Coexisting with Change: Wildlife Responses to Invaded Forest Communities in Southeastern Michigan

by

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ABSTRACT

Invasive plants are a major driver of biodiversity loss worldwide and are particularly widespread in southeastern Michigan, where woody invasive shrubs such as autumn olive (*Elaeagnus umbellata*), Amur honeysuckle (*Lonicera maackii*), common buckthorn (*Rhamnus cathartica*) and glossy buckthorn (*Frangula alnus*) are altering ecosystem structure and habitat composition. While the impacts of invasive plants on native vegetation are well documented, less is known about how wildlife respond behaviorally to invaded habitats. I aimed to clarify how invasive plants influence habitat use and behavior of two influential species, white-tailed deer (*Odocoileus virginianus*) and eastern coyote (*Canis latrans*). If invasive plants are changing the behavior of these species, it could have cascading effects throughout the ecosystem. For example, deer can strongly influence plant community composition through selective browsing or over browsing of certain plant species. Coyotes may alter prey behavior through predation or fear-mediated effects, making it important to understand how their habitat use is affected by invasive plants.

Specifically, I examined if invasive shrub cover predicted habitat use and browsing behavior of white-tailed deer and habitat use of coyotes. Additionally, I evaluated whether Floristic Quality Index (FQI), a commonly used measure of habitat quality based on plant community composition, predicted invasive shrub presence and wildlife site use. I investigated these questions at 16 1-hectare sites across southeastern Michigan in lands managed by the Michigan Nature Association. I used trail cameras to detect wildlife presence and performed a comprehensive vegetation survey at each site over a one-year period, once per season, between the summer of 2023 and the spring of 2024. I used linear mixed-effects models and AICc model selection to evaluate relationships between invasive shrub cover, plant community characteristics, season, and wildlife detections. I utilized linear and multiple linear regression models to understand how FQI scores were correlated with invasive plant cover at each field site.

Deer site use was positively associated with buckthorn cover and was greatest during the fall, possibly due to late season cover provided by buckthorn. Plant diversity was not correlated with deer site use. Deer browse was positively associated with honeysuckle, but not other invasive plants. Coyote site use was greatest in areas with buckthorn. FQI scores were not correlated with overall invasive shrub cover, and, unexpectedly, honeysuckle cover was positively associated with FQI.

My findings suggest that deer and coyotes both appear to utilize invasive resources and indicate wildlife behavior within invaded habitat may be highly specific to the invasive plant species. My findings demonstrate that species-specific responses to invasive plants must be considered when studying wildlife behavior, habitat use, and conservation in invaded ecosystems. Understanding how wildlife utilizes invaded habitats can improve management strategies for ecosystems increasingly dominated by invasive plants and help land managers better restore ecosystems.

Subject Category: Wildlife Ecology, Biology.

Key Words: Invasive Plants, Coyotes, Deer, Buckthorn, Habitat

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INTRODUCTION

Human activities have substantially altered ecosystems worldwide, resulting in habitat loss, species declines, and changes in community composition (Côté et al., 2004; McShea & Rappole, 1997). These changes can influence wildlife populations by modifying resource availability, habitat structure, and species interactions, often with cascading effects on ecosystem function. Among the most important drivers of these changes are invasive plant species, which can alter ecosystem structure and function through mechanisms such as shifts in nutrient cycling, reductions in forest productivity, and competition with native vegetation (Hayes & Holzmueller, 2012; Pyšek & Richardson, 2007; Rejmanek & Richardson, 1996). Invasive plants frequently form dense stands that reduce native plant diversity and modify habitat structure, with potential consequences for both plant and animal communities (Gorchov et al., 2021; Vilà et al., 2011). More broadly, invasive plants have been implicated in declines of threatened and endangered animal species in the United States (U.S) (United States Department of Agriculture, n.d.). As a result, understanding how invasive plants influence ecological processes and wildlife populations has become an important focus in forest ecosystems.

In addition to invasive plants, animals that exert strong ecological influence can further shape ecosystem structure and function. In the midwestern U.S, large herbivores such as white-tailed deer (*Odocoileus virginianus*) and meso-predators such as coyotes (*Canis latrans*) play important roles in structuring plant and animal communities through herbivory, predation, and habitat modification (Blossey & Gorchov, 2017; Kurta, 2017; Waller & Alverson, 1997). High densities of deer can reduce regeneration of preferred plant species and alter understory composition, potentially interacting with invasive plant dynamics (Averill et al., 2016; Côté et al., 2004; Gorchov et al., 2021; Waller & Alverson, 1997). These interacting drivers of ecological

change highlight the need to understand how invasive plants and wildlife jointly influence forest ecosystems.

Invasive plant species often possess traits such as rapid growth, high reproductive output, and the ability to establish in disturbed environments, which can facilitate their spread and persistence in novel habitats (Pyšek & Richardson, 2007; Rejmanek & Richardson, 1996). Several ecological mechanisms contribute to invasion success. The enemy release hypothesis suggests that invasive species may experience reduced pressure from their natural herbivores and pathogens in their introduced range, allowing them to allocate more resources toward growth and reproduction compared to native species (Keane & Crawley, 2002; Liu & Stiling, 2006). Similarly, invasive plants may benefit from competitive release, where reduced competition from native plants, herbivores, and pathogens in the introduced range, which did not evolve with this novel invasive, allows the invasive to thrive in its new environment (Hierro et al., 2005; Keane & Crawley, 2002). For example, garlic mustard (*Alliaria petiolata*) and Japanese barberry (*Berberis thunbergii*), are rarely browsed by deer, giving them an advantage over more palatable native plants in the midwestern U.S (Averill et al., 2016; T. Knight et al., 2009).

Many invasive plants exhibit characteristics associated with r-selected life history strategies, including high fecundity and rapid population growth, which enable them to quickly colonize and dominate disturbed habitats (Rejmanek & Richardson, 1996). For example, species such as Amur honeysuckle (*Lonicera maackii*) and buckthorn (*Rhamnus cathartica* and *Frangula alnus*) produce abundant fruit that is readily dispersed by birds, facilitating rapid spread across landscapes (Gorchov et al., 2021; K. S. Knight et al., 2007; Luken & Thieret, 1995). As a result of these traits and mechanisms, invasive plants can become dominant within

plant communities, reducing native species diversity and altering habitat structure and resource availability for wildlife (Pyšek & Richardson, 2007; Vilà et al., 2011).

The prevention and management of invasive plants is estimated to cost more than $148 billion annually in the United States (Pimentel et al., 2005). Management is often resource-intensive and requires long-term effort. This is especially difficult on privately owned lands, where coordinated control of invasives is extremely challenging. Even in managed systems, such as well funded parks, reinvasion from surrounding areas can limit the effectiveness of control efforts. Consequently, many land managers have shifted from eradication of invasives to long-term management strategies. Given the persistence of invasive plants, particularly woody species that substantially alter habitat structure, there is a growing need to understand their effects on wildlife. Although the impacts of invasive plants on native plant communities are well documented, their influence on wildlife behavior remains less well understood (Hayes & Holzmueller, 2012).

Invasive plants can alter how animals use their habitat. Invasive plants are known to alter habitat structure, which can impact native animals' foraging behavior and movement ability (Stewart et al., 2021). For example, invasive plants with herbivory defenses such as thorns or chemical defense are often avoided by deer, which can allow these plants to dominate without any natural control (Kronberget al. 1993, Stewart et al., 2021). If unpalatable invasives dominate by outcompeting native plants and deer avoid the invaded habitat, it may lead to less foraging opportunities for deer (Sample et al., 2023; Stewart et al., 2021). Invasive plant thickets also impact native animals' movement. Studies have suggested that smaller animals and some predators, like coyotes, will utilize invasive thickets, potentially to use as a source of cover,

while larger animals like deer avoid thickets which are hard to move within or to avoid areas where predators may lurk (Stewart et al., 2021; Vernon et al., 2014).

Native plants in North America are experiencing another stressor that can help invasive plants take root. White-tailed deer (*Odocoileus virginianus*) populations are at an historical high (Côté et al., 2004; McShea & Rappole, 1997). Native predators, such as wolves, bears and mountain lions, were eliminated from most of the deer range by the early 1900's. Although deer were almost hunted to extinction by commercial and recreational markets, establishment of state wildlife agencies and conservation measures that managed hunting allowed the deer to make a comeback in the last century (Kurta, 2017; McShea & Rappole, 1997). Increased agricultural, silvicultural and early successional habitat enhanced deer habitat within the past century, leading to very abundant deer populations (Alverson et al., 1988; Averill et al., 2017; McShea & Rappole, 1997; Waller & Alverson, 1997).

Currently, white-tailed deer in the Midwest occur at high densities, exerting sustained browsing pressure on native plant communities that leave legacy effects on forests, such as reduce regeneration and altered forest understory composition (Côté et al., 2004; T. Knight et al., 2009; McShea & Rappole, 1997; Russell et al., 2001; Waller & Alverson, 1997). White-tailed deer overpopulation leads to plant community disturbances that can open niches for invasive plants to take advantage of. For example, deer create heavy browse pressure on native plants, which can suppress native populations and assist invasive plant establishment (Averill et al., 2017; Blossey & Gorchov, 2017; Gorchov et al., 2021).

Heavy deer use at a localized site can cause changes to soil compaction, and deer waste can increase nutrient availability (Averill et al., 2017). These changes create favorable conditions for invasive earthworms, which can further modify soil structure and nutrient cycling, ultimately

affecting native plant recruitment (Dávalos et al., 2015). All these factors can help invasive plants get established in new ecosystems since there become less competition from native plants (Gorchov et al., 2021; T. Knight et al., 2009).

White-tailed deer do not uniformly suppress invasive plants; rather, browsing pressure varies strongly by species identity (Averill et al., 2016). In controlled feeding trials, deer selectively avoided some invasive species while readily consuming others, including bush honeysuckles (*Lonicera maackii*). However, high palatability does not necessarily lead to suppression, as invasive plants can compensate through rapid growth, increased leaf phenology or other traits (Averill et al., 2016; Blossey & Gorchov, 2017; Gorchov et al., 2021; T. Knight et al., 2009). On the other hand, some invasive plants are less palatable to deer and if co-occurring native species are heavily browsed, deer may indirectly promote invasion by creating a relative release from herbivory. Although the Enemy Release Hypothesis traditionally refers to escape from coevolved specialist enemies, selective avoidance by abundant native generalists may produce a similar ecological outcome for certain invaders (Averill et al., 2016; Keane & Crawley, 2002; Liu & Stiling, 2006). Studies focusing on wild deer browse are therefore necessary to determine whether the same pattern occurs in natural conditions. Additionally, other common invasives to the Midwest, including buckthorn (*Rhamnus cathartica* and *Frangula alnus*) and autumn olive (*Elaeagnus umbellata*) need to be studied to understand their interactions with deer.

In forest ecosystems, one important source of disturbance is herbivory by white-tailed deer, which can reduce native plant abundance and create conditions that facilitate invasive plant establishment (Bourg et al., 2017; Côté et al., 2004; Gorchov et al., 2021; T. Knight et al., 2009). Invasive plants have been described as “back-seat drivers” of ecosystem change, establishing in response to disturbances and subsequently reinforcing native species decline (Bauer, 2012). In

this framework, deer act as an initial disturbance that facilitates invasion, while invasive plants further alter ecosystem structure and function beyond the effects of deer alone. Although deer may contribute to the establishment and spread of invasive plants, less is understood about how wildlife behavior shifts in forests already dominated by invasive species (Hayes & Holzmueller, 2012).

Understanding how invasive plants influence wildlife is particularly important for species that exert strong ecological effects, such as white-tailed deer. If invasive plant dominance alters deer habitat use, browsing pressure may shift toward less-invaded areas, potentially redistributing disturbance across the landscape. Such shifts could reinforce invasion dynamics by facilitating the spread of invasive plants into previously less-impacted habitats. In addition to ecological consequences, changes in deer habitat quality may have economic implications in regions where deer are an important game species, including the Midwestern United States (Calantone, 2017).

Coyotes, in addition to deer, are a good animal to study to examine invasive plants effect on the wildlife community. Coyotes are one of the top predators in southeastern Michigan, and if invasive plants are changing where or how coyotes occur, it could have trickle down effects on the behavior of prey animals (Kurta, 2017), including effects on herbivore distribution and behavior. These predator-prey interactions are particularly relevant for species such as white-tailed deer, which directly shape plant communities through herbivory (Blossey & Gorchov, 2017; Waller & Alverson, 1997). Understanding whether invasive plants alter coyote habitat use is important for determining if these effects extend across trophic levels and vary among ecological contexts.

Although we know how wildlife interacts with some individual invasive plant species, less is known about how deer might interact with habitat that has co-occurring invasive plant species interactions. Understanding multi-invaded areas is particularly important because that is most often the type of invasion land mangers face (Kuebbing et al., 2013). This is because invasive plants in the area are typically found next to each other since they utilize similar disturbances, such as unstainable deer browsing, to establish and persist (Gorchov et al., 2021; T. Knight et al., 2009; Kuebbing et al., 2013). When multiple invasive shrubs dominate a site, cascading effects can occur. For example, dense honeysuckle and buckthorn thickets can reduce native seedling recruitment and understory diversity (Blossey & Gorchov, 2017; Hutchinson & Vankat, 1997; Knight et al., 2007). This can limit food resources for small mammals and birds (Blossey & Gorchov, 2017). Additionally, deer may shift their browsing to remaining native plants. This can further suppress native regeneration and indirectly facilitate the spread of less-palatable invasives like autumn olive (Averill et al., 2016; Blossey & Gorchov, 2017). These interactions illustrate how multi-invaded habitats can alter plant–herbivore dynamics and reshape forest community composition.

The focal invasive shrubs in my study—autumn olive, buckthorn (*Rhamnus cathartica* and *Frangula alnus*), and amur honeysuckle—each have distinct invasion histories and functional traits that may influence wildlife habitat use. Autumn olive (*Elaeagnus umbellata*) is a nitrogen-fixing shrub native to Asia that was introduced to North America during the twentieth century for erosion control, wildlife habitat improvement, and land reclamation plantings (Kurtz & Hansen, 2016). Its ability to fix atmospheric nitrogen allows it to establish in nutrient-poor soils and alter soil nutrient availability (Franke et al., 2019). Autumn olive is also a rapid colonizer of disturbed sites and can form dense stands that suppress native vegetation (Blossey & Gorchov, 2017).

