure strategy also significantly impacted ground prey availability. Ground prey abundance was lowest in no structure plots, especially for non-native plants. Although herb-layer vegetation cover is high in these plots, this community could be dominated by non-natives resulting in low food availability for herbivorous, ground-dwelling prey. Removal of invasive plants frequently leads to an increase in abundance and richness of other invaders in managed sites (Loh and Daehler 2007; McConnell et al. 2005; Runkle et al. 2007).

3.4.2 Arthropods

Since invasive plant identity, vegetation structure and white-tailed deer all alter environments, we sought to explore how these factors contribute to changes in arthropod communities. Invasive plants can impact arthropod communities through the alteration of any of the local or regional processes that influence community dynamics. However, most of these alterations have been attributed to a few large ecosystem changes that invasives create including reduced native plant diversity, plant structural changes, and alteration of the soil microclimate. Arthropod abundance and richness (total, ground, and aerial) was the highest in “undisturbed”, native, canopy intact, deer removed sites, which are most representative of the historical state of these environments. Both the presence of invasive woody shrubs (Hanula & Horn 2011a, b; Lindsay & French 2006; Ulyshen et al. 2010) and white-tailed deer have been implicated in decreased diversity, richness, or abundance of and altered community composition of insects (Suominen et al. 2013; Harris et al. 2004). Increased dominance by invasive plants and deer frequently results in a decrease of native plant diversity (Vila et al. 2011) and an overall alteration of vegetation composition. This can have large impacts on arthropod composition because many herbivorous species are oligophagus (Bernays & Graham 1988). In our study, alteration of plant dominance and deer browsing lead to distinct changes in the structure of the vegetation (increased branch density in honeysuckle and burning bush plots respectively; Loomis et al. 2014) and percent vegetation cover (highest in native, followed by honeysuckle, and then burning bush; reduced or unaffected in deer present plots; Toft et al. 2001). Increased dominance by invasive plants frequently results in a decrease of native plant diversity (Vila et al. 2011) leading to large negative impacts on arthropod composition, as arthropod diversity is strongly positively associated with plant species richness (Siemann et al. 1998; Haddad et al. 2001). As native plots supported higher levels of vegetation cover, these plots supported higher abundance and richness of arthropods due to increased food for herbivores. Reduced cover in honeysuckle plots was correlated with reduced abundance and richness of arthropods. Loomis and Cameron (2014) also showed this effect for honeysuckle, and this trend for invasives in generally is highly supported (Campbell et al. 2007; Hanula and Horn 2011). Burning bush dominated sites showed even lower levels of vegetation cover and arthropod abundance likely through its increased impacts on the physical and biotic environment. Through selective feeding, deer also reduce vegetation cover, change vegetation composition (Rooney 2009), reduce vertical structure (Suominen et al. 2003), and homogenize forest environments (Rooney & Waller 2003; Wiegmann & Waller 2006). Arthropod abundance and richness was further decreased in plots dominated natives, honeysuckle, and burning bush likely due to alterations in native plant cover leading to reductions in food availability (Baines et al. 1994), vegetation structure (Miyashita et al. 2004), and habitat (Allombert et al. 2005; Suominen et al 2003). Total arthropod community composition also differed between all three dominant plant types, with native plots tightly clustered, and burning bush plots most dissimilar to native plots. The largest differences between native and burning bush plots were the relative contribution of the Hymenoptera and Orthoptera orders. Burning bush plots favored these orders while native plots supported more even communities. Both Hymenoptera and Orthoptera are highly mobile orders of arthropods (Marshall 2006; Triplehorn & Johnson 2005). It is possible that these orders traverse through burning bush dominant areas without necessarily residing in these plots, increasing their relative contribution to the overall observed community composition of arthropods.

Changes in vegetation cover and composition may indirectly impact arthropods through changes in the microclimate, to which arthropods are very sensitive (Stewart 2001). This can include changes in light intensity, temperature, soil moisture, soil nutrients, salinity, pH, and the amount of leaf litter (Wolkovich et al. 2009; Gratton & Denno 2005). Leaf litter and nutrient changes, in particular, may alter detritivore assemblages, as they rely heavily on the quality of leaf litter (Talley et al. 2012). Native plots contained the highest level of leaf litter, adding habitat and food for detritivores, potentially resulting in the overall increase in total arthropods. Invasive plants have been shown to contribute favorably to detritivore abundance through microclimate changes and increased leaf litter (Longcore 2003; Levin et al. 2006). However, honeysuckle and burning bush both showed reduced leaf litter compared to native sites and supported lower abundance and richness of ground-dwelling arthropods. It is possible that the leaf litter produced by these species may negatively impact this group, as they are known to be high in or harbor novel secondary metabolites (Cipollini et al. 2008; Lieurance & Cipollini 2015; Roberson chapter 2) and in the case of honeysuckle, allelochemicals (Motard et al. 2015). The community composition of ground-dwelling arthropods differed between native, honeysuckle, and burning bush plots, although the largest difference was between native and burning bush sites. As previously discussed, hymenopterans and orthopterans contributed more highly to the community composition of burning bush plots. Collembolans were also more common in burning bush plots by a factor of two. This order of hexapoda is omnivorous and while they do not directly decompose leaf material, they contribute to this process through shredding (Triplehorn & Johnson 2006; Marshall 2006). The high abundance and dominance of this order in burning bush plots could be contributing to the low leaf litter observed. Additionally, this order flourishes in moist environments. Although we did not measure soil moisture, as burning bush plots supported the lowest level of ground cover, it is possible that these plots were moist, due to the reduced uptake of water by plants. Arthropod biomass, both total and ground-dwelling, was greater in native sites without deer. This was also true for non-native sites, but deer exclusion had a smaller impact on biomass. Overall, deer presence reduced litter depth, ground cover, ground, and aerial prey therefore plots without deer provided more food for decomposers and more habitat for ground dwellers. Aerial prey availability was higher where deer were present resulting in more food for aerial spiders or other shrub-dwelling predators. Deer did not affect ground-dwelling arthropods in honeysuckle-dominated plots, but deer presence increased ground cover in these plots. In these sites, increased habitat and/or food could reduce the effect of reduced prey availability on arthropod biomass. Future studies should examine in more detail the abiotic alterations of microclimate caused by plant and deer invasion to further elicit the causal impacts on arthropod communities.

Vegetation structure altered arthropod communities. When deer were removed, abundance and richness was highest in canopy intact plots regardless of plant type. In native dominated plots, arthropod abundance was higher in no structure plots than in structure only plots. No structure plots supported higher ground cover. In native plots, this is more likely to be native ground cover, leading to beneficial habitat, microclimate and food for native herbivorous arthropods, outweighing the negative impacts of the loss of branch density (less habitat). For non-natives, abundance decreased in structure only plots and further in no structure plots likely due to a sequential reduction of resources in these plot types: branch density (habitat), prey (food), and ground cover (food, habitat, microclimate). Although ground cover was highest in no structure plots, it is likely that this high ground cover is dominated by invasive species as invasives can facilitate the invasion of other nonnatives (Loh and Daehler 2007; McConnell et al. 2005; Runkle et al. 2007). Aerial arthropod community composition differed between dominant plant types. Opiliones and dipterans contributed highly to this pattern. Opiliones and dipterans were both more abundant in burning bush and honeysuckle plots compared to native plots. These groups likely rely more on vegetation structure for habitat for than foliage for food. These groups are also highly mobile and can therefore reside in areas of high coverage for habitat or protection and travel for food as required. As burning bush and honeysuckle had significantly higher branch density compared to native plots, it follows that Opiliones and dipterans would be more successful in these plots. Regardless, as arthropod abundance was higher in structure only plots than no structure plots in sites dominated by invasives, basal application of herbicide and the maintenance of standing dead woody vegetation is a good choice for management when deer are also excluded.

After deer exclusion, recovery happened incredibly fast – effects of the release from deer pressure began to emerge as early as 8 months after the installation of exclosures. However, deer exclusion is expensive and difficult on a large scale. When deer were present, total arthropod abundance and richness were similar when compared across all plant types, but differed between vegetation structure plots. When deer herbivory is present, foliage in the canopy intact plots could have highly expressed secondary defense metabolites as herbivory induced the production of these compounds (Motard et al. 2015). This foliage could act as a detrimental resource, reducing food quality, negating the positive impact of high resource native plots, and therefore reducing herbivorous arthropod abundance. Arthropod abundance and richness, although not different between plant types, did differ between vegetation structure strategy plots (highest in structure only, followed by no structure and canopy intact). Similar to the "intermediate disturbance hypothesis", structure only plots showed moderate levels of branch density, ground cover, and prey availability, when deer were present, suggesting these vegetation structure plots could represent a "sweet spot" of habitat characteristics leading to the highest abundance and richness of arthropods. Therefore, in terms of management, spraying and leaving standing dead mass could be a good choice, if deer exclusion is not an option (costly and not realistic over large spatial scales).

3.4.3 Beetles

Overall abundance and richness patterns of beetles were similar to total arthropods. This is unsurprising as beetles encompass all feeding guilds and trophic levels, thrive in both the ground and aerial environment and mimic overall arthropod community structure (Triplehorn & Johnson 2005; Evans 2014). The effect of deer on beetles in native plots was even more severe than for total arthropods. In these plots, deer reduced leaf litter, ground cover, and ground prey. Beetles rely heavily on these facets of the environment for food and shelter. Interestingly, deer presence resulted in higher biomass of beetles. This result is not rare in the literature, which implicates reduced leaf litter and ground cover caused by deer as drivers of this change. Reduced ground barriers lead to easier movement for ground beetles (Allombert et al. 2005; Suominen et al 2003). The ground beetle community composition differed between dominant plant types, although the overall composition of the community was dominated by three beetle families (Carabidae, Staphylinidae, Curculionidae, and Silphidae), regardless of the dominant plant type. Carabids were most abundant in honeysuckle plots. As these plots have the median amount of leaf litter and vegetation cover, it is possible that this provides a favorable microclimate while reducing barriers to movement, two factors important for Carabid success (Allombert et al. 2005; Suominen et al 2003). Silphids were 3.5 times and 7.5 times more abundant in native plots compared to burning bush plots and honeysuckle plots respectively. Silphids, or carrion beetles, feed primarily on carrion (including invertebrates), fungi, and dung (Evans 2014). It is possible that native plots support a higher abundance of non-arthropod animals (not sampled in this study). Invasive plants reduce animal diversity, abundance, growth, and fitness (Vila et al. 2011).

Honeysuckle, specifically, has been shown to support a lower abundance of birds (Gardner et al. 2017). The reduced success of animals in invaded areas could explain the low abundance of Silphidae, as potential food sources are reduced in invaded plots. Future studies should more closely examine the species-specific impacts of plant invasion and deer overabundance on beetle diversity, as we only examined abundance and family richness.

3.4.4 Spiders

Unlike overall arthropods and beetles, plant invasion, deer, or vegetation structure did not impact spider abundance, although alterations in richness were observed. Spiders are highly dependent on vegetation structure (Uetz 1991; Langellotto & Denno 2004) and richness has been shown to increase with increasing vegetation volume and density (Loomis et al. 2014; Heikkinen & MacMahon 2004). Increased vegetation structure was implicated as the driver of high spider abundance on honeysuckle compared to native plants (Loomis et al. 2014). Although we did not observe differences in abundance between any main or subplot effects, spider richness differed between vegetation structure plots strategies. Richness was highest in canopy intact plots, followed by structure only plots, then by no structure plots following the sequential decrease of vegetation structure in these plots suggesting that branch density is a driver of spider richness. Prey availability may also contribute to these results as canopy intact and structure only plots had higher prey than no structure plots. Although abundance and richness did not differ between plant types, community composition was significantly different. This is in line with previous research that found that spider composition responds significantly to alterations in vegetation (Uetz 1991; Langellotto & Denno 2004; Hatley & MacMahon 1980). Environmental characteristics were significantly different between native, honeysuckle, and burning bush plots. As spiders are sensitive to a variety of vegetation characteristics (height, density, volume, microclimate), it is likely that spider community composition is responding to these changes. The largest difference in community composition between plant types was the abundance of Tetragnathidae (more abundant in burning bush plots). Tetragnathidae are horizontal orb-weaving spiders. They frequently build their webs across gaps in vegetation, or high in vegetation where gaps are usually larger. Branch density was lowest in native plots as was the overall density of vegetation (personal observation). It is possible that these gaps were too large for the successful construction of Tetragnathidae webs. Additionally, the average height of burning bush is higher than that of spicebush, paw-paw, and sugar maple in our plots. As these spiders build their webs high in vegetation, native plot vegetation structure may not have been conducive to web construction. Future studies should further investigate the structure of these shrubs and their contribution to alterations in spider composition. Aerial spider biomass was highest in structure only plots. The reduced branch density in these plots likely allows spiders to create larger webs and the high aerial prey availability contributes to the maintenance of high body mass. As structure only plots still supported a high richness of large spiders, basal application and the leaving of dead mass intact may be a good management strategy to simultaneously remove invading plants while maintaining spider richness and size.

Ground spiders responded similarly to plant invasion as total and aerial spiders. Family richness was highest in native plots, which corresponded to the highest ground cover, prey, and leaf litter. This could suggest that these sites had more habitats, food, and a more favorable microclimate. Higher availability of resources could mean more niches, and greater diversity of spiders. This is supported as the available resources in honeysuckle and burning bush dominated sites declined, so did ground spider richness. Ground spider community composition differed between dominant plant types. Regardless of plant type, the spider composition was heavily dominated by Lycosidae (wolf spiders). The relative contribution of Theridiidae, Linyphiidae, and Thomisidae did differ between plant types. Theridiidae and Linyphiidae were more abundant in burning bush plots compared to native plots. These families contain small cob or sheet web-building spiders. These webs require many attachment points for construction. As burning bush plots contain less ground cover and leaf litter, it is possible that this environment allows for more effective construction of small webs built over leaf litter (Bradley 2012, Ubick et al. 2005). Thomisids were also more abundant in burning bush plots compared to either honeysuckle or native plots. The two most prevalent genera of Thomisids observed in this study (*Xysticus* and *Ozyptila*) are ambush predators that wander over open ground, rarely found on plants (Ubick et al. 2005). As burning bush plots contained, by far, the lowest level of vegetation cover, it follows that Thomisids would be most abundant in these areas.

Ground spider biomass varied between vegetation structure plots, suggesting that ground cover was highly important for determining spider size. Biomass was highest in no structure plots where ground cover was highest but supported the lowest prey availability. These plots are likely supporting fewer, larger individuals as these plots have plentiful habitat. Although no structure plots supported the lowest prey, ground spiders are frequently extremely mobile (Bradey 2012). These individuals are able to travel easily to other sites to find prey. Both structure only and canopy intact plots had smaller ground spiders than no structure plots, however, canopy intact plots supported the smallest spiders. These plots types supported similarly low ground cover and prey availability. It is possible that the intact canopy could negatively alter the microclimate (increased shade and humidity, lower temperature) for ground spiders. Live shrubs could also be leaching defense compounds into the soil in an allelopathic manner, reducing soil conditions for ground dwelling spiders (Trisel 1997; Dorning and Cipollini 2006; Cipollini et al. 2008). Regardless, use of basal spraying as a management technique, would simultaneously control invasive plants while maintaining ground spider biomass.

Plant invasion significantly altered multiple facets of novel ecosystems including vegetation structure, herb-layer vegetation cover, and litter depth. Although honeysuckle is a well-known and destructive invader, most habitat alterations were even more severe in burning bush invaded sites. The introduction of white-tailed deer into these interactions more often than not, further intensified these alterations. However, invasive plant management, especially the implementation of basal application of herbicide, was able to significantly mitigate some negative implications of plant invasion on the physical environment while preserving arthropod communities. Future studies need to examine the abiotic environmental characteristics altered by plant invasion to further understand the mechanisms behind community change.

3.5 REFERENCES

Adams, J.M., Fang, W., Callaway, R.M., Cipollini, D., Newell, E. 2009. A cross-continental test of enemy release hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its Europe. Biological Invasions 11:1105-1016.

Allombert, S., Stockton, S., Martin, J.L., 2005. A natural experiment on the impact of overabundant deer on forest invertebrates. Conservation Biology. 19(6): 1917-1929.

Arthur, MA., Bray, SR., Kuchle, CH., McEwan, RW. 2012. The influence of the invasive shrub, Lonicera maackii, of leaf decomposition and microbial community dynamics. Plant Ecology 213(10): 1571-1582.

Baines, D., Sage, R.B., Baines, M.M., 1994. The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. Journal of Applied Ecology. 31 (4): 776-783.

Bartuszevige, A.M., Gorchov, D.L. 2006. Avian seed dispersal of an invasive shrub. Biological Invasions 8: 1013-1022.

Bernays, E., Graham, M. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69: 886-892.

Blossey, B., Notzold, R. 1995. Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. Journal of Ecology 83: 887-89.

Bradley, RA. 2012. Common Spiders of North America. University of California Press, Las Angeles.

Brand, H., Lubell, J.D., Lehrer, J.M. 2012. Fecundity of winged Euonymus cultivars and their ability to invade various natural environments. HortScience 47(8): 1029-1033.

Bressette, J.W., Beck, H., Beauchamp, V.B., 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. Oikos. 121: 1749-1760.

Callaway, M., Ridenour, W.M. 2004. Novel Weapons: Invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2(8): 436-443.

Campbell J, Hanula JL, Waldrop TA (2007) Effects of pre- scribed fire and fire surrogates on floral visiting insects of the Blue Ridge province of North Carolina. Biol Conserv 134:393–404

Ciola, V., Cipollini, D. 2011. Distribution and host range of a powdery mildew fungus infecting garlic mustard, *Alliaria petiolata*, in Southwestern Ohio. American Midland Naturalist 166:40-52.

Cipollini, D., Stevenson, R., Enright, S., Eyles, A., Bonello, P. 2008. Phenolic metabolites in leaves of the invasive shrub, *Lonicera maackii*, and their potential phytotoxic and anti-herbivore effects. Journal of Chemical Ecology 34: 188-193.

Cipollini, K., Ames, E., Cipollini, D. 2009. Amur honeysuckle (*Lonicera maackii*) management method impacts restoration of understory plants in the presence of white-tailed deer (*Odocoileus virginianus*). Invasive Plant Science and Management 2: 45-54.

Collier, M.H., Vankat, J.L., Hughes, M.R. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. American Midland Naturalist 147: 60-71.

Conley AK, Watling JI, Orrock JL (2011) Invasive plant alters ability to predict disease vector distribution. Ecol Appl 21:329–334

CNPS. 2004. Vegetation rapid assessment protocol. https://cnps.org/cnps/vegetation/pdf/rapid_assessment_protocol.pdf

Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the roles of ecosystem engineers. OIKOS 97(2): 153-166.

Davidson, A.M., Jennions, M., Nicotra, A.B. 2011. Do invasive species show high phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14:419-431.

Davis, S., Cipollini, D. 2014. Do mothers always know best? Oviposition mistakes and resulting larval failure of Pieris virginiensis on Allaria petolata, a novel, toxic host. Biological Invasions, 16(9): 1941-1950.

Dirr, M. A. 1998. Manual of Woody Landscape Plants. Their Identification, Ornamental Characteristics, Culture, propagation and Uses. Stipes Publishing, Champaign, Illinois.

Dirr, M.A. 2001. Winged euonymus is a stalwart shrub for consistent fall color. Nursery Management and Production. 17:16-17, 91-95.

Doorduin, L.J., Vrieling, K. 2011. A review of the phytochemical support for the shifting defense hypothesis. Phytochemical Review 10(1): 99-106.

Dorning, M., Cipollini, D. 2006. Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of thee herbs with no autotoxic effects. Plant Ecology 184: 287-296.

Drenovsky, R.E., Grewell, B.J., D'Antonio, C.M.D., Funk, J.L., James, J.J., Molinari, N., Parker, I.M., Richards, C.L. 2012. A functional trait perspective on plant invasion. Annals of Botany 110: 141-153.

Ehrlich, P.R., Raven, P.H. 1964. Butterflies and plants: a study in coevolution. Evolution.

18:586-608.

Evans, AV. 2014. Beetles of Eastern North America. Princeton University Press. Princeton, United States.

Fryer, Janet L. 2009. Euonymus alatus. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2015, October 29].

Gardner, AM., Muturi, EJ., Leah, D. 2017. Large-scale removal of invasive honeysuckle decreases mosquito and avian host abundance. ECOHealth 14(4): 750-761

Gioria, M., Osborne, B.A. 2014. Resource competition in plant invasions: emerging patterns and research needs. Frontiers in Plant Science 5(501): 1-21.

Gorchov, D.L., Trisel, D.E. 2003. Competitive effects of the invasive shrub, *Lonicera maackii*, on the growth and survival of native seedlings. Plant Ecology 166: 13-24.

Gorchov, D.L. 2013. White-tailed deer (*Odocoileus virginianus*) disperse seeds of the invasive shrub, Amur honeysuckle (*Lonicera maackii*). Natural Areas Journal 33: 78-80.

Gordon, S.W. 1976. Population studies of the fall webworm in Ohio with development of life tables in relation to temperature. (Masters dissertation, Ohio State University).

Gratton, C., Denno, R.F. 2005. Restoring of arthropod assemblages in Spartina salt marsh following the removal of the invasive plant species *Phragmites australis*. Restoration Ecology 13: 358-372.

Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M., Knips, J.M.H. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. American Naturalist 158: 17-35.

Hanula JL, Horn S (2011) Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. For Ecol Manag 262:674–680

Hanula JL, Horn S (2011) Removing an invasive shrub (Chi- nese privet) increases native bee diversity and abundance in riparian forests of the southeastern United States. Insect Conserv Divers 4:275–283

Harris RJ, Toft RJ, Dugdale JS, Williams PA, Rees JS (2004) Insect assemblages in a native (kanuka—Kunzea ericoides) and an invasive (gorse—Ulex europaeus) shrubland. N Z J Ecol 28:35–47

Hartman, K.M., McCarthy, B.C. 2007. A dendro-ecological study of forest overstory productivity following the invasion of the non-indigenous shrub, *Lonicera maackii*. Applied Vegetation Science 10:3-14.

Hatley, CL., MacMahon. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. Environmental Entomology 9: 632-639

Heikkinen, MW., MacMahon, JA. 2004. Assemblages of spiders on models of semi-arid shrubs. Journal of Arachnology 32: 313-323

Hottes, Frederick, & Theodore Frison (1931) "The plant lice, or Aphiidae, of Illinois." Bulletin of theIllinois Natural History Survey, 19(3), pp. 123-448.

Huenneke, LF. 1997. Outlook for plant invasions: Interactions with other agents of global change. Assessment and management of plant invasions. New York, NY. USA: Springer-Verlag, 95-1-3.

Kalisz, S., Spigler, R.B., Horvitz, C.C. In a long-term experimental demography study: excluding ungulates reversed invader's explosive population growth and restored natives. Proceedings of the National Academy of Sciences 111(12): 4501-4506.

Keane, R.M., Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. Trends on Ecology and Evolution. 17: 164-170.

Knight, Harry H. (1941) "Plant bugs, or Miridae, of Illinois." Bulletin of the Illinois Natural HistorySurvey, 22(1), pp. 1-234.

Langellotto, GA., Denno, RF. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139: 1-10.

Lankau, R.A., Rogers, W.E., Siemann, E. 2004. Constraints on the utilization of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. Ecological Entomology 29: 66-75.

Levin, L., Neira, A.C., Grosholz, E.D. 2006. Invasive cordgrass modifies wetland trophic function. Ecology 87: 419-432.

Lieurance, D. 2004. Leaf phenology, fecundity, and biomass allocation of the invasive shrub *Lonicera maackii* (rupr.) maxin in contrasting light environments. Masters thesis, Ohio University

Lieurance, D., Chakraborty, S., Whitehead, S.R., Powell, J.R., Bonello, P., Bowers, M.D., Cipollini, D. 2015. Comparative herbivory rates and secondary metabolite profiles in the leaves of native and non-native *Lonicera.* Journal of Chemical Ecology 41:1069-1079.

Lieurance, D., Cipollini, D. 2012. Damange levels from arthropod herbivores on *Lonicera maackii* suggest enemy release in its introduced range. Biological Invasions 14: 863-873.

Lieurance, D., Cipollini, D. 2013a. Environmental influences on growth and defense responses of the invasive shrub, *Lonicera maackii*, to simulated and real herbivory in the juvenile stage. Annals of Botany 112:741-749.

Lieurance, D., Cipollini, D. 2013b. Exotic *Lonicera* species both escape and resist specialist and generalist herbivores in the introduced range in North America. Biological Invasions 15: 1713-1724.

Lindsay EA, French K (2006) The impact of the weed Chry- santhemoides monilifera ssp. rotundata on coastal leaf litter invertebrates. Biol Invasions 8:177–192

Litt, A.R., Cord, E.E., Fulbright, T.E., Schuster, G.L. 2014. Effects of invasive plants on arthropods. Conservation Biology 28(6): 1532-1549.

Loh, R. K. and C. C. Daehler. 2007. Influence of invasive tree kill rates on native and invasive plant establishment in a Hawaiian forest. Rest. Ecol. 15:199-211.

Longcore, T. 203. Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub (California, USA). Restoration Ecology 11: 397-409.

Loomis, J.D., Cameron, G.N. 2014. Impact of the invasive shrub Amur honeysuckle (*Lonicera maackii*) on shrub-layer insects in a deciduous forest in the eastern United States. Biological Invasions 16:89-100

Loomis, J.D., Cameron, G.N., Uetz, G.W. 2014. Impact of the invasive shrub *Lonicera maackii* on shrub-dwelling Araneae in a deciduous forest in eastern North America. American Midland Naturalist 171: 204-218.

Luken, JO. Thieret, JW. 1996. Amur honeysuckle, its fall from grace. Bioscience 46:18-24.

Luken, J.O., Tholemeier, T.C., Kuddes, L.M. 1995. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* in contrasting light environments. Canadian Journal of Botany 73: 1953-1961.

Luken, J.O., Kuddes, L.M., Tholemeier, T.C., Haller, D.M. 1997. Compatative responses of *Lonicera maackii* and *Lindera benzoin* to increased light. American Midland Naturalist 138:331-343.

Mack, RN. 2000. Cultivation fosters plant neutralization by reducing environmental stochasticity. Biological Invasions 2: 111-122

Mack, RN., Lonsdale, WM. 2001. Humans as global plant dispersers: Getting more than we bargained for. Bioscience 51: 95-102

McConnell, A.L., A. M. Monteer, H. R. Owen, and B. L. Todd. 2005. Influence of stem cutting and glyphosate treatment on *Lonicera maackii*, an exotic and invasive species, on stem regrowth and native species richness. Trans. Ill. State Acad. Sci. 98:1-17.

McEwan, RW., Birchfield, MK., Schoergendorfer, A., Arthur, MA. 2009. Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. Journals Torrey Botanical Society 136: 212-220

McKinney AM, Goodell K (2010) Shading by invasive shrub reduces seed production and pollinator services in a native herb. Biol Invasions 12:2751–2763

Miller, K.E. and D. L. Gorchov, D.L. 2004. The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139:359-375.

Miyashita, T., Takada, M., Shimazaki, A., 2004. Indirect effects of herbivory by deer reduce abundance and species richness of web spiders. Ecoscience. 11(1): 74-79.

Motard, E., Dusz, S., Geslin, B., Akpa-Vinceslas, M., Hignard, C., Babiar, O., Clair-

Maczulajtys, D., Michel-Salzat, A., 2015. How invasion by *Ailanthus altissima* transforms soil and litter communities in a temperate forest ecosystem. Biological Invasions 17: 1817-1832.

OIPC. 2008. Ohio Invasive Plant Assessment Protocol. http://www.oipc.info/uploads/5/8/6/5/58652481/ohio_invasive_plant_assessment_final2013.pdf

Peebles-Spencer, JR., Grochov, DL., Crist, TO. 2017. Effects of an invasive shrub, Lonicera maackii, and a generalist herbivore, white-tailed deer, on forest floor plant community composition. Forest Ecology and Evolution 402: 204-212.

Reichard, S.H., Hamilton, C.W. Predicting invasions of woody plants introduced into North America. Conservation Biology 11(1): 193-203.

Roberson, E.J., Chips, M.J., Carson, W.P., Rooney, T.P. 2016. Deer herbivory reduces web-building spider abundance by simplifying forest vegetation structure. PeerJ 4:e2538; DOI 10.7717/peerj.2538

Rogerson, H. 1912. Chemical examination of the bark of Euonymus atropurpureus. Journal of the Chemical Society, Transactions. 101: 1040-1052.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management. 181: 165-176.

Rooney, T.P., 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology. 202:103-111.

Runkle, J.R., A. DiSalvo, Y. Graham-Gibson, and M. Dorning. 2007. Vegetation release eight years after removal of *Lonicera maackii* in West-Central Ohio. Ohio J. Sci. 105:125-129.

Schaffner, U., Ridenour, W.M., Wolf, V.C., Bassett, T., Muller, C., Muller-Scharer, H., Sutherland, S., Lortie, C.J., Callaway, R.M. 2011. Plant invasions, generalist herbivores, and novel defense weapons. Ecology 92: 829-835.

Sharp, B.R., Whittaker, R.J. 2003. The irreverable cattle-driven transformation of a seasonally flooded Australian savanna. Journal of Biogeography 30: 783-802.

Siemann, E., Tilman, D., Haarstad, J., Ritchie, M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. The American Naturalist 152: 738-750.

Sikes, K.G., Evens, J.M. 2014. Plant community characterization and ranking of fens in the Lake Tahoe Basin, California and Nevada. California Fish and Game 100(1): 114-137.

Stewart, A.J.A., 2001. The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. Forestry. 74(3): 259-270.

