

**INTERACTIVE EFFECTS OF LANDSCAPE CONTEXT, NON-NATIVE
PLANTS, AND DEER ABUNDANCE ON FOREST PLANT
COMMUNITIES IN CENTRAL INDIANA**

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Dedicated to my wife for supporting and dealing with my academic endeavors.

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ABSTRACT

Landscape context (land use and fragmentation), high densities of white-tailed deer, and non-native plants have all contributed to reductions in native plant diversity in forests across the eastern United States. These processes and their impacts on plant communities have produced ecological, economic, social, and human-health concerns, emphasizing the need to better understand these processes and their impacts to effectively guide management across the rural-urban gradient. However, management is further complicated due to the related and interactive nature of these processes. While some research has examined interactions among landscape context and invasive species, as well as invasive species and white-tailed deer, we found few studies that simultaneously considered all three of these threats to native forest plant communities.

We studied forest patches in central Indiana in both agricultural (rural) and urban matrices to determine how deer herbivory varied with landscape context. Specifically, we examined how deer abundance, browse on woody species, non-native plant species cover and densities, land cover, and forest patch area/shape impacted herbaceous-layer and sapling-layer species diversity. Our results demonstrated that woody browse available to deer differed between rural and urban forest patches. Additionally, we found that deer browsed the invasive shrub, Amur honeysuckle (*Lonicera maackii*) at a higher rate in urban forest patches compared to agricultural patches. We also observed that deer, non-native plant densities and cover, and landscape context were all associated with changes in native plant species diversity. Higher rates of deer browse, non-native plant density/cover, and increased forest edge were associated with declines in diversity. Interestingly, we found that the proportion of forest land cover in close proximity to forest patches was not only correlated with increased native plant species, but also associated with reduced negative effects on diversity from non-native species. We did not observe any interactions between deer and non-native plants or deer and landscape context variables. Both rural and urban landscapes in our study were highly fragmented and adding a heavily forested landscape would contribute to an improved understanding of how landscape context, deer herbivory, and non-native plant species affect native plant communities. Managers should be aware that forest patches with increased edge and a lack of other forest land cover located within 500 m are susceptible to declines in diversity associated with non-native plants. While observed rates of deer browsing in our urban forest patches were low compared to examples in the literature, managers should also be aware

that deer often exceed desired densities in urban settings, which could further harm at-risk plant communities.

CHAPTER 1. INTRODUCTION

1.1 Introduction

Plant communities provide essential ecosystem services such as water filtration and soil stabilization (Myers, 1997; Matteo et al., 2006), and are primary producers in food webs. Higher plant diversity is associated with improved production and efficiency of ecosystem services (Quijas et al., 2010; Isbell et al., 2011). Additionally, higher plant diversity is associated with improved ecosystem resilience (Elmqvist et al., 2003). In the face of anthropogenic modifications to the environment, maintenance of diversity in ecosystems is critical to sustaining ecological services. Effective conservation requires knowledge of how multi-scale processes and conditions affect plant species diversity.

Over the past century, forest plant communities in the eastern United States have experienced changes in landscape context (e.g. fragmentation, land cover; Riitters et al., 2012), increased white-tailed deer (*Odocoileus virginianus*) densities (Côté et al., 2004), and invasion by non-native plant species (Oswalt et al., 2015), all of which have been associated with reductions in native plant diversity. Thus, successful conservation and management strategies depend on identifying how these factors drive reductions in diversity within forest patches. Each of these factors (landscape context, non-native plants, white-tailed deer) impact plant communities differently, through a variety of direct and indirect processes and interactions.

White-tailed deer directly impact plant communities through the consumption of plant tissue and indirectly by preferentially browsing some species and reducing their competition with other species. This phenomenon has been widely documented with white-tailed deer consuming native species and reinforcing the dominance of non-native species (Webster et al., 2008; Dávalos et al., 2015; Shen et al., 2016; Blossey and Gorchov, 2017). In addition to shifting plant community composition, white-tailed deer can also, through time, alter vegetation structure (Horsley et al. 2003). Through alterations to the plant community, white-tailed deer can also impact the abundance and species richness of other animal taxa (Allombert et al., 2005; Martin et al., 2010, Shelton et al. 2014). In addition to direct impacts on vegetation, white-tailed deer can also indirectly impact plant communities and the environment through increased soil compaction (Heckel et al. 2010), and altered nutrient cycling (Rooney and Waller, 2003).

Landscape context (e.g. fragmentation, land use) influences plant communities through a variety of processes. Fragmentation causes spatial separation of forest patches, which can inhibit seed dispersal (Matlack, 2005). Additionally, fragmentation creates disturbed edge habitats that provide opportunities for non-native species to establish and advance into the forest interior (Gavier-Pizarro et al., 2010). Urban land cover and roads also facilitate the spread of non-native species plant species (Trombulak and Frissel, 2001; Aronson et al., 2015). Urbanization can also alter the environmental conditions, such as carbon dioxide concentrations and temperature (Bereitschaft and Debbage, 2013).