Common buckthorn (*Rhamnus cathartica*) was introduced from Europe as an ornamental shrub and for hedgerows and has since become a dominant component of many forest understories (Gorchov et al., 2021; Kurylo et al., 2007). Glossy buckthorn (*Frangula alnus*) was also introduced from Europe, Africa and central Asia, being utilized as an ornamental plant in gardens and for wildlife habitat improvement (Mehrhoff et al. 2003; Webster et al. 2006). Common and glossy buckthorn frequently co-occur in Midwestern U.S. forests and are sometimes treated collectively as invasive understory shrubs while studying their range and ecological effects (Becker et al., 2012). I combined these species for analysis to evaluate their joint effects on wildlife, hereafter referred to as "buckthorn" or "buckthorn (*Rhamnus cathartica* and *Frangula alnus*)". They are functionally similar species, competing for light, water, and nutrients in both forest edge and understory habitats, although glossy buckthorn is better adapted to wet sites (Kalkman et al., 2019; McClain 1996). Both species of buckthorn can form dense, nearly monospecific thickets that outcompete native shrubs and tree seedlings (Converse 1984; Heneghan et al., 2006; T. M. Knight et al., 2009). Buckthorn alters soil chemistry and nutrient cycling, particularly in stands dominated by common buckthorn, and both species exhibit extended leaf phenology, retaining leaves longer than many native species (Richburg et al. 2001; Heneghan et al., 2006). Both buckthorn species have fruits that are readily consumed and dispersed by birds, facilitating rapid spread across landscapes (Catling and Porebski 1994; K. S. Knight et al., 2007; T. Knight et al., 2009; Kurylo et al., 2007).

Amur honeysuckle was introduced from Asia as an ornamental shrub for wildlife plantings and is now widespread across Midwestern forests (Donoso et al., 2024; Kurtz et al., 2015; Luken & Thieret, 1995). Like buckthorn, honeysuckle exhibits extended leaf phenology, allowing it to leaf out earlier in spring and retain foliage later into fall than many native shrubs (Kurtz et al.,

2015; Mcewan et al., 2009; McNeish & McEwan, 2016). Honeysuckle thickets can reduce the amount of rainwater and the chemistry of water that reaches the forest floor, leading to changes in forest nutrient cycling (McEwan et al., 2012). It often becomes a dominant shrub in invaded forest understories and has been shown to reduce native woody seedling recruitment and understory diversity (Hutchinson & Vankat, 1997; Martinod & Gorchov, 2017).

The Floristic Quality Index (FQI) is a widely used metric to assess the ecological integrity of plant communities (Herman et al., 2001; Swink & Wilhelm, 1994). FQI integrates both species richness and the presence of native species that are sensitive to disturbance, with higher scores generally indicating higher-quality, less-disturbed habitats. In Michigan and other Great Lakes states, FQI has been shown to effectively discriminate among wetlands of differing ecological condition and to serve as a reliable indicator of habitat integrity (Bourdaghs et al., 2006; Diller & Schriever, 2025). However, the ability of FQI to detect the impacts of invasive species is debated, as invaded sites may retain native flora while still undergoing significant compositional or functional shifts, leading to unexpectedly high FQI scores (M. J. Cohen et al., 2004; Miller & Wardrop, 2006). Given that FQI is already used by many land managers and conservation agencies, understanding how it responds to invasive plant cover in forested communities is critical to determining whether it remains a reliable indicator of habitat quality under invasion pressure.

There were four primary objectives in this study. First, I investigated how FQI scores are impacted by invasive plants in southeastern Michigan. I predicted that the Floristic Quality Index (FQI) would be negatively associated with invasive shrub cover. The remaining objectives were exploratory. I developed models to evaluate whether honeysuckle cover, buckthorn (*Rhamnus cathartica* and *Frangula alnus*) cover, autumn olive cover, FQI, and plant diversity were

associated with (a) deer habitat use, (b) deer browse, and (c) coyote habitat use. By evaluating these relationships across multiple seasons, I aimed to clarify how invasive plants influence deer habitat use, deer foraging behavior, and coyote habitat use in invaded forests. This work aims to advance the understanding of invasion dynamics, specifically untangling potential consequences of invasive plants on wildlife populations and how management can help preserve native biodiversity.

METHODS

Site description

My research was conducted at three Michigan Nature Association (MNA) nature sanctuaries, Dauner Martin, Mary and Lyle Rizor, and Sharon Zahrfeld Memorial, located across Genesee and Livingston Counties in Southeastern Michigan (Figure 1, Figure 3a, Figure 3b). The sanctuaries were all characteristic of a dry-mesic southern forest, as defined by the Michigan Natural Features Inventory, with dominant vegetation including red maple (*Acer rubrum*), black cherry (*Prunus serotina*), red oak (*Quercus rubra*), and gray dogwood (*Cornus foemina*) (Cohen et. al, 2020; Kost et. al, 2007). Dauner Martin consists of 155 acres of protected area and had 8 1-ha sites (Figure 4a). Mary and Lyle Rizor in Livingston County consists of 30 acres of protected area and had 4 1-ha sites (Figure 2, Figure 4b). Shannon Zahrfeld Memorial in Genesee County consists of 55 acres of protected area and had 4 1-ha sites (Figure 4c).

Field Methods

I surveyed vegetation and deer activity using the same method at all 16 sites. Each site was defined as a 1-ha plot selected along a gradient of invasive plant presence, ranging from

little invasion to heavy invasion. To ensure site independence, sites were spaced at least 75 m apart, which is similar to other studies that examine deer interaction with invasive plants (Christopher et al. 2014). Deer and coyotes have large home ranges, with deer home ranges in our area being 70-120 ha and coyotes being 10-40 ha, ensuring that wildlife had access to all sites within each nature sanctuary and our observations reflected site-use choices made by wildlife (Hiller & Campa, 2008).

Vegetation sampling

I sampled vegetation at each site once per season. Following other studies that examined invasive plants and wildlife (Vernon et al., 2014), the summer sampling season took place from July to August 2023, fall from October to November 2023, winter from January to February 2024, and spring from April to May 2024.

I sampled understory and overstory vegetation to assess plant community composition within each site. Specifically, I sampled 5 $10m^2$ subplots within each 1-hectare site, spaced at 25m intervals to ensure adequate vegetation sampling (Christopher et al., 2014) (Figure 5a). Each $10m^2$ subplot had nine $1m^2$ quadrats spaced 3.3m apart, where we sampled understory vegetation and canopy cover to species (Figure 5b, Figure 5c). This ensured that each hectare had $45m^2$ of vegetation sampling, which is similar compared to other studies that examined deer and landscape vegetation (Frerker et al., 2013). We selected this "grid" sampling method over a transect-based approach based on preliminary species accumulation curves, where grid sampling more effectively captured species richness in our study sites.

I recorded woody and herbaceous species that fell within a quadrat to species (Christopher et al., 2014; Knight et al., 2009). Grasses and sedges (Monocots) were recorded to species if they comprised more than 25% of a quadrat (Filazzola et al., 2014). I recorded cover

class of each species in the quadrat using a modified Braun Blanquet cover–abundance scale (Braun-Blanquet, 1932, Figure 14) for understory, or plants below 2 meters, and overstory plants.

Deer browse survey

All herbaceous and woody plants within each quadrat were visually examined for deer browsing once per season. I employed a "direct browse" sampling method, counting evidence of consumption on shoots, twigs, and leaves as "browse". This required me to identify browse through characteristic patterns such as bite marks, broken stems, or missing buds on woody stems (Figure 6, Figure 13) (Patton et al., 2018). Browse observations were restricted to vegetation occurring below 2 meters in height, which represents the maximum typical deer browse height (Donoso et al., 2024; Frelich & Lorimer, 1985). Eastern cottontail (*Sylvilagus floridanus*) and deer forage were differentiated by assessing leaf damage patterns (Skoták et al., 2025, figure 13). Specifically, rabbits tend to leave "clean" 45-degree angle bite marks, where deer browse is often characterized by teared off stems (Skoták et al., 2025). Finally, to quantify browse pressure, we calculated the proportion of browsed plants per species relative to the total number of plants available at each site, providing a standardized metric of browsing intensity.

Camera trap sampling

I deployed passive infrared camera traps at every 1-hectare plot to monitor wildlife activity, providing a measure of deer detection in relation to the vegetation characteristics (Figure 7). I randomly deployed camera traps at one of the five subplots within each hectare (Figure 5a). I placed camera traps 10m south of a subplot so the camera could observe all activity within the 10x10m subplot area. I placed cameras facing north to minimize false triggers by the sun (Vernon et al., 2014; Wilton, 2021). I deployed the cameras for 30 days each season during the

same time periods as vegetation sampling during all sampling seasons. I placed camera traps 1 m high on a suitable tree and set to capture 3 photos based on motion detection every 10 seconds (Vernon et al., 2014; Wilton, 2021). Trail cameras were set to camera mode with a three-shot burst, medium sensitivity, a 10-second lag time, 20 MP resolution, a 120° detection angle, and images saved in JPEG format.

Data Analysis

Calculating the invasive plant cover variables

I summed Braun-Blanquet cover for each plant species in all 5 subplots during each season and calculated relativized invasive cover (cover of invasive species/sum of cover for all species at a site) for each hectare (Knight et al., 2009). This process helps standardize comparisons between sites and is common in ecological data analysis of this type, allowing for meaningful comparisons of invasive dominance within the plant community while controlling for variation in total vegetation abundance (Shanholtzer, 1978). Using this method, I calculated the mean Braun Blanquet cover of honeysuckle, buckthorn (*Rhamnus cathartica* and *Frangula alnus*) and autumn olive and relativized each against the Braun Blanquet sum of all plant cover in each hectare. This created the overall invasive cover, buckthorn cover, autumn olive cover and honeysuckle cover variables for each site during every season.

For the buckthorn cover variable, both common and glossy buckthorn were utilized. These species were identified separately in the field, which was helpful to obtain individual browse numbers. However, for abundance analysis, cover values for both species were combined to represent total buckthorn cover at each site for each season. I chose this approach because both buckthorn species typically co-occurred at our field sites and grew together to create dense, monospecific stands that could impact wildlife. This approach was used because both species frequently co-occur in Midwestern U.S. forests and are often treated collectively in ecological

studies due to their similar growth form and understory dominance (Becker et al., 2012; Kalkman et al., 2019).

Calculating Simpson's Diversity Index

I calculated Simpsons index of diversity per hectare of the entire plant community and for understory plants only. This was done because deer can only browse understory plants, so understory plant diversity might have a bigger impact on predicting deer habitat use than overall plant diversity. Calculations were done in R studio (Posit Team, 2024).

Calculating Floristic Quality Index (FQI)

I used the University of Michigan College of Literature, Arts and Sciences Herbarium plant database to assign a floristic quality index score (FQI) score to each plant observed (University of Michigan LSA Herbarium, 2024). The floristic quality index is a conservation tool that uses coefficients of conservatism (C-values) assigned to species to measure community integrity and vulnerability to disturbance. We took the FQI of each site during every season to use as a predictor of deer and coyote habitat use.

FQI scores are calculated using the formula $FQI=C\sqrt{n}$, where C is the mean of the conservatism values of species observed at a site and n is the total number of plant species observed at that site. Conservation values of each species were obtained from the University of Michigan's LSA Herbarium's Michigan Flora database (University of Michigan LSA Herbarium, 2024).

Camera trap data

Camera trap data was sorted by season and site. I utilized Megadetector v1.2.0 an open-source object detection model designed for wildlife image classification (Beery et al., 2019).

Megadetector is a deep-learning–based object detection model designed to rapidly classify camera-trap images by identifying the presence of humans, vehicles, and animals, thereby reducing the time required for manual image review. Megadetector has been used for a variety of trail camera surveys and can increase photo tagging efficiency by 500% (Fennell et al., 2022; Tuia et al., 2021; Wilton, 2021). I applied MegaDetector with a 70% confidence threshold to identify deer and coyote, which is slightly more inclusive than the 90% threshold used by other studies (Fennell et al., 2022). This lower threshold was chosen to reduce the risk of false negatives, particularly for wildlife detections, while still maintaining reasonable precision for my study species. Once photos were sorted by Megadetector, all animal photos were manually tagged to species by our research team using DigiKam (version 6.2.0) and the metadata downloaded using to a .csv file using Exif Tool (version 11.87) (Caullier, 2019; Harvey, 2016).

To ensure temporal independence of each wildlife detection and avoid repeated triggers of the same individual, I chose a minimum delta time of 5 min (Bargabos et al., 2023). I used the recordTable function in the camtrapR package (Niedballa et al., 2016). Consecutive images were grouped into the same event unless they were separated by at least 5 minutes, with independence assessed relative to the last independent record. Within each 5-minute interval, the image containing the maximum number of individuals was used to represent that event. For example, if one image contained a single deer and another image taken 4 minutes later contained three deer, the event was recorded as three individuals. This approach minimizes overcounting when animals remain in front of the camera while still capturing peak animal use during a visit.

Deer and coyote photos were relativized to create our habitat use variable. This is typical for camera trap studies because the habitat-use variable accounts for camera trap effort at each site (Wilton, 2021). Specifically, to create our deer use variable I used the following equation (#

deer observations at a site/30 sampling days). The same equation was used to create our coyote use variable. It is important to note that although some cameras were deployed for longer than 30 days, due to lag time in picking up cameras, I constrained my analysis to the same 30 days per season for every camera to ensure equal sampling effort.

Statistical Methods and Models

Hypothesis 1: FQI will be negatively associated with invasive plant cover

I tested whether floristic quality (FQI) was related to invasive shrub cover. First, I examined total invasive cover as a predictor of FQI scores using a linear regression model in RStudio (Posit Team, 2024). Then, I ran a multiple linear regression model. This model considered individual variables—Amur honeysuckle, buckthorn (*Rhamnus cathartica* combined with *Frangula alnus*), and autumn olive as predictors of FQI scores. To assess multicollinearity among predictor variables, I calculated the variance inflation factor (VIF) and removed variables with VIF values >4 (Fox & Weisberg, 2019). Tests were performed using R studio version 4.3.3, open-source software with the the nlme package (Posit Team, 2024).