Stireman, J.O. III, Devlin, H., Doyle, A.L. 2014. Habitat fragmentation, tree diversity, and plant invasion interact to structure forest caterpillar communities. Oecologia. 176: 207-224.

Strayer, D.L., Eviner, V.T., Jeschke, J.M., Pace, M.L. 2006. Understanding the long-term effects of species invasions. TRENDS in Ecology and Evolution 21(11): 645-651.

Sultan, S.E. 2001. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. Ecology 82: 328-343.

Suominen, O., Niemela, J., Martikainen, P., Kojola, I., 2003. Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. Ecography. 26: 503-513.

Tallamy, D.W. 2004. Do alien plant species reduce insect biomass? Conservation

Biology 18: 1689-1692.

Talley, T.S., Nguyen, K.C., Nguyen, A. 2012. Testing the effects of an introduced palm on a riparian invertebrate community in southern California. PLoS ONE 7(8): e42460.

Theoharides, K.A., Dukes, J.S. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist 176: 256-273

Thomas PA, El-Barghathi M, Polwart A. 2011. Biological Flora of the British Isles. J Ecol 99:345-365. doi: 10.1111/j.1365-2745.2010.01760.x

Tiley, G.E.D., Dodd, F.S., Wade, P.M. 1996. *Heracleum mantegazzianum* Sommier and Levier. Biological flora of the British Isles. Journal of Ecology 84: 297-319.

Toft, R.J., Harris, R.J., Williams, P.A. 2001. Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand. Biological Conservation 102: 31-46.

Triplehorn, CA., Johnson, NF. Introduction to the Study of Insects. Thomson Brooks/Cole. United States of America.

Trisel, D.E. 1997. The invasive shrub *Lonicera maackii*: factors contributing to its success and its effect on native species. PhD Thesis, Miami University, Oxford, OH.

Ubick, D., Paquin, P., Cushing, PE., Roth, V. (eds) 2005. Spiders of North America: an identification manual. American Arachnological Society, Keene (New Hampshire)

Uetz, GW. 1991. Habitat structure and spider foraging, p. 325-348. Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London

Ulyshen MD, Horn S, Hanula JL (2010) Response of beetles (Coleoptera) at three heights to the experimental removal of an invasive shrub, Chinese privet (Ligustrum sinense), from floodplain forests. Biol Invasions 12:1573–1579

USDA, Natural Resources Conservation Service. Invasive Plant Database. http://plants.usda.gov/core/profile?symbol=LOMA6

Vellend, M. 2010. Conceptual synthesis in community ecology. Quarterly Review of Biology 85: 183-206.

Vila, M., Espinar, J.L., Hajda, M., Hulma, P.E., Jarosek, V., Maron, J.L., Pergl, J., Sun, Y., Pysek, P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities, and ecosystems. Ecology Letters 14: 702-708.

Vitousek, P.M. 1990. Biological invasions and ecosystem properties: towards an integration of population biology and ecosystem studies. OIKOS 57: 7-13.

Vitousek, P.M., D'Antionio, C.M., Loope, L.L., Westbrooks, R. 1996. Biological invasions as global environmental change. American Scientist 84: 469.478.

Wagner, D.L., Van Driesche, R.G. 2010. Threats posed to rare or endangered insects by invasions of nonnative species. Annual Review of Entomology 55: 547-568.

Webster, C.R., Jenkins, M.A., Rock, J.H. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation 125: 297-307.

Wiegmann, S.M., Waller, D.M., 2006. Fifty years of change in northern upland forest understories: Identity and traits of "winner" and "loser" plant species. Biological Conservation. 129: 109-123.

Williamson, M.H., Fritter, A. 1996. The varying success of invaders. Ecology 77, 1661-

66.

Wolkovich, E., Bolger, M., Holway, D.T. 2009. Complex responses to invasive grass litter by ground arthropods in a Mediterranean scrub ecosystem. Oecologia 161(4): 697-708.

Yadav RKP, Karamanoli K, Vokou D (2005) Bacterial coloni- zation of the phyllosphere of mediterranean perennial species as influenced by leaf structural and chemical fea- tures. Microb Ecol 50(2): 185

Zhau-hui, Y., Zhu-zhen, Z., Xian-qing, H., et al. 2013. Chemical constituents of Euonymus alatus. Chemistry of Natural Compounds. 49(2): 340-342.

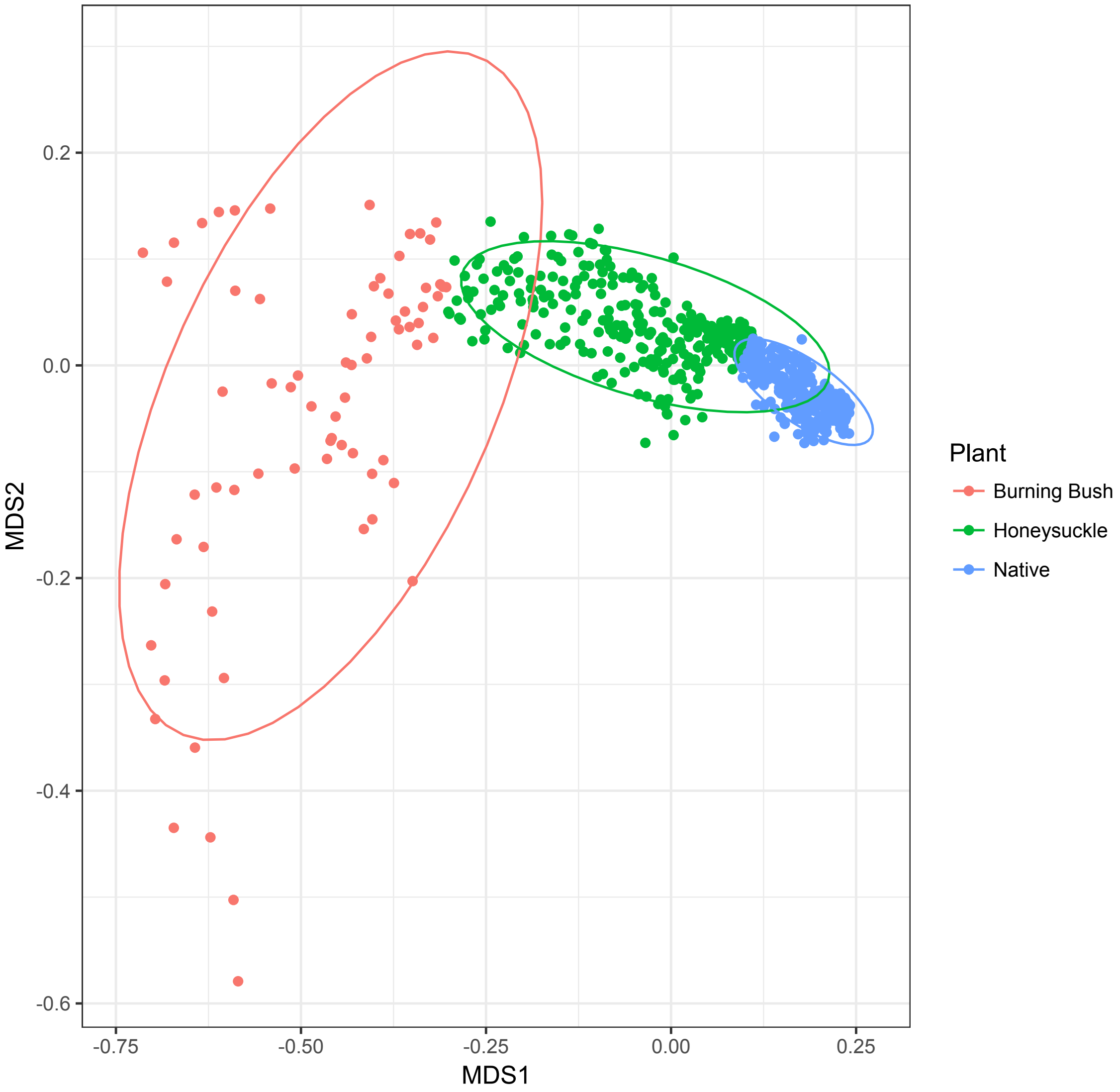

Fig 3.2: ANOSIM of arthropod orders in each dominant plant plot; abundance of each order was averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year; visualized using NMDS

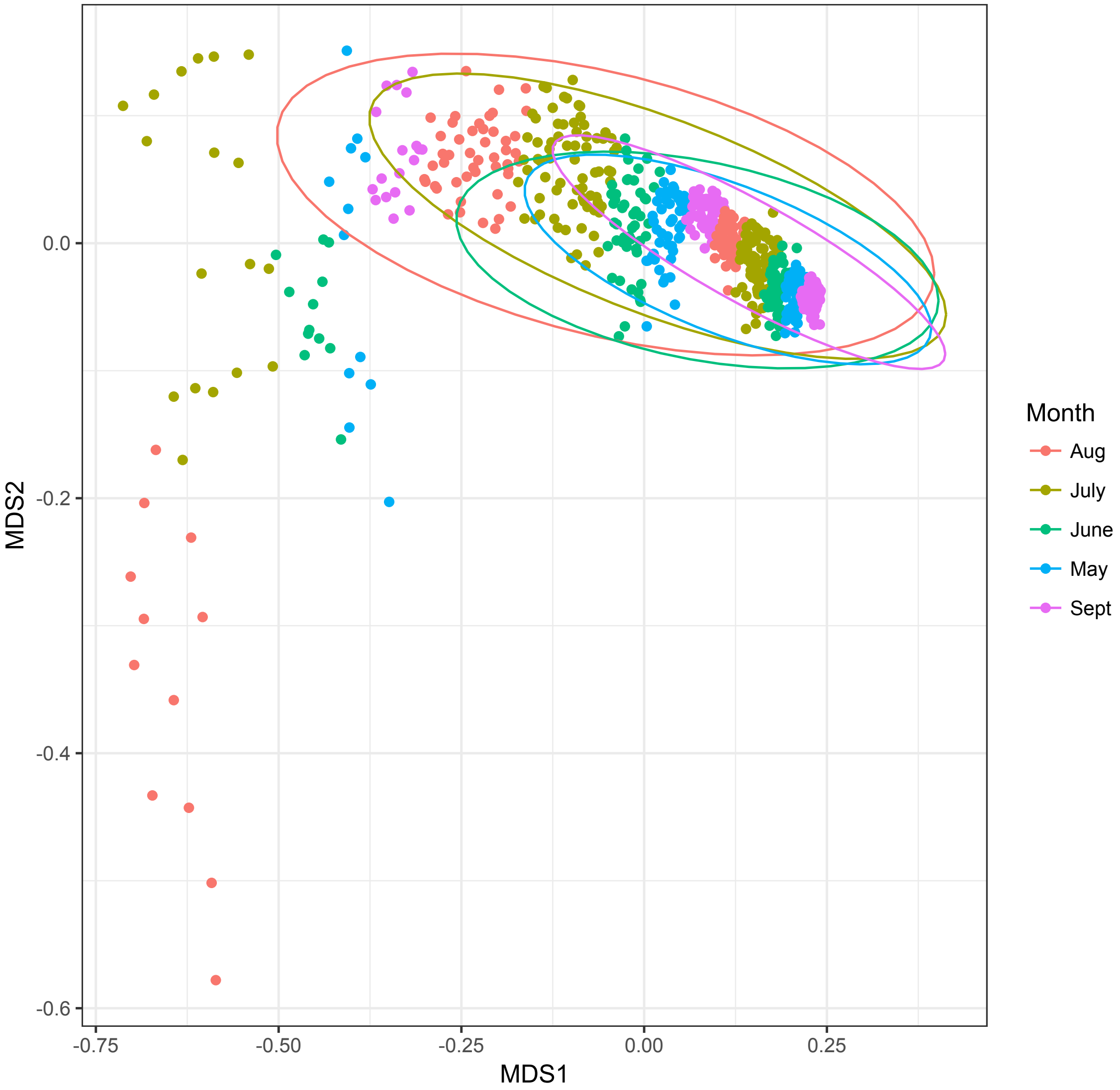

Fig 3.3: ANOSIM of arthropod order community composition across sampling months; abundance of each order was averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year; visualized using NMDS

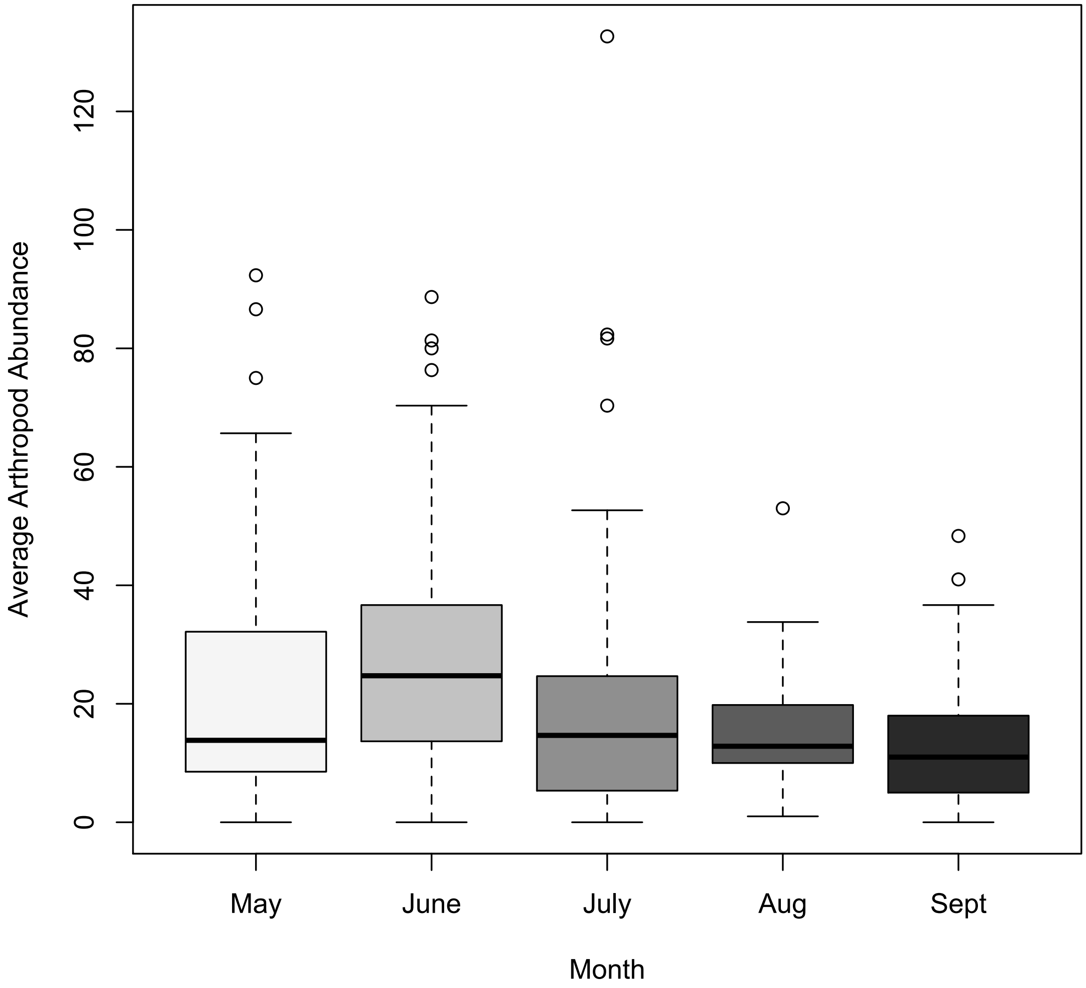

Fig 3.4: Total arthropod abundance in each sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

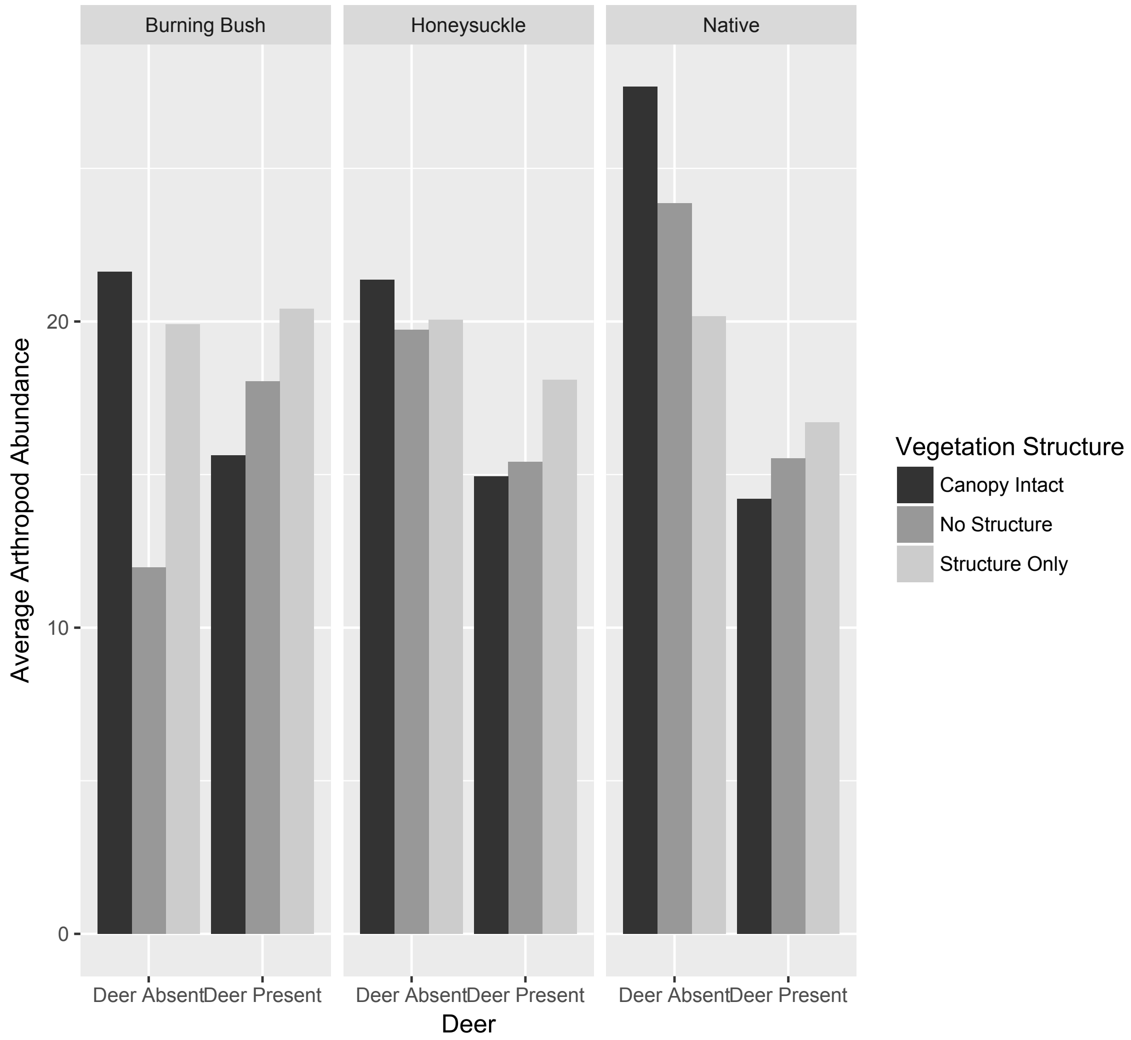

Fig 3.5: Total arthropod abundance for the interaction of dominant plant type, deer presence/absence, and plant management treatment; samples were averaged across all plots in each site for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

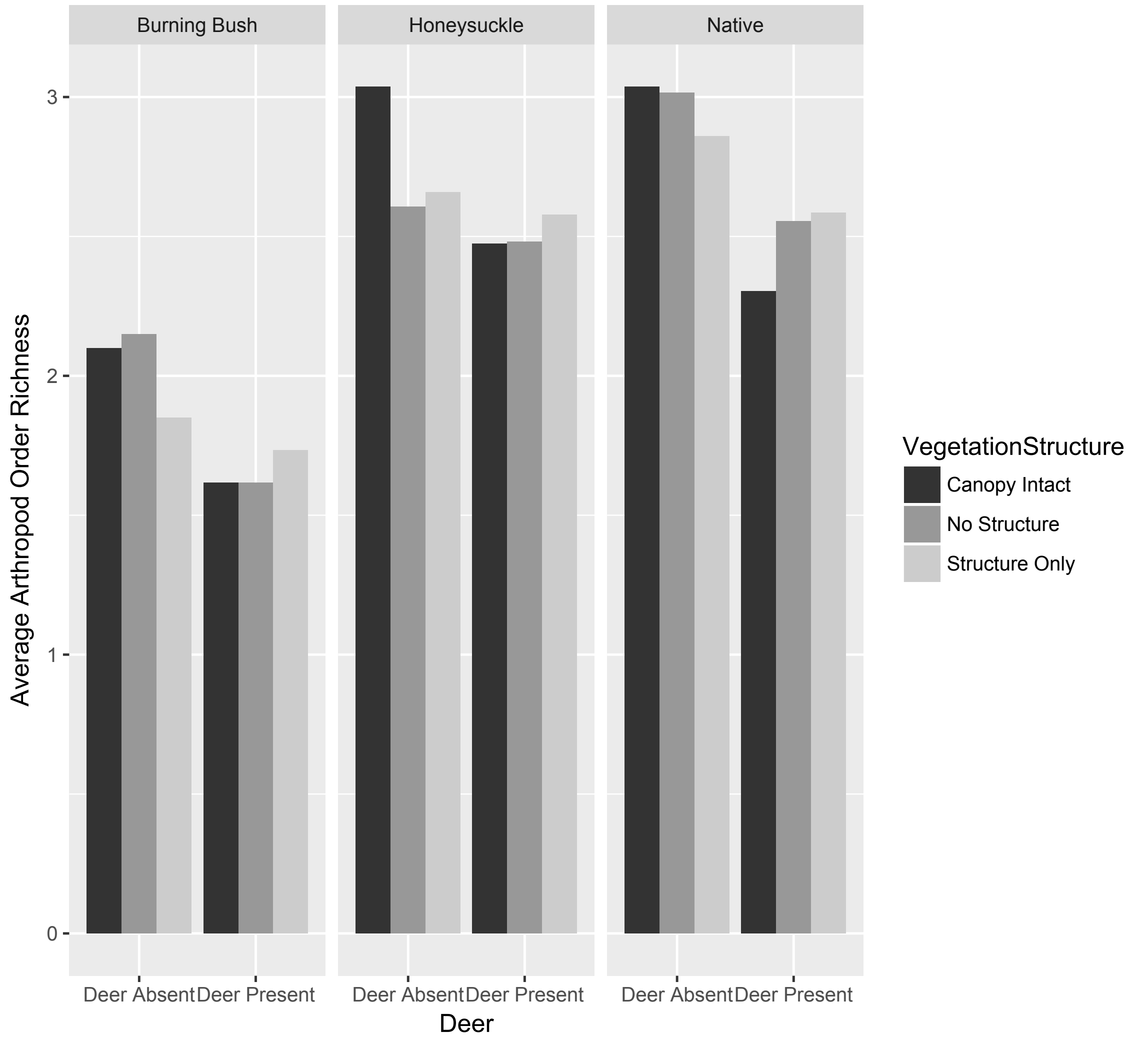

Fig 3.6: Total arthropod order richness for the interaction of dominant plant type, deer presence/absence, and plant management treatment; samples were averaged across plots in each site for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

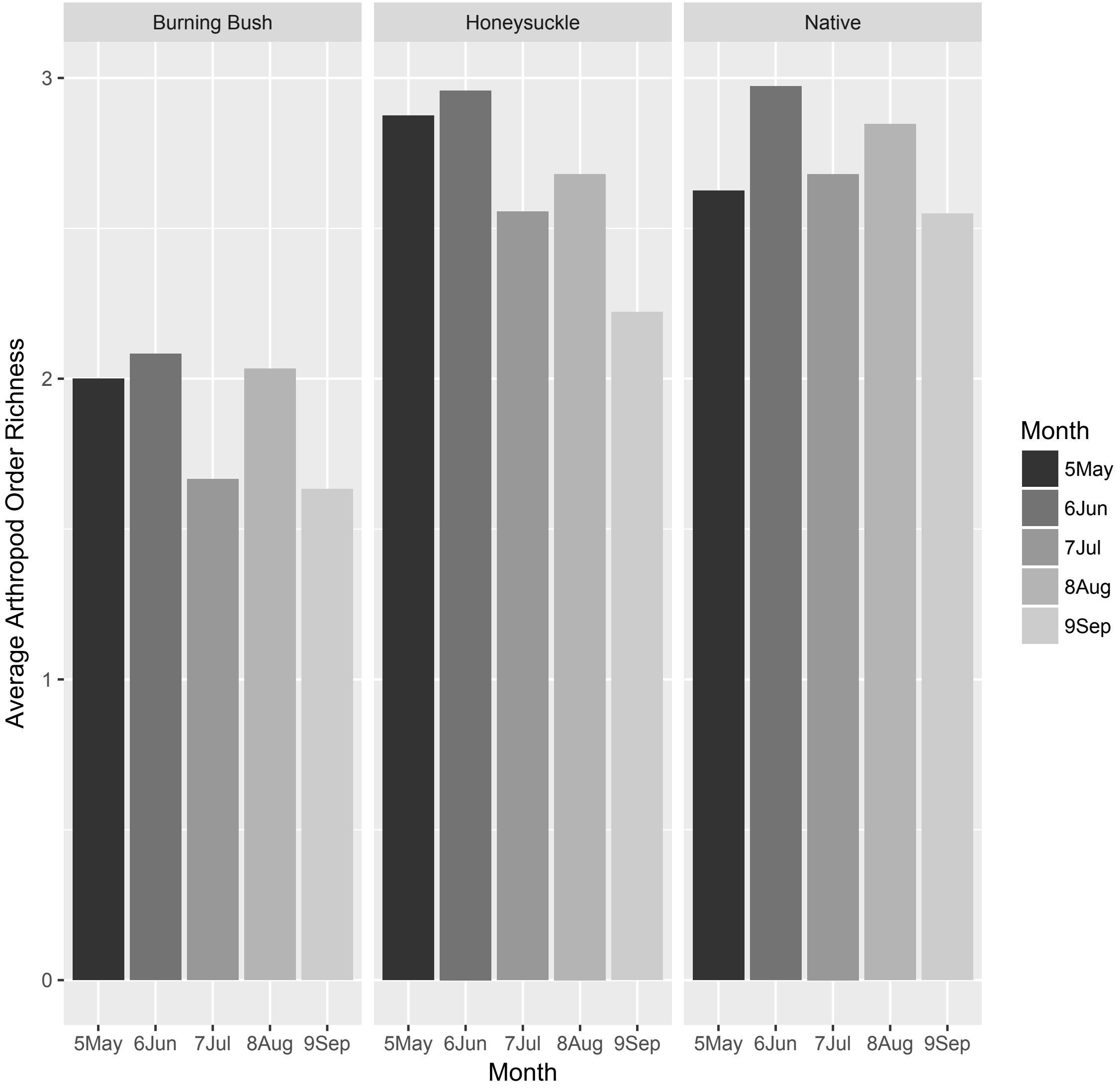

Fig 3.7: Arthropod order richness for the interaction of dominant plant type, and sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

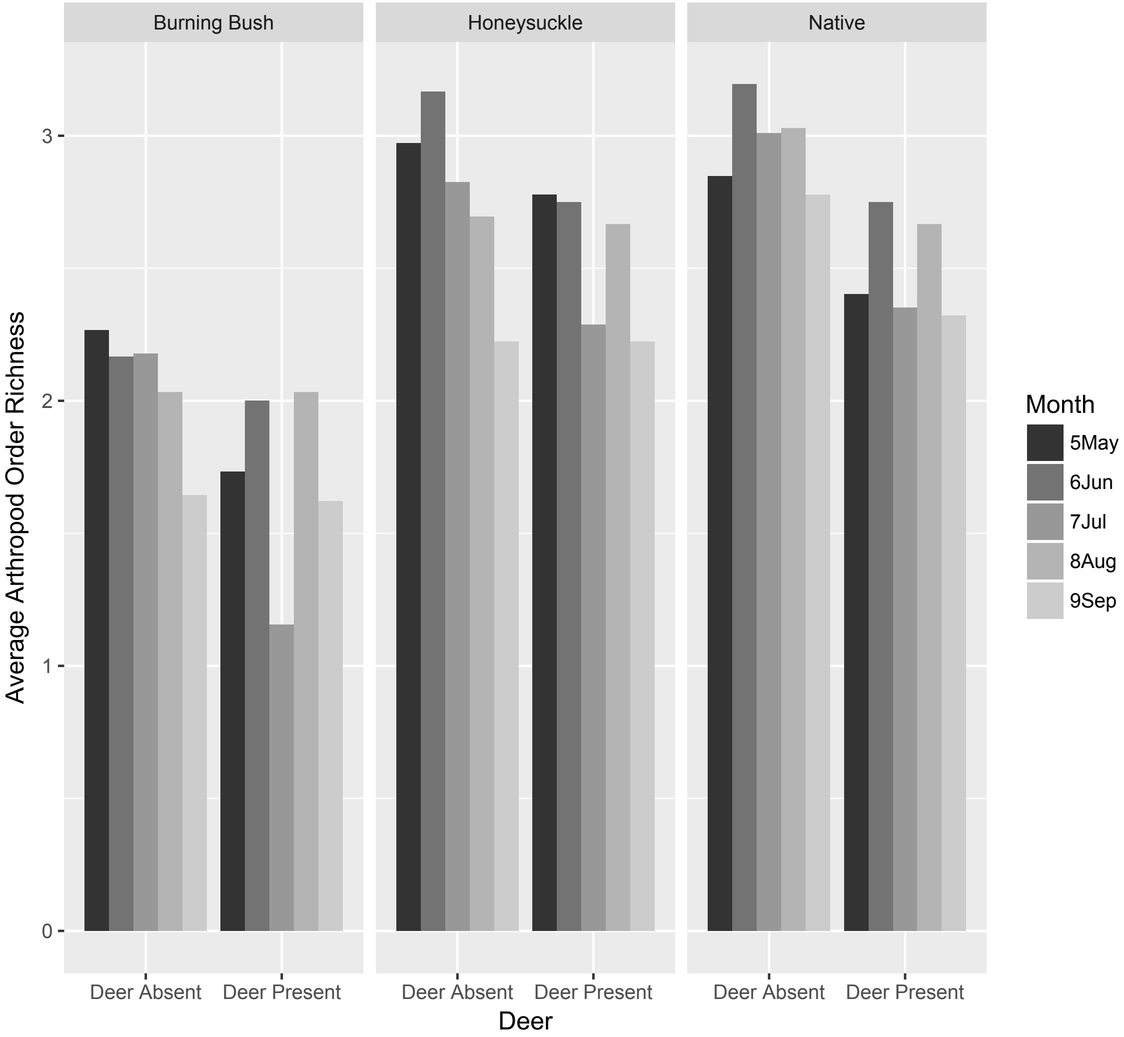

Fig 3.8: Arthropod order richness for the interaction of dominant plant type, and sampling month, and deer presence/absence; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