Non-native plants can reduce native plant diversity and density through direct competition. Non-native plants often display extended leaf phenology, which provides them with a photosynthetic advantage over native species (Fridley, 2012). Additionally, non-native plants can impact nutrient cycling (Ehrenfeld, 2003) and deter native plant establishment through with allelopathy (Hierro and Callaway, 2003).

In addition to their individual effects, these factors frequently interact, lending greater complexity to their overall effects on plant communities. White-tailed deer and some non-native plant species have shown a synergistic effect in reducing native plant cover and diversity (Webster et al., 2008). Additionally, non-native plants are associated with urbanization which provides the opportunity for simultaneous impacts on plant communities from these factors. Deer often occur at high densities in urban areas, but it remains unclear if the impacts of deer interact with ecosystem stress from urbanization to reduce plant species diversity. Studies that simultaneously examined the impacts of all of three factors (landscape context, white-tailed deer, non-native plants) on plant communities in both rural and urban landscapes are lacking in the literature.

Due to the prevalence of urban land cover (McKinney, 2006), high abundances of deer in many urban areas (Urbanek et al., 2011), and the spread of non-native species across the United States (Oswalt et al., 2015), we designed our study to examine how these factors affect native plant communities in urban forests in comparison to rural forests, with the goal of informing management across the rural-urban interface. We measured variables associated with white-tailed deer abundance and herbivory, land cover composition and urbanization, fragmentation (forest patch area and shape), and non-native plant species cover and density and examined plant community responses in urban and rural forests (in an agriculture matrix). In chapter 2 we address how the availability of browse species changes in the rural to urban gradient and, subsequently, if

white-tailed deer browsing preferences and browse pressure changes in the rural to urban gradient. In chapter 3 we examine the diversity of the herbaceous and sapling layers in response to individual and interactive effects of fragmentation impacts (e.g. forest patch area, perimeter-area ratio), land cover composition surrounding forest patches, white-tailed deer abundance and browse on woody stems, and the cover and density of non-native plant species.

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CHAPTER 2. WOODY BROWSE PRESSURE AND PREFERENCES BY DEER IN RURAL AND URBAN FOREST PATCHES

2.1 Introduction

Structure and ecological function within rural and urban landscapes are inherently different and have differing effects on forest plant communities. Urbanization alters forest processes such as seed dispersal and seedling establishment (Trentanovi et al., 2013; Williams et al., 2009) and increases nitrogen deposition, CO₂ concentration, and temperature (Bereitschaft and Debbage, 2013; Brazel et al., 2000; Savva et al., 2010). Additionally, invasive plant species are often more prevalent in urban areas (Aronson et al., 2015) due to increased importation of materials and anthropogenic modifications that favor habitat generalists (Mckinney, 2006). Thus, it is not surprising that urban forests display different species composition and structure (Burton et al., 2005; Pennington et al., 2010). Differing plant composition is likely to result in different woody browse availability and deer browsing pressure and preferences between rural and urban forests. If urban forest browse composition shifts to less preferred species, deer may shift to other sources of food such as ornamental plants and gardens, which would increase human-wildlife conflicts. For both ecological and practical reasons, we posit that understanding how woody browse composition and preference differ between urban and rural forests is critical to the successful management of forests across the urban-to-rural gradient.

White-tailed deer (*Odocoileus virginianus*), hereafter deer, are keystone herbivores that impact ecosystem components and processes such as nutrient cycling (Pletscher et al., 1989), plant community composition, tree regeneration (Horsley et al., 2003; Rooney and Dress, 1997; Waller and Alverson, 1997), and assemblages of other fauna (DeCalesta, 1994). Thus, management of deer is consequential to ecosystem structure and function. The impacts of deer herbivory on plant species diversity, regeneration and survival of woody plants, and the interactive effects of deer and invasive species have been extensively studied (Blossey and Gorchov, 2017; Rooney, 2001; Royo et al., 2010; Waller, 2014). However, many of these studies focused on rural landscapes with high forest landcover (Miller et al., 2009; Royo et al., 2017) or mixed forest and agricultural landcover (Hurley et al., 2012), while fewer studies have examined deer impacts on forests in urban landscapes (Morrison, 2017).