Objectives 1-3: Deer and Coyote Models

I used linear mixed-effects models (LME) in R using the nlme package (Posit Team, 2024) to address all three exploratory questions: how deer-use, deer herbivory, and coyote-use are influenced by invasive plants and other environmental variables. To assess multicollinearity among predictor variables, I calculated the variance inflation factor (VIF) and removed variables with VIF values >4 for each of the following models (Fox & Weisberg, 2019).

My first objective was to create a model that explored how deer site use was impacted by the invasive plant and other environmental variables. Diagnostic checks for multicollinearity

using variance inflation factors (VIFs) indicated no issues. I used an LME to test deer use, which was the response variable, and autumn olive cover, buckthorn cover (*Rhamnus cathartica* and *Frangula alnus*), honeysuckle cover, Simpsons diversity of the plant community, FQI, and season as predictors in the saturated model. Site was included as a random effect nested within its relative nature preserve.

For my second objective, I created a model to test what variables impacted deer herbivory. VIF tests found covariance between honeysuckle and FQI, so I removed FQI from the model so that the effects of honeysuckle on deer herbivory could still be examined. I created an LME with response variable of deer herbivory and the predictor variables being deer capture rate, Simpsons diversity of the plant community, autumn olive cover, buckthorn cover, honeysuckle cover and season. Site was a random effect nested with its relative nature preserve.

For my third objective, I created an LME to explore coyote use. VIF tests found no multicollinearity concerns. Coyote site use was the response variable and predictor variables included autumn olive cover, buckthorn (*Rhamnus cathartica* and *Frangula alnus*) cover, honeysuckle cover, Simpsons diversity of the plant community, FQI and season. Site was a random effect nested within its relative nature preserve.

Once I created each linear mixed effects model, I used Akaike Information Criterion corrected for small sample sizes (AICc) to identify predictors in the model of best fit. AICc is becoming more widespread by ecologists and is particularly useful in behavioral ecology when exploring multivariate models (Symonds & Moussalli, 2011). This exploratory approach is well suited for AICc, which can determine what variables may be associated with wildlife habitat preference. I used AICc for small sample sizes since I had 16 field sites in total (Symonds & Moussalli, 2011).

After fitting each LME, I performed AIC-based model selection (Venables , 2002). To identify the most influential predictors, I conducted a model selection process using the dredge function from the 'MuMIn' package in R studio (Bartoń 2024, Posit Team, 2024). We ranked the top models using Akaike Information Criteria with small sample size correction (AICc). Models with $\Delta AICc < 2$ are not effectively different (Burnham and Anderson, 2011), so I employed model averaging using the 'AICcmodavg' and 'car' packages (Fox et al., 2023; Mazerolle, 2023). I took the results of model averaging and reported 95% confidence intervals for each variable.

To assess whether coyote and deer site use were associated, a post hoc correlation analysis was conducted between coyote and deer detection rates across sites using a Spearman rank correlation. This analysis performed to evaluate potential co-occurrence patterns between the two species. A Spearman rank correlation was selected due to the non-normal distribution of coyote detection data.

RESULTS

Our camera traps captured 99,249 images across 16 sites over four seasons, of which 23,999 photos were retained for manual species identification using digiKam, after running MegaDetector at a 70% confidence threshold to eliminate photos with no animals. I identified 5,327 deer and 84 coyotes throughout the project. Other wildlife detections were dominated by chipmunks (*Tamias striatus*; 250 detections), raccoons (*Procyon lotor*; 137), eastern gray squirrels (*Sciurus carolinensis*; 50), and eastern fox squirrels (*Sciurus niger*; 35), along with birds (44 songbirds, 10 wild turkey (*Meleagris gallopavo*), and 4 barred owls (*Strix varia*). Less frequent detections included red fox (*Vulpes vulpes*; 1) and skunk (*Mephitis mephitis*; 1), while

other species such as opossums (*Didelphis virginiana*; 17), mice (3), and groundhogs (*Marmota monax*; 3) which only occurred only sporadically.

The field team and I identified 19,961 individual plants to species while recording cover and location information. 491 plant species were identified across all field sites and seasons. Non-native species comprised 63 of 491 taxa represented (~13%). Buckthorn (*Rhamnus cathartica* and *Frangula alnus*), autumn olive, and honeysuckle accounted for 1,019 occurrences in total, collectively representing ~5% of all recorded plant observations. 2,529 instances of deer browse were observed on plants across all sites and seasons. FQI scores at my field sites ranged 2-20 (Table 8). Simpson's diversity index, ranged from 0.39- 0.98, reflecting high variability in plant community diversity across sites and seasons.

Hypothesis 1: FQI will be negatively associated with invasive plant cover

The results of a linear regression model testing invasive cover as a predictor of FQI scores showed a weak positive relationship between total invasive cover and FQI ($\beta = 0.994 \pm 0.519$ SE, $t = 1.917$, $p = 0.059$).

I also tested a multiple regression model, where I tested individual invasive variables—amur honeysuckle, buckthorn., and autumn olive as predictors of FQI. The results revealed a significantly positive effect of amur honeysuckle ($\beta = 1.472 \pm 0.626$ SE, $t = 2.353$, $p = 0.021$) on FQI scores. Buckthorn showed a nonsignificant effect ($\beta = -1.088 \pm 0.964$ SE, $p = 0.263$) and autumn olive did not have an effect ($\beta = 1.862 \pm 1.079$ SE, $p = 0.089$) on FQI scores. Overall, the model explained a small proportion of variation in FQI (adjusted $R^2 \approx 0.073$).

Objective 1: What factors influence white-tailed deer detection?

I used AICc to explore what variables influence white-tailed deer detection at our field sites. Our maximal model included deer browse as the response variable and the cover of buckthorn, autumn olive, honeysuckle, FQI, Simpson Diversity Index of the plant community

and season as predictor variables, with site being a random effect nested within its respective park location. The top four models were within 2 ΔAICc units and together accounted for more than 99% of the model weight (Table 1).

In the model-averaged estimates, buckthorn cover had a positive relationship with increased deer detections (β = 57.0 ± 24.9 SE, p = 0.022, 95% CI = 8.2–105.9). In contrast, autumn olive (*Elaeagnus umbellata*) was not supported as an important predictor of deer detections (β = –38.0 ± 24.8 SE, *p* = 0.126, 95% CI = –86.6–10.6). Interestingly, honeysuckle (*Lonicera maackii*) was not associated with deer detections either (β = 4.0 ± 15.5 SE, *p* = 0.795) (Figure 8, Table 2). Neither Floristic Quality Index (β = –1.6 ± 3.4 SE, *p* = 0.643, 95% CI = –8.2–5.0) nor Simpson's diversity (β = 93.6 ± 91.7 SE, *p* = 0.308, 95% CI = –86.2–273.4) were associated with deer detections (Figure 8, Table 2).

I also examined the effect of season on deer detections. Fall served as the reference season. Compared to fall, deer detections were lower in spring (β = –99.0 ± 33.3 SE, p = 0.003, 95% CI = –164.3 to –33.7), summer (β = –79.5 ± 34.7 SE, p = 0.022, 95% CI = –147.4 to –11.6), and winter (β = –127.0 ± 33.4 SE, p < 0.001, 95% CI = –192.4 to –61.6) (Figure 8, Table 2).

Objective 2: What factors influence deer browse?

Deer herbivory was most prevalent at sites 1, 5, and 14, which had dense understory vegetation (Figure 9). The most frequently browsed species included invasive plants such as autumn olive (*Elaeagnus umbellata*), oriental bittersweet (*Celastrus orbiculatus*), glossy buckthorn (*Frangula alnus*), common buckthorn (*Rhamnus cathartica*), as well as the native black cherry (*Prunus serotina*). Invasive species accounted for most browsed stems, with native species less affected (Figure 10).

We evaluated predictors of deer browse across all seasons using AICc-based model selection and model averaging. Our full model included deer browse as the response variable and

autumn olive, honeysuckle cover, and buckthorn (*Rhamnus cathartica* and *Frangula alnus*) cover, as well as deer detection, FQI and Simpson's diversity of the vegetation and deer capture rate as predictor variables. No single model received overwhelming support (ΔAICc < 2 for multiple candidates, all weights < 0.15), so model-averaged coefficients were used (Table 3). Looking at predictors within the model averaging results, relative cover of honeysuckle was the only predictor that did not cross the zero-effect threshold, with sites containing more honeysuckle showing greater browsing pressure ($\beta = 20.87 \pm 10.17$ SE, 95% CI = 0.42–41.33, $p = 0.045$) (Figure 11, Table 4). Winter exhibited a positive trend ($\beta = 43.28 \pm 22.89$ SE, 95% CI = –2.79–89.35, $p = 0.066$) (Figure 11, Table 4). Other predictors, including cover of buckthorn, autumn olive, Floristic Quality Index, Simpson diversity, and deer capture rate, showed no clear effects, with confidence intervals overlapping zero (Figure 11, Table 5).

Objective 3: What factors influence coyote site use?

I recorded 84 coyote detections during the study period. To evaluate coyote site use, I used linear mixed-effects models with AICc-based model selection, including site as a random effect. The top candidate models (ΔAICc ≤ 2) consistently included relative buckthorn cover, while floristic quality (FQI) and other vegetation variables (autumn olive, honeysuckle, and Simpson's diversity) appeared in a subset of models (Table 5). Season was not included in any top-supported models.

Model-averaged estimates indicated that buckthorn cover was positively associated with coyote detections ($\beta = 0.0125 \pm 0.0042$ SE, $p = 0.003$, 95% CI = 0.00419–0.02079). Floristic quality showed a weak and uncertain relationship with coyote detections ($\beta = 0.00078 \pm 0.00045$ SE, $p = 0.082$, 95% CI = -0.00010–0.00165), as confidence intervals overlapped zero. In contrast, autumn olive, Amur honeysuckle, and Simpson's diversity were not associated with

coyote detections. Seasonal effects were not supported, as seasons were not retained in top models and coefficients did not differ from the reference season of fall (Figure 12, Table 6).

To further explore potential spatial relationships between coyotes and deer, a post hoc Spearman rank correlation was conducted between deer detections and coyote detections across sites. There was no significant association between deer detections and coyote detections (ρ (rho) = 0.13, $p = 0.315$), indicating weak or no site-level relationship between the two species at the spatial scale of this study.

DISCUSSION

Overall, invasive shrub cover, particularly buckthorn (*Rhamnus cathartica* and *Frangula alnus*), emerged as a key predictor of deer and coyote use. Deer and coyote site use were not correlated, possibly due to the low coyote density in the study area. Seasonal shifts were pronounced for deer. Importantly, deer interacted directly with invasive plants through herbivory (Figure 10). Model results further indicated that deer herbivory was positively associated with honeysuckle, suggesting that this invasive species may contribute to sustained browsing pressure within these systems. FQI was associated with honeysuckle, although the relationship was surprisingly positive, indicating that higher honeysuckle abundance corresponded with higher FQI values. In general, vegetation metrics such as Simpson's diversity index and FQI were generally less predictive of deer activity, though they may still play a role in shaping coyote habitat use.

FQI scores were generally low, indicating disturbed plant communities (Table 7). Although many field sites included several high-conservatism forest species, the community was dominated by low C-value generalists and invasive species, which likely contributed to reduced Floristic Quality Index (FQI) scores across sites. Field sites were one hectare each, and the

presence of invasive species or low C-value species within portions of these large sampling areas, such as site edges or localized patches, may have reduced overall FQI scores even when higher-quality remnant vegetation was present elsewhere within the same hectare.

Hypothesis 1: Testing how FQI scores relate to invasive plants

I predicted that Floristic Quality Index (FQI) scores would be lower in invaded areas, reflecting the low ecological value of invasive plant species. Contrary to this expectation, FQI values increased with honeysuckle cover, suggesting that standard FQI calculations may not fully capture the ecological effects of shrub invasion. This was surprising, since invasive honeysuckle is associated with a low coefficient of conservatism (CC) score. However, this pattern is consistent with previous research demonstrating that FQI can be biased by high value natives that may overestimate habitat quality in disturbed or invaded systems (M. J. Cohen et al., 2004; Cretini et al., 2012; Miller & Wardrop, 2006).

One explanation for this unexpected relationship is that invaded sites may retain several high CC native species while also supporting many invasive plants. Sites containing a few high-quality native species alongside numerous invasive species can still yield elevated FQI values (Cretini et al., 2012; Maginel et al., 2016; Miller & Wardrop, 2006). In such cases, FQI scores may obscure ecological degradation by emphasizing species presence of rare natives rather than dominance of invasives or functional impact (Bowles & Jones, 2006). For this reason, FQI may be more fit for finding remnant communities rather than assessing current disturbance.

Another possible explanation is that honeysuckle invasion in the study sites may be in a early-stage localized invasion, during which invasive shrubs have established but have not yet fully displaced native species (Larkin, 2012; Mack et al., 2000). During this stage, native plants may persist beneath or alongside invasive shrubs, allowing FQI values to remain high despite ongoing structural and functional changes to the plant community. Over time, continued

honeysuckle expansion may lead to declines in native abundance, richness, and recruitment, potentially producing stronger negative relationships between invasive cover and FQI that were not yet evident in this study.

These findings highlight important limitations of using FQI alone to assess habitat quality in invaded systems. While FQI remains widely used in Michigan and other Great Lakes states for conservation planning and wetland assessment (Bourdaghs et al., 2006; Diller & Schriever, 2025; Herman et al., 2001; Rice, 2023), its reliance on species presence rather than abundance may reduce its sensitivity to invasion impacts. Developing or applying modified FQI metrics that incorporate species cover or relative abundances, such as those demonstrated by Cretini et al. (2012), could improve the reliability of floristic assessments in invaded Midwestern ecosystems. These modified indices may better reflect ecological condition by weighing dominant invasive species more heavily and reducing the inflation of FQI scores driven by residual native richness.

Future research should examine whether relationships between FQI and invasive cover strengthen over longer timescales, at higher invasive densities, or under varying levels of herbivory and disturbance. This could clarify when FQI is most informative and when alternative metrics are necessary for effective management decisions.