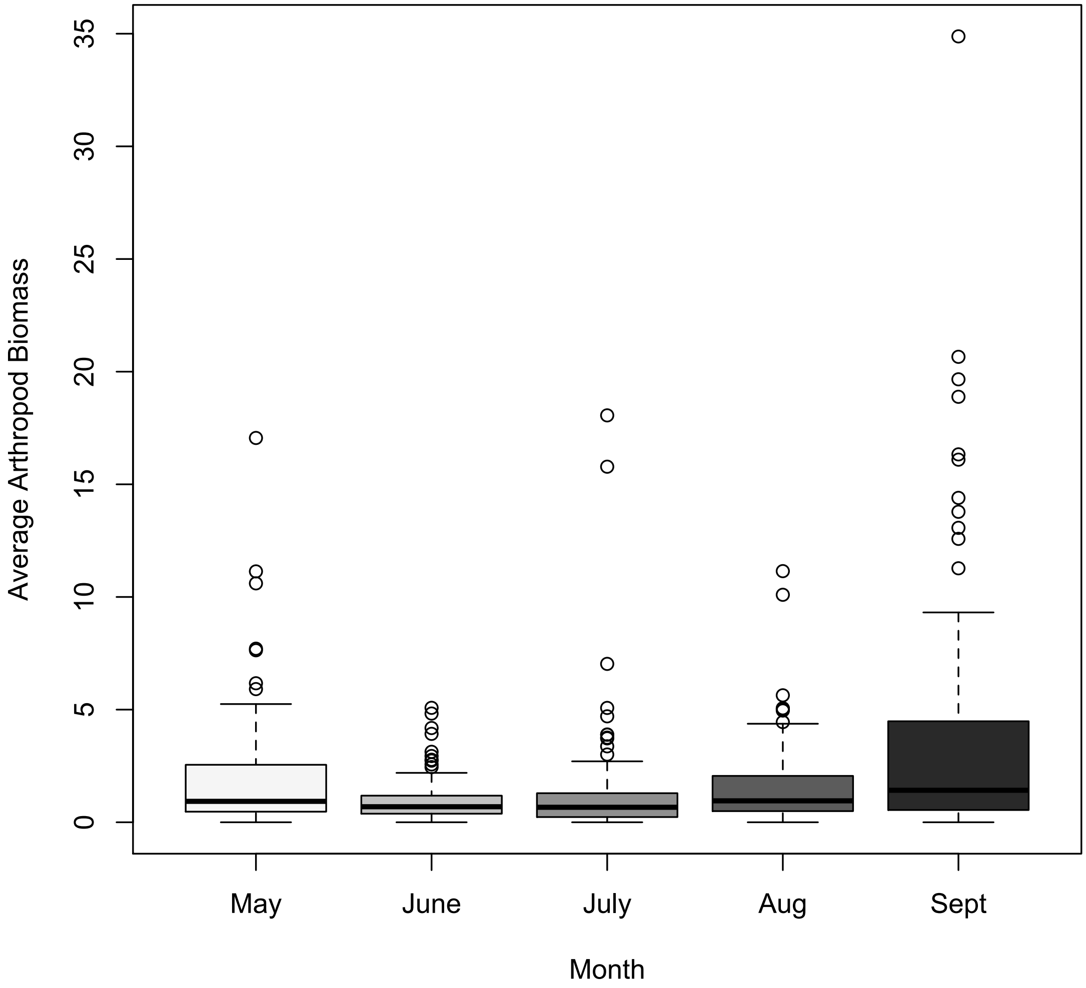

Fig 3.9: Average per individual arthropod biomass in each sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

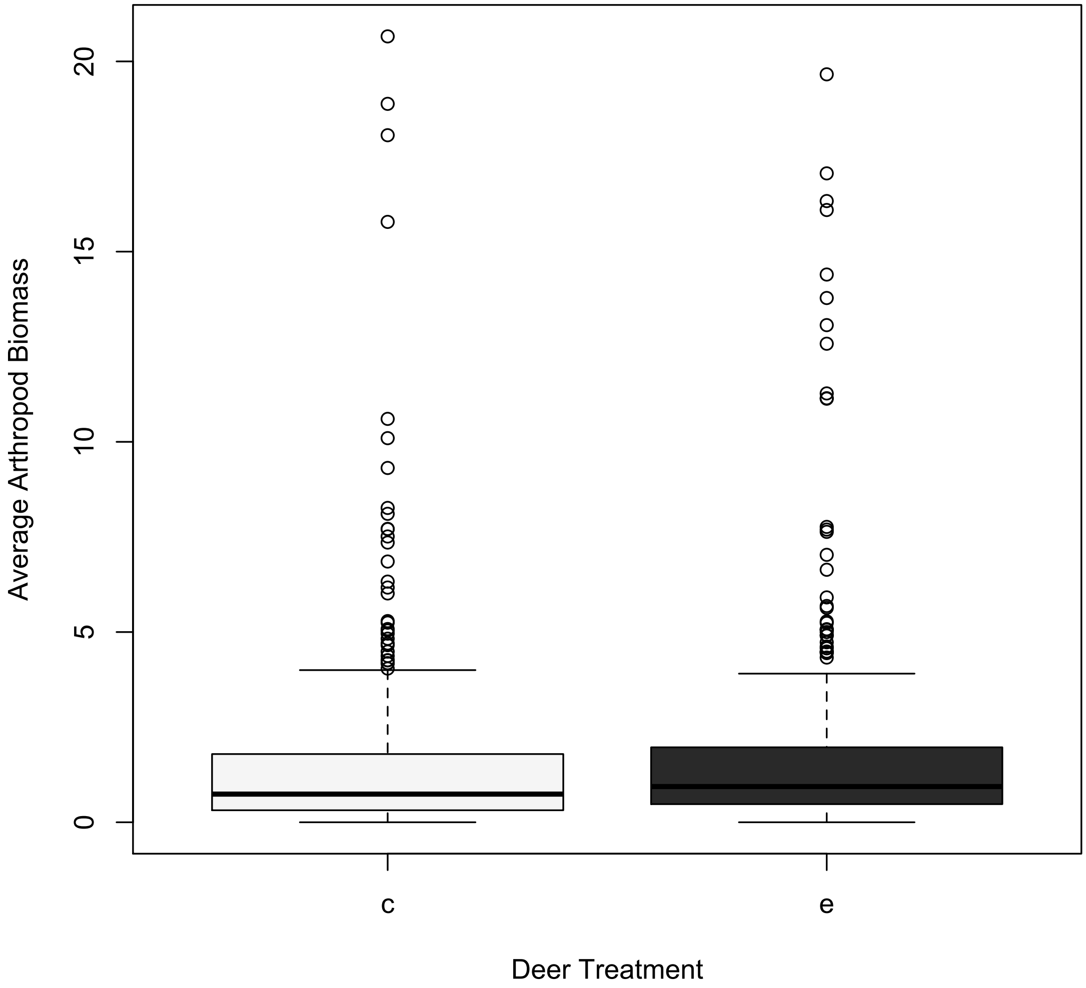

Fig 3.10: Per individual arthropod biomass (mg) deer treatments (c = deer present; e = deer absent); samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

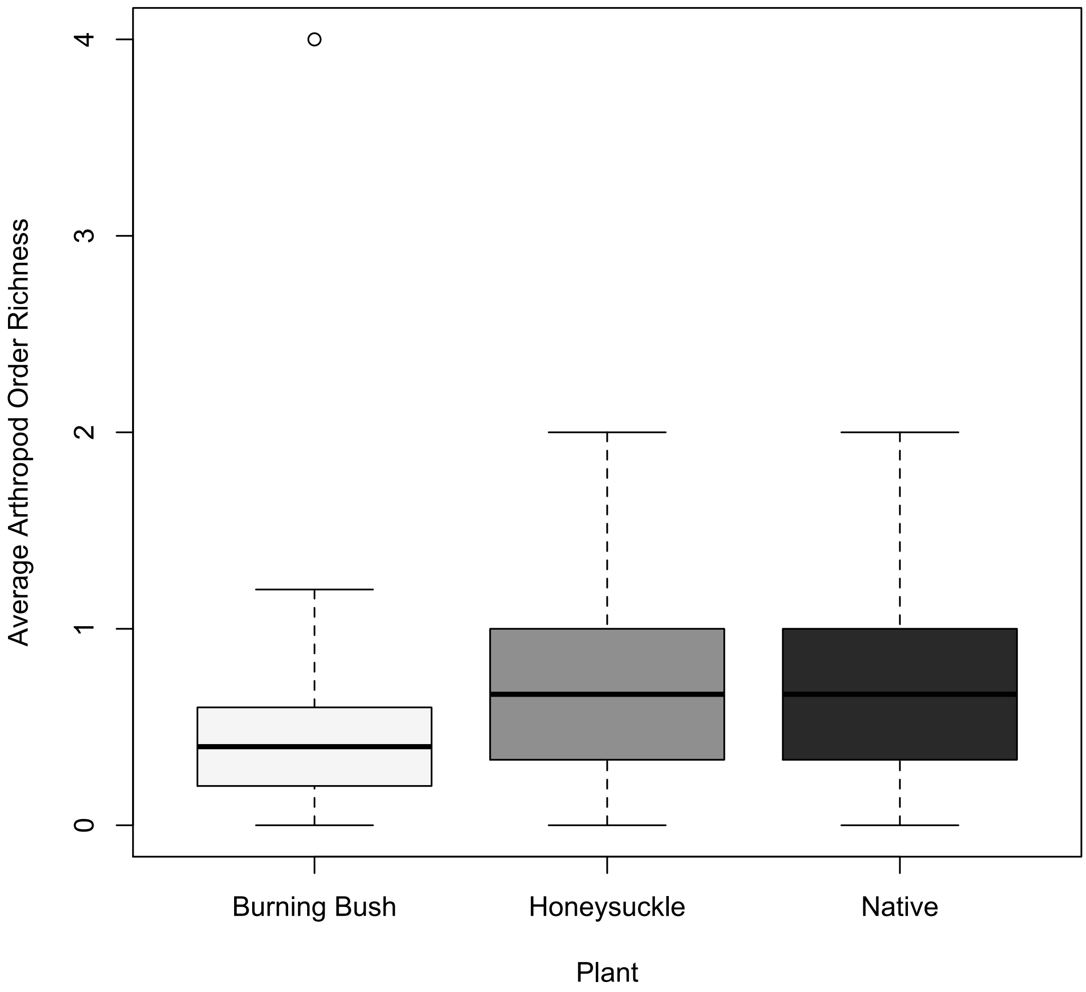

Fig 3.11: Richness of aerial arthropods in dominant plant treatments; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

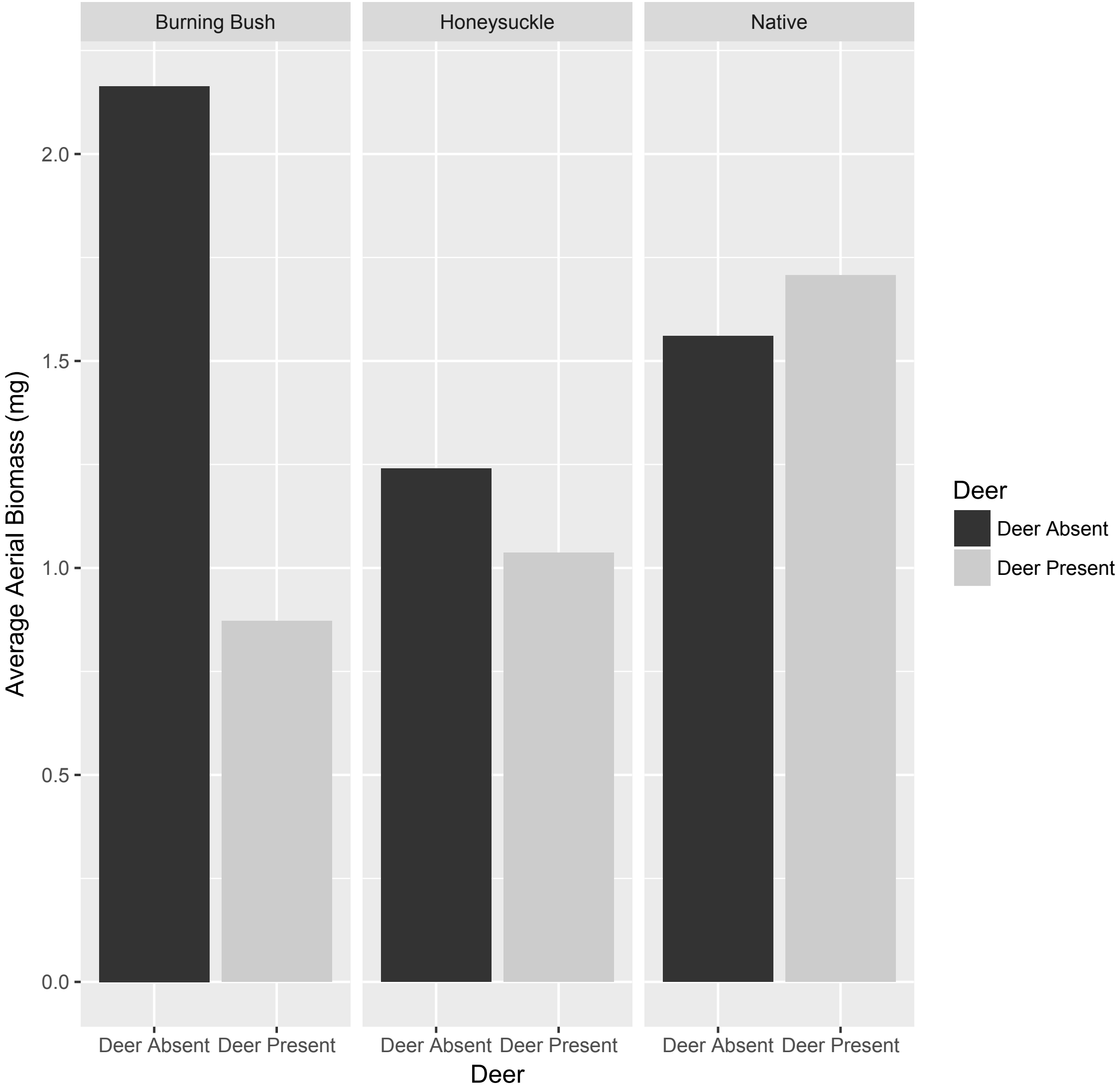

Fig 3.12: Aerial arthropod biomass (mg) between the interaction of plant species and deer treatment; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

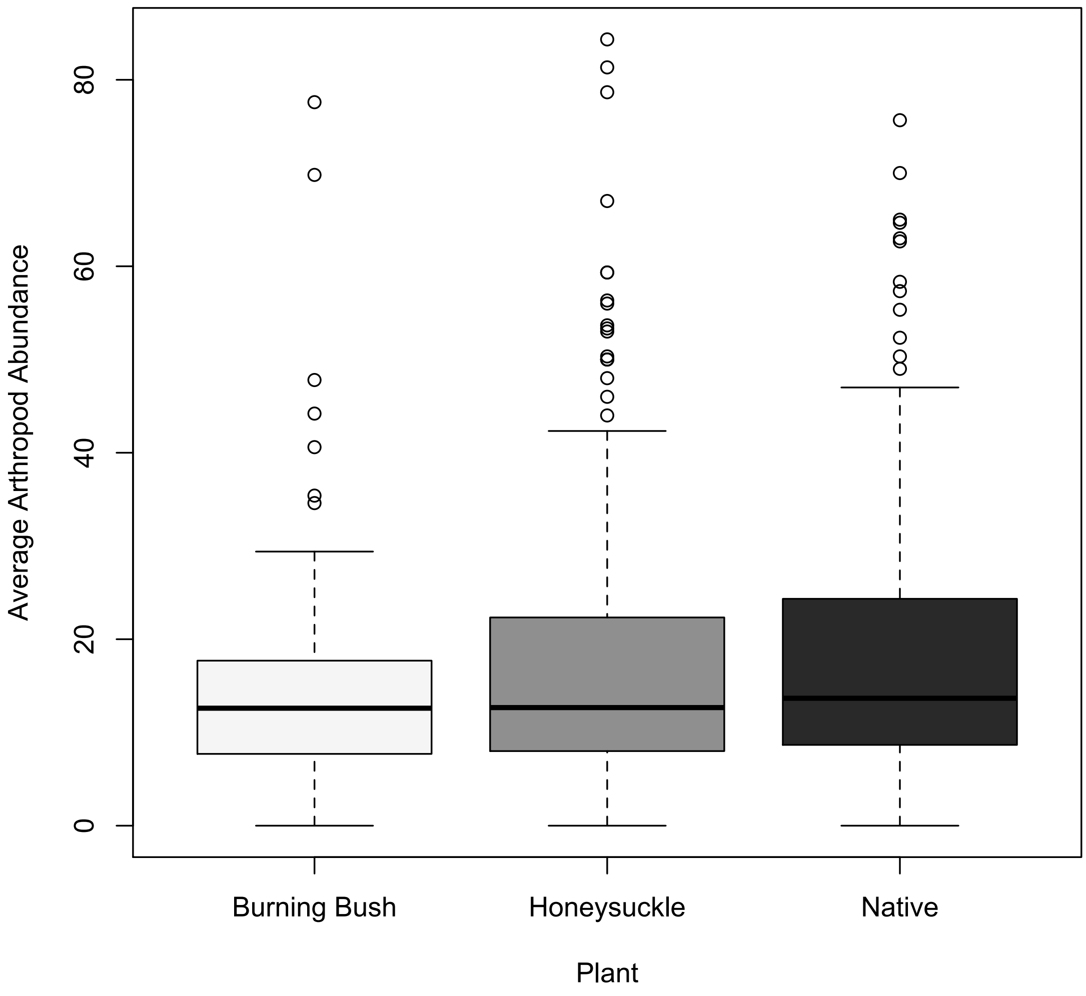

Fig 3.13: Ground arthropod abundance across dominant plant species; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

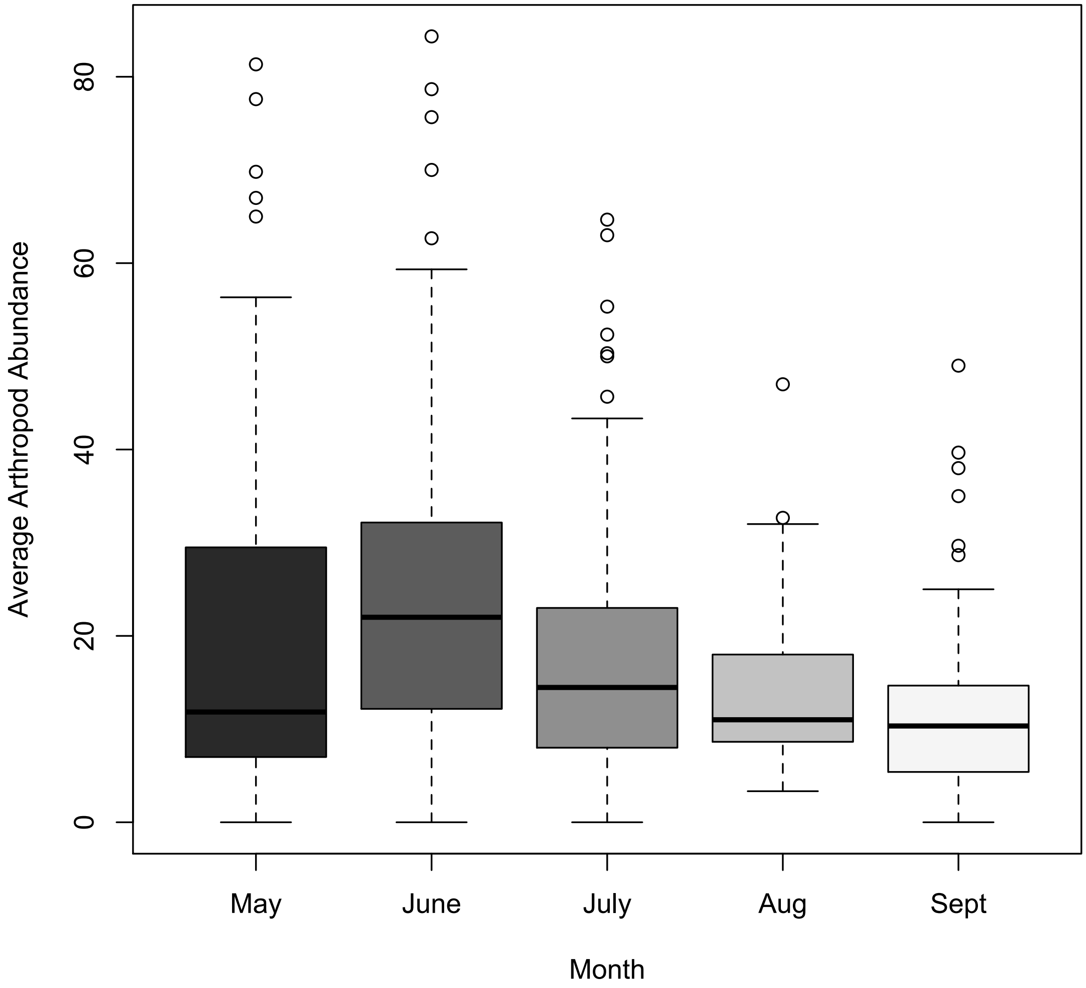

Fig 3.14: Ground arthropod abundance across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

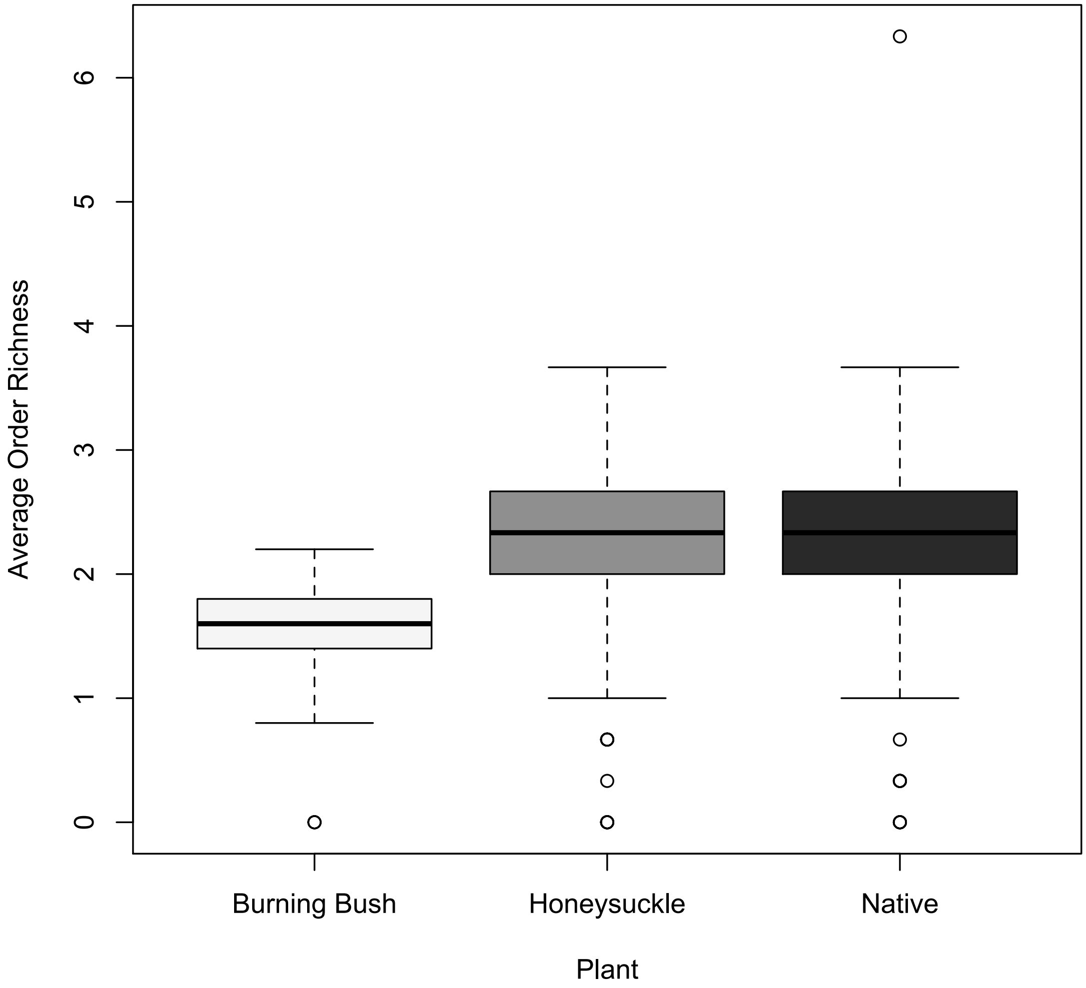

Fig 3.15: Ground arthropod richness across dominant plant species; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

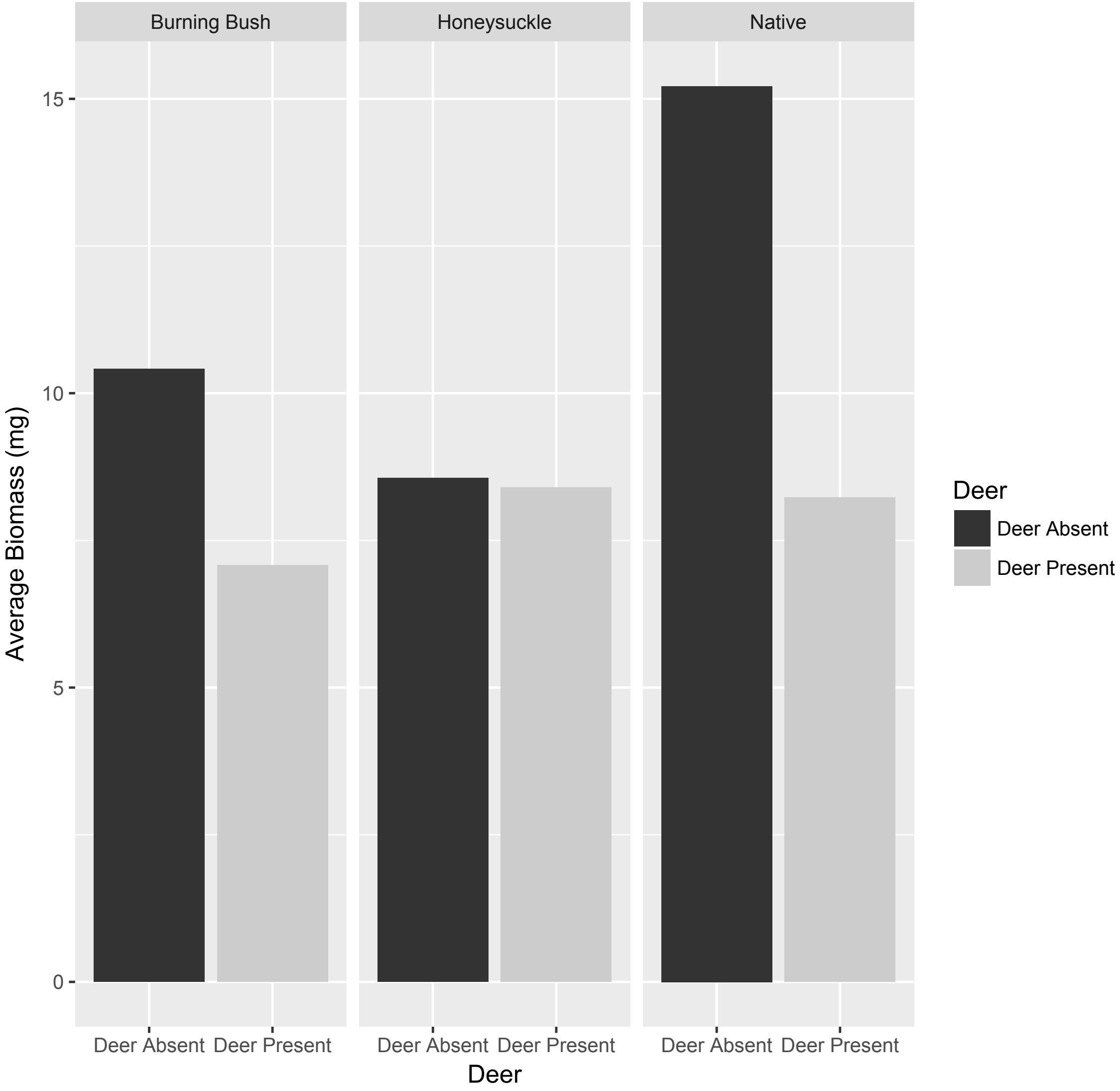

Fig 3.16: Average ground arthropod biomass across the interaction of dominant plant species and deer treatment; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