While little studied, the effects of deer on forests in urbanized landscapes are often problematic. First, deer in urban environments often exceed desired densities, with 33 out of 34 deer biologists in states with white-tailed deer indicating that urban and suburban deer populations are a management concern (Urbanek et al., 2011). Deer-vehicle collisions are another concern with urban and suburban deer populations. Although the distance to urban areas was not a reliable factor in a review of studies examining deer-vehicle collisions (Pagany, 2020), Stewart (2011) found that 39% of respondents to a survey in three Midwestern cities indicated that a family member had been involved in a deer-vehicle collision, which was an important factor in determining attitudes towards urban deer. Another human health concern with urban and suburban deer is elevated abundance of tick species (Allan et al., 2010; Rand et al., 2003) and increased human risk of zoonotic diseases, such as Lyme disease (Kilpatrick et al., 2014) and ehrlichiosis (Allan et al., 2010). In addition to human health and safety concerns, deer in urban areas also produce ecological concerns. Deer in urban landscapes exhibit behavioral and demographic differences compared to deer in rural landscapes, such as smaller home range sizes (Grund et al., 2002; Storm et al., 2007), differences in genetic relatedness (Blanchong et al., 2013), and differences in the causes and rates of herd mortality (Etter et al., 2002). Based on a review of the literature we have found few studies that have examined whether these differences translate to different ecological impacts on plant communities by deer in urban forests compared to rural forests. Because deer in urban areas exhibit smaller home ranges coupled with high survival rates and a general lack of hunting (Etter et al., 2002), deer may exert heavier browsing pressure on woody forest plants in urban areas. In fact, Barrett and Stiling (2006) found lower densities of preferred woody forage and higher browse pressure in urban areas compared to exurban/rural areas in hardwood hammocks of Florida.

The availability of alternate food sources outside of forest understories also differs in rural versus urban landscapes. In rural (agricultural) landscapes of the Midwest, row crops (i.e. corn and soybeans) and cover crops provide alternate food sources, whereas ornamental plants, gardens, fertilized lawns, and potentially human handouts, provide alternate food sources in urban landscapes (Swihart et al., 1995; Barret and Stiling, 2006). Differences in type, seasonality, and nutritional quality of these alternative food sources could also affect the relative impacts of browsing on forest understories in rural and urban settings, even if deer abundances are similar.

As noted previously, increased abundance of invasive plants in urban areas can contribute to changes in browse composition and intensity, which further alters the dynamics of deer

herbivory in urban forests. Deer display differing preferences for invasive plants, preferring some while avoiding others (Averill et al., 2016). Some invasive plant species, such as Amur honeysuckle (*Lonicera maackii*), may be neither preferred nor avoided by deer. Amur honeysuckle is not a preferred browse species (Wright et al., 2019) however, it can compose 14 - 47% of annual deer diets (Martinod and Gorchov, 2017). This shrub species is widely distributed across the eastern United States (USDA, NRCS 2020), highly abundant in urban areas (Borgmann and Rodewald, 2005; White et al., 2014), and displays extended leaf phenology (ELP; McEwan et al., 2009) that affords it a competitive advantage over native competitors (Fridley, 2012). Amur honeysuckle can be an important food resource in early spring when it flushes leaves while native plants are still dormant and less nutritious (Martinod and Gorchov, 2017). Thus, it is possible that Amur honeysuckle and native plants are in a food-mediated apparent competition where honeysuckle provides an important temporal resource in early spring that could improve deer survival and increase population densities, and as a result, increase the browsing pressure on native plants (Martinod and Gorchov, 2017). Examining the landscape conditions associated with browse on Amur honeysuckle and native competitors simultaneously is necessary to understand browsing effects along urban-to-rural landscapes gradients in the eastern United States.

To better understand whether woody browse pressure by deer, browse composition, and browse preference differ between urban and rural landscapes, we address three questions: 1) Are there differences in browsing pressure by deer in forests in urban landscapes versus rural landscapes? 2) Do deer browse Amur honeysuckle at a higher rate in urban forests compared to rural forests? 3) Are there differences in browse composition in forests in urban versus rural landscapes and if so, which woody species do deer prefer, avoid, or neutrally browse in each landscape? To address these questions, we examined the relationship between agricultural landcover, urban landcover, deer pellet group counts (a proxy of deer abundance), and woody browsing intensity in forests in rural and urban landscapes in central Indiana. We predicted that browse composition will differ between urban and rural forests. We also predicted a higher level of deer browse in urban forests. Similarly, we predicted that browse on Amur honeysuckle will be higher in urban forests because ELP offers a unique temporal resource to deer when native species are dormant and agriculture is not present as an extra food source. Because we hypothesize that land cover and within-patch variables (such as Amur honeysuckle browse, availability of twigs

browsed, etc.) are both important in predicting deer browse, we tested for interactions among significant land cover and within-patch predictors.

2.2 Methods

2.2.1 Study Area

Our study was conducted in west-central Indiana in the Grand Prairie and Central Till Plain Natural Regions (Homoya et al., 1985), which have glacial soils. Row crop agriculture occupies most of the land in the study area, with scattered fragments of forest (hereafter we refer to a single forest fragment as a “forest patch”) occurring throughout the area. Our study area also contains an urbanized zone in Tippecanoe County comprised of the cities Lafayette and West Lafayette (hereafter Greater Lafayette area) with population estimates of 71,721 and 50,996, respectively (122,717 combined population; US Census Bureau 2018; US Census Bureau 2019). We classified our sampled forest patches in the Greater Lafayette Area as “urban” forest patches, due to the high density of urban land cover in a 500 m buffer surrounding the forest patches we sampled (Table 2.1). In nearby Warren, Montgomery, Carroll, Newton, Benton, and White counties, we sampled forest patches in an agriculture-dominated matrix and refer to these as “rural” forest patches based on the low cover of urban land cover and the high cover of agriculture surrounding the forest patches (Table 2.1).