Objective 1:Deer site use in relation to invasive plants and other site variables

We found that white-tailed deer detection was influenced by specific species rather than overall vegetation quality. Surprisingly, our best fitting models suggested that deer were positively associated with buckthorn cover, while FQI and Simpson diversity were poor predictors of deer detection (Figure 8). This result indicates that deer are not necessarily avoiding invaded habitats and instead may preferentially use sites dominated by buckthorn. This was surprising, since I assumed invasive plants, especially with low palatability, such as buckthorn,

would offer little value for deer and they would avoid these areas (Nitzsche et al., 2019; Vernon et al., 2014).

The positive association between deer detections and buckthorn cover was unexpected, particularly given previous work demonstrating the opposite pattern in systems with strong predator effects. A study in the Chicago metropolitan area found that deer avoided buckthorn-dominated sites in suburban landscapes, while coyotes preferentially used these areas, presumably due to increased perceived predation risk (Vernon et al., 2014). Vernon suggested that coyote presence may influence deer habitat use through perceived predation risk of neonates. In contrast, our study found that both deer and coyotes were positively associated with buckthorn, suggesting that predator-mediated avoidance may be context dependent. For example, coyote populations at our site may not be high enough for deer to avoid buckthorn sites. Alternatively, high deer densities may reduce the ability of individuals to avoid otherwise risky habitats. Additionally, deer may be more likely to avoid habitats with coyotes only during the spring and summer months when fawns are most vulnerable to coyote predation.

I found that autumn olive and honeysuckle were not associated with deer detection, but buckthorn was associated with increased deer detection. Both buckthorn species function as a small understory tree or tall shrub and can be successful in closed-canopy forest interiors and forest gaps, where it can form dense subcanopy layers (Fagan & Peart, 2004; K. S. Knight et al., 2007). In contrast, autumn olive and amur honeysuckle are shrub species more commonly associated with forest edges, canopy gaps, and open or early successional habitats and may be less competitive than buckthorn under closed-canopy forest conditions (Hayes & Holzmueller, 2012; Munger, 2003) . White-tailed deer frequently select early- to mid-successional forested habitats that provide both concealment cover and abundant browse in the form of stems and

shoots, conditions that may coincide with areas where buckthorn is more prevalent relative to other invasive shrub species (Alverson et al., 1988; Côté et al., 2004; Waller & Alverson, 1997). Together, these findings suggest that deer responses to invasive plants are species-specific and mediated by vegetation structure and habitat context, rather than invasive status alone.

Seasonal patterns further support this interpretation, as deer detections were highest during the fall. This could be because the fall is a period associated with increased movement of deer during the rut to find mates, and shifting resource availability as many plants that were used for cover or food will lose their leaves and become dormant (Rogers et al., 1981; Webb et al., 2010). Buckthorn may provide an important late-season resource, as it retains leaves later into the fall and winter than many native species (Kurylo et al., 2007) and can offer both cover (Zouhar, 2011) and low-quality forage when preferred food sources become limited. Consistent with this idea, we observed high levels of herbivory damage buckthorn, suggesting that deer may be using it as a survival food, especially during late fall and winter when native forage is depleted (Figure 10). Buckthorn herbivory may be more prevalent in areas with deer overpopulation when compared to areas with lower deer density, which might prefer higher quality forage.

However, these seasonal patterns may also be influenced by the absence of hunting pressure at study sites. Hunting was not allowed at the parks my field sites were located within. This could have reduced perceived risk and allowed deer to use the study area more frequently during the fall. In hunted landscapes, white-tailed deer often alter space use and activity patterns to avoid hunters, including reducing their movement and using smaller areas more intensely (Kilgo et al., 1998; Little et al. 2015). The study sites within this study were surrounded by

private farmland and forests, and Dauner Martin nature sanctuary is located within a few miles of Seven Lakes State Park, where hunting pressure would have occurred.

Seasonal variation in predation risk may also contribute to patterns of buckthorn use by deer. Deer association with buckthorn-dominated areas were highest during fall, a period when fawn vulnerability to predation is substantially lower compared to summer, when fawn survival is lowest (Ballard et al., 1999). Decrease in fawn predation in fall and winter paired with the need for resources, such as thermal cover and food may help explain seasonal variation in deer buckthorn use. This seasonal shift suggests that deer use of invasive vegetation may reflect changing trade-offs between resource acquisition and predation risk across the year.

From a management perspective, my findings suggest that deer in southeastern Michigan are actively using invaded habitats, particularly those dominated by buckthorn. Although deer are generalists and can utilize these sites, buckthorn should still be removed because of the damage it causes to native ecosystems. For example, a study at Tifft Nature Preserve on the eastern coast of Lake Erie found that deer presence in buckthorn habitats leads to increased herbivory on nearby native plant species (Warren et al., 2025). Over time, buckthorn can further limit higher-quality native food sources for deer by reducing seedling recruitment and forming dense monoculture stands (Côté et al., 2004; Fagan & Peart, 2004; Kurylo et al., 2007).

Because buckthorn increases pressure on native plants and reduces available native food sources, restoration efforts should prioritize re-establishing native vegetation. Experimental removal of invasive shrubs in Pennsylvania led to increased diversity and regeneration of native understory plants and tree seedlings, demonstrating that native communities can rebound following invasive removal (Maynard-Bean & Kaye, 2019). In addition, revegetation treatments using native trees and shrubs in Minnesota have been shown to substantially suppress buckthorn

re-establishment in forest understories, highlighting the importance of planting native woody species as part of long-term restoration (Schuster et al., 2025).

Managers should be prepared for increased deer pressure and browse on native plants after removing invasives, as deer may have been utilizing invasives for cover or browse (Averill et al., 2016, 2017; Bourg et al., 2017; Gorchov et al., 2021). It will be key for successful restorations to utilize deer exclosures or deer tubes to protect them from herbivory and rubbing. For example, deer exclusion increased recruitment and growth of native tree seedlings in Ohio and was recommended as a tool for restoration management (Hay & Gorchov, 2026). Long-term deer exclosure experiments in Virginia and Pennsylvania deciduous forests found that excluding deer enhanced native understory richness, helped reduce invasive abundance (Bourg et al., 2017) and increased oak regeneration despite higher deer abundances (Yuska et al., 2008). Protective tubes have been shown to increase oak seedling survival by 21% in Georgia (Thyroff et al., 2022). These proven strategies could allow land managers to restore habitats while accounting for additional pressure on native plants after invasive removal.

A potential limitation of this study is the high white-tailed deer density characteristic of southeastern Michigan, which may reduce the detectability of strong habitat selection patterns. In systems with elevated deer abundance, individuals may use a wider range of available habitats, including suboptimal or degraded areas, due to increased competition for resources (Côté et al. 2004; Rooney and Waller 2003). As a result, observed use of invasive-dominated habitats may reflect both habitat availability and density-driven expansion of use, rather than strong selection for specific vegetation characteristics. This context should be considered when interpreting patterns of habitat use in this study.

Future research should utilize population surveys of wildlife to test whether these patterns persist in landscapes with lower deer densities. Additionally, they could incorporate additional invasive species into model selection frameworks, such as multiflora rose or oriental bittersweet. Increasing camera replication within sites may also improve inference about fine-scale habitat use and detection patterns. Together, these findings emphasize that deer responses to invasive plants are complex and context dependent, shaped by interactions among forage availability, cover, seasonality, and potentially even population dynamics.

Objective 2: Deer browse in relation to invasive plants and other site variables

The deer browse observations in this study suggest that invasive shrubs play a complex role in deer–plant interactions. Our best fitting model showed that honeysuckle was positively associated with deer browsing. The most frequently browsed species across all sites were invasive plants, particularly autumn olive and oriental bittersweet (Figure 10). White-tailed deer have been shown to browse invasive shrubs, even when those species are not considered high-quality forage (Averill et al., 2016). For example, an Ohio study found that honeysuckle comprised between 14% and 47% of annual deer diet, indicating that invasive shrubs can represent a substantial component of deer forage in invaded systems (Martinod & Gorchov, 2017). Although browsing on autumn olive has been reported less consistently, it is nonetheless documented as a forage species for deer (Munger, 2003).

Importantly, browsing pressure on invasive shrubs does not necessarily translate into suppression of these species. Many invasive shrubs resprout vigorously following herbivory, and deer browsing can disproportionately suppress native plant species, thereby contributing to invasive persistence rather than control (Averill et al., 2016; Gorchov et al., 2021; Knight et al., 2009).Similarly, studies examining the combined effects of deer and invasive shrubs have shown

that sites with both deer access and invasive shrub presence often exhibit higher invasive cover and reduced native shrub and forb abundance compared to deer-excluded plots (Averill et al., 2017; Blossey & Gorchov, 2017; Bourg et al., 2017; Donoso et al., 2024). Together, these findings suggest that deer herbivory may indirectly facilitate invasive shrub dominance by disproportionately impacting native vegetation. Deer browse on invasives could lead to a similar pattern, leading to increased success of invasive plants at our field sites.

Autumn olive accounted for the highest number of browse observations in raw count data, but only honeysuckle emerged as a predictor of deer browsing in the AIC-selected model (Figure 10, Figure 11, Table 6). Although autumn olive was browsed frequently, it was also widespread and abundant across sites. High browse counts may therefore reflect availability rather than a strong site-level association with browsing intensity. In contrast, honeysuckle presence was more strongly associated with increased browsing after accounting for other environmental variables with my AIC models. These results suggest that deer readily browse autumn olive when encountered, but that honeysuckle may play a stronger role in structuring where browsing activity is concentrated across the landscape.

It is important to note that deer browse could have been double counted on the same plant between seasons. For example, if a stem that was browsed in the fall did not regrow, it could have been counted again in the winter season, since we sampled the same area each season. This could lead to an overestimation of browsing pressure. Despite this limitation, the consistency of methods across all sites allows for meaningful relative comparisons.

Deer consumed invasive species extensively, including plants not traditionally considered preferred forage, suggesting that assumptions about forage quality and avoidance may oversimplify these interactions. However, this study did not evaluate nutritional quality, fitness

consequences, or survival outcomes associated with invasive plant use. Determining whether browse on invasive shrubs functions as a valuable resource, neutral component or low value browse that potentially create ecological traps, will require targeted research. This research could focus on diet quality, body condition, reproductive success, and survival of deer across invaded and uninvaded landscapes.

Future research should explicitly examine whether repeated deer browsing increases resprouting and stem density of invasive shrubs over time. Tracking stem counts across multiple years would help determine whether herbivory promotes compensatory growth that allows invasive species to persist or expand. Additionally, incorporating deer diet analyses using fecal DNA metabarcoding would allow for direct quantification of invasive versus native plant consumption and help clarify whether deer preferentially consume invasive shrubs or rely on them opportunistically when native forage is limited. Finally, experimental approaches that assess browsing preference in pristine, invaded and mixed plant communities—where invasive and native species occur side by side—would provide valuable insight into whether deer actively select invasive shrubs even when native alternatives are available.

Objective 3: Coyote site use in relation to invasive plants and other site variables

Coyotes are also utilizing sites with buckthorn cover, similarly to our results for deer (Table 9, Figure 12). Coyotes in suburban areas have been found to use buckthorn, presumably as a cover source while hunting (Vernon et al., 2014). Vernon et al. (2014) found that coyotes were more likely to use buckthorn-invaded sites in suburban Chicago, particularly during spring and summer, and suggested that this pattern was driven by seasonal increases in prey availability associated with invasive shrub structure.

Similarly, I found increased coyote use of buckthorn-invaded sites in a Michigan forest system; however, I did not observe unique seasonal differences (Figure 12). However, buckthorn's extended leaf phenology relative to native shrubs may provide enhanced thermal and concealment cover, especially in colder months (K. S. Knight et al., 2007).

Beyond its role as structural cover, buckthorn may influence coyote habitat use indirectly by altering small mammal activity patterns. For example, Japanese barberry increased small mammal foraging activity (Utz et al., 2020), and autumn olive and Amur honeysuckle demonstrated extended autumn foraging and increased activity in eastern chipmunks (*Tamias striatus*) and white-footed mice (*Peromyscus leucopus*) within shrub-invaded forests (Connolly et al., 2024). Similarly, buckthorn has been shown to alter white-footed mouse spatial behavior, reducing reliance on woody debris cover during granivory activity (Guiden & Orrock, 2017). In one case, plots with buckthorn had three times as many detections of white-footed mouse (Guiden & Orrock, 2019). Although evidence for buckthorn directly increasing small mammal population density remains limited, invasive shrubs do seem to be altering the behavior of small mammals. Additionally, earthworm abundance and bird nest predation is increased in buckthorn habitat (Schmidt & Whelan, 1999; Vernon et al., 2014). Such shifts in prey behavior and activity could influence coyote use of buckthorn-dominated areas as coyotes search for additional food sources.

Models of best fit showed that FQI was not associated with coyote site use. Coyotes are generalists, able to adapt to a wide range of conditions and prey (Kurta, 2017). Therefore, it would make sense that coyotes use both high quality and disturbed habitats. Additionally, FQI is more strongly correlated with species richness than with the mean Coefficient of Conservatism, which can obscure changes in community composition and lead to unexpected or

counterintuitive results (Bowles & Jones, 2006; Maginel et al., 2016). Previous work has shown that FQI may be relatively insensitive to invasive plant impacts, suggesting that modified FQI should be used in the future when using FQI as a tool to determine habitat value for wildlife (Bourdaghs et al., 2006; Cretini et al., 2012; Miller & Wardrop, 2006). For example, even if coyotes use sites with buckthorn, FQI scores may not strongly reflect buckthorn invasion if high-quality native species persist within the sampling area. These mechanisms help explain why our models indicate that coyotes are associated with buckthorn but not FQI.

Autumn olive and honeysuckle were not predictors of coyote use in our top models. Differences in shrub structure, phenology, or understory complexity may limit their ability to provide comparable forage or thermal cover, which could help explain why coyotes were associated with Buckthorn but not the other invasive shrubs in this study. Future studies should test if autumn olive and honeysuckle have the same ability to support small mammal populations. If not, it could help explain why coyotes were associated with only buckthorn. Additionally, the current study has shown deer are most associated with buckthorn in the fall, so coyotes may be following deer into buckthorn habitat as a food resource.