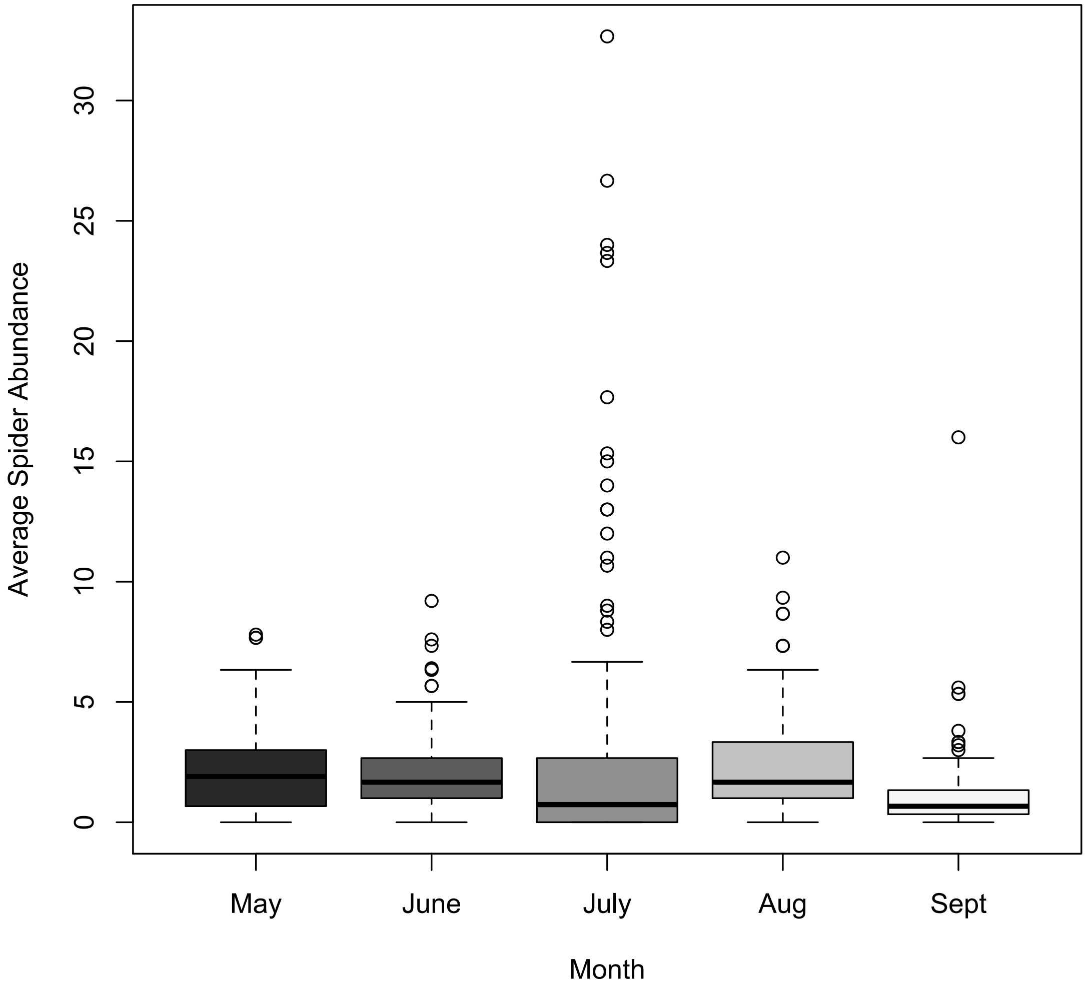

Fig 3.17: Total spider abundance in each sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

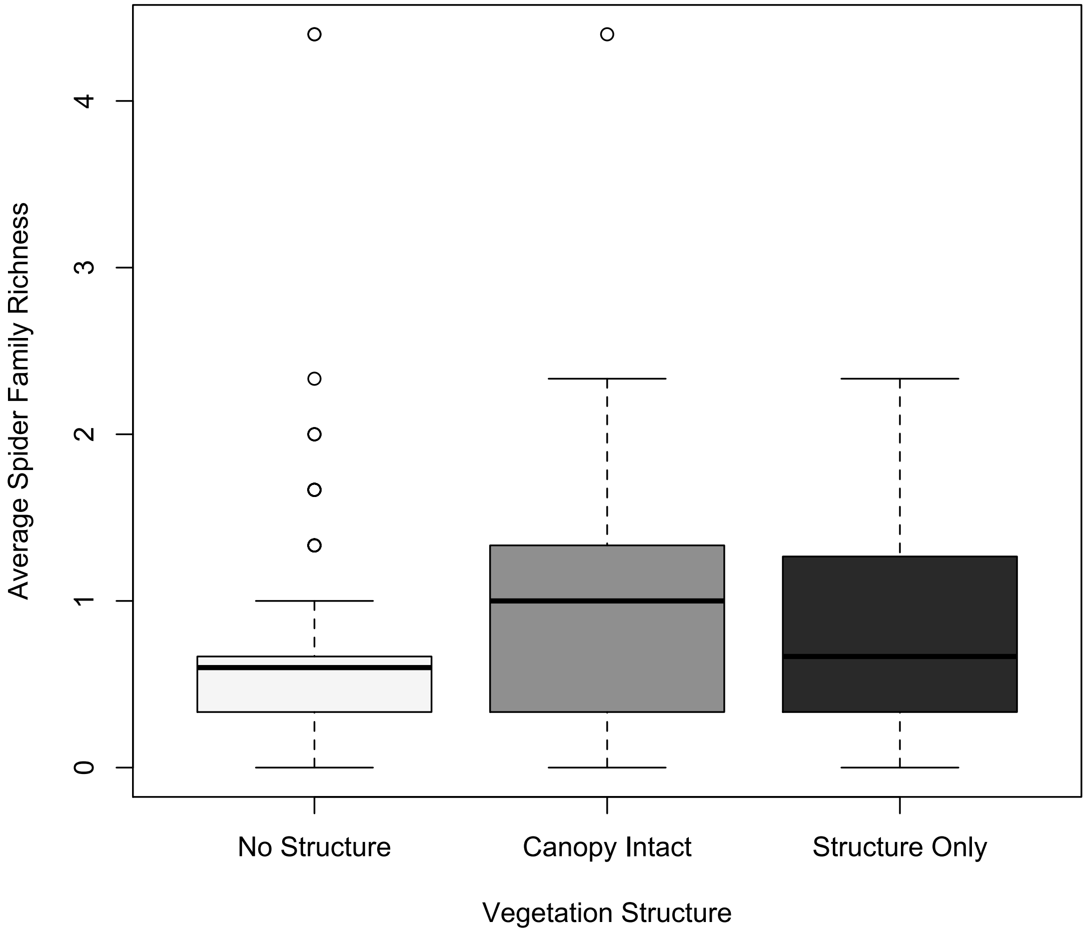

Fig 3.18: Spider family richness in invasive plant management treatments; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

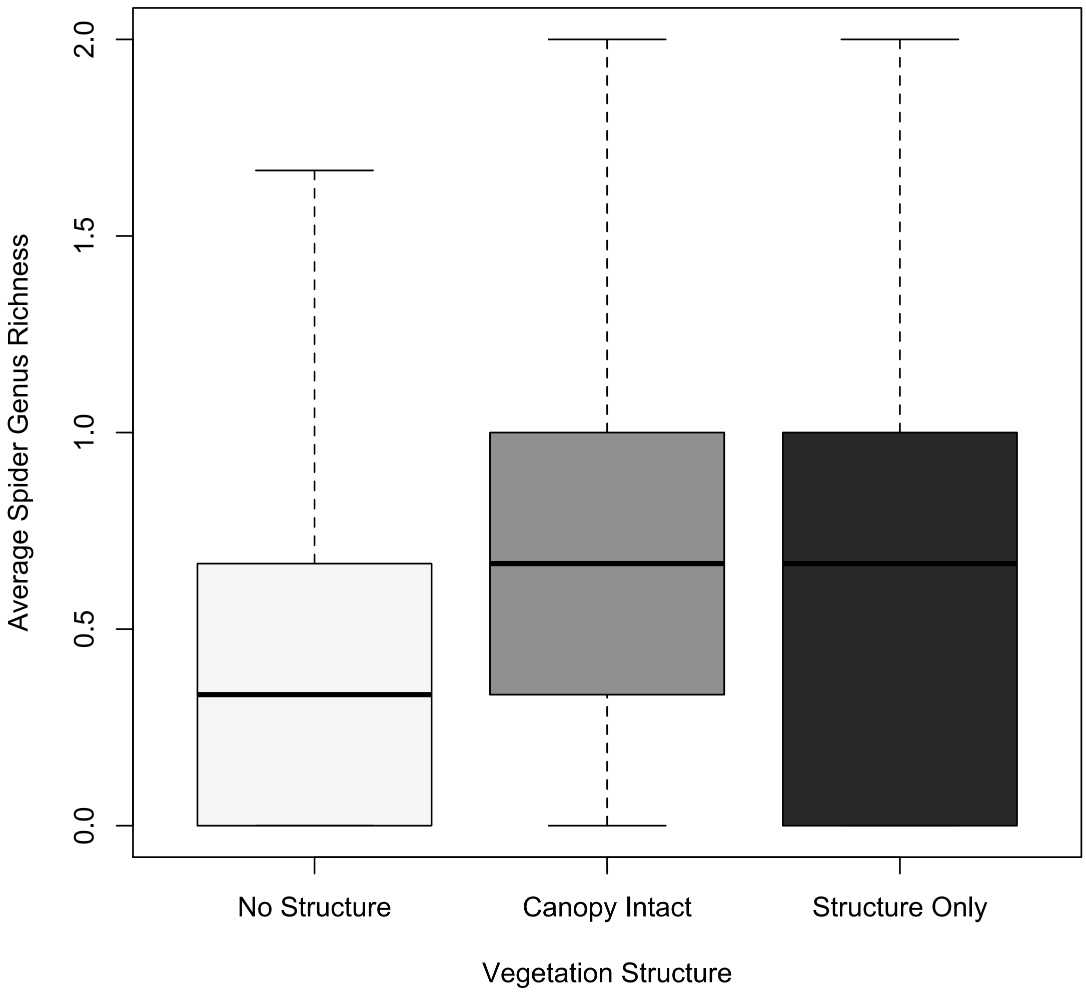

Fig 3.19: Spider genus richness in invasive plant management treatments; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

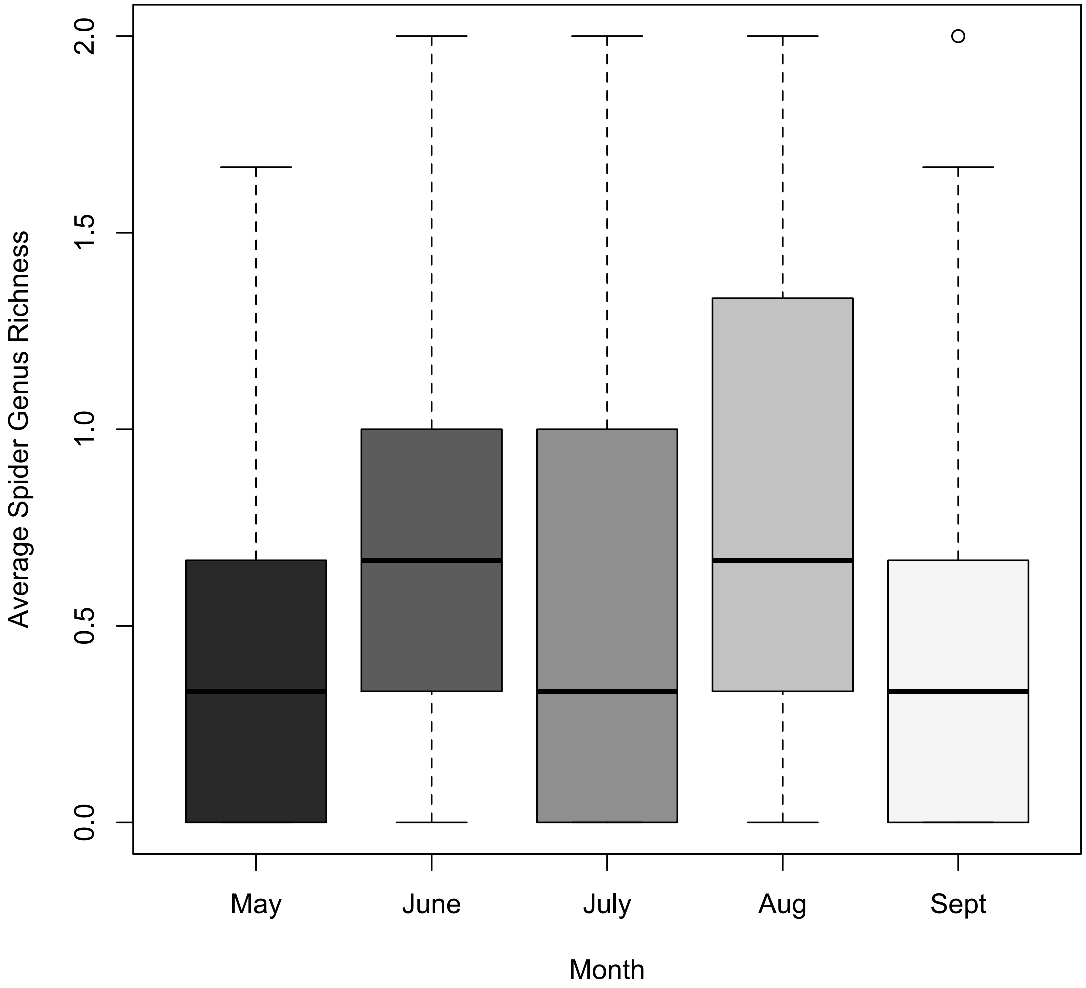

Fig 3.20: Spider genus richness in each sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

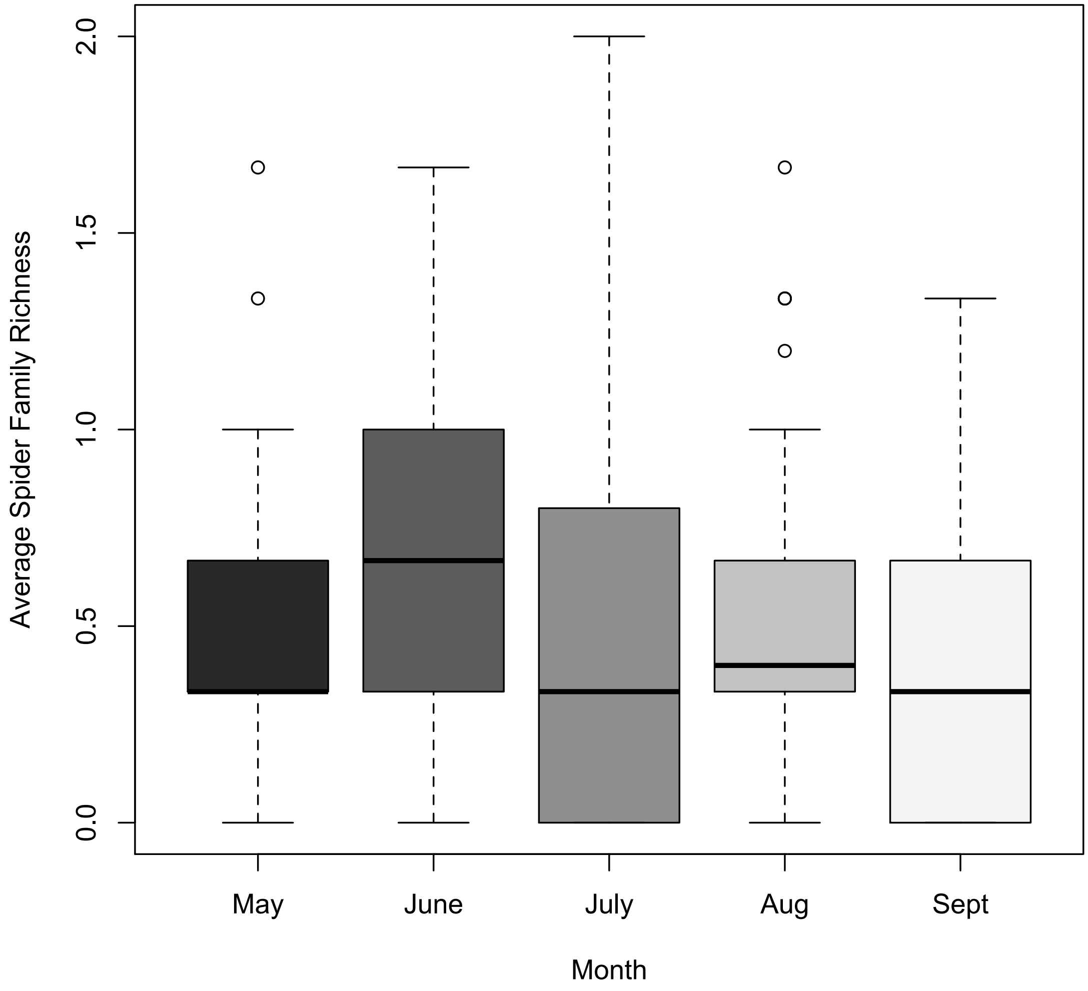

Fig 3.21: Aerial spider family richness across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

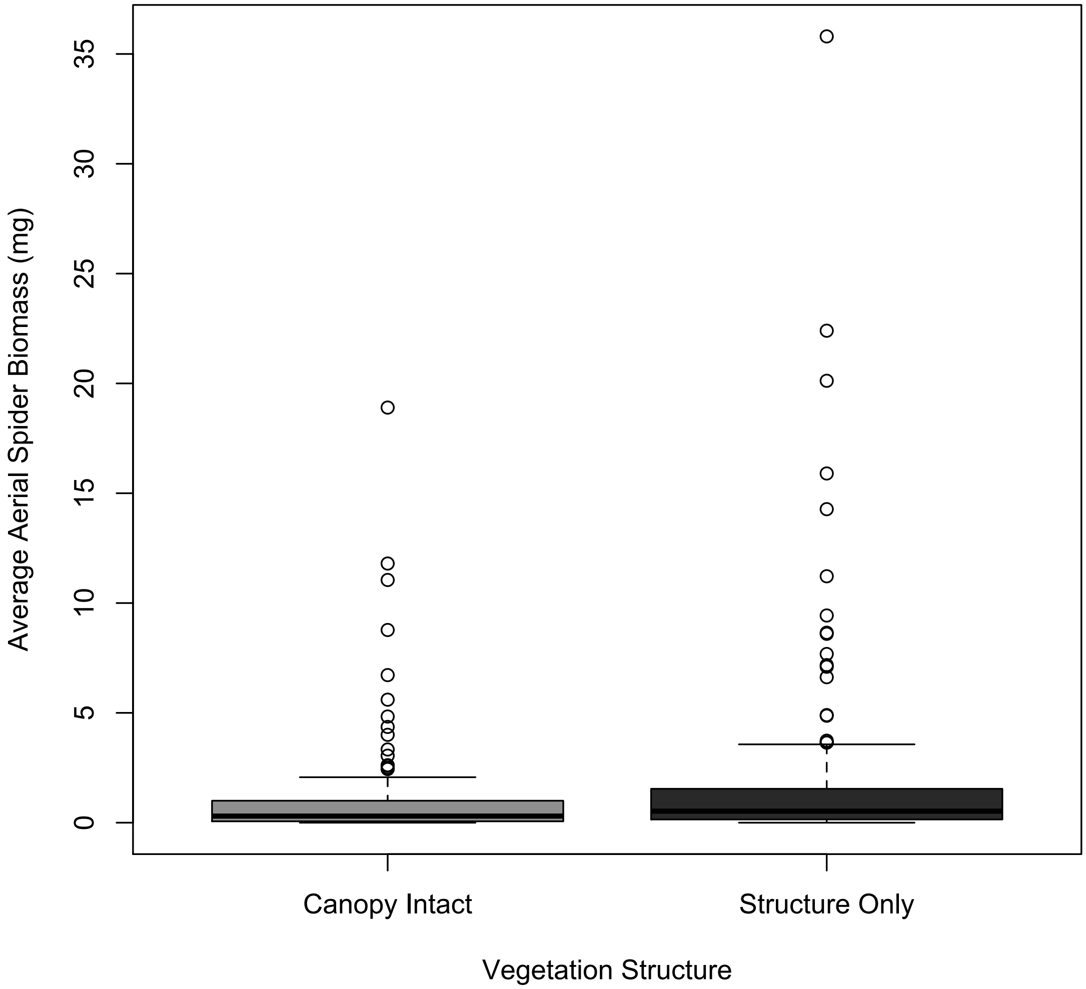

Fig 3.22: Aerial spider biomass of vegetation structure subplots; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

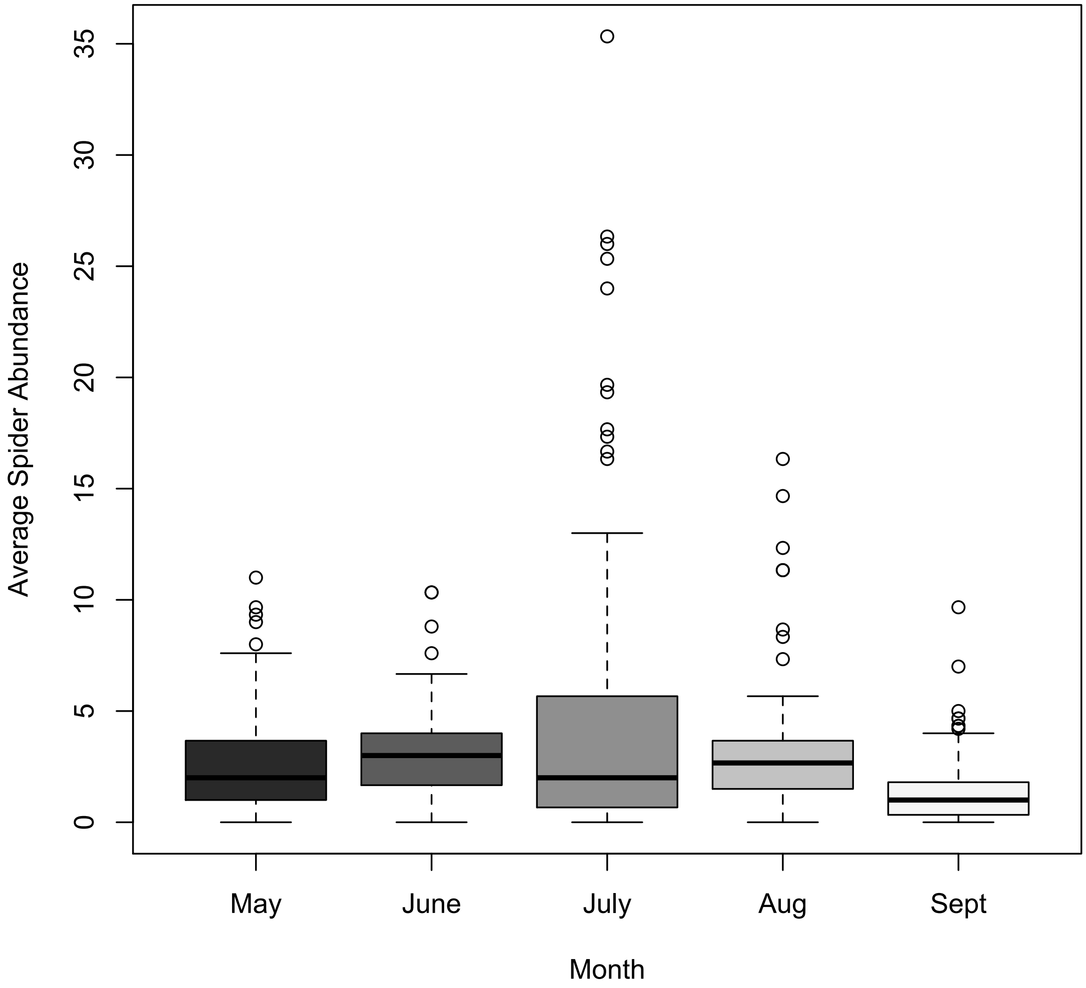

Fig 3.23: Ground spider abundance across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

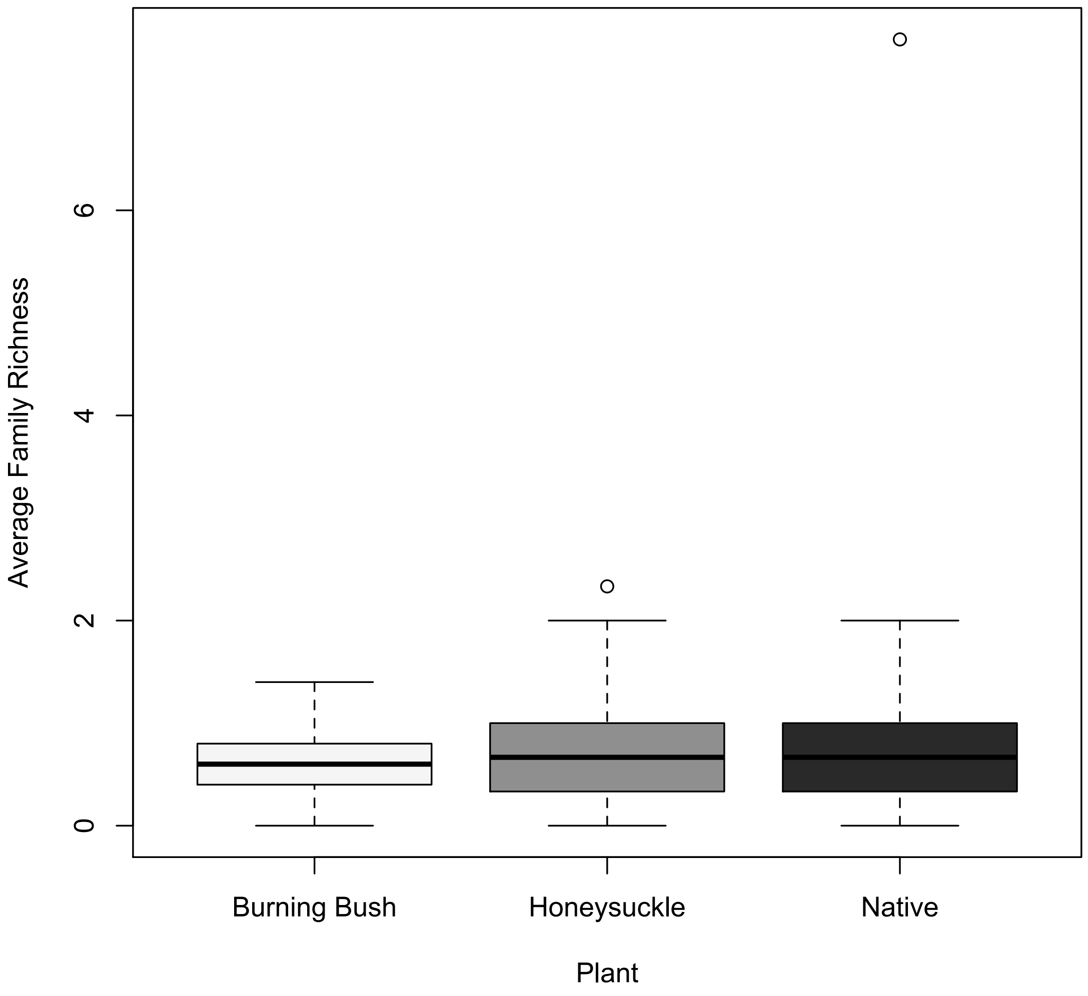

Fig 3.24: Ground spider family richness across dominant plant species; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

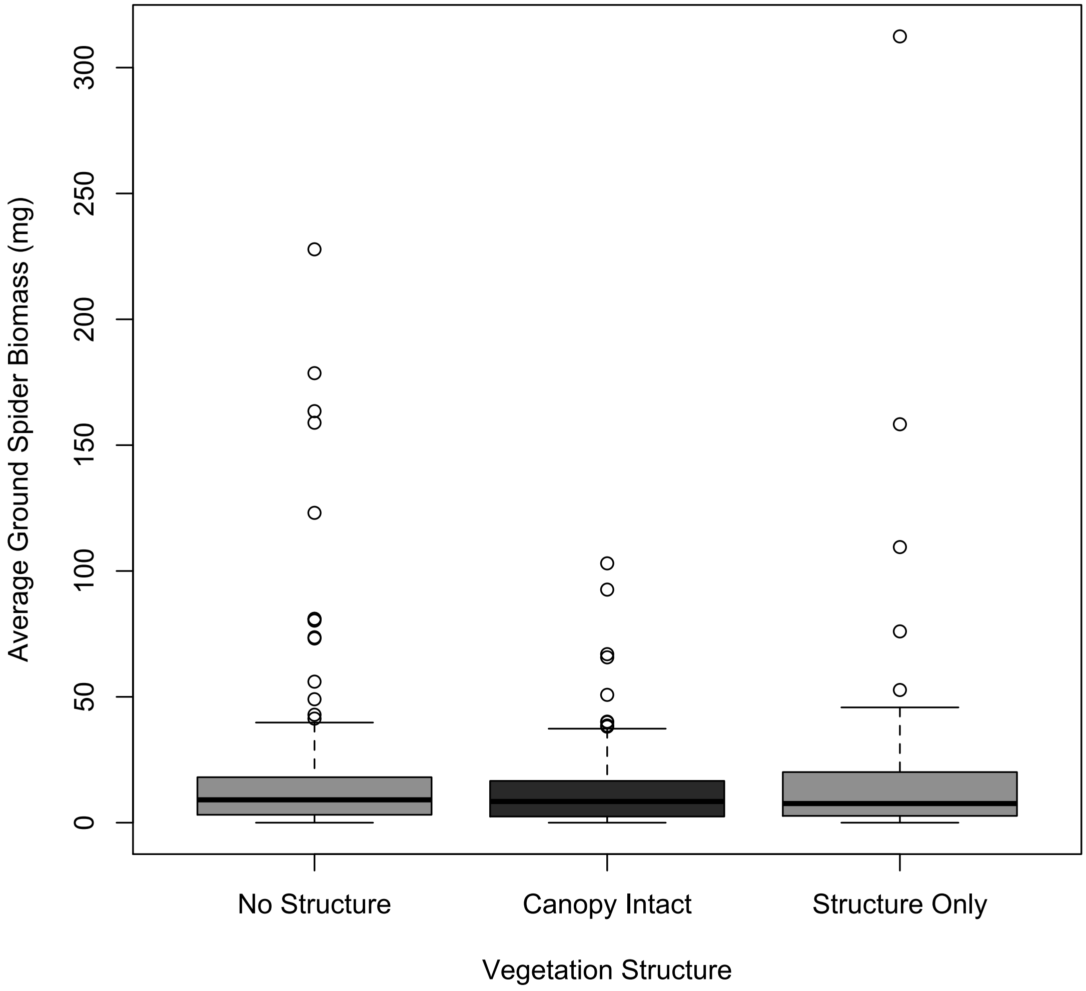

Fig 3.25: Ground spider biomass across invasive plant management plots; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