Upland forest sites in this region are often composed of oak/hickory species (*Quercus* spp./*Carya* spp.) with associated species such as black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), and American basswood (*Tilia americana*). Bottomland sites frequently have overstories of American sycamore (*Platanus occidentalis*), Ohio buckeye (*Aesculus glabra*), eastern cottonwood (*Populus deltoides*), and silver maple (*Acer saccharinum*). Well-drained bottomlands or mesic slopes also contain black walnut (*Juglans nigra*). Ash species (*Fraxinus* spp.) were common in the overstory of both upland and bottomland sites, however, most ash trees have died from the non-native insect, emerald ash borer (*Agrilus planipennis*). Most forests in this region are secondary forests, at one point having been cleared for agriculture. Historical disturbances to forests in this region during the last century included grazing by cattle and timber harvests (Carman, 2013).

2.2.2 Site Selection and Study Design

We sampled a total of 41 rural forest patches over two years (32 in 2019 and 9 in 2020) that were part of a regional management unit within of a larger, state-wide integrated deer management project. Regional management units were created for Indiana using county data of land cover, hunter densities, other human-caused mortality of deer, expert opinion, and a partial contiguity constraint (Swihart et al., 2020). Within this regional management unit composed of nine counties, ten 3.22×3.22 km sample areas were randomly placed within the regional management unit. Within these sample areas we sampled any forest patches where we were able to obtain permission to sample from the landowner; most rural forest patches were privately owned.

We sampled a total of 28 urban forest patches (17 in 2019 and 11 in 2020) in the Greater Lafayette area. Urban forest patches sampled in 2019 were primarily open to the public, whereas in 2020 we sampled urban forest patches that were privately owned and were selected from a county property ownership map by identifying forest areas with a closed-canopy and a minimum size of 0.6 ha. Between both years, we sampled 41 rural forest patches and 28 urban forest patches for a total of 69 patches sampled.

2.3 Vegetation Sampling

We used 50 × 1 m belt transects to collect vegetation and woody browse data. We sampled the minimum number of transects in each forest patch to satisfy the inequality $A/t < 2t$, where A is forest patch size (ha) and t is the number of transects assigned to a forest (Table 2.2). We randomly generated transect starting points using ArcMap (v. 10.8, ESRI Corporation, Redlands, CA, USA) and randomly generated the direction of the transect but constrained the direction parallel to the contour of any slopes to avoid elevation changes.

We tallied all saplings (diameter at breast height [dbh, 1.37 m] < 10 cm; total height > dbh height) by species within each belt transect. In addition, we recorded whether each sapling contained live branches in the height range with the greatest browsing intensity, known as the “molar zone” (20 – 180 cm; Frerker et al., 2013). We calculated the density of saplings with branches in the molar zone in each belt transect (saplings/50 m²). We also calculated the total density of Amur honeysuckle saplings and the density of Amur honeysuckle saplings with

evidence of deer browse. We averaged sapling densities of all transects within each forest patch to have a patch-level average.

We tallied seedlings (woody stems < 1.37 m in height) by species within 1 m² quadrats placed every 10 m in the belt transect for a total of five quadrats per transect. Seedlings were tallied into two classes based on height: < 20 cm (class 1), and 20 - 130 cm (class 2). We calculated seedling density for each class by averaging the number of seedlings of all quadrats within a forest patch (seedlings/m²) to obtain a patch-level average.

Within the 3-dimensional space in the molar zone above each 1 m² quadrat, we counted the total number of twigs available and the number of twigs browsed for each species encountered. We only counted live twigs and twigs that showed obvious evidence of browse (approximately within the past year). Dead twigs or otherwise broken twigs without clear evidence of deer browse were not included in our counts.

2.3.1 Landcover and Landscape Metrics

To capture the proportions of agriculture, forest, urban, and forage-rich landcover around forest patches, we reclassified 2016 national land cover database (NLCD) 30 m resolution landcover data (Dewitz, 2019) into nine classes (Table 2.3). We then calculated the proportion of each reclassified landcover in a 500 m buffer around each forest patch. We selected a 500 m buffer because this buffer size best explained native plant cover in response to deer and interspersed forage habitat in the landscape surrounding Indiana state parks (Hurley et al., 2012) and was similar in size to a buffer used to approximate the radius of average deer home range across seasons in Midwestern landscapes (Urbanek and Nielsen, 2013). We also used patch level statistics in FRAGSTATS (McGarigal et al., 2012) to calculate forest patch area and shape index (the perimeter of a patch divided by the minimum possible perimeter a patch with the same area).