Future studies would benefit from measuring population sizes of coyotes and deer while investigating their habitat use patterns. Vernon et al (2014) found that deer avoid buckthorn because coyotes use buckthorn. We did not find deer and coyote site use to be correlated. Perhaps in my study, the coyote population has not met a certain threshold to prevent deer site use via fear mediated effects. It would be interesting to track seasonal effects to see if sites with high coyote populations lead to deer avoiding buckthorn more in the fawning season only, where predation is highest, or if deer would avoid buckthorn habitats with higher coyote populations year-round.

The association between coyotes and buckthorn-invaded habitats raises future questions about the potential for coyotes to influence other mesocarnivore dynamics through trophic cascades. Coyotes, which have relatively recently expanded into regions historically dominated by wolves, including much of the eastern United States and Michigan, may partially fill this ecological role (Kurta, 2017). Raccoons (*Procyon lotor*) are known to negatively impact native bird and reptile populations (Suraci et al., 2014; Urbanek et al., 2016) and are also commonly associated with these buckthorn habitats, likely due to increased availability of invertebrates and bird nests (Vernon et al., 2014). This suggests that coyotes, including those utilizing buckthorn sites, could have a cascading effect on ecosystem health either through direct predation or by impacting raccoon behavior. If coyotes exert top-down pressure on raccoons in their shared habitats, they could indirectly benefit lower trophic levels and improve ecosystem function. However, recent evidence suggests that coyotes may not commonly prey on raccoons, indicating that shared habitat use does not necessarily imply strong predatory interactions (Chitwood et al., 2020). Future research should examine whether coyotes in this region can suppress raccoon populations, especially in buckthorn habitats where they may co-occur.

Conclusion

My study has shown that wildlife will utilize invaded habitats, but interactions are species-specific. Deer and coyotes continue to use areas degraded by invasive species, with each invasive species affecting wildlife differently. Buckthorn was positively associated with both deer and coyote site use. Stronger effects were observed for deer in the fall, likely due to buckthorn's extended leaf cover providing shelter and late-season forage. Autumn olive and honeysuckle were not associated with habitat use, although both species were browsed extensively.

Floristic Quality Index performed poorly for inferring wildlife habitat use and quantifying invasive pressure. Elevated FQI scores in invaded sites may be because invasive shrubs have not yet shaded out high-ranking native species, rather than true ecological condition. Additionally, FQI can be biased towards species richness, reflecting limitations in conveying the ecological threat of invasives (Bowles & Jones, 2006; Cretini et al., 2012; Miller & Wardrop, 2006). These findings highlight the need for caution when using FQI alone to assess habitat quality in invaded systems.

Although deer actively browsed invasive shrubs and used buckthorn-dominated stands for cover, this use should not be interpreted as evidence that invaded habitats provide equivalent nutritional or ecological value to native-dominated systems. In the long term, reliance on low-diversity, invasive-dominated habitats may be detrimental if these systems provide reduced forage quality or function primarily as structural refugia. Deer use of invasive shrubs may reflect short-term behavioral flexibility rather than long-term suitability.

The association between coyotes and buckthorn-dominated habitats further suggests that invasive plants may alter predator space use and potentially influence predator–prey interactions. By concentrating both cover and prey resources, invasive shrubs such as buckthorn may shape wildlife community dynamics in ways that extend beyond direct plant–herbivore interactions. These findings highlight the need for future research examining how invasive vegetation influences trophic interactions and behavioral responses across multiple species.

My study focused on deer and coyotes, although the trail cameras captured a broader community including raccoons, opossums, squirrels, and turkeys. Future research could improve efficiency by grouping species according to functional roles or ecological guilds, enabling broader inference about community responses to invasion. Overall, these findings underscore

that invasive plants reshape ecosystems in species-specific ways, and understanding wildlife responses requires integrating plant and animal data across seasons.

Invasive plants are among the greatest threats to biodiversity today. However, my study revealed an unexpected story of perseverance. Deer and coyotes continue to survive and even use habitats heavily altered by invasive species. Their presence, however, does not mean these habitats provide the same ecological value as native systems; instead, it highlights the resilience of wildlife facing altered landscapes. These findings reframe our understanding of invasive plant–animal interactions: wildlife do not merely avoid invasives, but engage with them in complex, species-specific ways, with potentially long-lasting impacts on the ecological community. By documenting these patterns, this work lays the foundation for future research exploring how altered plant communities influence wildlife behavior, species interactions, and trophic cascades in invaded ecosystems. Ultimately, understanding these dynamics is essential for managing both invasive plants and wildlife in ways that support resilient, functioning ecosystems.

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TABLES AND FIGURES

Table 1. *Deer Detection:* Candidate models evaluating predictors of deer detections across sites, ranked by AICc. Model factors are listed for each candidate model; *K* is the number of parameters, AICc is the corrected Akaike Information Criterion, ΔAICc is the difference from the top model, and *W* is the model weight (relative support). All models included a random effect of site.

Model Factors	K	AICc	ΔAICc	W
(Intercept), Autumn Olive, Buckthorn, Season	8	766.4	0	0.349
(Int), Buckthorn, Season	7	766.7	0.3	0.3
(Int), Autumn Olive, Buckthorn, Season, Diversity	9	767.3	0.93	0.219
(Int), Buckthorn, Season, Diversity	8	768.3	1.95	0.132

Table 2: *Deer Detection*: Model-averaged parameter estimates (β), standard errors (SE), *p*-values, and 95% confidence intervals (CI) for predictors of deer detections across 16 sites over four seasons. Fall served as the reference category for seasonal comparisons. Estimates are based on top-ranked candidate models (ΔAICc < 2). Significant predictors ($p < 0.05$) are shown in bold.

Predictor	Estimate (β)	SE	p-value	95% CI (lower–upper)
Intercept	121.9	71.1	0.087	–17.5 – 261.3
Buckthorn	57.0	24.9	0.022	8.2 – 105.9
Autumn Olive	–38.0	24.8	0.126	–86.6 – 10.6
Honeysuckle	4.0	15.5	0.795	–26.4 – 34.4
Season (Spring)	–99.0	33.3	0.003	–164.3 – –33.7
Season (Summer)	–79.5	34.7	0.022	–147.4 – –11.6
Season (Winter)	–127.0	33.4	<0.001	–192.4 – –61.6
Simpson's diversity	93.6	91.7	0.308	–86.2 – 273.4
FQI	–1.6	3.4	0.643	–8.2 – 5.0

Table 3. *Deer browse*: List of the top models ranked by AICc for the model examining what environmental variables impact deer browse. Model factors are listed for each candidate model; AICc is the corrected Akaike Information Criterion, ΔAICc is the difference from the top model, and W is the model weight (relative support). Species names are italicized. All models included a random effect of site.

Variables Included	K	AICc	ΔAICc	Weight
Amur honeysuckle cover + Season + Plant diversity (Simpson's Index)	7	713.33	0	0.137
Floristic Quality Index (FQI) + Amur honeysuckle cover + Plant diversity (Simpson's Index)	5	713.79	0.46	0.109
Deer detection rate + Amur honeysuckle cover + Season + Plant diversity (Simpson's Index)	8	714.46	1.13	0.078
Season + Plant diversity (Simpson's Index)	6	714.91	1.58	0.062

Table 4. *Deer browse*: Model-averaged estimates (β), standard errors (SE), p-values, and 95% confidence intervals (CI) for predictors of white-tailed deer browse across 16 sites over four seasons. Fall was the reference season. Significant predictors ($p < 0.05$) are shown in bold.

Predictor	Estimate (β)	SE	95% CI (Lower)	95% CI (Upper)	p-value
Intercept	4.72	7.58	-10.18	19.62	0.531
Honeysuckle	**20.87**	**10.17**	**0.42**	**41.33**	**0.045**
Buckthorn	-11.24	18.66	-47.90	25.42	0.548
Autumn Olive	12.40	15.35	-18.69	43.50	0.430
FQI	-0.46	0.66	-1.76	0.84	0.484
Simpson diversity	-2.26	8.41	-18.76	14.23	0.784
Deer capture rate	-0.02	0.02	-0.06	0.02	0.278
Season (Fall)	9.17	17.49	-25.23	43.57	0.599
Season (Spring)	8.05	22.92	-37.06	53.15	0.727
Season (Summer)	-1.66	23.64	-48.00	44.67	0.943
Season (Winter)	43.28	22.89	-2.79	89.35	0.066

Table 5. Coyote site use: Candidate models evaluating predictors of coyote detections across sites, ranked by AICc. Model factors are listed for each candidate model; *K* is the number of parameters, AICc is the corrected Akaike Information Criterion, ΔAICc is the difference from the top model, and *W* is the model weight (relative support). All models included a random effect of site.

Model	Model Factors	K	AICc	ΔAICc	w
10	(Int), FQI, Rhamnus	5	-348.5	0	0.262
12	(Int), FQI, Elaeagnus, Rhamnus	6	-348.2	0.28	0.228
9	(Int), Rhamnus	4	-347.8	0.73	0.181
44	(Int), FQI, Elaeagnus, Rhamnus, SDA	7	-346.9	1.57	0.12
42	(Int), FQI, Rhamnus, SDA	6	-346.7	1.79	0.107
41	(Int), Rhamnus, SDA	5	-346.6	1.89	0.102

Table 6. *Coyote site use:* Model-averaged estimates (β), standard errors (SE), p-values, and 95% confidence intervals (CI) for predictors of coyote site use across 16 sites over four seasons. Fall was the reference season. Significant predictors ($p < 0.05$) are shown in bold.

Predictor	β (Estimate)	SE	p-value	95% CI
Intercept	-0.005	0.0115	0.663	-0.0275, 0.0175
FQI	0.00078	0.00045	0.082	-0.00010, 0.00165
Buckthorn	0.01249	0.00424	0.003	0.00419, 0.02079
Autumn Olive	-0.00577	0.00443	0.193	-0.01445, 0.00291
Simpson Diversity	0.0145	0.01498	0.333	-0.01486, 0.04386
Honeysuckle	-0.00113	0.00275	0.683	-0.00652, 0.00427
Season (Spring)	-0.005	0.0061	0.413	-0.01696, 0.00696
Season (Summer)	-0.00779	0.00672	0.247	-0.02097, 0.00539
Season (Winter)	-0.00396	0.00582	0.497	-0.01537, 0.00745

Table 7. FQI scores for each site during each season. FQI is calculated using the formula (FQI=C√n), where C is the mean conservation values of native species observed at a site and n is the total number of native plant species observed at that site. Conservation values of each species were obtained from the University of Michigan's LSA Herbarium's Michigan Flora database (University of Michigan LSA Herbarium, 2024). Bolded text indicates that score is an average of all seasons within a site.

Site	FQI	Site	FQI	Site	FQI
1_1	**11.54101058**	7_Fall	**11.66726189**	13_Spring	20.10910988
1_Fall	10.12920852	7_Spring	10.85027796	13_Summer	**20.34020192**
1_Spring	14.88627451	7_Summer	15.7435663	13_Winter	7.849062223
1_Summer	14.83945999	7_Winter	6.654721524	**14_14**	**12.6542**
1_Winter	6.30909928	**8_8**	**7.6861**	14_Fall	9.592972662
2_2	**8.498865746**	8_Fall	7.11738529	14_Spring	11.24483352
2_Fall	7.083333333	8_Spring	**7.273098321**	14_Summer	18.03827751
2_Spring	12.01355075	8_Summer	11.35583488	14_Winter	11.74052144
2_Summer	12.8985789	8_Winter	3	**15_15**	**13.1724**
2_Winter	2	**9_9**	**17.7642**	15_Fall	11.00806449
3_3	**10.8129**	9_Fall	19.72708071	15_Spring	16.375
3_Fall	5.725490196	9_Spring	25.33783784	15_Summer	20.08283586
3_Spring	12.54345942	9_Summer	19.99197627	15_Winter	5.225578118
3_Summer	15.21694983	9_Winter	6	**16_16**	**9.9913**
3_Winter	9.763636364	**10_10**	**12.3215**	16_Fall	8.514508765
4_4	**10.7087**	10_Fall	11.35943991	16_Spring	15.86916235
4_Fall	7.602729371	10_Spring	15.80707043	16_Summer	12.1470444
4_Spring	12.44160889	10_Summer	15.387941	16_Winter	3.434518651
4_Summer	14.05409452	10_Winter	9.797958971		
4_Winter	**8.736513416**	**11_11**	**15.3146**		
5_5	**12.0485**	11_Fall	13.67104859		
5_Fall	11.47767156	11_Spring	17.57057422		
5_Spring	12.84336807	11_Summer	20.0423195		
5_Summer	18.02381691	11_Winter	9.972447249		
5_Winter	7.849056604	**12_12**	**12.0182**		
6_6	**7.7972**	12_Fall	13.45132926		
6_Fall	8.598733668	12_Spring	15.45977011		
6_Spring	11.80535131	12_Summer	6.350852961		
6_Summer	9.944444444	12_Winter	12.81081081		
6_Winter	6.639528096	**13_13**	**14.3163**		
7_7	**11.2285**	13_Fall	10.96900106		