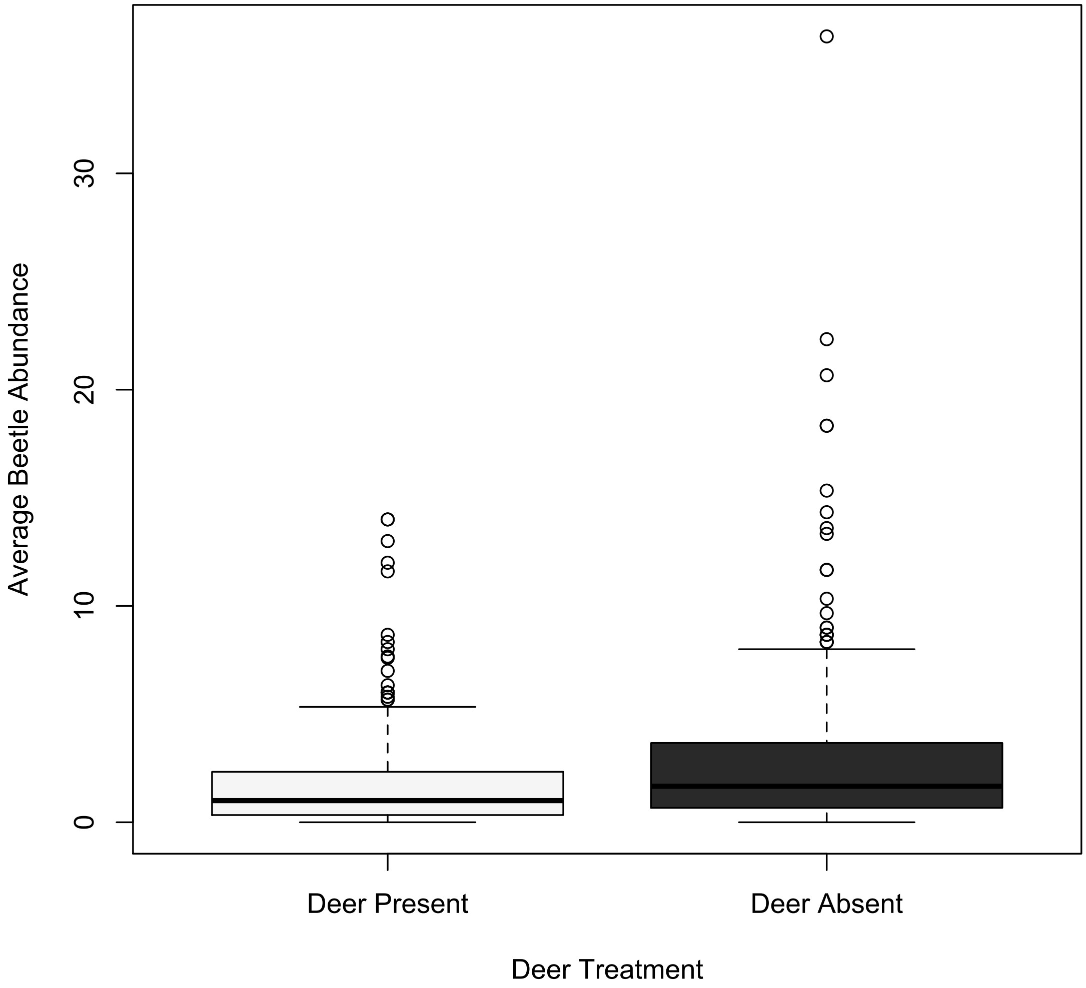

Fig 3.26: Beetle abundance between deer treatments; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

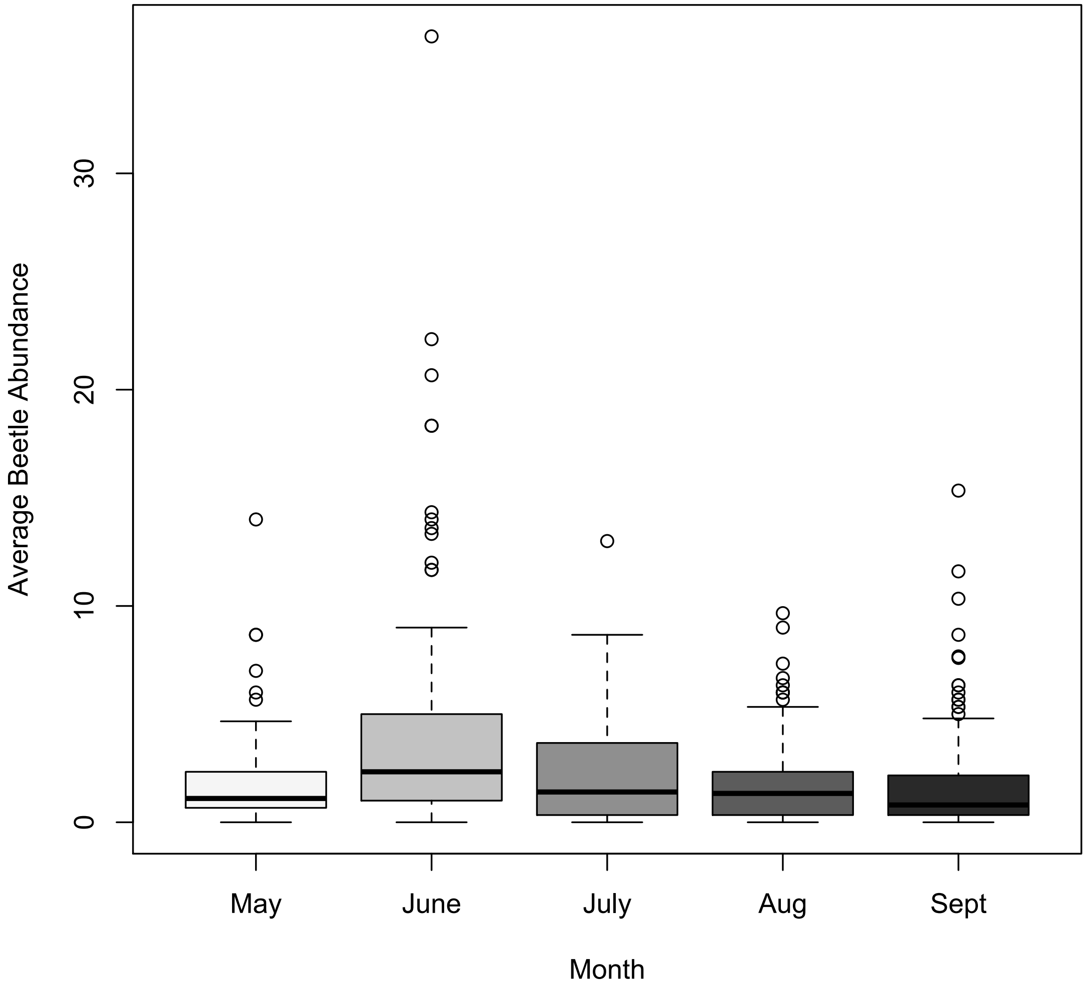

Fig 3.27: Beetle abundance in each sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

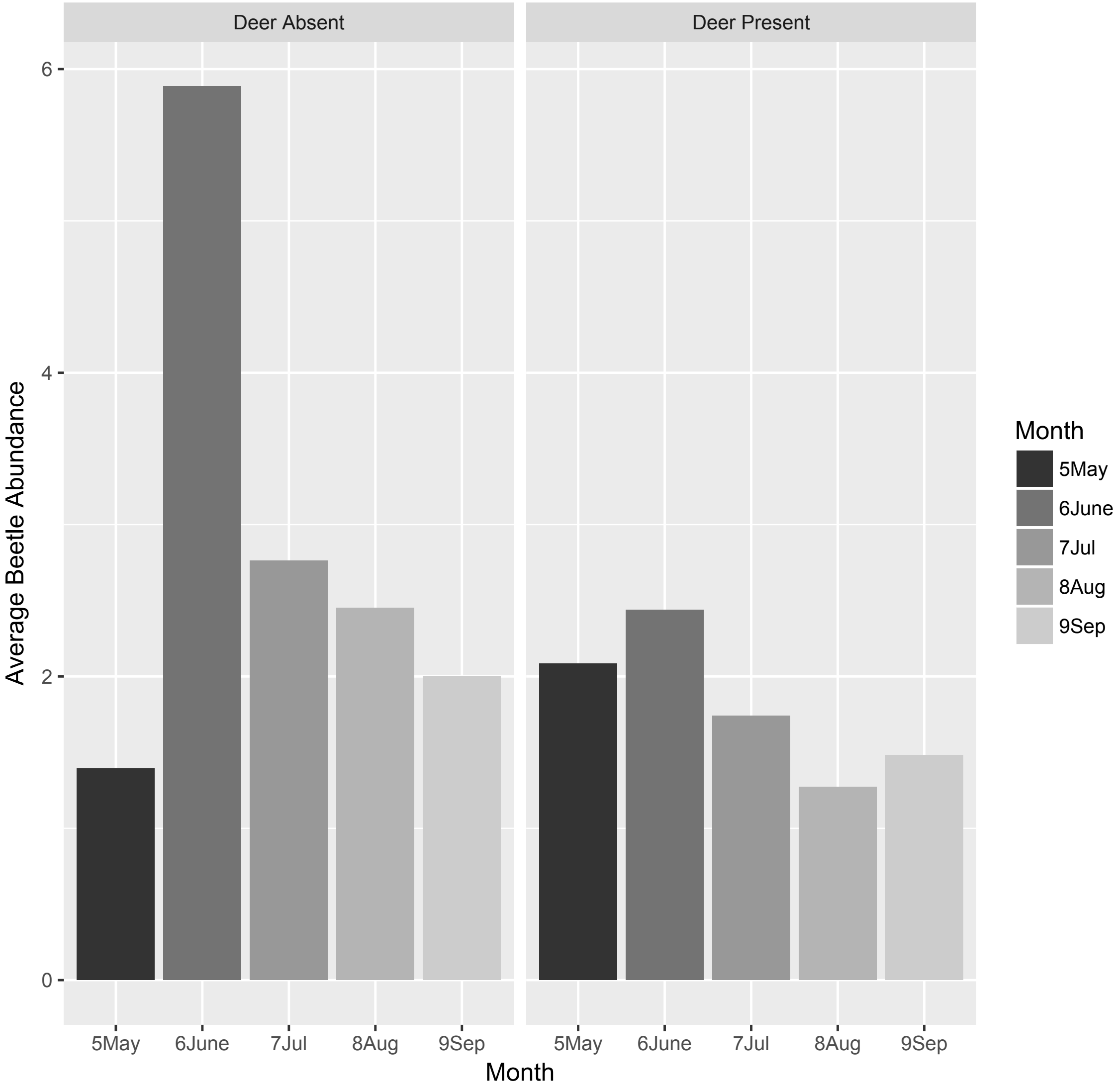

Fig 3.28: Average beetle abundance across the interaction of sampling month, and deer presence/absence; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

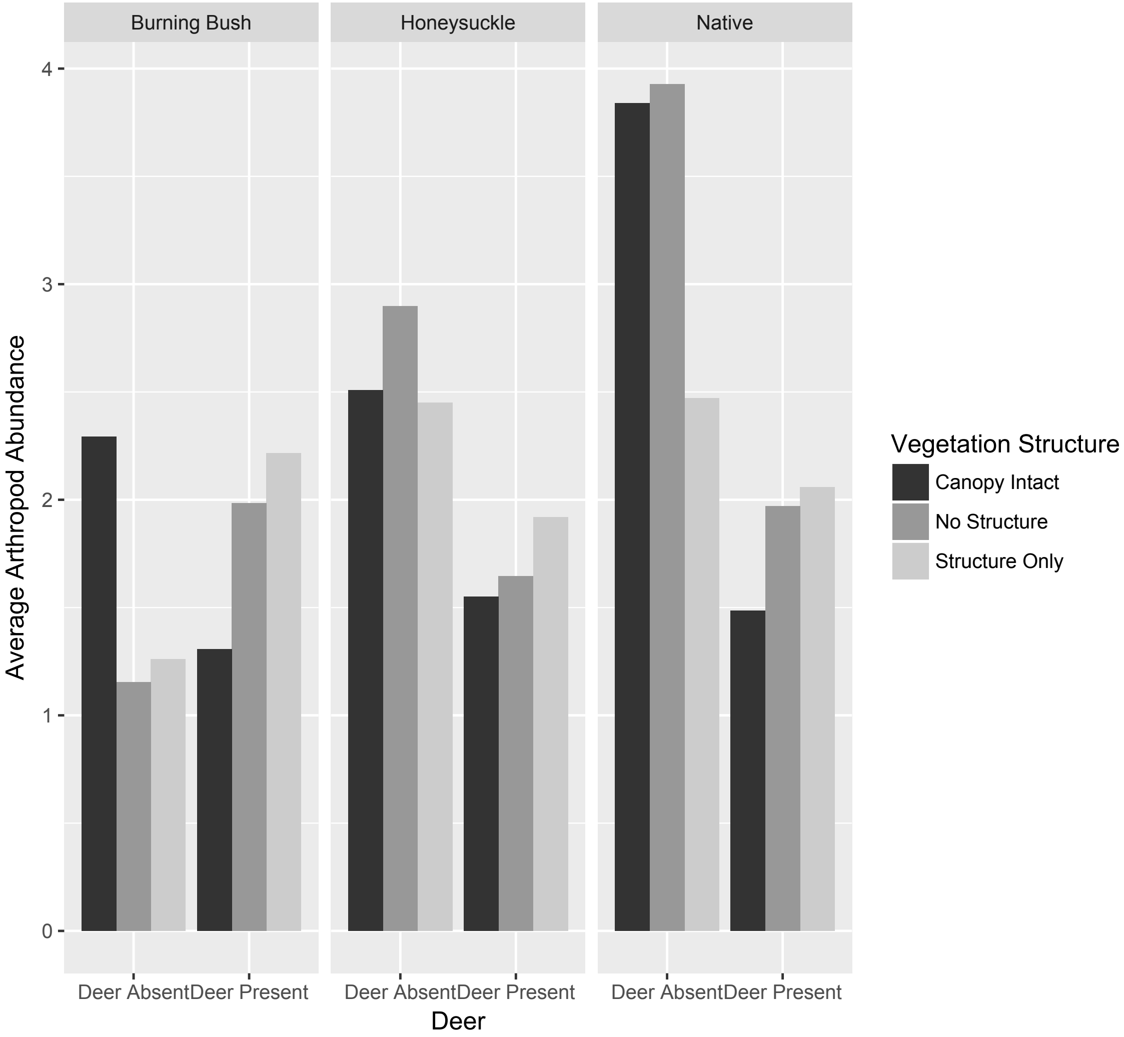

Fig 3.29: Average beetle abundance for the interaction of dominant plant type, deer presence/absence, and plant management treatment; samples were averaged across plots in each site for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

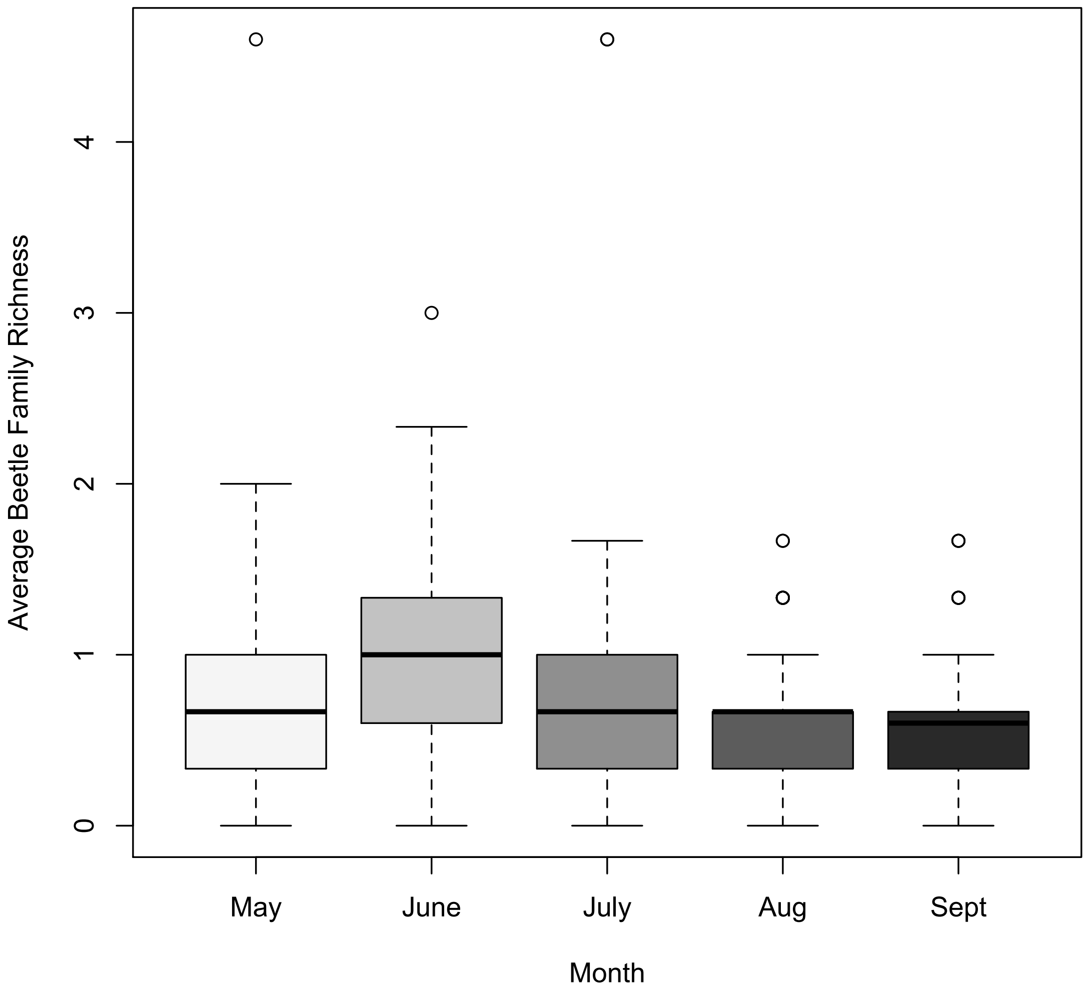

Fig 3.30: Beetle family richness in each sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

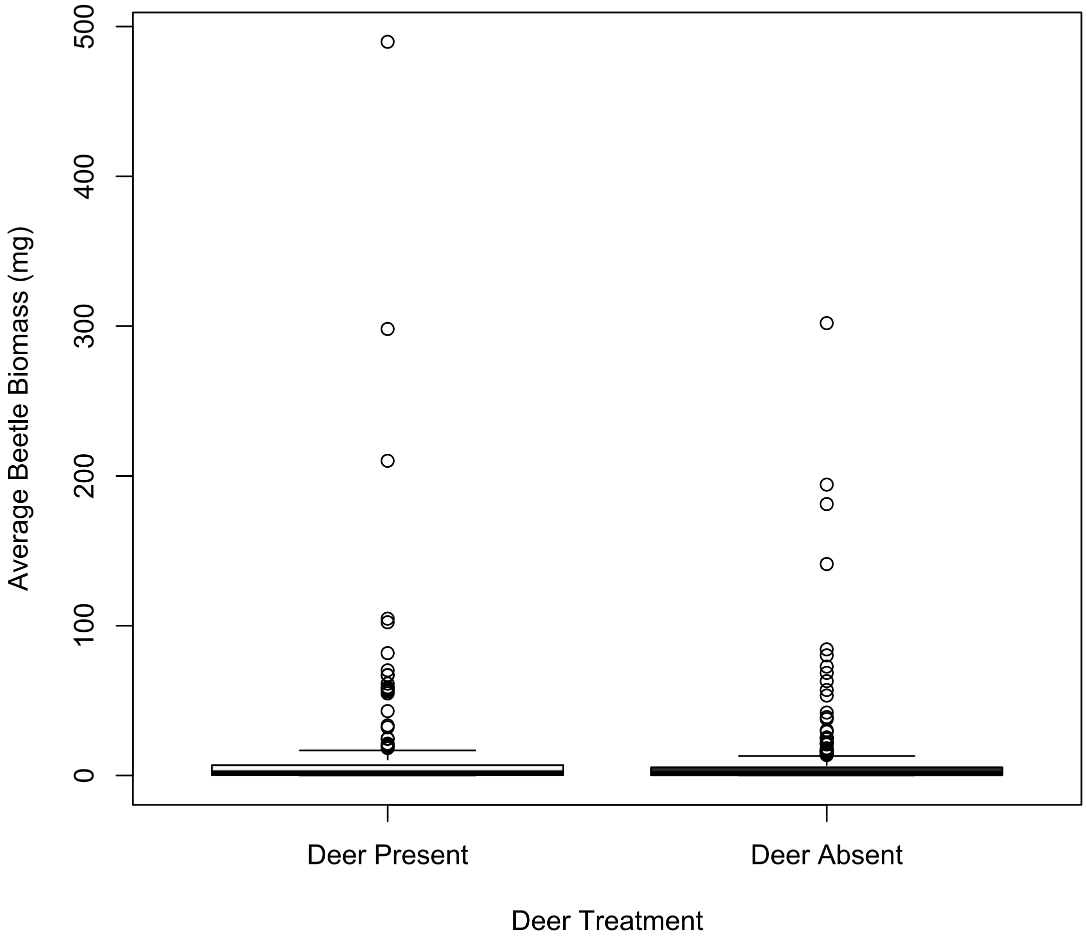

Fig 3.31: Average beetle biomass (mg) between deer treatments; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

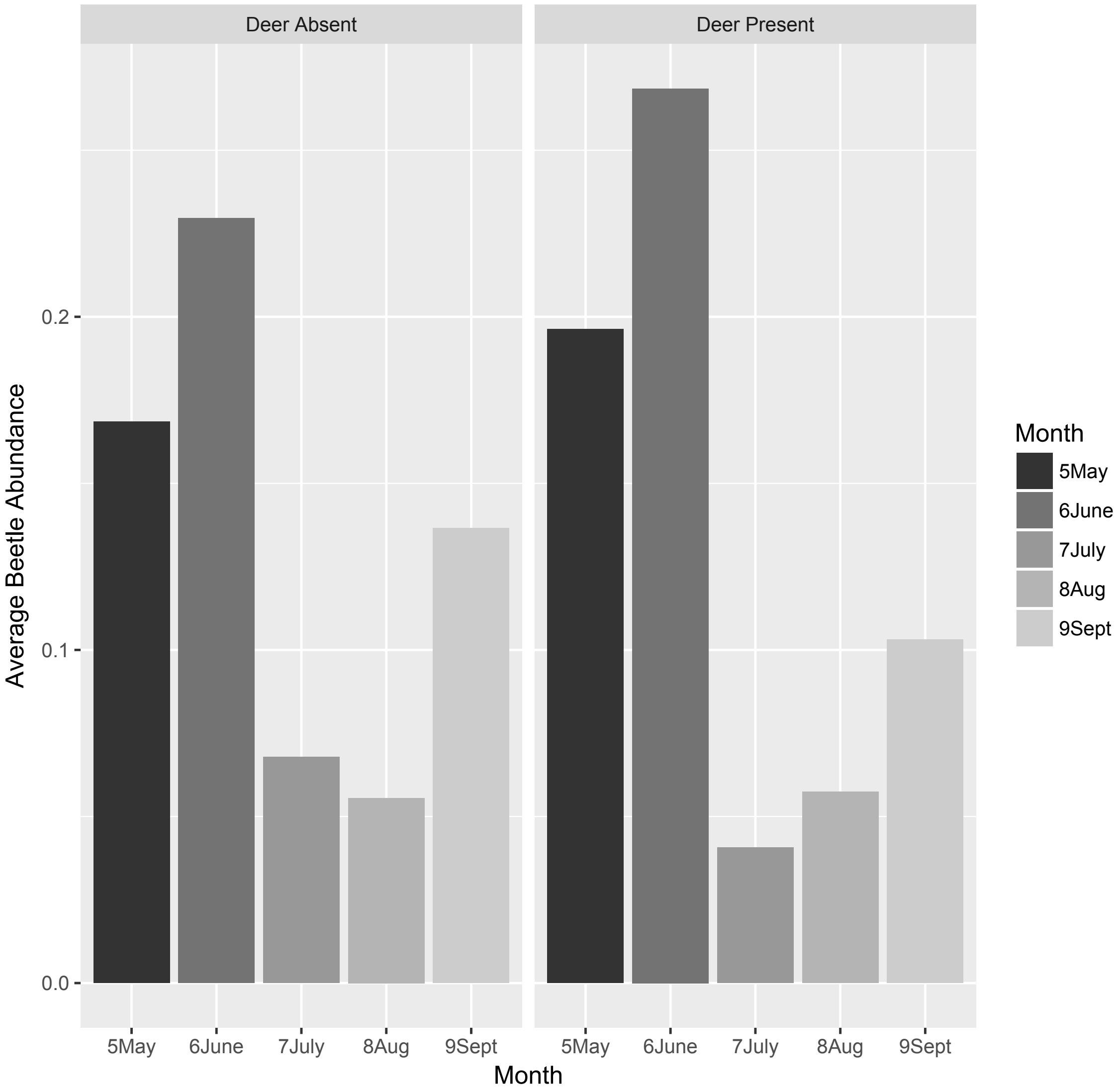

Fig 3.32: Average aerial beetle abundance between the interaction of deer presence/absence and sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

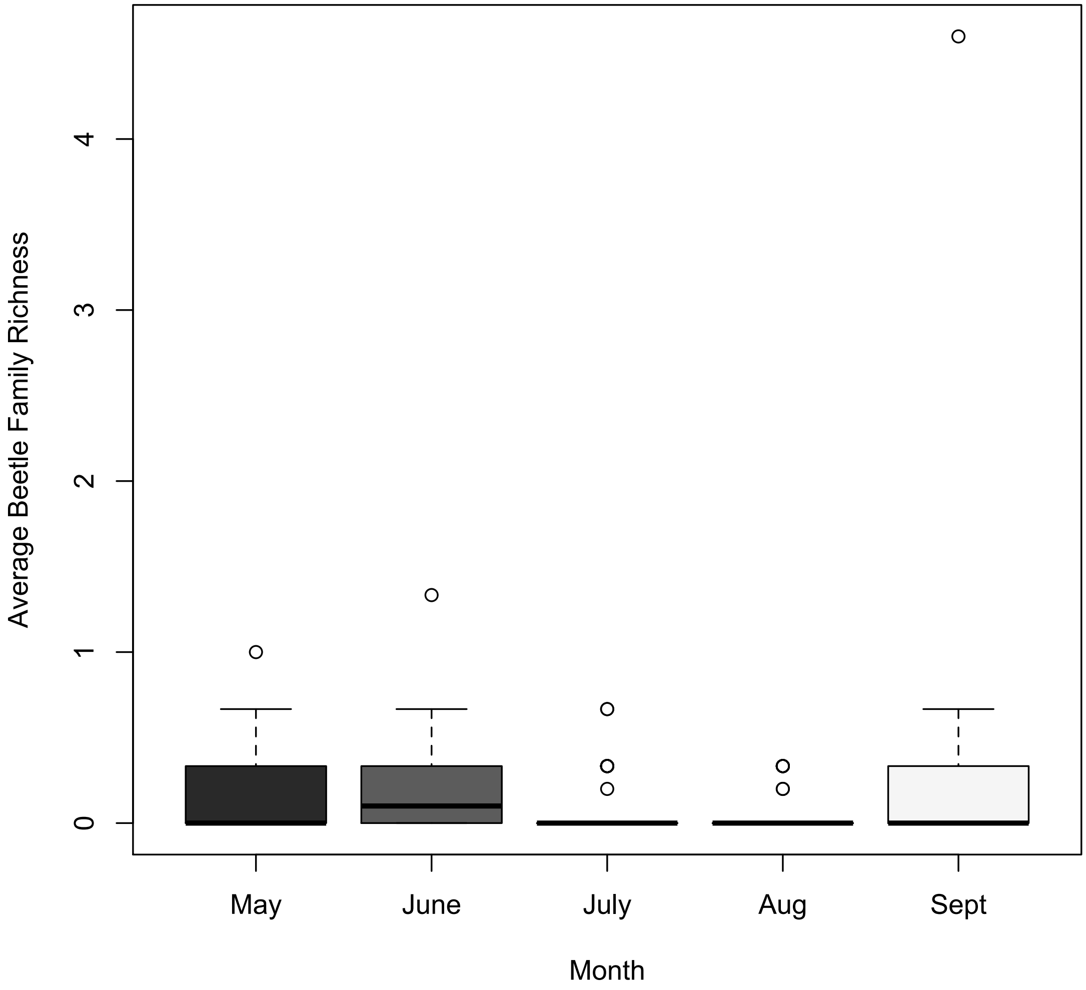

Fig 3.33: Aerial beetle family richness across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