2.3.2 Pellet Sampling

To estimate a proxy for deer abundance, we used a distance sampling framework and recorded pellet groups along 200 m transects. We used ArcMap to randomly place pellet transects. To conduct a pellet transect, the observer walked down the transect looking on each side for pellet groups and recorded the perpendicular distance from the transect to the center of each detected

pellet group. We used the degree of degradation, color, and size of pellets to differentiate among groups. Pellet group density estimates for our forest patches and clusters had high variances. Rather than using unreliable density estimates, we opted to use a simple index of the number of pellets detected per transect as a proxy of deer abundance.

As mentioned previously, rural forest patches were sampled as part of a larger, state-wide deer project. Pellet transects in this state-wide project were used to estimate deer densities at large spatial scales greater than that of an individual forest patch (Z. Delisle, unpublished data). As a result, some rural forest patches did not contain a pellet transect, while other rural forest patches contained multiple pellet transects. For models including pellets per transect as a predictor, we excluded the 11 rural forest patches that did not contain pellet transects. Urban forest patches in our study were not part of the larger deer project. Therefore, we assigned each urban forest patch one pellet transect due to logistical constraints. While the distance sampling framework is designed for calculating a density using an estimated detection function, we did not have enough detected pellet groups to have a reliable detection function for our collective urban forest patches. Thus, we averaged the number of pellets found per transect in forest patches with multiple pellet transects to have a patch-level index value for deer abundance.

2.3.3 Statistical Analysis

To analyze forest patches independently, we used the 500 m buffers around each forest patch that reflected the radius of a deer home range size. When buffers around forest patches overlapped, we clustered forest patches and designated cluster as a random intercept term in our generalized linear mixed model analysis. If buffers of two forest patches did not directly overlap, but both overlapped with a third forest patch buffer, we clustered the whole group of forest patches (Fig. 2.1). We performed all statistical analyses using R (R Core Team 2019) except for a non-metric multidimensional scaling ordination that we performed using PC-ORD (version 5.31; McCune and Mefford 2011).

Browse Composition and Preference

We calculated the sum of twigs available and twigs browsed by deer for each woody species for three analyses: all forest patches combined (overall), all rural forest patches (rural), and

all urban forest patches (urban). We only included species for analysis if we sampled ≥ 30 total twigs available for the species and if the species was present in more than one forest patch. The overall, rural, and urban analyses had 39, 27, and 19 species, respectively, that met these criteria. For each analysis, we divided the total number of twigs browsed by the total number of twigs available of all species combined, which yielded our observed browsing proportion. We then multiplied this observed browsing proportion by the number of twigs available for each species to determine an expected number of twigs browsed.

We used a post-hoc analysis of residuals of Pearson's chi-square test for count data using the observed number of twigs browsed and expected number of twigs browsed for each species with the `chisq.posthoc.test` function (Ebbert 2019). We performed this test for each analysis (overall, urban, and rural) to create browse preference lists. To create browse preference classes, we classified any species with no significant difference between observed and expected number of twigs browsed as "neutral." We classified species that had significant differences between observed and expected number of twigs browsed as "preferred" and "avoided" for species browsed at either higher or lower proportions, respectively, than the average observed proportion.

To further examine browse composition, we ran a non-metric multidimensional scaling (NMS) ordination of forest patches using the total number of available twigs of each species in a forest patch divided by the number of quadrats sampled in a forest patch. We used autopilot mode in PC-ORD and completed 250 random runs and 250 runs with real data using the Sørensen distance measure and 0.0000001 stability criterion (Jenkins et al., 2014). We also examined correlations between the axes of the NMS and environmental variables of urban 1 land cover, urban 2 land cover, urban 3 land cover, urban 4 land cover, forest land cover, forage land cover, agricultural land cover, forest patch area, forest patch shape index, non-native sapling density, the proportion of twigs browsed of neutral or preferred species (classes from the chi square analysis), and overstory basal area.

Woody Browse Pressure

To examine woody browsing pressure across forest patches, we first defined a group of "intermediately" browsed species. We did this to have a representative suite of species that were common throughout forest patches and browsed at similar rates. We did not include preferred species in this group because some forest patches did not contain preferred species and we would

be comparing species with different preferences across forest patches. To be considered intermediately browsed, a species was required to be classified as neutral in each previously-mentioned browse preference chi-square analyses in which it was included. In addition, intermediately browsed species had to have an overall browse proportion > 0.05 and < 1 standard deviation above the average browse rate between species in any of the three chi-squared analyses in which the species was included. Species that met these criteria and were considered intermediate include American plum (*Prunus americana*), black cherry, black raspberry (*Rubus occidentalis*), blackhaw (*Viburnum prunifolium*), boxelder (*Acer negundo*), downy serviceberry (*Amelanchier arborea*), gooseberry (*Ribes* spp.), hazelnut (*Corylus americana*), ironwood (*Ostrya virginiana*), musclewood (*Carpinus caroliniana*), northern red oak (*Quercus rubra*), Ohio buckeye, sassafras, slippery elm (*Ulmus rubra*), swamp dewberry (*Rubus hispidus*), winged burningbush (*Euonymus alatus*), and witchhazel (*Hamamelis virginiana*). We then pooled the number of available and browsed twigs from these species in each forest patch.