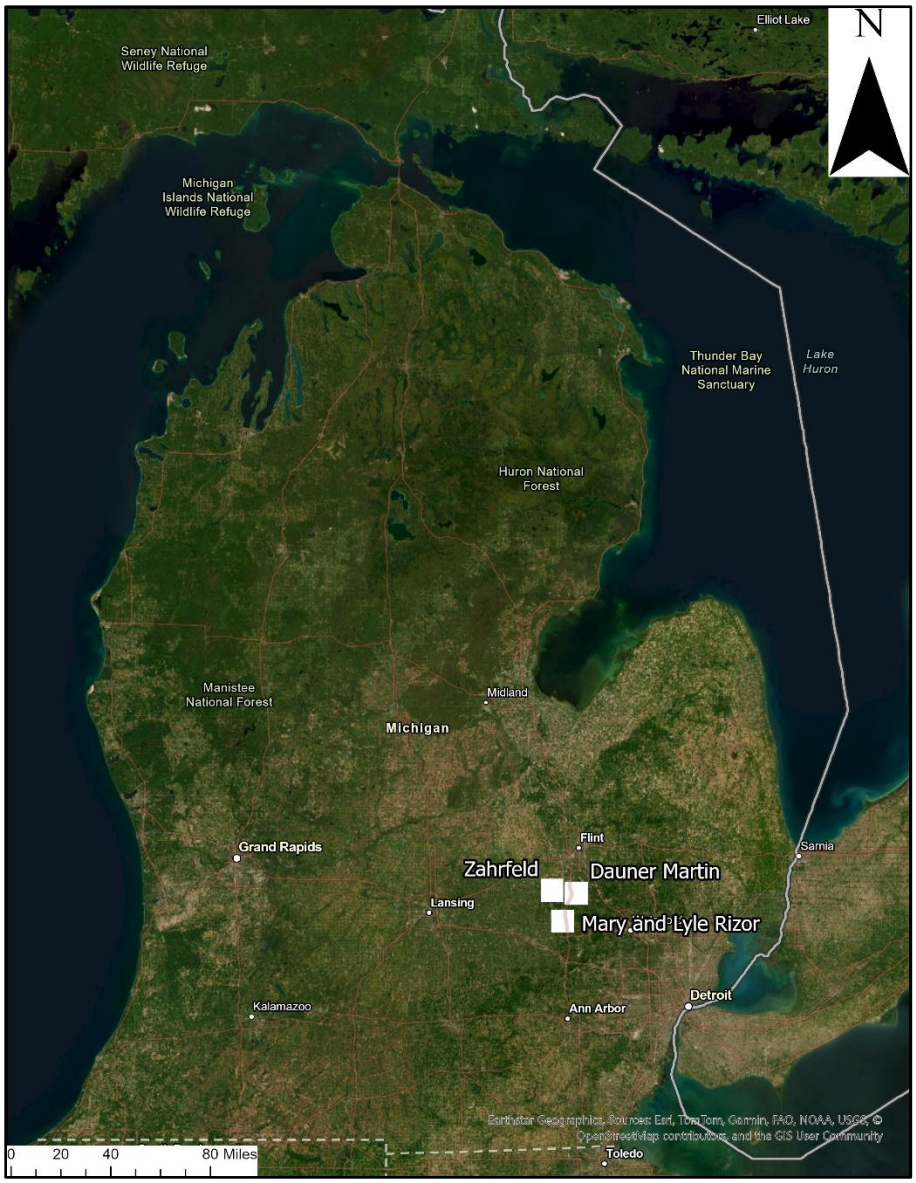


Figure 1. The locations of the three Michigan Nature Association sanctuaries used for this project are represented by gray squares, relative to the lower peninsula of Michigan. Squares are not to scale.



Figure 2. Photograph of spring ephemerals at Mary and Lyle Rizor in Livingston County.

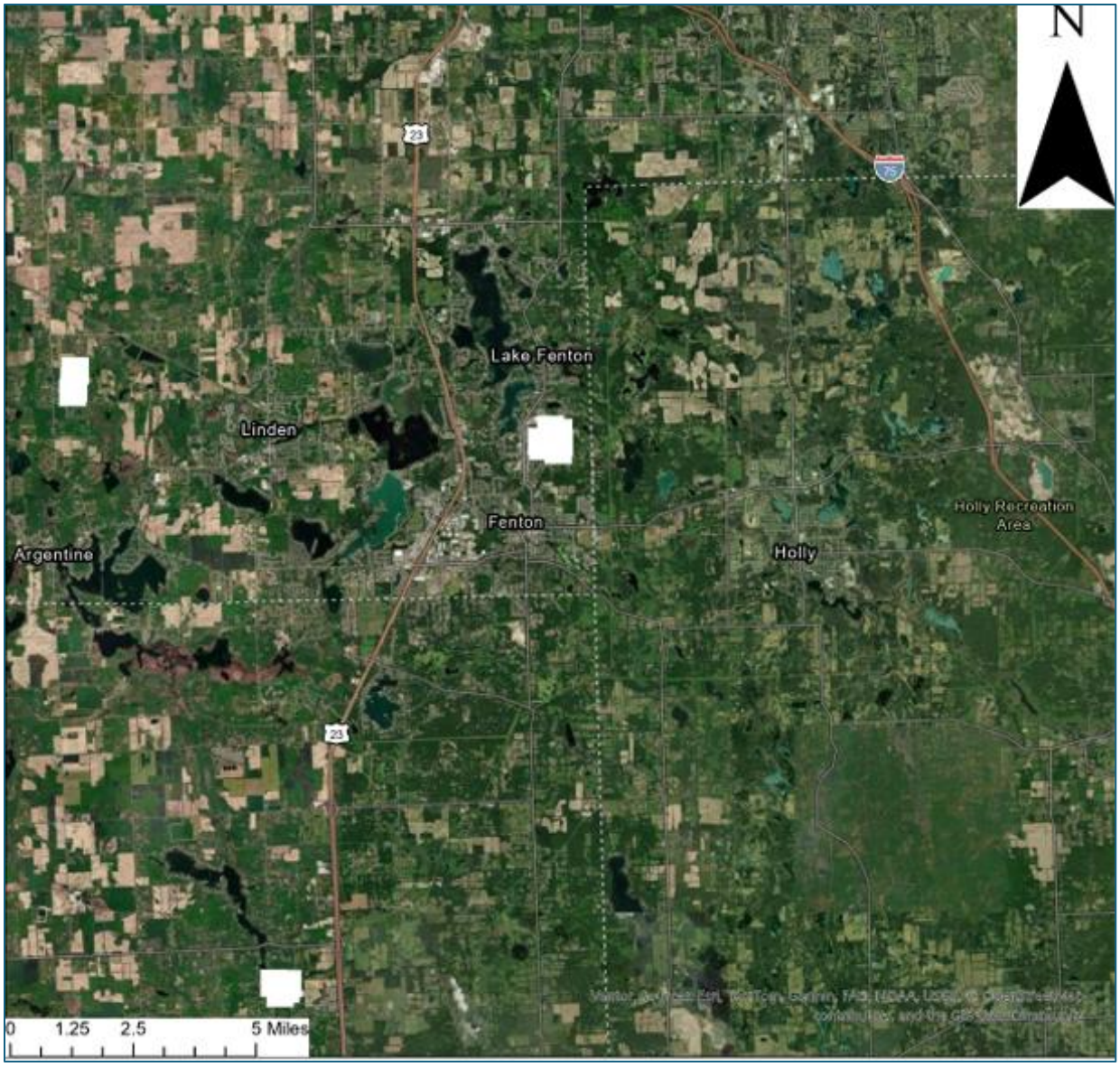


Figure 3a. Locations of all field sites, located in southeastern Michigan. There were 16 sites in total. Each site is represented by a square, although at this scale the squares are shown overlapping. Squares are not to scale.

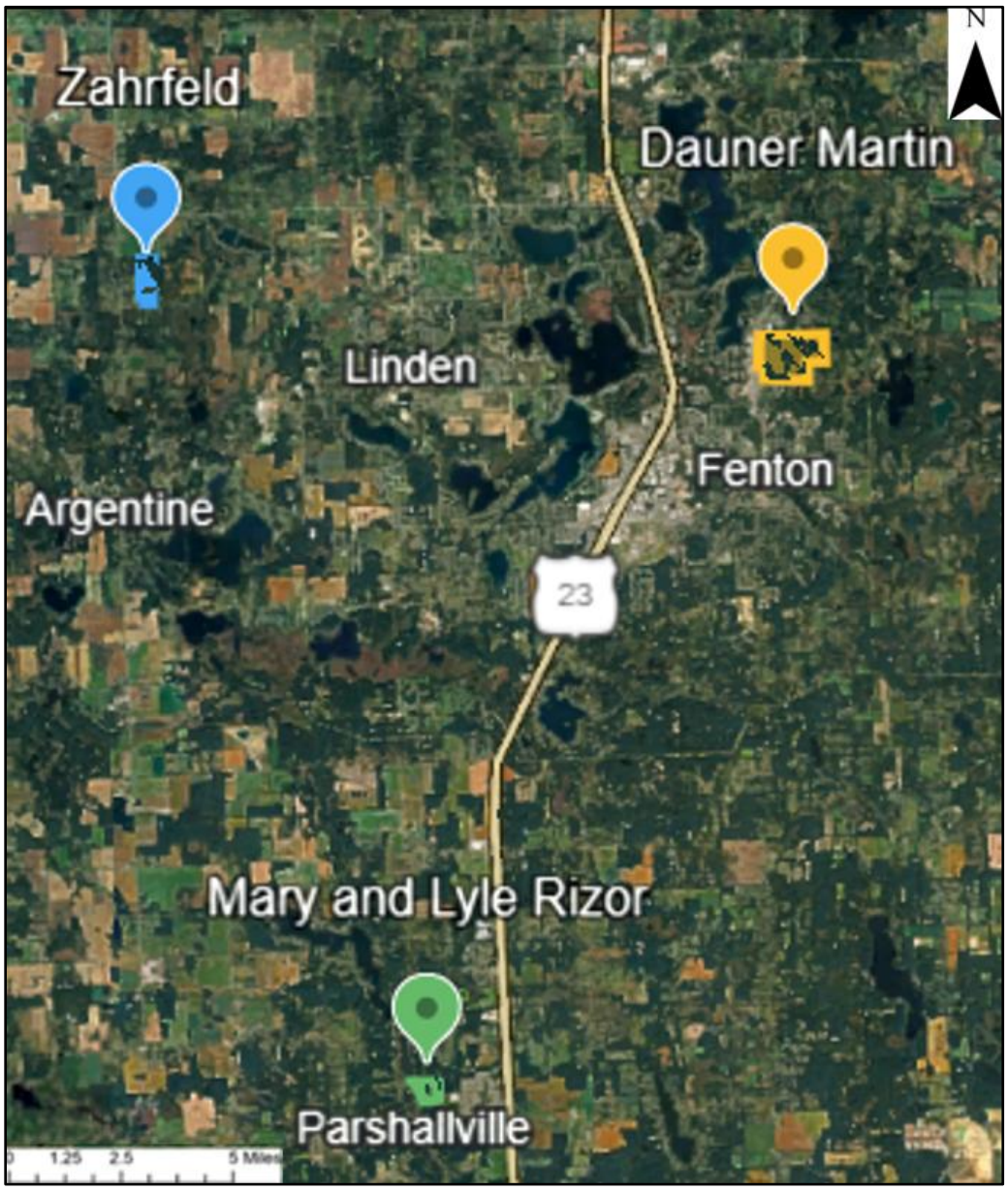


Figure 3b. The locations and outlines of each of the MNA park boundaries relating to the local area. Dauner Martin had 8 field sites, Mary and Lyle Rizor had 4 field sites and Zahrfeld had 4 field sites.



Figure 4a. Location of 1-ha sites within Dauner Martin Nature Sanctuary, located within Fenton township, Genesee County, Michigan. Plots were chosen to ensure a spectrum of invasion was sampled throughout the study.



Figure 4b: Location of 1-ha sites within Mary and Lyle Rizor field sites. Mary and Lyle Rizor Nature Sanctuary is near Parshallville in Hartland township, Livingston County, Michigan.



Figure 4c. Field sites located at the Michigan Nature Association's Zahrfeld Nature Sanctuary, located in Argentine Township within Genessee County, Michigan. Each square represents one hectare.

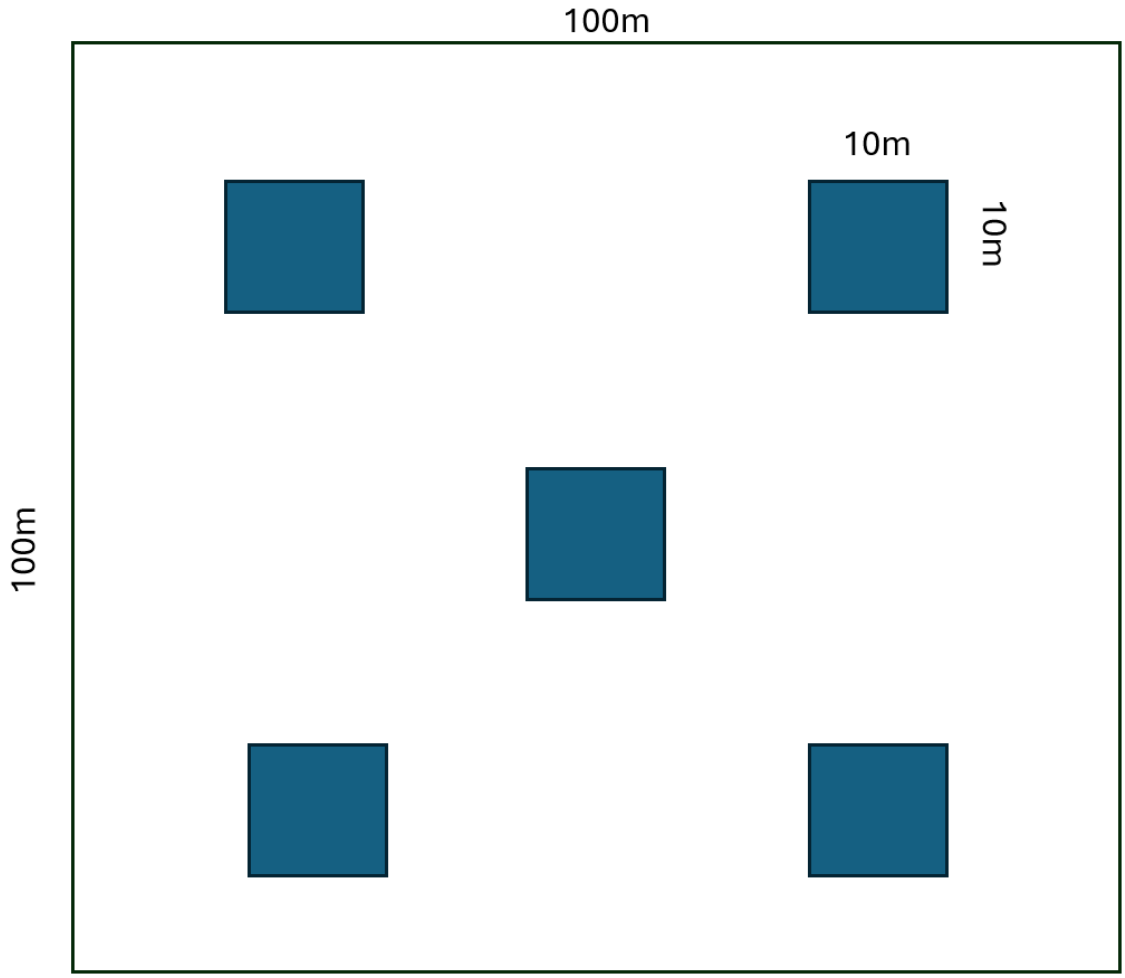


Figure 5a. Example of the five $10m^2$ subplot grid within one hectare. All subplots were 25m from each other. Camera traps were placed at a random subplot.