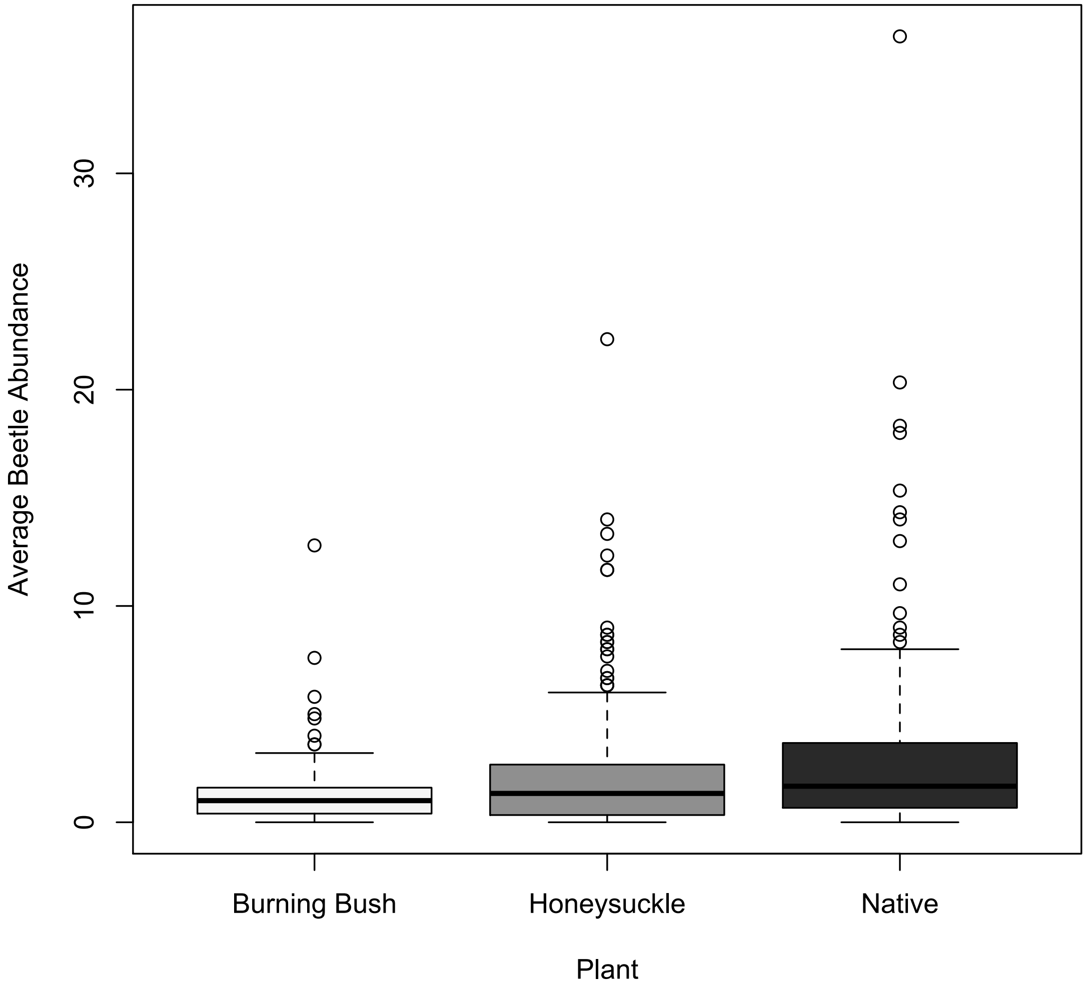

Fig 3.34: Ground beetle abundance across dominant plant plots; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

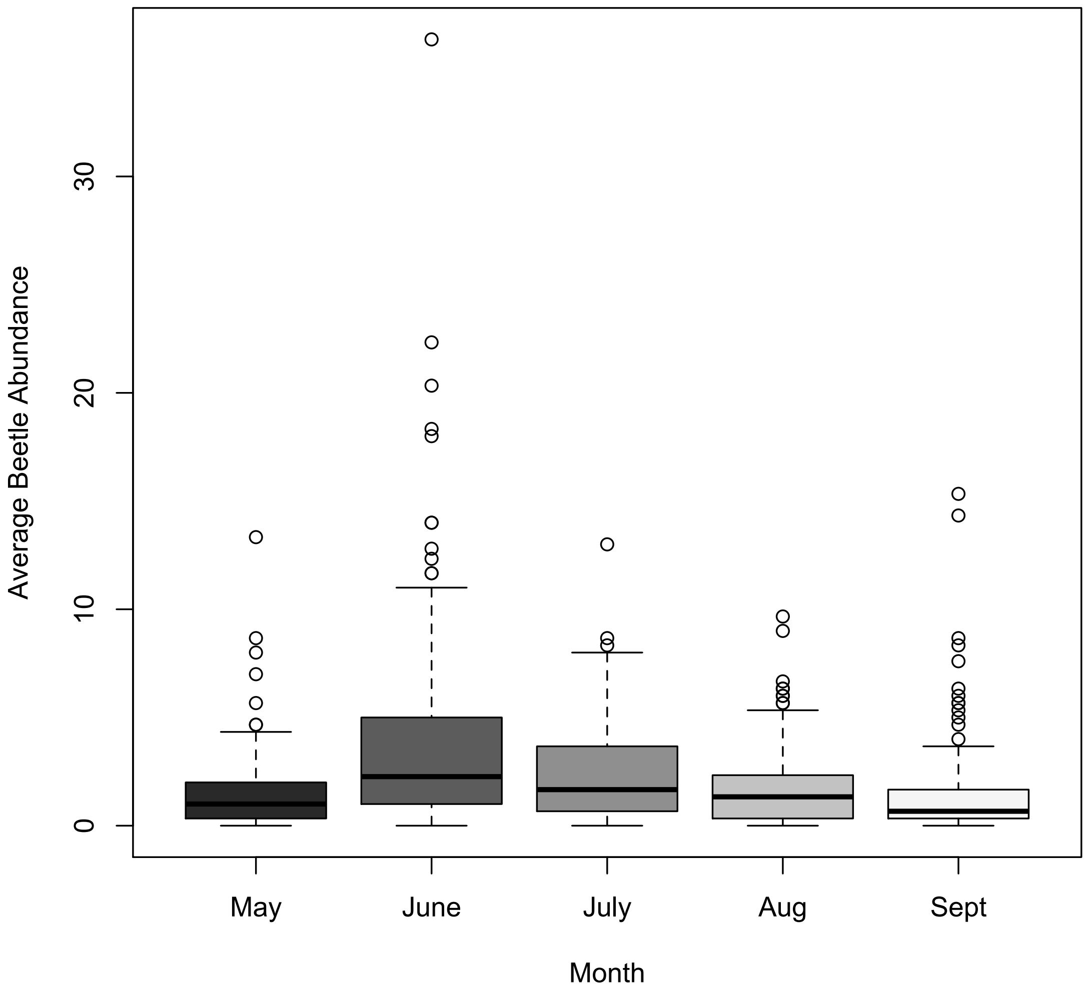

Fig 3.35: Ground beetle abundance across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

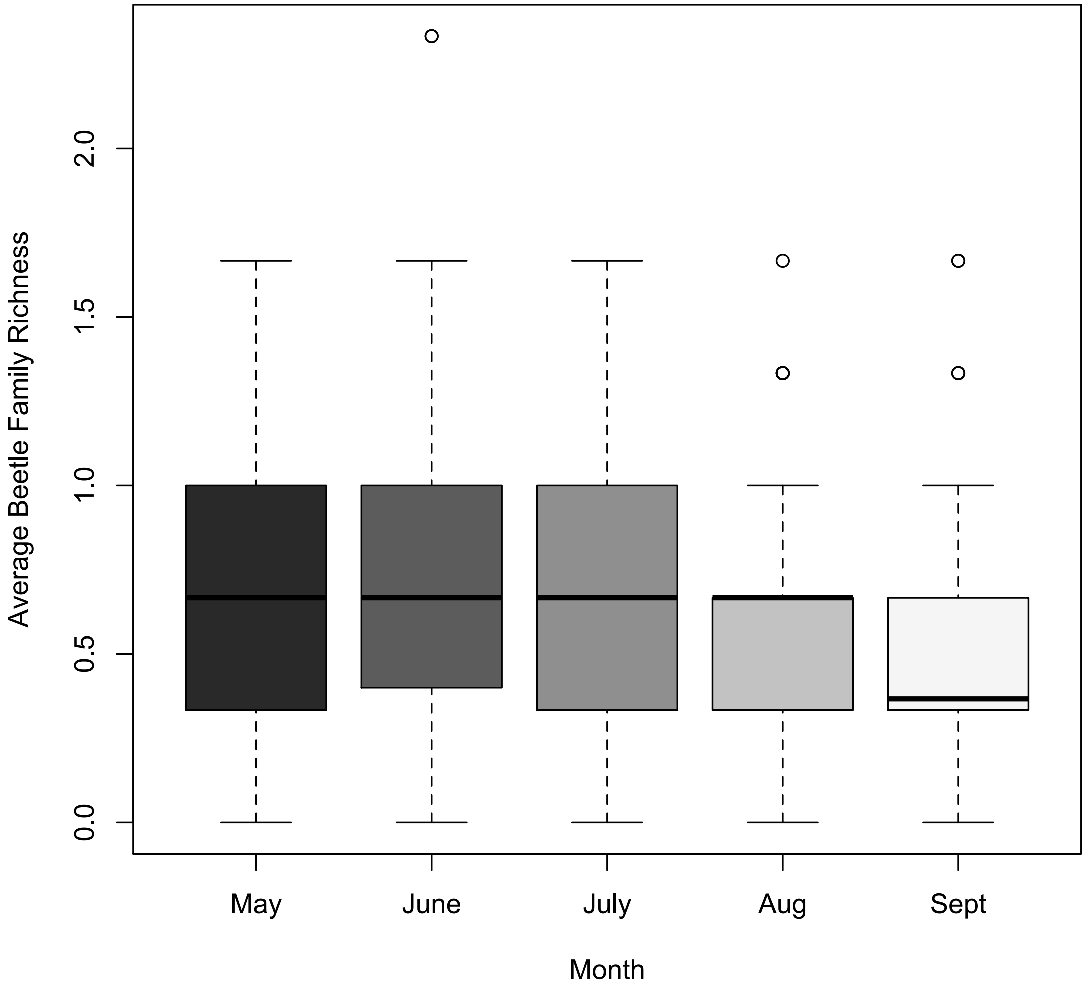

Fig 3.36: Ground beetle family richness across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

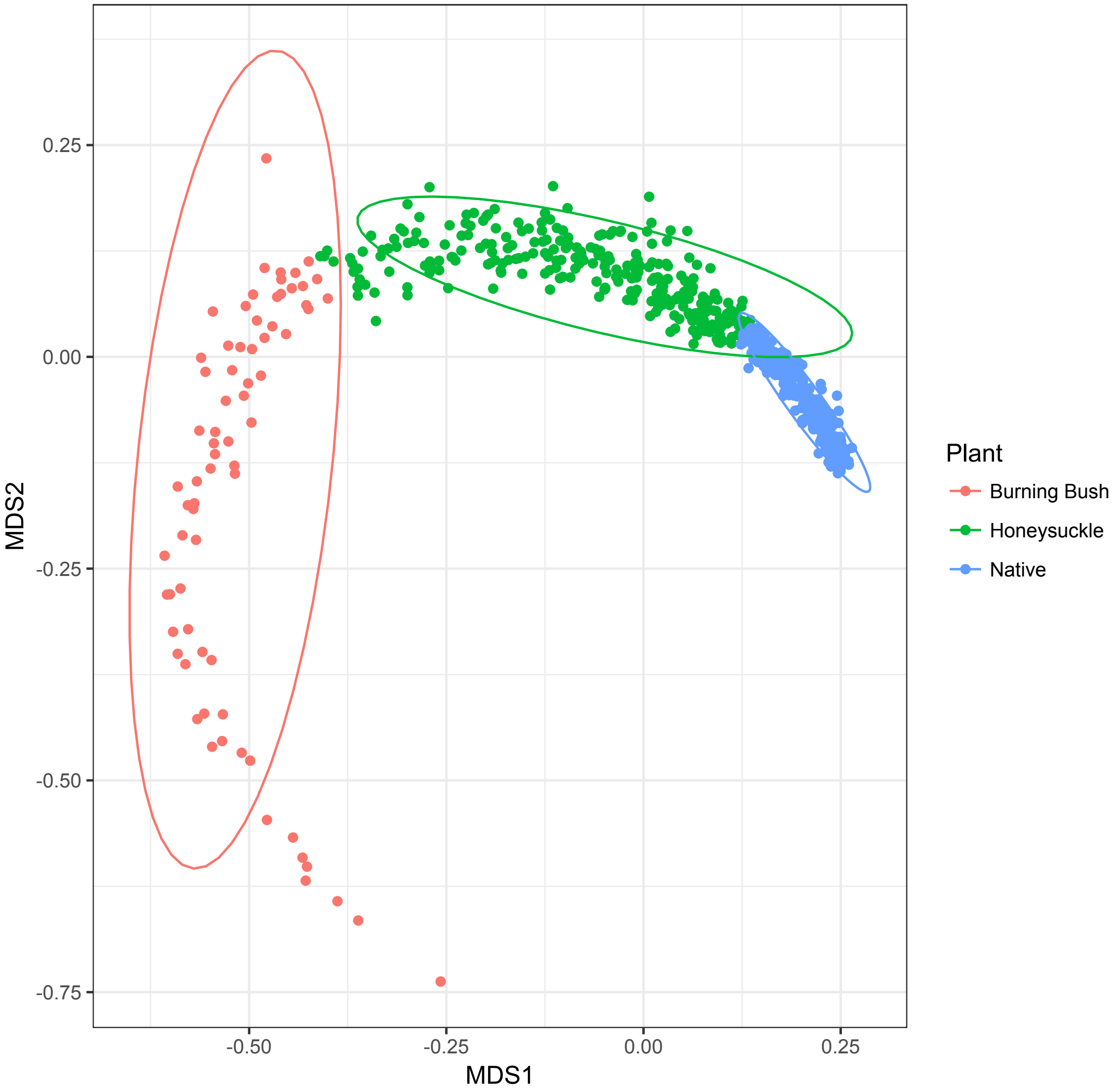

Fig 3.37: ANOSIM of environmental characteristics in dominant plant plot; abundance of each order was averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year; visualized using NMDS

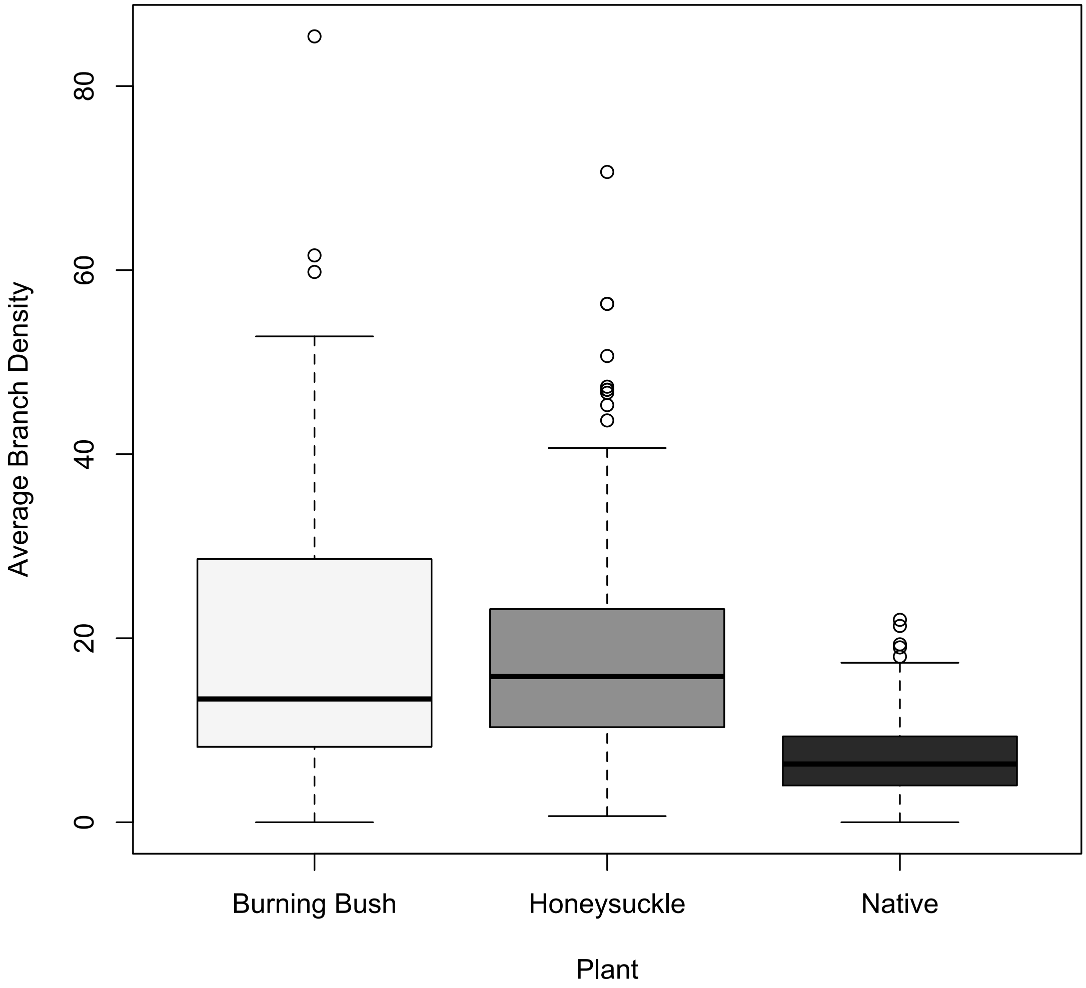

Fig 3.38: Branch density across dominant plant species; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

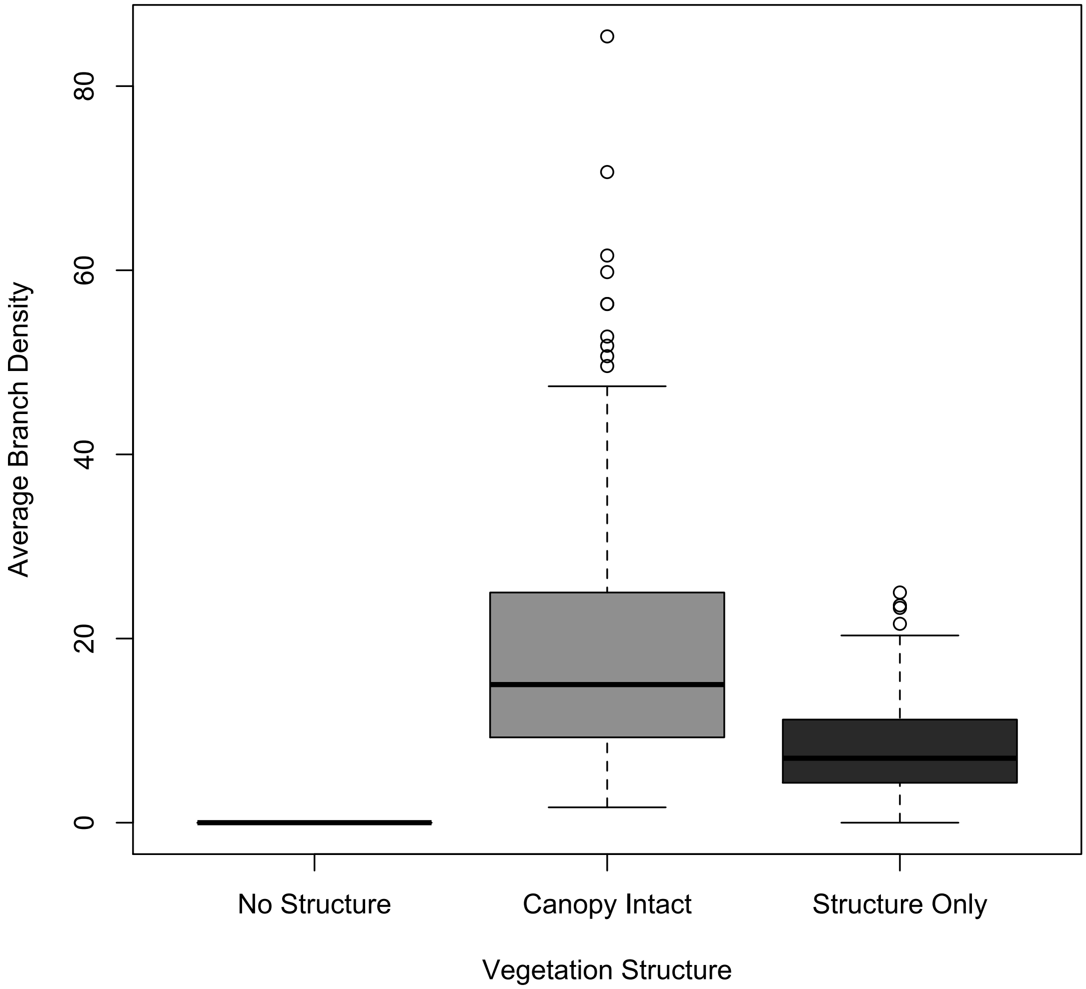

Fig 3.39: Branch density across invasive plant management treatments; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

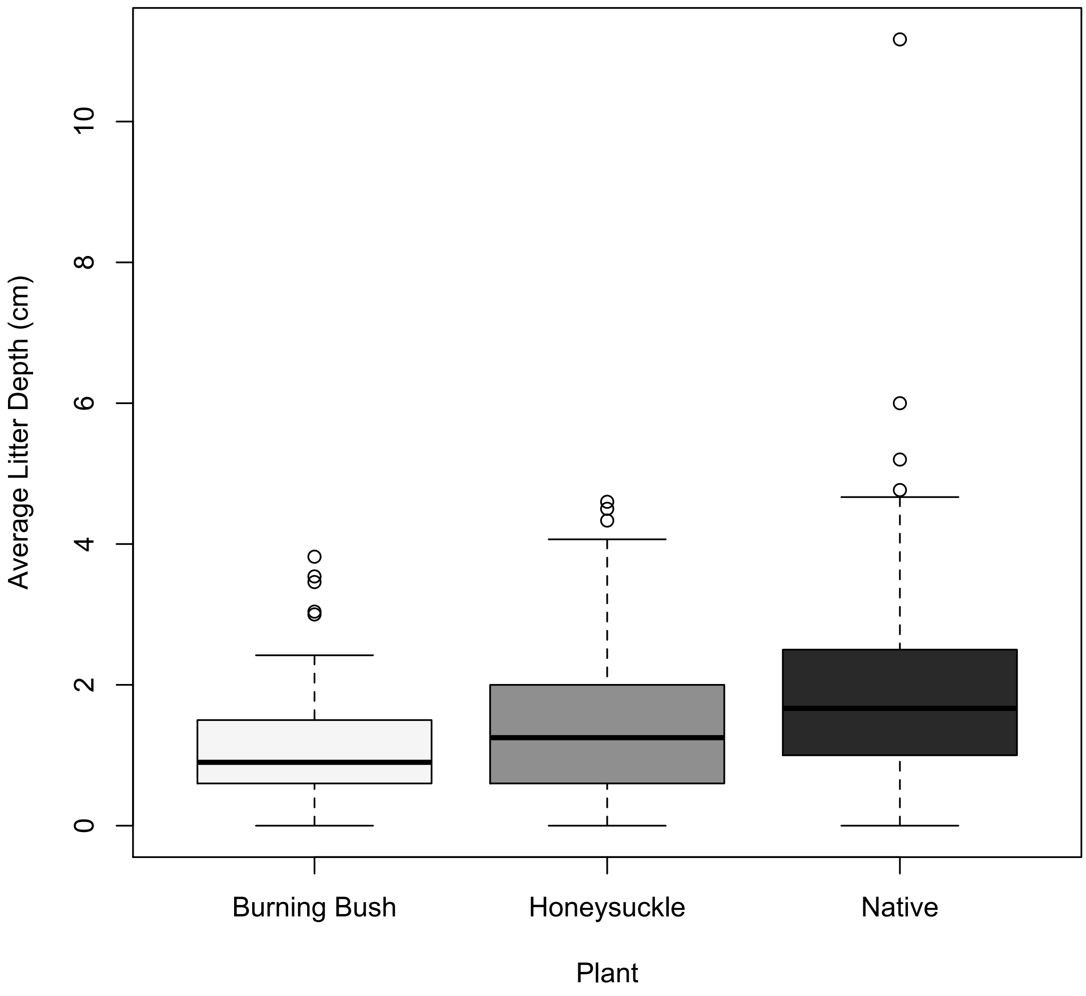

Fig 3.40: Average litter depth across dominant plant species; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

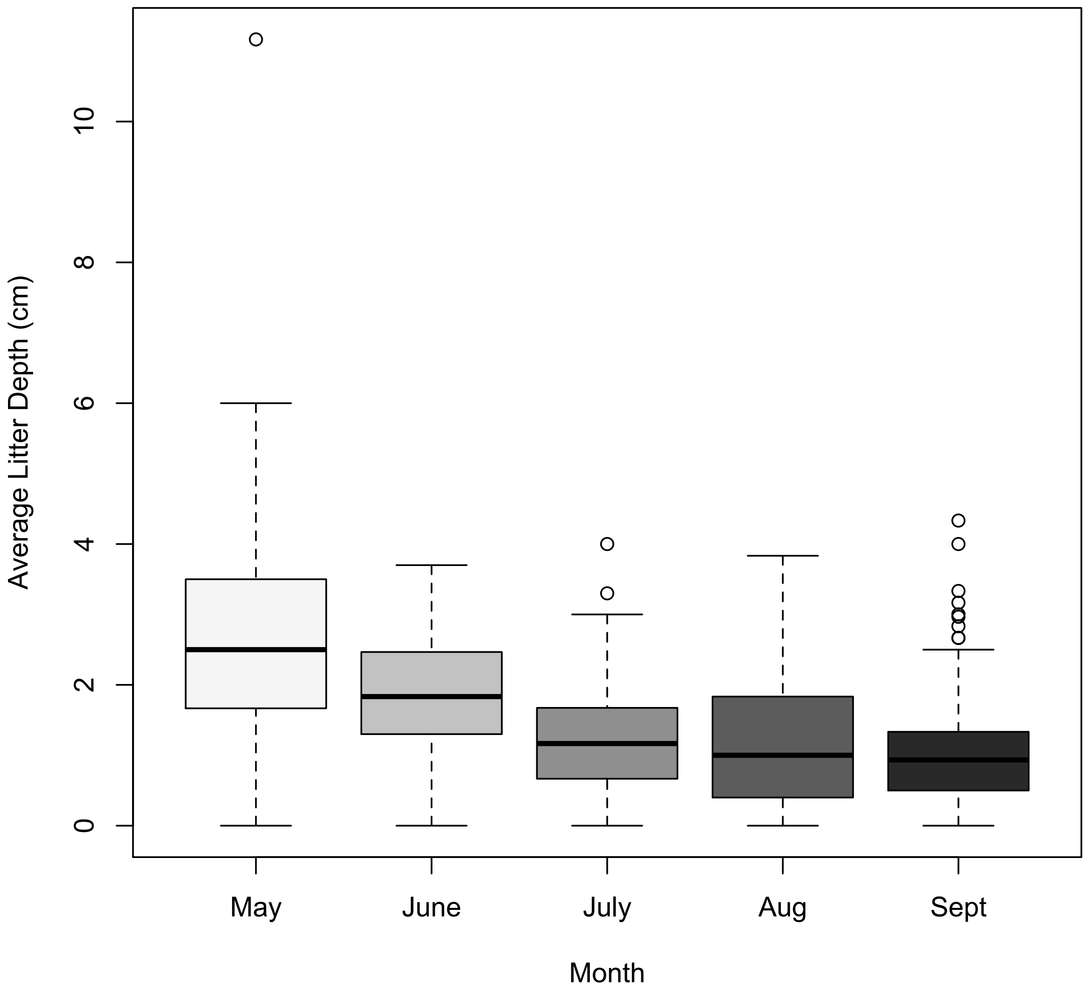

Fig 3.41: Average litter depth across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