Using the package lme4 (Bates et al. 2015), we modeled the proportion of browse of intermediately preferred species using binomial family generalized linear mixed models. Each response variable was a binary response of each available intermediate twig in a forest patch as not browsed (0) or browsed (1). We designated cluster as a random intercept in all models. Because deer browse is sensitive to deer abundance, we included pellets detected per transect as a predictor in all models. We then constructed seven models with each model including the proportion of one land cover class of interest in forest patch buffers (urban 1, urban 2, urban 3, urban 4, forest, forage, and agriculture) as predictors. We also constructed three models including within-patch level predictors: (1) the density of class 2 seedlings and density of saplings with branches in the molar zone, (2) the total density of Amur honeysuckle saplings, and (3) the density of browsed Amur honeysuckle saplings. Because we were interested in the simultaneous impacts of land cover and deer browse, we tested for interactions between significant land cover and within-patch scale predictors.

We compared models with Akaike information criterion (AIC), then for the best models examined goodness of fit using the Hosmer-Lemeshow Goodness of Fit Test and simulated residuals for the entire model to test uniformity. Lastly, we checked model performance using area under the curve (AUC) and the more recent metric, H measure (Hand, 2009).

Browse on Amur Honeysuckle

We also used binomial family generalized linear mixed models with cluster as a random intercept for constructing models of honeysuckle browse. The model had a binary response variable of honeysuckle twigs being browsed or not browsed (1 and 0 respectively). Similar to woody browse pressure models, we used pellet groups detected as a predictor in all models and built seven models with each including the proportion of one land cover class of interest in forest patch buffers as predictors (urban 1, urban 2, urban 3, urban 4, forest, forage, and agriculture). We also built two within-patch models, one with the number of neutral and preferred (determined by the chi-squared analysis of preference) twigs available as a predictor, and another with the proportion of neutral and preferred twigs browsed. We also tested for interactions between significant land cover and within-patch scale predictors. We used the same model comparison and diagnostics described for woody browse pressure models.

2.4 Results

2.4.1 Browse Composition and Preference

NMS Ordination of Browse Composition

The NMS ordination revealed differences of the composition of available twigs between rural (Benton, Carrol, Montgomery, Newton, Warren, and White Counties) and urban (Tippecanoe County) forest patches (Fig. 2.2). The NMS recommended a 3-dimensional solution and had a final stress equal to 15.67. Axes 1, 2, and 3 accounted for 71.4% of variance with axes 1 and 3 explaining the most variance, 17.4% and 40.7%, respectively. Environmental variables urban 1, urban 2, and urban 3 land cover were negatively correlated with axis 3, while agricultural land cover was positively correlated with axis 3 (Table 2.4). Non-native sapling density was negatively correlated with axes 1 and 3. Forest land cover and agricultural land cover showed the strongest correlations with axis 2, which were both negative (Table 2.4). Most urban forest patches (82%) had negative values on axis 3 while most rural forests patches (76%) had positive values on axis 3.

Species scores on the same ordination axes revealed a higher number of species associated with the proportion of agriculture than those associated with urban land cover (Fig. 2.3), supporting our hypothesis that rural forest patches may have more species available for browse. Rural and

urban forest patches also generally contained available twigs from different non-native species. Amur honeysuckle associated more with urban forest patches and a few forest patches from Newton County. Autumn olive (*Elaeagnus umbellata*) and multiflora rose (*Rosa multiflora*) were associated agricultural land cover, while winged burningbush was associated with urban land cover. Native species that were most strongly associated with urban land cover include blue ash (*Fraxinus quadrangulata*), Ohio buckeye, northern red oak. Native species strongly associated with agricultural land cover include downy serviceberry, northern catalpa (*Catalpa speciosa*), deerberry (*Vaccinium stamineum*), and pin oak (*Quercus palustris*). While poison sumac (*Toxicodendron vernix*) was also associated with agricultural land cover, we only observed twigs available of this species in one forest patch.