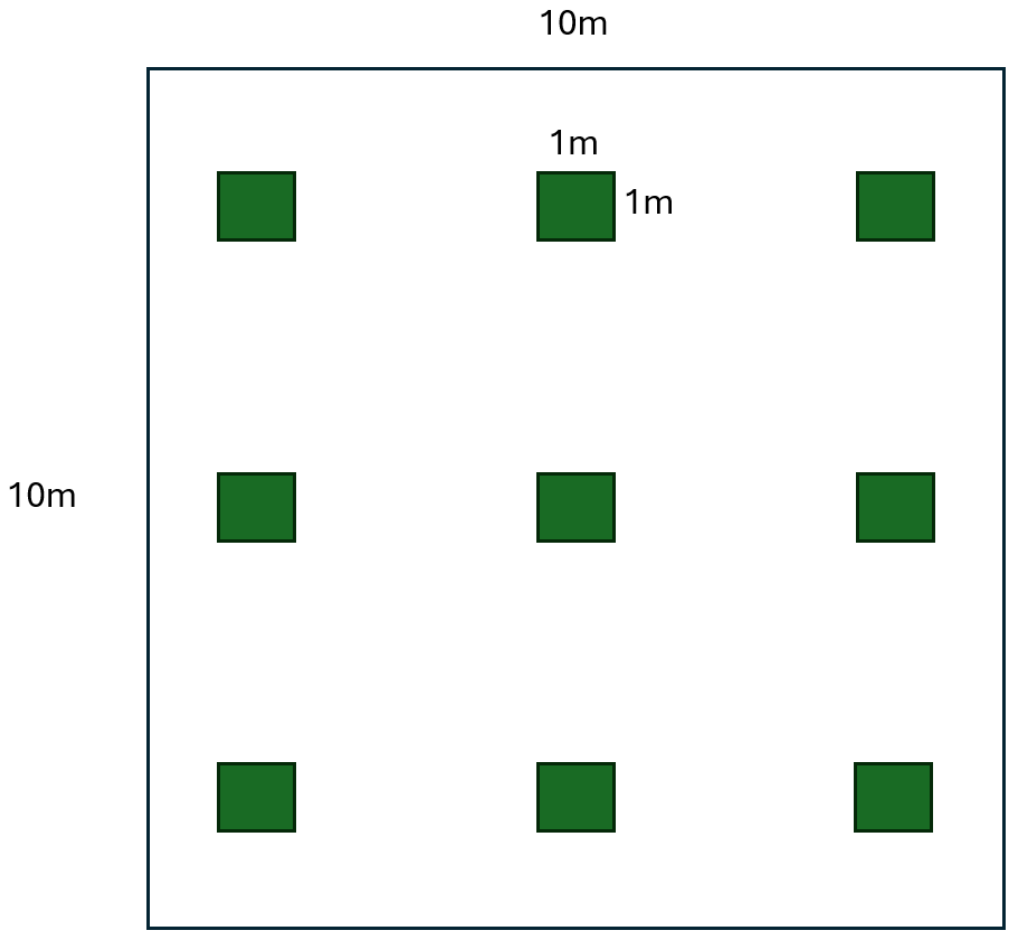


Figure 5b. Example of quadrat placement inside a 10x10m subplot. Vegetation sampling occurred within each quadrat.



Figure 5c. Image of a field researcher setting up a $10m^2$ subplot with vegetation sampling quadrats placed every 3.3m. A field tape was used to ensure accurate quadrat spacing. Note that only 2 out of 9 quadrats are shown in this picture. PVC Quadrat tools are shown divided in half for easier transportation.



Figure 6. This is an example of deer browse. Deer tends to leave jagged and torn stems, compared to cottontail rabbits who would leave clean 45-degree bite marks (Skoták et al., 2025). All plants within our sampling quadrats were visually examined for damage. We counted the number of browsed stems and leaves per plant. Rabbit and deer forage were differentiated by assessing stem damage patterns while considering height of browse.



Figure 7: Image of a camera trap at site 1, located with Dauner Martin Nature Sanctuary in February of 2024. Camera traps were operated for 30 days each season and faced north to avoid the direct glare from the sun.

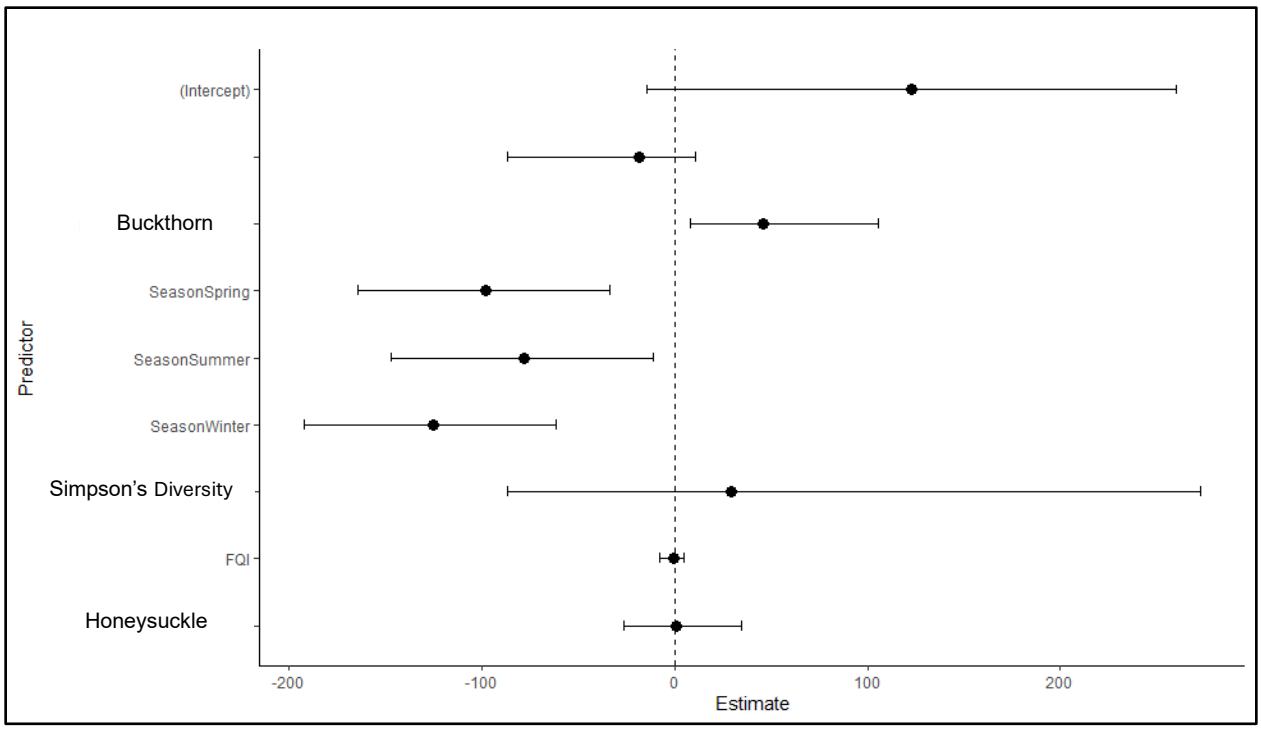


Figure 8. Forest plot of the deer use model averaged affects (95% Confidence Interval). Note that buckthorn had a positive association with deer site use.

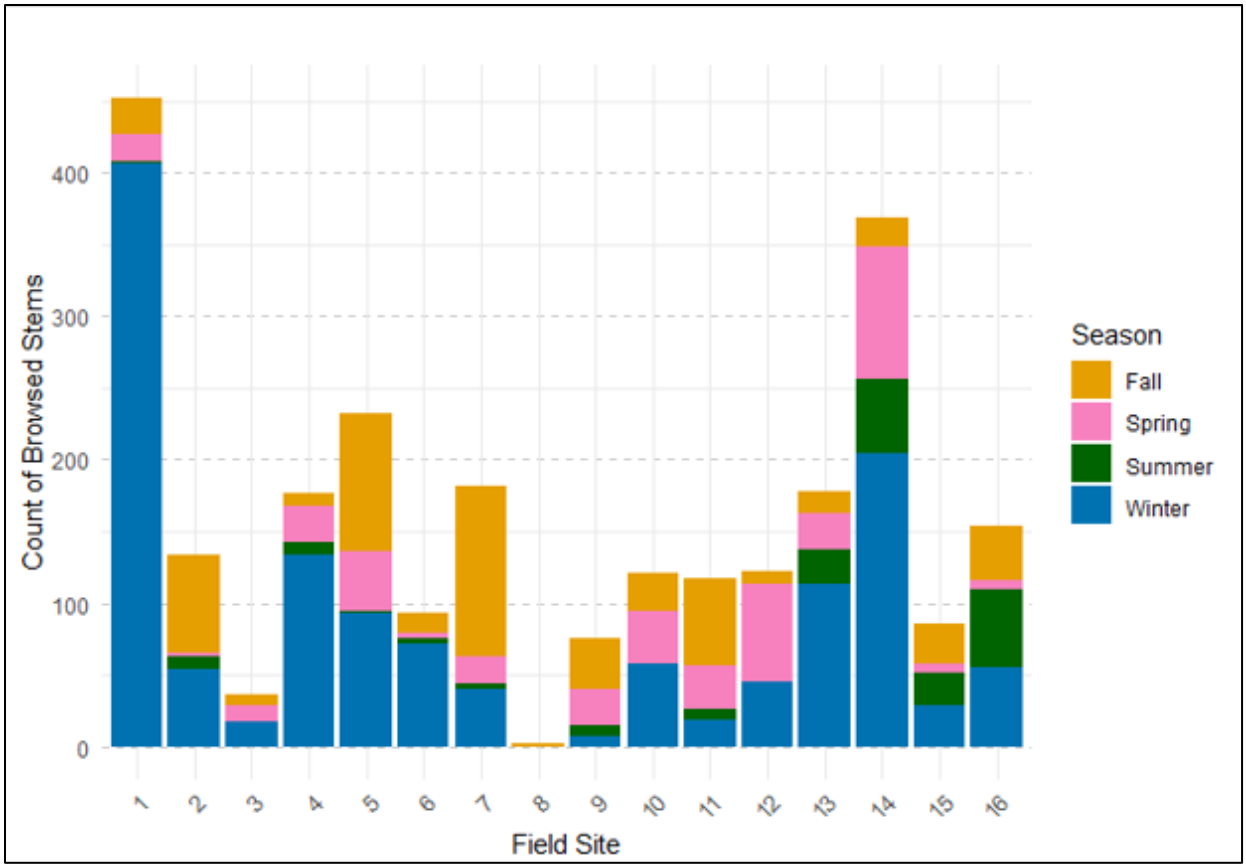


Figure 9. This figure shows browsed stems observed at each site, with each column subdivided based on the number of browsed stems per season. Sites 1 at Dauner Martin and 14 at Zarhfeld experienced the most browsed stems. Both sites could be considered early successional habitat with numerous saplings and shrubs within deer browse height.

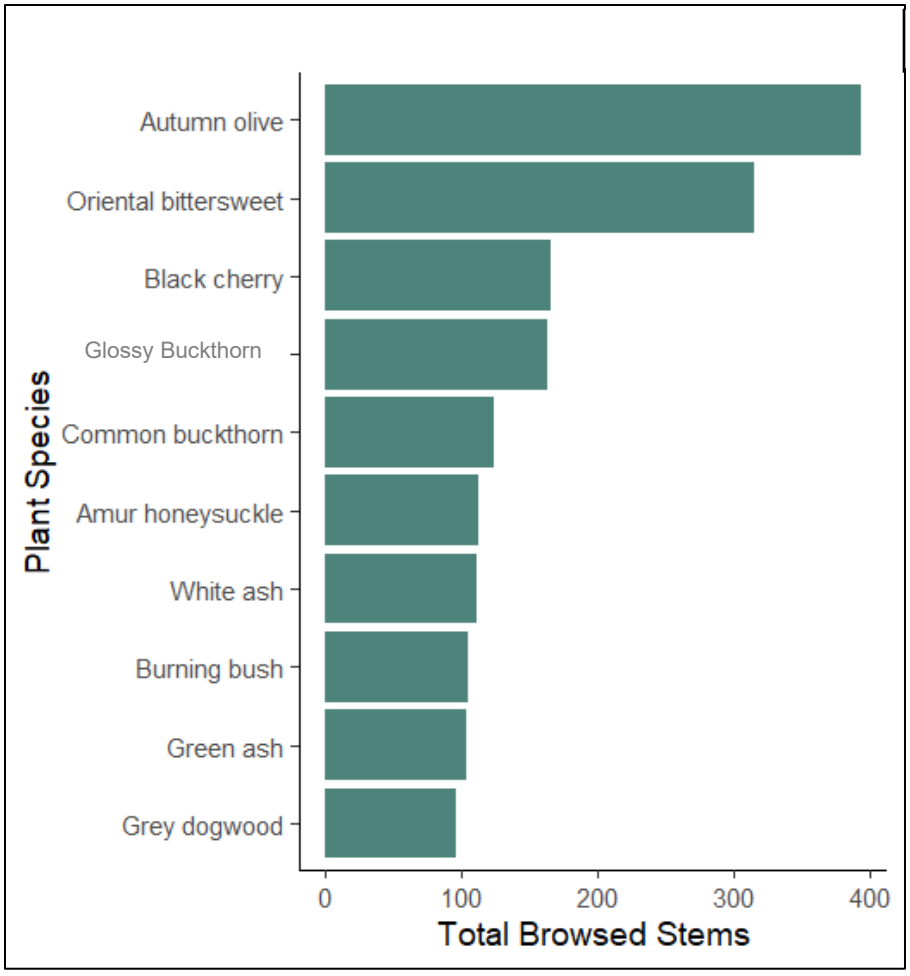


Figure 10. Counts of browsed stems from the top 10 browsed plant species. The most herbivory damage was observed on autumn olive and oriental bittersweet, two invasives that occurred commonly in our research sites. Aside from black cherry (*Prunus serotina*), invasive plants made up the most browsed species. Note that this data is pooled from 16 one-hectare field sites occurring at 3 unique nature preserves throughout all seasons.