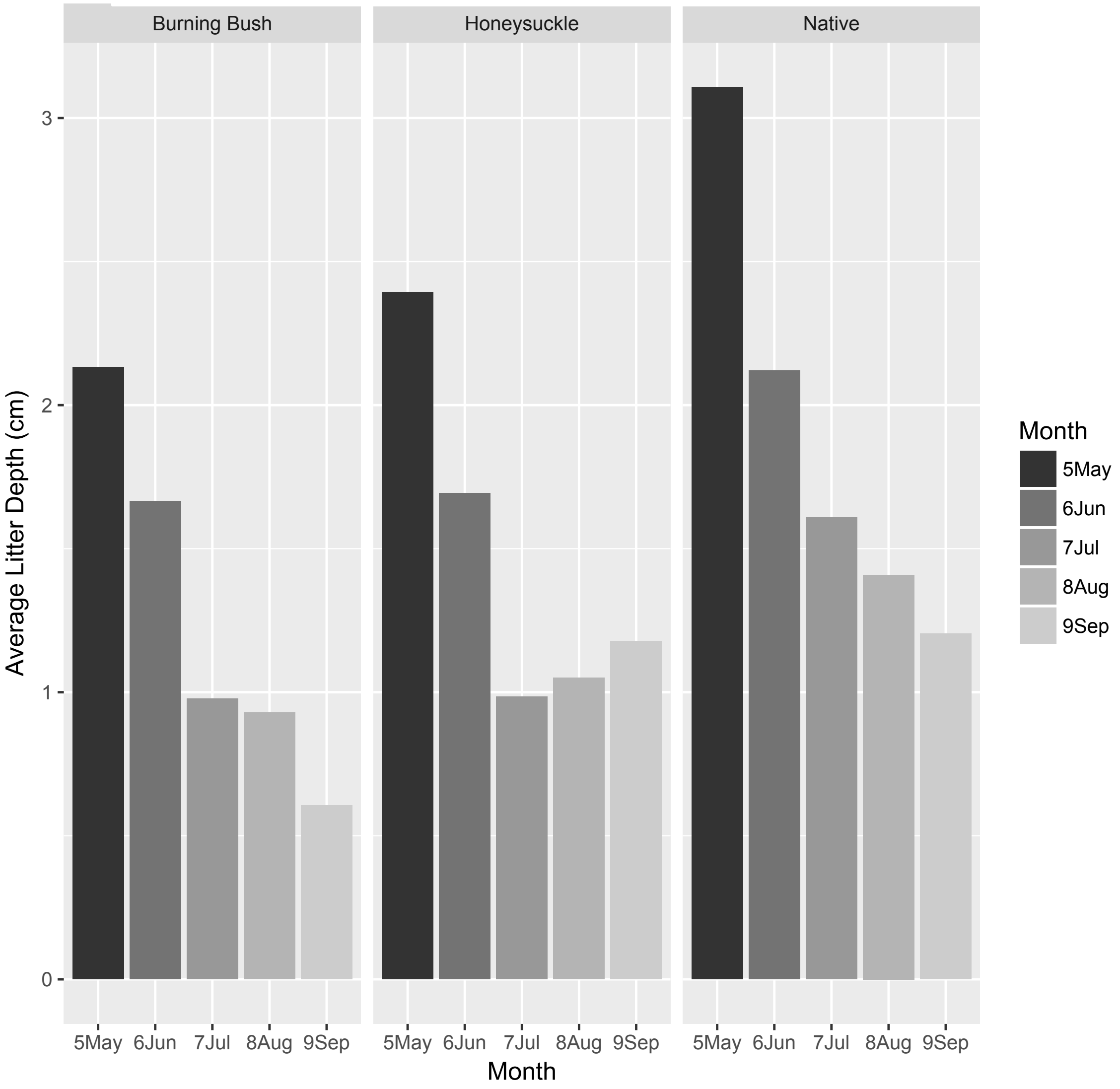

Fig 3.42: Average litter depth across the interaction between dominant plant species and sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

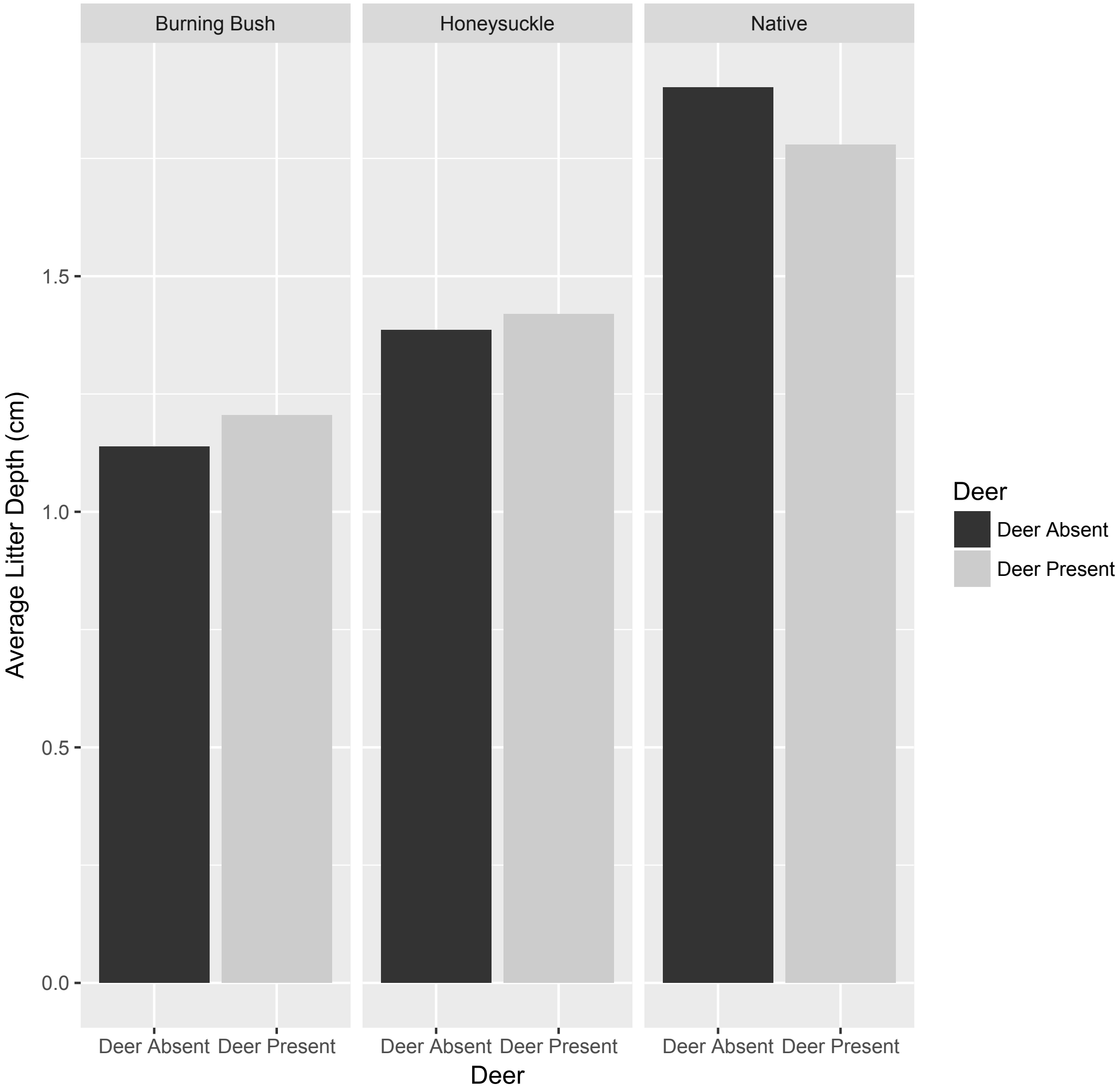

Fig 3.43: Litter depth between dominant plant and deer presence treatments; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

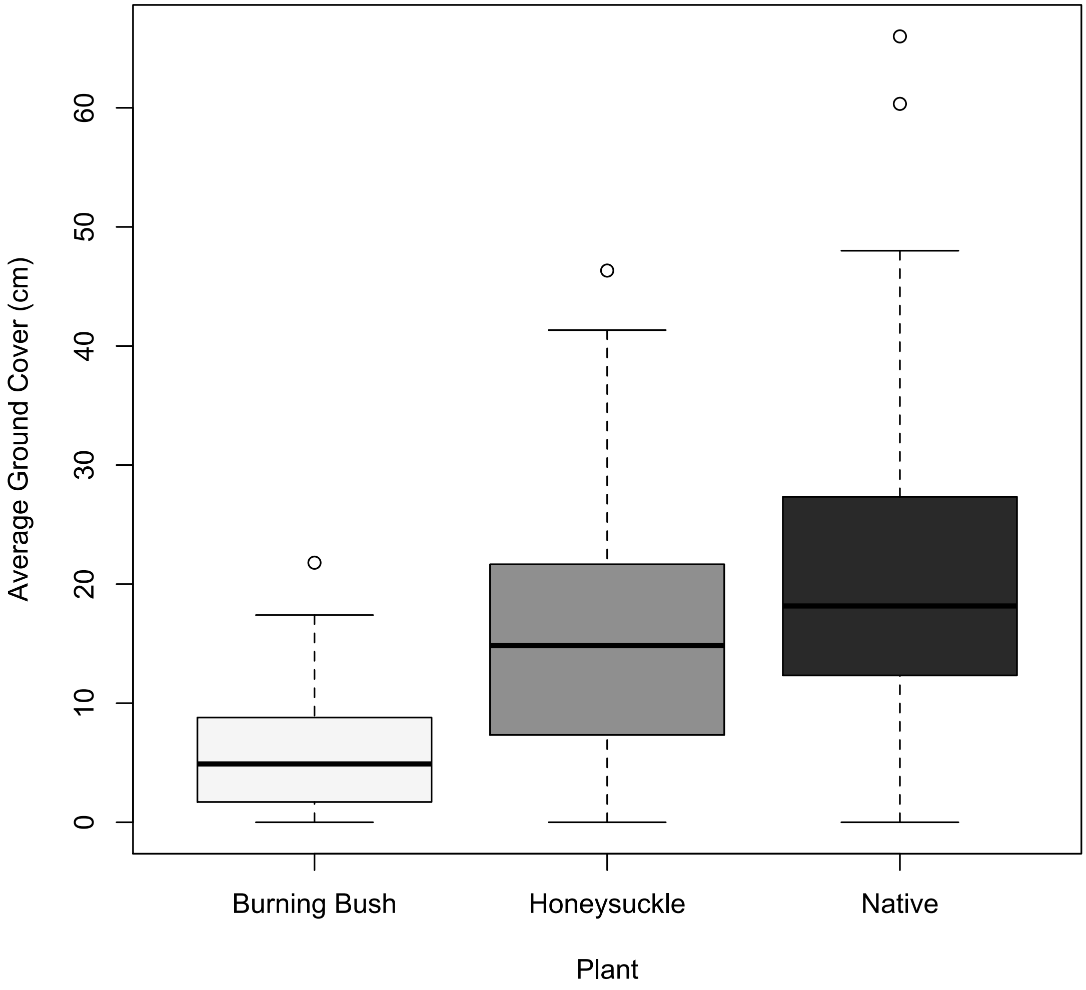

Fig 3.44: Vegetation cover across dominant plant species; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

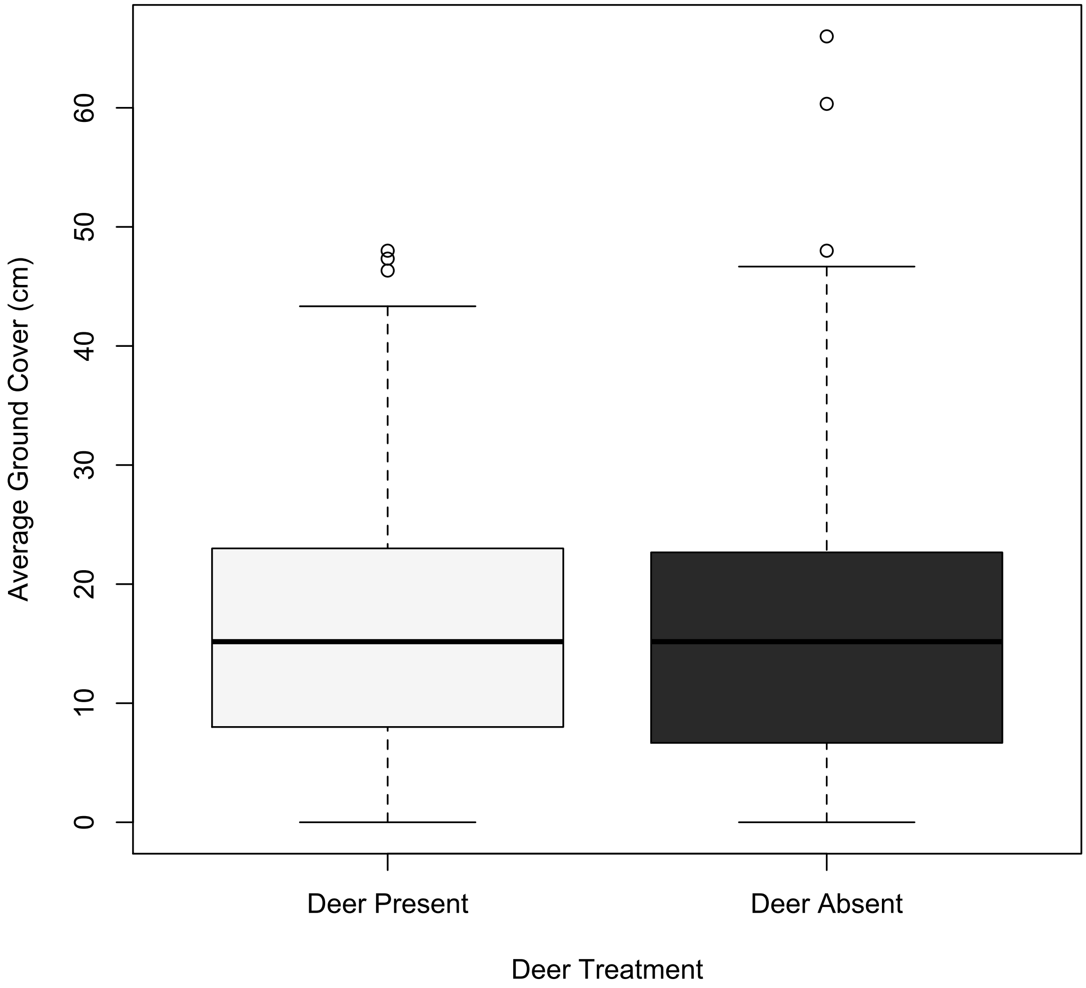

Fig 3.45: Vegetation cover differences between deer presence; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

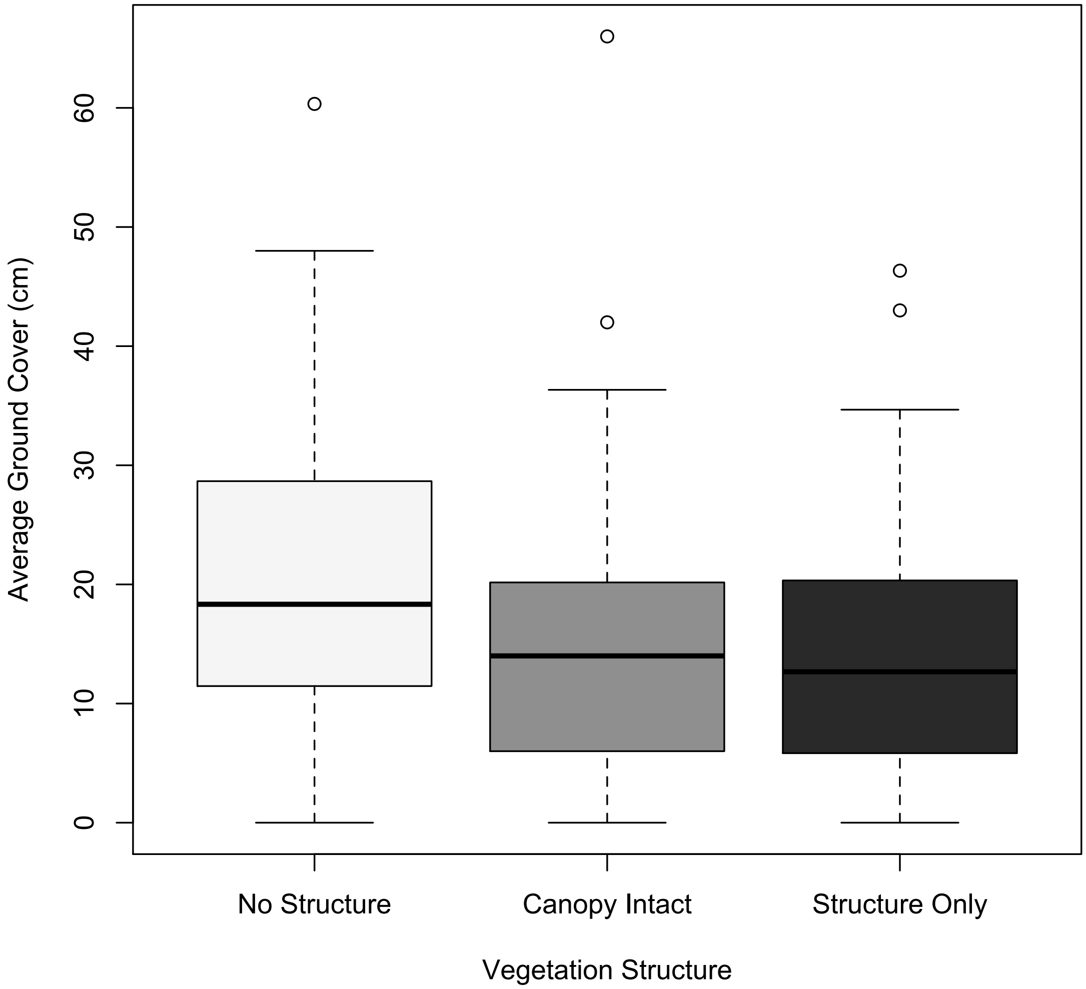

Fig 3.46: Vegetation cover differences between invasive plant management strategies; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

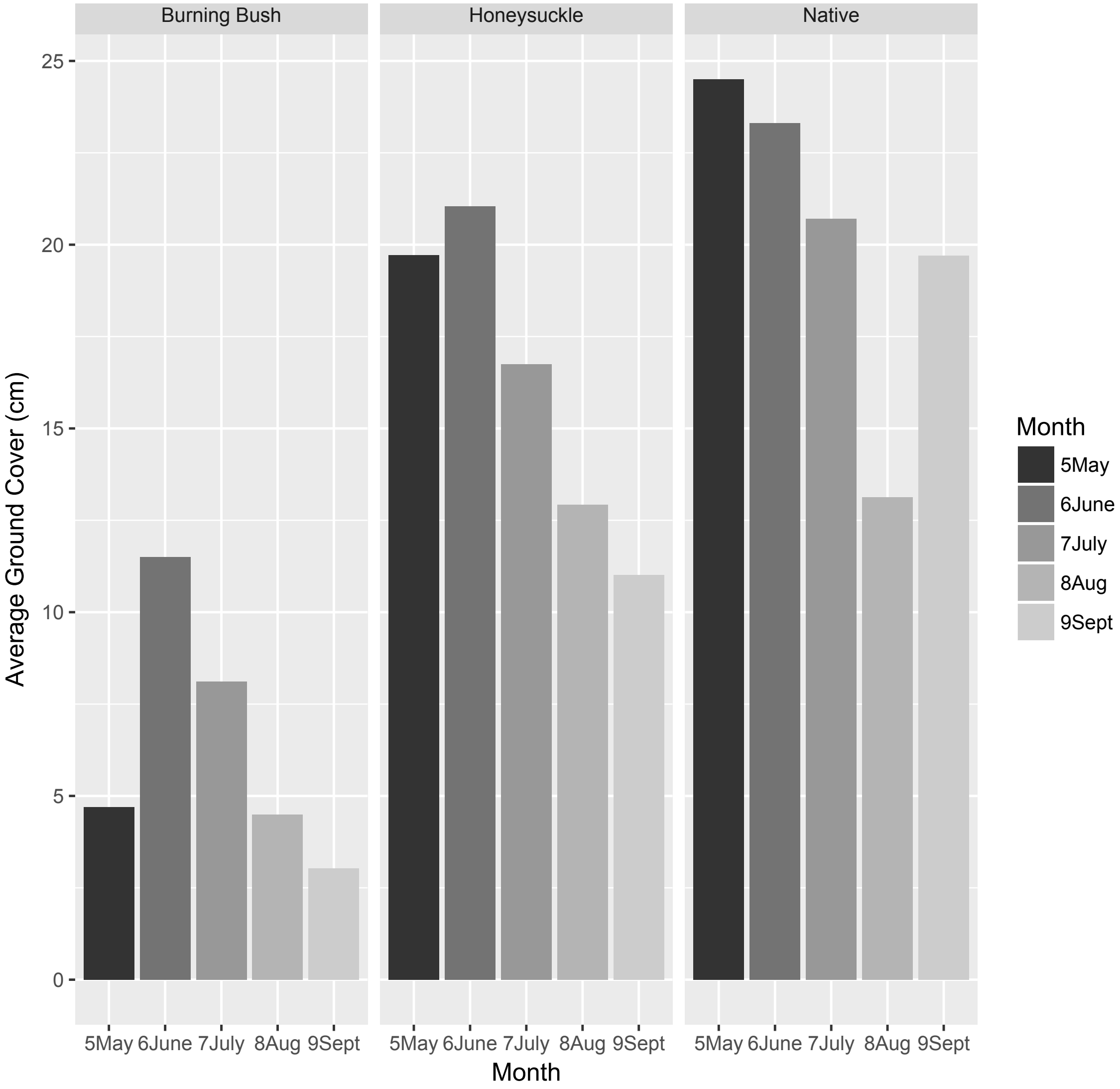

Fig 3.47: Herb-layer vegetation cover between the interaction of dominant plant and sampling month; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

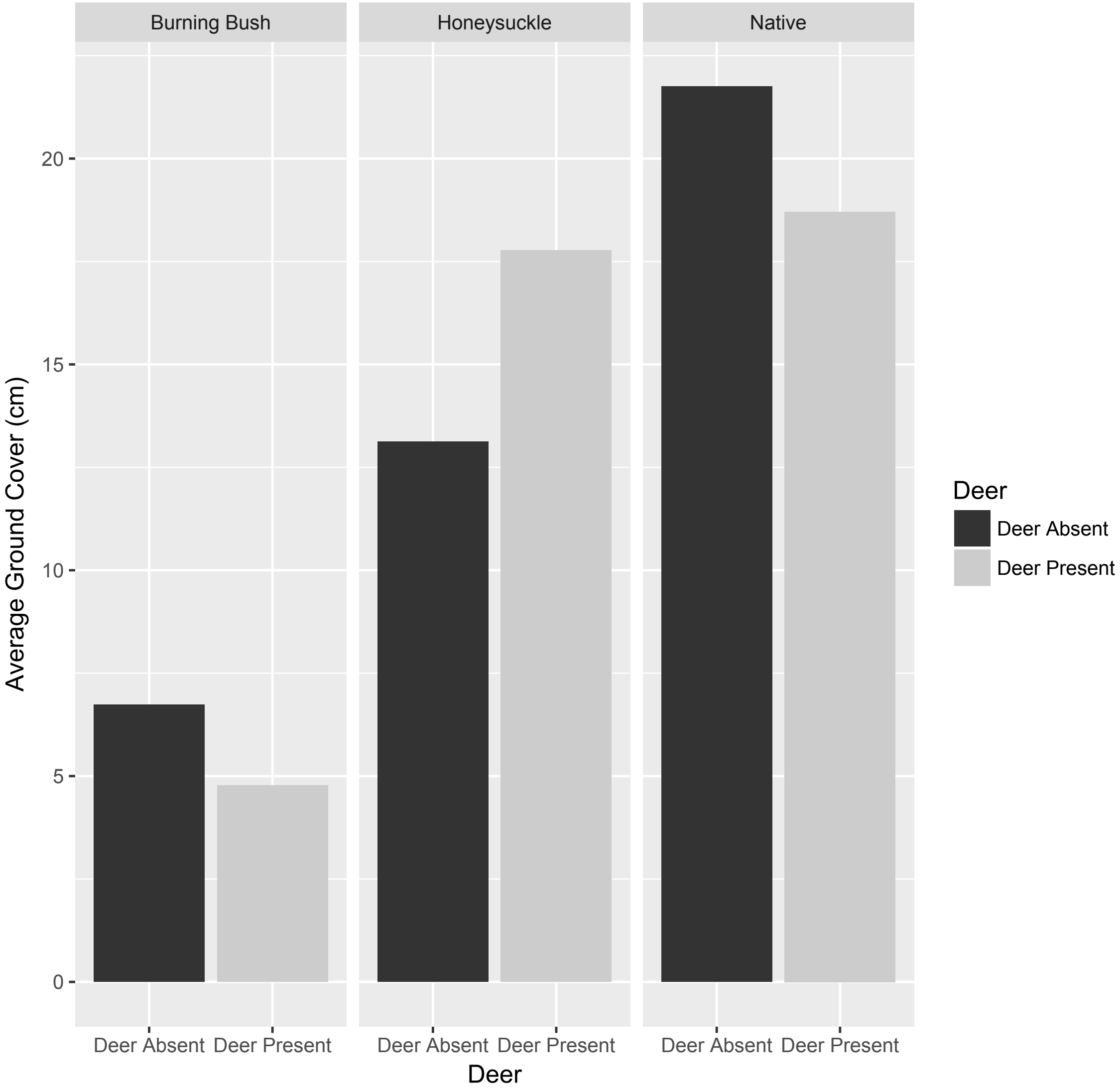

Fig 3.48: Average herb-layer vegetation ground cover measured between the interaction of dominant plant and deer presence; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

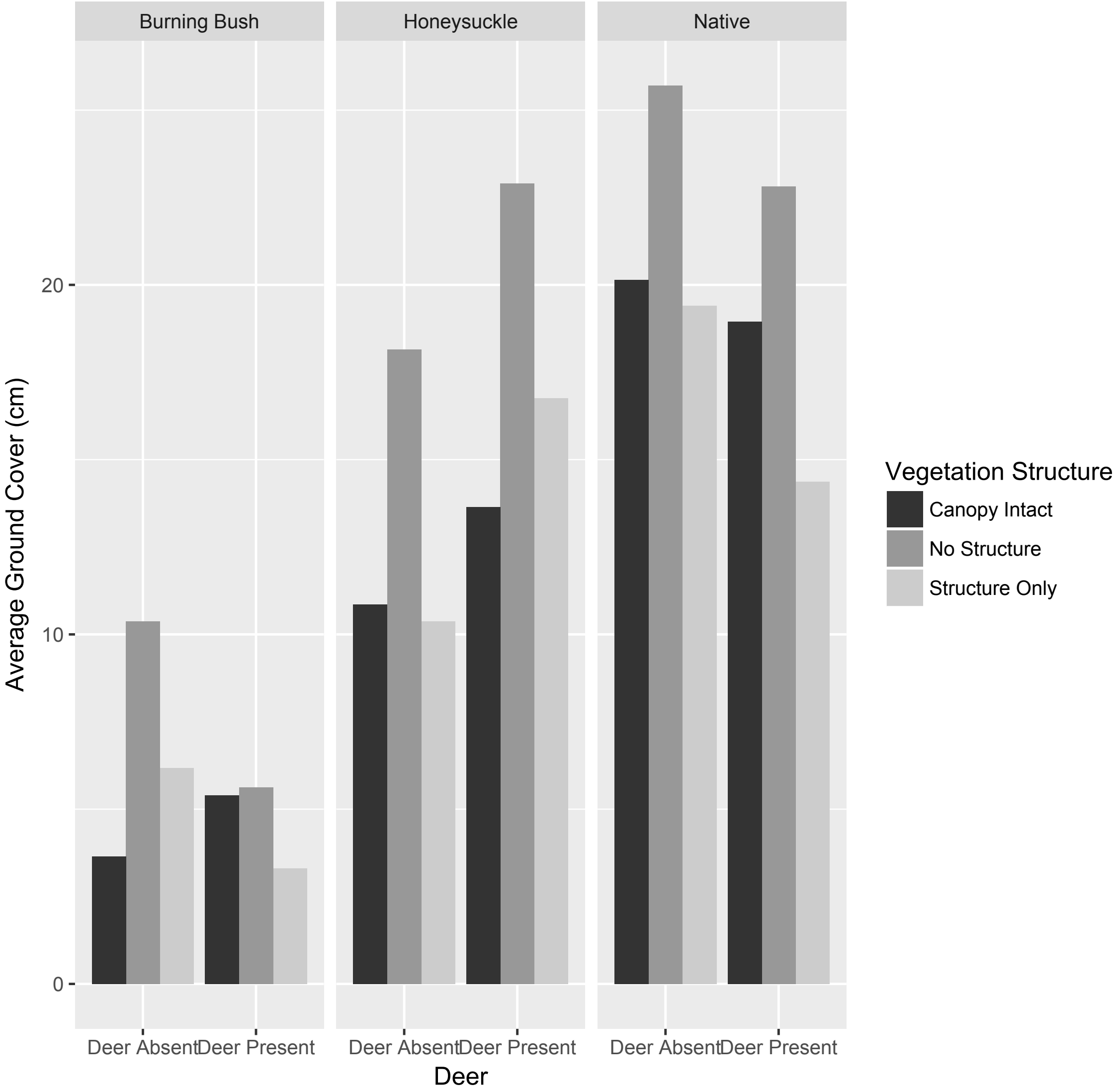

Fig 3.49: Average herb-layer vegetation ground cover measured between the interaction of dominant plant, deer presence, and invasive plant management; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