Woody Browse Preference

The Pearson's chi-squared tests of expected twigs browsed and observed twigs browsed revealed significant differences among species overall (urban and rural forest patches; $X^2 = 427.33$, $p < 0.001$), in rural forest patches ($X^2 = 277.77$, $p < 0.001$), and in urban forest patches ($X^2 = 114.5$, $p < 0.001$). Post hoc analyses on Pearson's chi-squared residuals of browse preference of species overall (urban and rural forest patches combined) revealed 21% of species were preferred, 10% were avoided, and 69% were neutral (Fig. 2.4). Post-hoc analysis for rural forest patches identified 15% of species were preferred, 15% were avoided, and 70% were neutral (Fig. 2.5). Post-hoc analysis of urban forest patches revealed 10% of species were preferred species, 16% were avoided, and 74% of species were neutral (Fig. 2.6). Deer browsing preference among species changed between rural forest patches and urban forest patches. Multiflora rose and sugar maple were neutral in preference in rural forest patches but avoided in urban forest patches. Deer avoided Amur honeysuckle in rural forest patches; however, preference of the species was neutral in urban forest patches. Lastly, green ash (*F. pennsylvanica*) was neutral in rural forest patches and preferred in urban forest patches.

2.4.2 Browse Pressure

Browsing pressure did not increase with urbanization. Coefficient z-values for each urban land cover predictor were not significant ($p > 0.05$). The only significant landscape-scale predictor

was forest land cover, while many forest patch-scale predictors were significant. The number of deer pellet groups detected was not a significant predictor except in the two models that included the total density of Amur honeysuckle and the density of browsed Amur honeysuckle as predictors. This is due to us limiting models with Amur honeysuckle predictors to forest patches that contained observations of Amur honeysuckle because we were interested in how deer browse pressure responded to varying levels of Amur honeysuckle. Our response variable of browse pressure of intermediate species was negatively related to the density of class 2 seedlings, the density of saplings with branches in the molar zone, the density of browsed Amur honeysuckle saplings, and the total density of Amur honeysuckle saplings (Table 2.5). However, each of these models demonstrated a lack of goodness of fit according to the Hosmer-Lemeshow goodness of fit test. Models had uniformity of residuals except for the models that included total Amur honeysuckle density and the density of browsed Amur honeysuckle as predictors.

We observed significant interactions between forest land cover and both total density of Amur honeysuckle and density of browsed Amur honeysuckle. In each interaction when Amur honeysuckle densities were low, browse on intermediate species increased with the proportion of forest land cover, but when Amur honeysuckle densities were high, browse on intermediate species decreased with forest land cover (Table 2.5; Fig. 2.7 and 2.8). We also observed a significant interaction between forest land cover and density of saplings with branches in the molar zone, but this model had a lower AUC and H measure than the two previously mentioned interaction models (Table 2.5). The interaction models with total density of Amur honeysuckle and the density of browsed Amur honeysuckle had the highest AUC and H measure values of all models demonstrating the best model performance (Table 2.5), and also passed Hosmer-Lemeshow goodness of fit tests ($X^2_{(8)} = 10.046$, $p = 0.26$ and $X^2_{(8)} = 5.127$, $p = 0.74$ respectively), however, the residuals lacked uniformity.

2.4.3 Browse on Amur honeysuckle

Land cover and the proportion of twigs of neutral and preferred species browsed were significant predictors of the proportion of Amur honeysuckle twigs browsed. Contrary to our hypothesis, the proportions of urban 2 and urban 3 landcover were negatively related to the proportion of Amur honeysuckle twigs browsed (Table 2.6). Also contrary to what we expected, the proportion of forage land cover was positively related to the proportion of Amur honeysuckle

twigs browsed (Table 2.6). The proportion browse of neutral and preferred species was negatively related to the proportion of Amur honeysuckle twigs browsed (Table 2.6). The number of available twigs of neutral and preferred species and deer pellet groups detected were not significant predictors of the proportion of Amur honeysuckle twigs browsed.

Because browse on neutral and preferred species and the proportion of land cover of urban 2 and urban 3 were significant predictors, we tested for interactions and identified a significant interaction between both the proportion of urban 2 and urban 3 land cover and the proportion browse of neutral and preferred species (Table 2.6). In the interaction model with urban 2 land cover, when urban land cover was low, the proportion browse of neutral and preferred species had a positive relationship with Amur honeysuckle browse, but as urban 2 landcover increased, this relationship became negative (Fig. 2.9). In the interaction model with urban 3 land cover, at low levels of urban 3 land cover, the proportion browse on Amur honeysuckle did not change with the proportion browse of neutral and preferred species. However, at high levels of urban 3 land cover, the proportion browse of Amur honeysuckle decreased with an increase in the proportion browse of neutral and preferred species.

Hosmer-Lemeshow Goodness of Fit Test revealed a lack in fit in our top models with urban 2 landcover ($X^2_{(8)} = 33.394, p < 0.001$), urban 3 landcover ($X^2_{(8)} = 41.289, p < 0.001$), proportion browse of neutral and preferred species ($X^2_{(8)} = 29.108, p < 0.001$), and the interaction of urban 3 landcover and the proportion browse of neutral and preferred species ($X^2_{(8)} = 22.794, p = 0.003$). However, the model with the interaction between urban 2 land cover and the proportion browse of neutral and preferred species demonstrated a good fit ($X^2_{(8)} = 6.597, p = 0.581$). All models demonstrated uniformity of residuals. We checked AUC and H measure for each of these top models. Values for AUC were all close to 0.7 (Table 2.6), indicating fair model performance. However, the models with the interaction terms had the best model performance with the highest AUC and H measure.