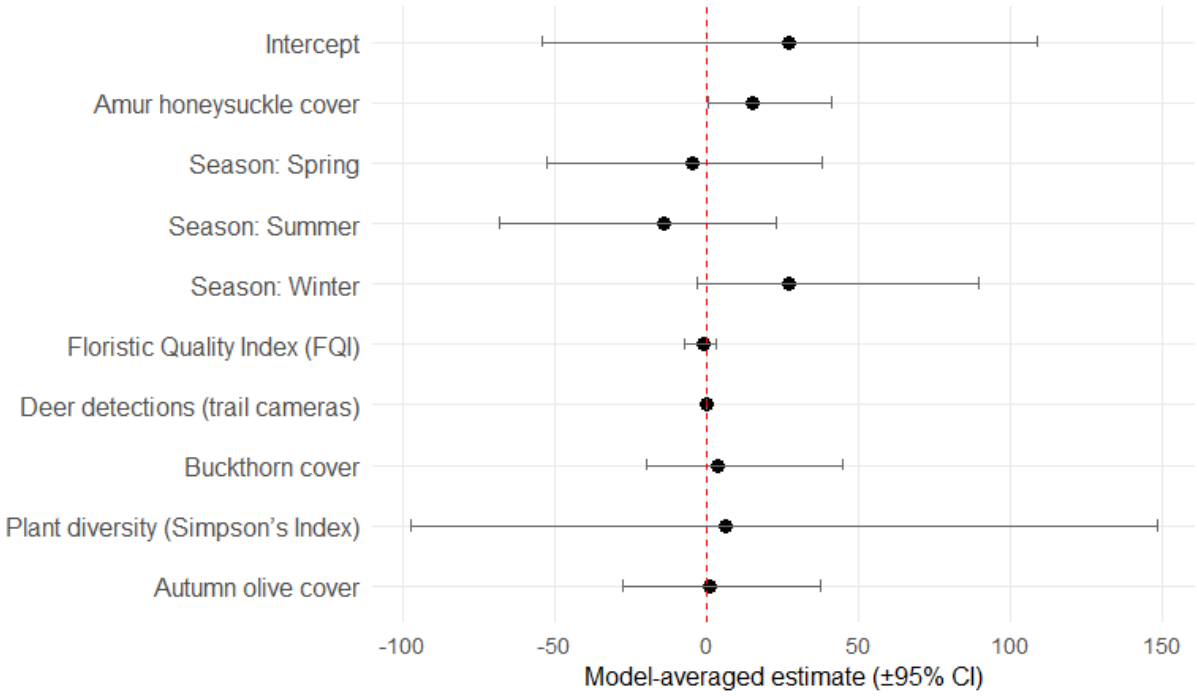


Figure 11. Forest plot showing the predictors of deer browse from the deer browse model averaged affects (95% Confidence Interval). Fall was the reference season. Honeysuckle cover was positively associated with deer browse.

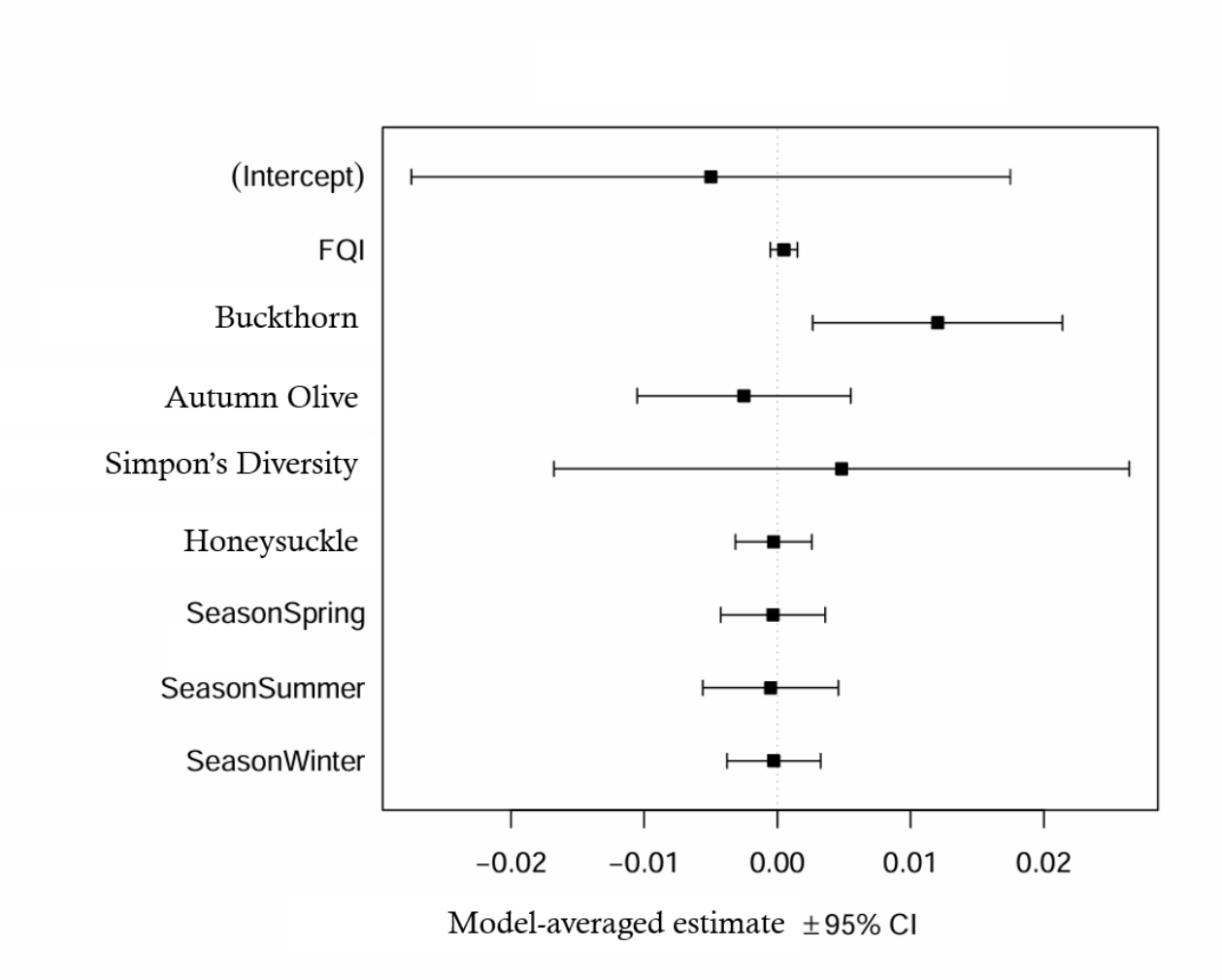


Figure 12. Forest plot illustrates the 95% confidence intervals of the variables in the model of best fit for predicting coyote site use. Note that FQI buckthorn cover has a positive association with coyote site use.

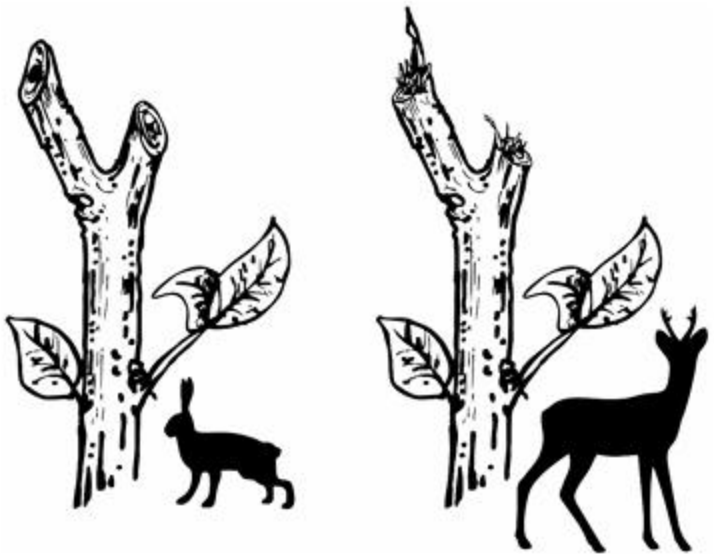


Figure 13. Examples of browse damage on twigs that are browsed by rabbits (clean cut) and deer (ragged tear) (Skoták et al., 2025).

Percent cover	0	0+	1+	5+	25+	50+	75+	95+	99+
Cover class	0	1	2	3	4	5	6	7	8

Figure 14. The modified Braun-Blanquet cover class scores that were used for identifying vegetation cover class.

Appendix: Supplemental Information

White-tailed Deer Site Use – Understory Sub Model

To better evaluate the relative contribution of plant diversity on deer detection, a separate model was run. This model included deer site use as the response variable and diversity of the forest understory (plants less than 6ft were included), autumn olive cover, buckthorn cover, honeysuckle cover, FQI, and season as predictor variables. Site was kept as a random effect. This was done to see if the understory vegetation, which deer could directly interact with in the form of food or cover, would have a stronger effect on deer detection than the overall diversity, which was not predictive of deer site use in the main model (Figure 8). Once this subset model was ran, only two candidate models were strongly supported ($\Delta AICc \leq 2$) (Table S1).

This model closely mirrored the results of the full deer site use model that utilized Simpsons diversity index of the entire plant community. Buckthorn (*Rhamnus* spp.) remained positively associated with deer detections ($\beta = 55.7 \pm 24.7$ SE, $p = 0.024$). Autumn olive (*Elaeagnus umbellata*) ($\beta = -35.4 \pm 24.8$ SE, $p = 0.154$) and Honeysuckle (*Lonicera maackii*) ($\beta = 4.2\text{-}15.2$ SE, $p = 0.78$) had no significant effect on deer detection. Seasonal effects were similarly consistent, with deer site use peaking in fall, and all other seasons seeing significantly less deer. However, understory vegetation was not significant predictor of deer ($\beta = -53.8 \pm 88.63$ SE, $p = 0.55$) (Table 4). This result was the same as the main model that included Simpsons diversity index of the entire plant community, showing that understory diversity is not a better predictor of deer site use than overall plant diversity.

White-tailed deer herbivory- Winter sub model

Because winter browse counts were much higher than other seasons (Fig. 9), we tested a winter browse-only model set to evaluate whether different environmental variables were more important during this season when compared to the main model. Initial VIF calculations indicated high multicollinearity for FQI (VIF = 7.36) for some invasive shrub cover variables (Relative Lonicera maackii = 5.18, Relative Elaeagnus umbellata = 9.57). To reduce multicollinearity, FQI was removed from the model. After removal, VIF values for the remaining predictors were not above 2.02, indicating no multicollinearity concern. In this analysis, no predictors were significantly associated with deer browse (Table S3). The null model was top-ranked, and all confidence intervals spanned zero. These null results may reflect low power from limited replication (n = 16 winter plots) as well as seasonal differences in plant availability and browsing behavior. To accurately test this winter only model we would need more site replication.

Table S1: White-tailed Deer Site Use – Understory Sub Model: Candidate models after running a AICc test on a white-tailed deer site use model that included only understory diversity, instead of diversity of all the plants. This was done since I thought deer might be more impacted by the diversity of plants they can directly browse. Candidate models are evaluating predictors of deer detections across sites, ranked by AICc. Model factors are listed for each candidate model; K is the number of parameters, AICc is the corrected Akaike Information Criterion, ΔAICc is the difference from the top model, and W is the model weight (relative support). Species names are italicized. All models included a random effect of site.

Model Factors	**K**	**AICc**	**ΔAICc**	**W**
(Int), Elaeagnus, Rhamnus, Season	8	766.4	0	0.538
(Int), Rhamnus, Season	7	766.7	0.3	0.462

Table S2. *White-tailed Deer Site Use – Understory Sub Model*: Model-averaged estimates (β), standard errors (SE), p-values, and 95% confidence intervals (CI) for predictors of white-tailed deer detections across 16 sites over four seasons. Fall was the reference season. Significant predictors ($p < 0.05$) are shown in bold. Note that this model utilizes Simpson diversity of low and medium height vegetation (includes plants that were less than 6ft). Spring, summer and winter experienced significantly lower deer detection than fall.

Predictor	**Estimate (β)**	**SE**	**p-value**	**95% CI (lower–upper)**
(Intercept)	161.73	54.89	0.003 **	54.15 – 269.30
Relative Elaeagnus umbellata	-35.36	24.78	0.154	-83.93 – 13.22
Relative Rhamnus spp.	55.71	24.67	0.024 *	7.36 – 104.07
Season Spring	-98.25	33.36	0.003 **	-163.62 – -32.87
Season Summer	-78.96	34.8	0.023 *	-147.16 – -10.76
Season Winter	-129.94	33.55	<0.001 ***	-195.69 – -64.18
Simpson Low-Med	-53.81	91.09	0.555	-232.35 – 124.73
FQI	-1.5	3.4	0.658	-8.17 – 5.16
Relative Lonicera maackii	4.28	15.65	0.784	-26.39 – 34.95

Table S3: *White-tailed deer herbivory- Winter sub model:* Estimates are model-averaged across all candidate models with random effect of Site. Confidence intervals are 95%. Full average includes zero for predictors not in all models; conditional average includes only models where predictor was included.

Predictor	**Full Average Estimate**	**Std. Error**	**Conditional Average Estimate**	**Std. Error**	**95% CI**
Intercept	68.31	55.09	68.31	55.09	-39.65 – 176.28
Honeysuckle Cover	8.26	21.20	34.52	31.19	-26.61 – 95.66
Autumn Olive Cover	1.84	20.42	14.99	56.49	-95.73 – 125.71
Deer capture rate	0.03	0.44	0.26	1.24	-2.16 – 2.69
SimpsonDivAll	2.36	46.66	19.73	133.55	-242.02 – 281.47
Buckthorn Cover	-0.77	23.40	-6.55	67.80	-139.43 – 126.34