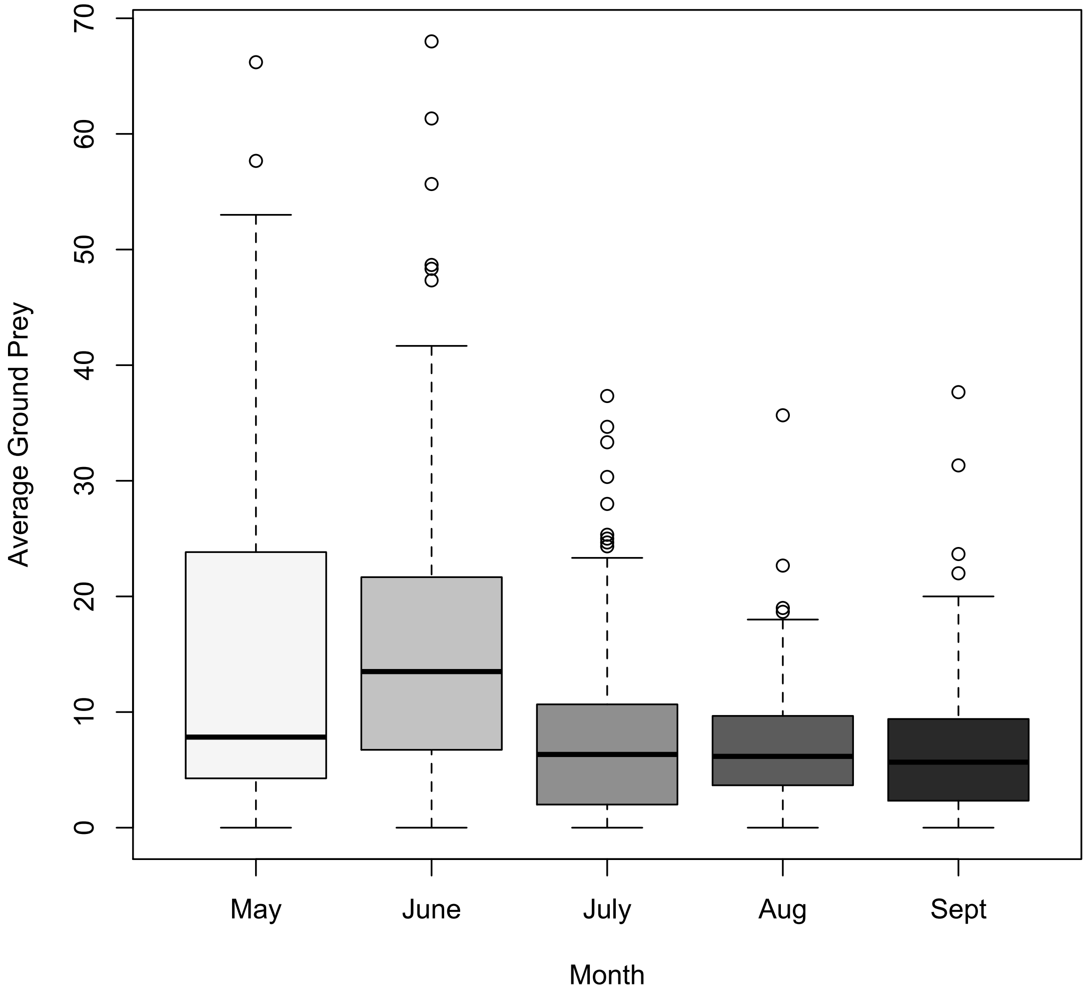

Fig 3.50: Ground prey abundance across sampling months; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

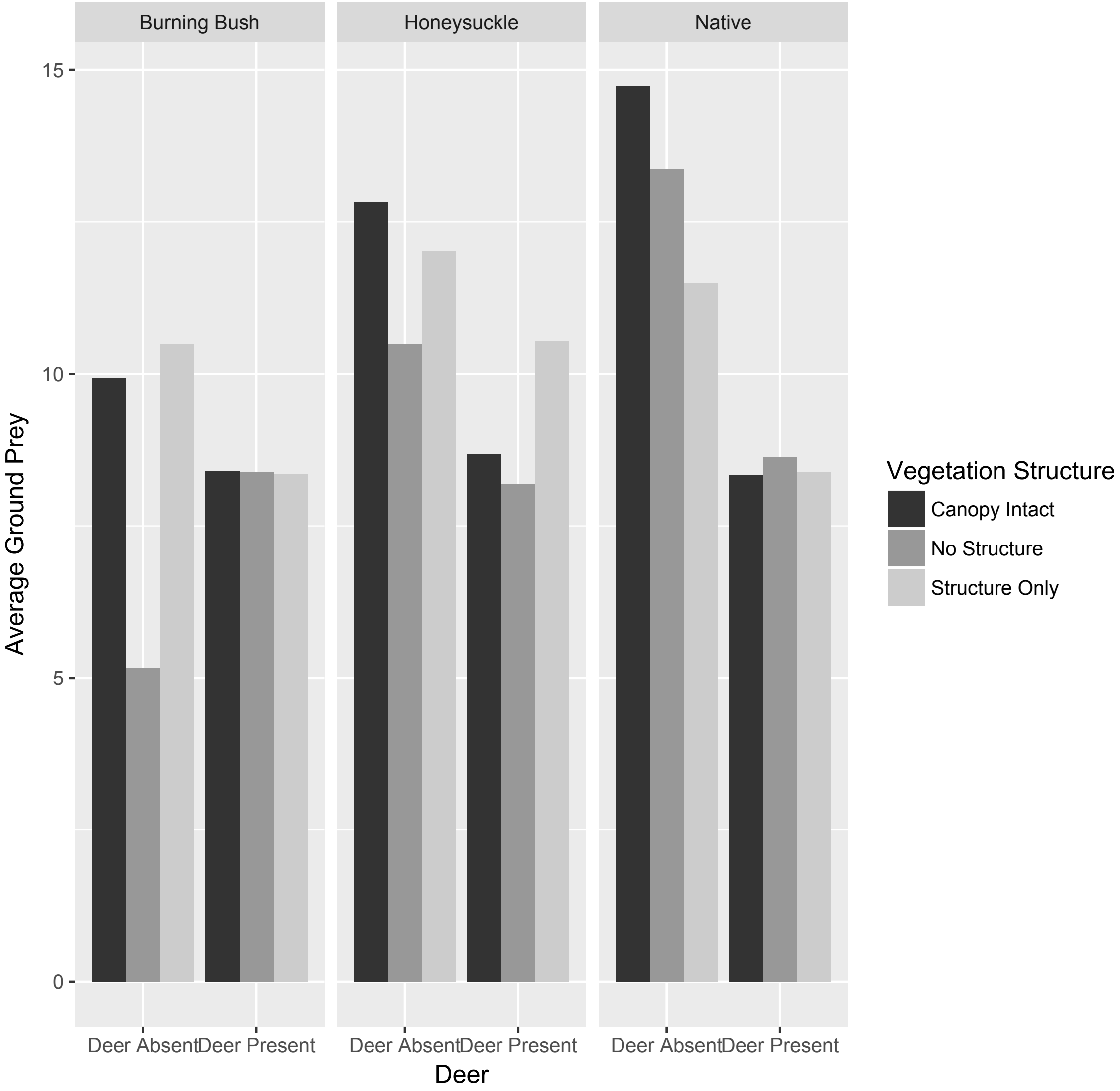

Fig 3.51: Ground prey measured between the interaction of dominant plant, deer presence, and invasive plant management; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

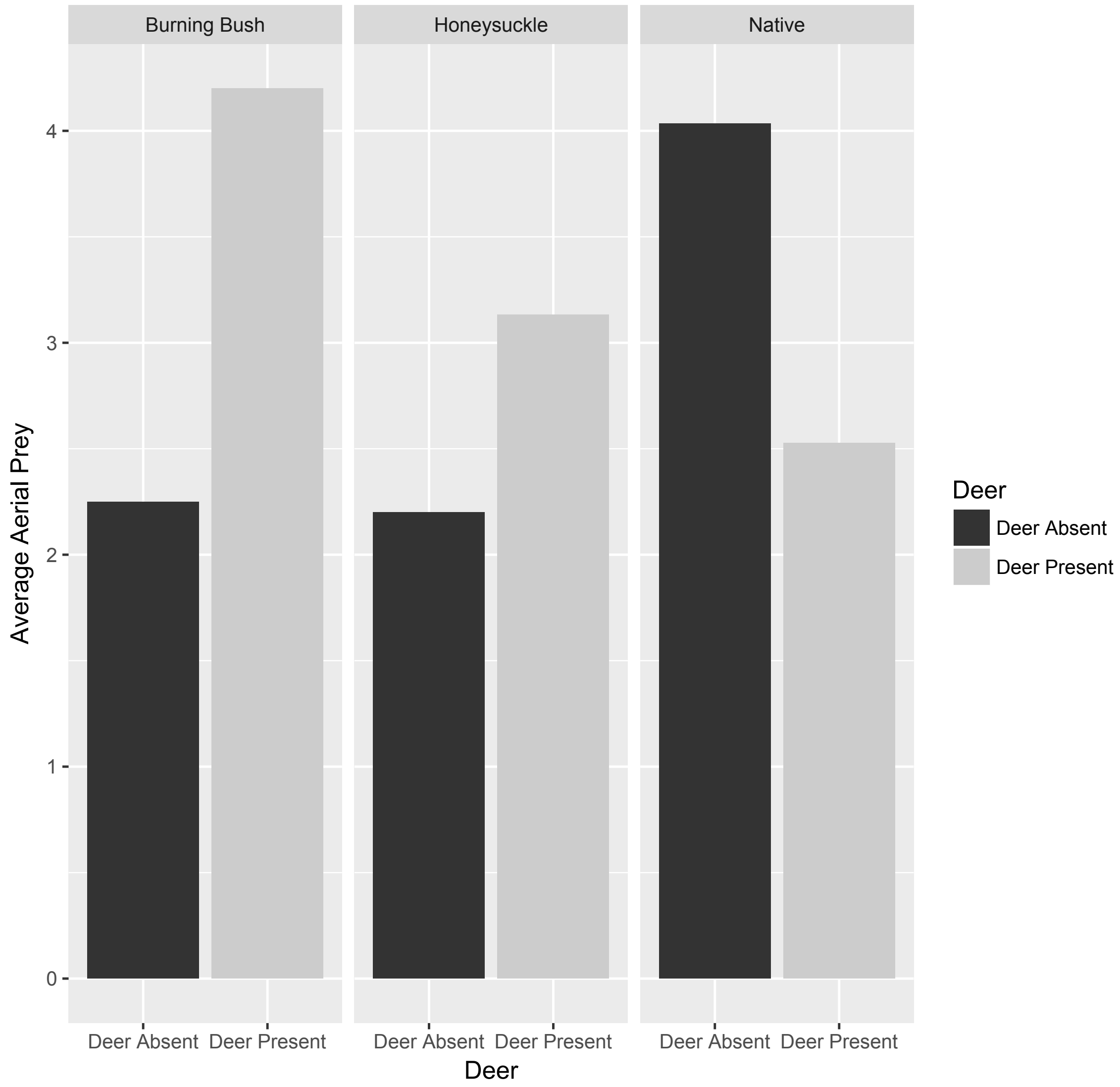

Fig 3.52: Aerial prey measured between the interaction of dominant plant and deer; samples were averaged across all plots for each combination of dominant plant type, deer presence/absence, and management strategy and sampling year

Dominant Plant	Coleoptera	Hemiptera	Hymenoptera	Orthoptera	Diptera	Isopoda	Collembola	Dermaptera	Opiliones	Araneae
BB	**7.42**	**1.77**	**7.86**	**4.43**	**8.97**	**3.59**	**24.17**	**0.29**	**8.64**	**11.40**
May	6.00	1.09	6.73	10.27	6.82	1.55	79.82	0.18	12.82	14.50
Aug	7.00	1.17	10.17	3.33	9.08	5.58	11.17	0.00	9.25	13.83
June	14.83	4.75	7.17	5.92	14.42	5.33	34.83	0.17	11.50	17.25
July	5.00	0.75	7.50	2.19	4.63	3.06	5.63	0.25	7.25	12.28
Sept	5.78	1.50	7.78	2.61	10.44	2.83	8.22	0.67	5.00	2.94
HS	**6.62**	**1.48**	**4.90**	**2.07**	**6.12**	**4.74**	**15.02**	**0.98**	**5.94**	**6.06**
May	6.25	1.83	3.88	3.40	4.21	4.13	33.10	1.63	7.71	6.38
Aug	5.63	0.44	4.31	1.38	4.21	5.60	5.75	0.21	5.38	6.69
June	11.98	3.44	5.35	2.25	11.10	9.06	29.31	0.71	5.73	6.00
July	6.18	1.51	6.08	1.81	4.08	3.29	7.68	1.85	8.24	7.90
Sept	3.67	0.31	4.35	1.70	7.81	2.63	4.28	0.19	2.00	2.81
N	**7.85**	**1.36**	**5.18**	**2.68**	**8.39**	**5.29**	**12.21**	**1.30**	**5.16**	**6.26**
May	4.67	1.38	2.25	1.83	3.94	2.10	23.58	2.00	4.25	5.81
Aug	5.90	0.54	4.63	2.58	6.85	7.23	6.31	0.42	4.44	6.67
June	13.90	3.02	4.71	3.04	14.38	7.25	19.35	1.17	5.98	5.77
July	8.35	1.40	8.21	3.26	6.15	5.39	8.25	2.08	8.51	9.36
Sept	6.37	0.54	4.65	2.41	11.35	4.54	6.28	0.56	1.41	2.57

Table 3.2: total arthropod community composition (aerial- and ground-dwelling) for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant orders; values are averages per plot

Dominant Plant	Coleoptera	Opiliones	Psocoptera	Diptera	Hemiptera	Araneae
BB	**0.35**	**0.52**	**0.02**	**0.67**	**0.06**	**6.02**
May	0.50	1.50	0.13	0.63	0.00	5.38
Aug	0.25	0.50	0.00	0.13	0.00	10.63
June	1.00	0.38	0.00	1.00	0.38	3.50
July	0.08	0.42	0.00	0.58	0.00	5.42
Sept	0.17	0.08	0.00	0.92	0.00	5.67
HS	**0.49**	**0.49**	**0.11**	**0.49**	**0.25**	**4.08**
May	0.75	1.78	0.00	0.75	0.50	3.25
Aug	0.19	0.09	0.34	0.41	0.22	5.69
June	0.91	0.59	0.09	0.41	0.28	2.13
July	0.19	0.19	0.04	0.38	0.21	3.50
Sept	0.56	0.00	0.11	0.56	0.08	5.89
N	**0.31**	**0.31**	**0.04**	**0.41**	**0.17**	**4.25**
May	0.41	0.81	0.06	0.38	0.31	2.56
Aug	0.16	0.09	0.03	0.44	0.03	7.50
June	0.63	0.59	0.00	0.53	0.19	2.63
July	0.17	0.17	0.08	0.38	0.17	3.31
Sept	0.25	0.00	0.00	0.36	0.17	5.56

Table 3.3: Aerial Arthropod community composition for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant orders; values are averages per plot

Dominant Plant	Coleoptera	Hemiptera	Hymenoptera	Diptera	Opiliones	Araneae	Collembola	Archeognatha	Orthoptera	Isopoda
BB	**11.82**	**1.72**	**7.85**	**9.10**	**9.57**	**4.39**	**26.99**	**0.08**	**5.06**	**3.65**
May	10.33	1.17	5.92	8.67	15.17	4.00	91.92	0.00	12.83	1.50
Aug	13.67	0.92	9.92	8.58	9.00	4.75	11.17	0.00	3.25	5.58
June	29.58	4.42	7.17	14.25	11.50	10.17	35.50	0.08	5.75	5.50
July	8.72	1.00	8.56	4.94	9.06	2.94	7.17	0.22	2.72	3.06
Sept	2.83	1.56	7.50	10.44	5.44	2.00	8.39	0.06	2.94	3.17
HS	**10.73**	**1.36**	**4.88**	**5.93**	**5.72**	**3.51**	**15.09**	**0.51**	**2.03**	**4.84**
May	11.25	1.54	3.65	3.98	6.79	1.38	33.50	0.00	3.31	4.13
Aug	11.33	0.40	4.13	3.94	5.29	5.88	5.71	0.63	1.33	5.83
June	22.29	3.29	5.33	10.81	5.50	3.63	29.13	0.04	1.98	9.29
July	8.14	1.40	6.21	4.15	8.14	4.54	7.76	1.04	1.90	3.33
Sept	2.93	0.28	4.48	7.46	2.13	1.83	4.37	0.59	1.72	2.63
N	**12.51**	**1.29**	**5.33**	**8.37**	**5.04**	**3.36**	**12.19**	**0.79**	**2.74**	**5.49**
May	8.19	1.23	1.85	3.46	3.71	2.81	23.27	0.00	1.92	1.96
Aug	11.56	0.50	4.58	7.02	4.38	3.44	6.25	1.00	2.58	7.25
June	27.90	2.94	4.60	14.33	5.67	2.77	19.13	0.27	2.85	7.25
July	11.75	1.38	9.10	6.17	8.65	4.83	8.57	1.75	3.43	5.99
Sept	4.56	0.44	4.69	11.59	1.44	2.33	6.30	0.46	2.57	4.85

Table 3.4: Ground arthropod community composition for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant orders; values are averages per plot

Dominant Plant	Lycosidae	Theridiidae	Agelenidae	Thomididae	Araneidae	Salticidae	Linyphiidae	Anyphaenidae	Tetragnathidae	Corinnidae	All Araneae
BB	**6.61**	**0.35**	**0.22**	**0.26**	**2.77**	**0.25**	**0.25**	**0.32**	**0.30**	**0.23**	**11.40**
May	7.00	0.09	0.91	0.00	6.64	0.27	0.00	0.27	0.09	0.00	14.50
Aug	6.58	0.92	0.17	0.17	3.75	0.25	0.17	0.83	0.25	0.50	13.83
June	8.58	0.50	0.25	1.25	3.67	0.42	0.75	0.17	0.92	0.42	17.25
July	11.31	0.38	0.00	0.00	0.56	0.25	0.25	0.19	0.31	0.06	12.28
Sept	0.89	0.00	0.00	0.06	1.11	0.11	0.11	0.22	0.06	0.22	2.94
HS	**2.97**	**0.60**	**0.06**	**0.21**	**1.06**	**0.14**	**0.20**	**0.20**	**0.17**	**0.21**	**6.06**
May	3.31	0.19	0.23	0.06	1.79	0.15	0.04	0.17	0.02	0.21	6.38
Aug	2.71	1.77	0.04	0.17	0.85	0.13	0.21	0.15	0.25	0.17	6.69
June	2.44	0.94	0.02	0.38	1.10	0.19	0.33	0.10	0.25	0.02	6.00
July	4.99	0.26	0.01	0.26	0.85	0.13	0.22	0.26	0.26	0.42	7.90
Sept	0.70	0.09	0.04	0.19	0.85	0.13	0.19	0.28	0.06	0.13	2.81
N	**3.23**	**0.56**	**0.09**	**0.18**	**0.99**	**0.09**	**0.27**	**0.22**	**0.13**	**0.22**	**6.26**
May	2.83	0.13	0.21	0.02	1.48	0.08	0.29	0.21	0.04	0.23	5.81
Aug	1.58	2.06	0.10	0.19	1.04	0.02	0.48	0.46	0.10	0.35	6.67
June	1.75	0.48	0.06	0.44	1.40	0.13	0.29	0.23	0.27	0.17	5.77
July	7.38	0.21	0.03	0.17	0.54	0.10	0.22	0.11	0.18	0.18	9.36
Sept	0.83	0.17	0.06	0.09	0.74	0.09	0.11	0.15	0.02	0.20	2.57

Table 3.5: Total spider community composition (aerial- and ground-dwelling) for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant families; values are averages per plot

Dominant Plant	Theridiidae	Thomisidae	Pisauridae	Araneidae	Salticidae	Linyphiidae	Anyphaenidae	Tetragnathidae	Ulubrionidae
BB	**1.21**	**0.08**	**0.17**	**3.04**	**0.15**	**0.08**	**0.42**	**0.52**	**0.21**
May	1.25	0.13	0.00	1.38	0.13	0.38	0.13	1.75	0.13
Aug	1.25	0.13	0.25	6.88	0.13	0.00	1.38	0.25	0.00
June	0.75	0.00	0.50	1.13	0.13	0.00	0.25	0.63	0.00
July	0.75	0.00	0.08	3.17	0.25	0.00	0.08	0.33	0.67
Sept	1.92	0.17	0.08	2.75	0.08	0.08	0.42	0.00	0.08
HS	**0.83**	**0.09**	**0.04**	**2.15**	**0.22**	**0.07**	**0.37**	**0.22**	**0.04**
May	0.97	0.13	0.03	1.16	0.34	0.22	0.31	0.06	0.00
Aug	2.53	0.13	0.03	1.94	0.28	0.03	0.41	0.22	0.09
June	0.09	0.13	0.06	1.03	0.19	0.03	0.00	0.47	0.00
July	0.25	0.04	0.04	2.08	0.15	0.00	0.54	0.29	0.10
Sept	0.64	0.08	0.03	4.31	0.19	0.08	0.47	0.03	0.00
N	**1.04**	**0.06**	**0.12**	**2.06**	**0.13**	**0.06**	**0.34**	**0.29**	**0.06**
May	1.19	0.06	0.00	0.69	0.09	0.13	0.16	0.03	0.00
Aug	3.25	0.09	0.16	2.63	0.13	0.00	0.56	0.41	0.16
June	0.59	0.03	0.03	0.97	0.06	0.09	0.09	0.66	0.03
July	0.35	0.04	0.23	1.79	0.15	0.06	0.25	0.33	0.08
Sept	0.25	0.08	0.14	4.08	0.19	0.03	0.64	0.03	0.03

Table 3.6: Aerial spider community composition for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant families; values are averages per plot

Dominant Plant	Lycosidae	Theridiidae	Agelenidae	Thomisidae	Linyphiidae	Corinnidae	Araneae
BB	**2.75**	**0.21**	**0.13**	**0.35**	**0.42**	**0.28**	**4.39**
May	2.25	0.17	0.00	0.42	0.25	0.50	4.00
Aug	3.33	0.17	0.00	0.17	0.58	0.25	4.75
June	7.33	0.17	0.17	0.92	0.67	0.50	10.17
July	1.28	0.39	0.06	0.33	0.50	0.22	2.94
Sept	1.11	0.11	0.33	0.06	0.17	0.06	2.00
HS	**2.66**	**0.09**	**0.07**	**0.13**	**0.15**	**0.20**	**3.51**
May	0.94	0.04	0.08	0.04	0.02	0.08	1.38
Aug	4.85	0.10	0.10	0.10	0.25	0.17	5.88
June	1.83	0.21	0.04	0.46	0.29	0.52	3.63
July	3.89	0.06	0.03	0.10	0.15	0.10	4.54
Sept	1.33	0.04	0.09	0.00	0.06	0.20	1.83
N	**2.38**	**0.06**	**0.11**	**0.15**	**0.22**	**0.21**	**3.36**
May	1.81	0.13	0.25	0.04	0.13	0.23	2.81
Aug	2.23	0.02	0.08	0.17	0.33	0.33	3.44
June	1.46	0.08	0.25	0.25	0.21	0.25	2.77
July	3.85	0.04	0.03	0.15	0.28	0.19	4.83
Sept	1.89	0.02	0.02	0.15	0.13	0.09	2.33

Table 3.7: Ground spider community composition for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant families; values are averages per plot

Dominant Plant	Carabidae	Staphylinidae	Curculionidae	Scarabaeidae	Silphidae	Nitidulidae	Tenebrionidae	Geotrupidae
BB	**1.41**	**4.12**	**0.68**	**0.09**	**0.10**	**0.72**	**0.03**	**0.01**
May	0.82	2.18	2.36	0.18	0.09	0.18	0.00	0.00
Aug	2.08	3.92	0.17	0.00	0.17	0.58	0.00	0.00
June	1.67	10.17	0.42	0.08	0.17	1.42	0.17	0.00
July	0.94	2.25	0.31	0.19	0.13	1.13	0.00	0.00
Sept	1.56	3.06	0.50	0.00	0.00	0.33	0.00	0.06
HS	**1.61**	**3.02**	**0.49**	**0.10**	**0.06**	**0.95**	**0.05**	**0.04**
May	1.58	2.06	1.63	0.29	0.00	0.29	0.04	0.04
Aug	2.02	2.31	0.17	0.04	0.06	0.85	0.00	0.10
June	2.17	7.10	0.42	0.19	0.23	0.75	0.17	0.02
July	0.79	2.83	0.21	0.03	0.01	2.15	0.04	0.04
Sept	1.85	1.13	0.20	0.02	0.02	0.19	0.00	0.02
N	**1.26**	**4.12**	**0.42**	**0.05**	**0.46**	**1.19**	**0.06**	**0.08**
May	1.38	1.88	0.79	0.08	0.00	0.27	0.02	0.00
Aug	1.31	3.75	0.27	0.00	0.00	0.38	0.00	0.15
June	1.56	8.21	0.23	0.13	2.44	0.75	0.17	0.06
July	0.85	3.35	0.47	0.04	0.08	3.29	0.03	0.10
Sept	1.39	3.83	0.33	0.00	0.02	0.33	0.07	0.09

Table 3.8: total beetle community composition (aerial- and ground-dwelling) for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant families; values are averages per plot

Dominant Plant	**Carabidae**	**Staphylinidae**	**Circirlionidae**	**Silphidae**
BB	**1.44**	**4.31**	**0.60**	**0.13**
May	0.83	2.00	2.00	0.08
Aug	2.08	3.92	0.17	0.17
June	1.75	10.58	0.33	0.17
July	0.83	2.89	0.22	0.22
Sept	1.83	3.33	0.50	0.00
HS	**1.61**	**3.03**	**0.42**	**0.06**
May	1.58	2.06	1.48	0.00
Aug	2.04	2.33	0.10	0.06
June	2.17	7.10	0.31	0.23
July	0.79	2.85	0.22	0.01
Sept	1.83	1.13	0.11	0.02
N	**1.32**	**4.27**	**0.37**	**0.46**
May	1.45	1.91	0.81	0.00
Aug	1.35	3.79	0.19	0.00
June	1.54	8.56	0.19	2.44
July	0.99	3.39	0.43	0.10
Sept	1.41	4.09	0.24	0.02

Table 3.9: Ground beetle community composition for the three dominant plant types (BB – burning bush; HS – honeysuckle, N – native) represented by the most abundant families; values are averages per plot

Arthropod Order	Total
Coleoptera	4412
Trichoptera	17
Mecoptera	81
Lepidoptera	109
Hemiptera	889
Hymenoptera	3263
Orthoptera	1588
Diptera	4536
Isopoda	2958
Collembola	9021
Archaeognatha	364
Lithobiomorpha	136
Blattodea	47
Chordeumatida	320
Psocoptera	31
Dermaptera	637
Acari	976
Opiliones	3593
Araneae	4146

Table 3.10: Total community composition of arthropod orders; values are total abundance collected over the entirety of the study

Beetle Families	Total
Carabidae	871
Staphylinidae	2212
Curculionidae	293
Trogossitidae	15
Scarabaeidae	47
Silphidae	147
Nitidulidae	628
Tenebrionidae	30
Chrysomelidae	20
Meloidae	4
Geotrupidae	35
Elateridae	9
Latridiidae	12
Pyrochroidae	2
Cerambycidae	15
Anobiidae	6
Leiodidae	7
Lampyridae	10
Ptilodactylidae	11
Melandryidae	1
Anthicidae	13
Ptiliidae	12
Coccinellidae	12

Table 3.11: Total community composition of beetle families; values are total abundance collected over the entirety of the study

Spider Families	Total
Lycosidae	2131
Gnaphosidae	47
Theridiidae	339
Theridiosomatidae	0
Segestriidae	0
Agelenidae	55
Thomididae	124
Pisauridae	34
Araneidae	745
Salticidae	78
Linyphiidae	144
Anyphaenidae	135
Philodromidae	7
Clubionidae	23
Tetragnathidae	102
Dysderidae	0
Corinnidae	132
Hahniidae	8
Dictynidae	10
Ulubrionidae	23
Liocranidae	4
Cybaeidae	5

Table 3.12: Total community composition of spider families; values are total abundance collected over the entirety of the study

Classification	Total
Lycosidae	
Gladicosa	60
Trebacosa	16
Geoclyosa	6
Pirata	453
Schizocosa	282
Hogna	7
Trebeops	6
Pardosa	6
Alllocosa	1
Rabidosa	3
Gnaphosidae	
Haplodrassus	1
Sergiolus	7
Drassyllus	9
Micaria	4
Talanites	1
Gnaphosa	4
Theridiidae	
Thymoites	12
Pholcomma	4
Enoplognatha	8
Achaearanea	15
Neospintharus	12
Theridion	229
Anelosimus	0
Dipoena	2

Spintharus	1
Robertus	1
Agelenidae	
Agelenopsis	49
Wadotes	2
Coras	2
Thomisidae	
Ozyptila	18
Xysticus	52
Tmarus	15
Mecaphesa	2
Misumenoides	22
Pisauridae	
Dolomedes	13
Pisaurina	13
Araneidae	
Mangora	243
Araneus	76
Micrathena	32
Cyclosa	26
Verrucosa	4
Metazygia	1
Argiope	2
Metepeira	3
Larinioides	3
Araniella	1
Salticidae	
Salticus	5
Marpissa	6

Sassacus	10
Thiodina	33
Maevia	2
Synemosyna	1
Hentzia	5
Chinattus	3
Chalcoscirtus	1
Attidops	1
Pelegrina	5
Phidippus	3
Habronattus	1
Linyphiidae	
Neriene	10
Macrargus	2
Maro	1
Lepthyphantes	2
Pityohyphantes	1
Ceraticelus	4
Islandiana	6
Walckenaeria	1
Bathyphantes	52
Agyneta	12
Helophora	1
Centromerus	3
Frontinella	1
Porrhomma	1
Ceratinopsis	2
Neriene	10

Anyphaenidae	
Anyphaena	2
Wulfila	127
Arachosia	1
Hibana	5
Philodromidae	
Tibellus	2
Philodromus	4
Clubionidae	
Clubiona	20
Tetragnathidae	
Leucauge	85
Tetragnatha	13
Pachygnatha	4
Corinnidae	
Phrurotimpus	10
Trachelas	2
Castianeria	96
Myrmecotypus	22
Hahniidae	
Antistea	8
Dictynidae	
Cicurina	9
Emblyna	1
Uloboridae	
Hyptiotes	17
Uloborus	6
Liocranidae	

Agroeca	4
Cybaeidae	
Cybaeota	5

Table 3.13: Total community composition of spider genera; values are total abundance collected over the entirety of the study