2.5 Discussion

2.5.1 Browse Availability and Preference

We observed differences in the composition of available twigs for browse in urban forest patches and rural forest patches, supporting our prediction. These results are similar to other

studies that demonstrated different riparian woody species compositions between urban and rural areas and decreased woody species diversity as urbanization around riparian forests increased (Burton and Samuelson, 2008; Pennington et al., 2010; White et al., 2014). These studies found that non-native species were generally more dominant in urban areas, however, we did not find this general association. Rather, Amur honeysuckle and winged burningbush were associated with our urban forest patches while multiflora rose and Autumn olive were associated with rural forest patches. Both multiflora rose and Autumn olive were planted for wildlife in rural areas, which could explain why these species were more prevalent in rural forest patches. The common use of Amur honeysuckle and winged burningbush as ornamental plants may explain their prevalence in urban forest patches. A native species associated with recent disturbances, black raspberry, was strongly associated with agricultural land cover, while midstory, shade-tolerant ironwood and musclewood were strongly associated with urban land cover. These associations suggest that disturbances may have been more recent and possibly more frequent in rural forest patches compared to urban patches, which could also contribute to our observed differences of the composition of available woody twigs between rural and urban forest patches.

In addition to differences in the composition of available browse between urban and rural forest patches, we also observed differences in the browse preferences of species. The shift in the browse preference of Amur honeysuckle from avoided in rural forest patches to neutral in urban forest patches supports our hypothesis that browse on Amur honeysuckle would be higher in urban areas. This could be due to fewer alternate food sources from agriculture and the nutritional advantages (increased crude protein) associated with ELP of Amur honeysuckle (Martinod and Gorchov, 2017). Sugar maple was neutral in rural forest patches but avoided in urban forest patches. This is likely attributable to one urban forest patch that contained 33% of all sugar maple twigs for the urban chi-square analysis, but only had 3% of sugar maple twigs browsed within the forest patch. We were surprised that multiflora rose changed preference between landscapes, being neutrally selected in rural forest patches but avoided in urban forest patches. A study in central Illinois in an agricultural landscape observed multiflora rose as a preferred browse species (Strole and Anderson, 1992). However, another study employing feeding trials found multiflora rose to be neither preferred or avoided (Averill et al., 2016). One possibility for the discrepancy of multiflora rose and Amur honeysuckle browse between urban and rural forest patches is consistent availability. Our sampled quadrats contained browsable twigs of multiflora rose in 25 rural forest

patches, while only 12 rural forest patches contained browsable twigs of Amur honeysuckle. Conversely, 21 urban forest patches contained browsable twigs of Amur honeysuckle while only four urban forest patches contained browsable twigs of multiflora rose. Thus, each of these species was neutrally preferred where it was more available across forest patches and avoided where availability was lower across forest patches. Multiflora rose has also demonstrated characteristics of ELP (Bodawatta et al., 2019), and may provide an important temporal food resource in rural forest patches similar to our hypothesis about Amur honeysuckle in urban forest patches.

2.5.2 Browse Pressure

Contrary to our hypothesis, we did not observe increased browse pressure of intermediate species as urban landcover increased. One study using preferred browse species in areas with high deer densities (18 – 22 deer/km²) observed higher browse pressure in hardwood hammock stands < 400 m from urbanized areas than in stands > 500 m from urbanized areas (Barrett and Stiling 2006). Hygnstrom et al. (2011) documented further evidence of high levels of woody browse pressure in urban areas with high deer densities (27 deer/km²), with as much as 60% of available twigs in the understory browsed by deer. We observed browse on 14% of available twigs in urban forest patches, suggesting lower browsing pressure in our study area than the aforementioned studies.

We were surprised to find a positive relationship between the proportion of forest land cover in buffers and browse pressure on intermediate species for two reasons. First, more forest landcover within 500 m of a forest patch would likely indicate a higher number of available twigs in the landscape around that patch for deer to browse, which would decrease the proportion of twigs browsed. Second, this would not be optimal foraging behavior because deer in forest patches with more forest land cover within 500 m would have shorter travel time between patches, and thus not forage as long as in a more isolated forest patch (low proportion of forest cover < 500 m away) with longer travel times. The reason these results were contrary to our expectations could be related to the amount of forest land cover for patches in this analysis, with mean forest land cover within buffers of 12% and a range of 0 – 36%. It is possible that there is a threshold of forest cover on the landscape, above which deer browse intensity would decrease with as forest land cover increases. Additionally, deer shift summer diets to herbs and crops (Vercauteren and Hygnstrom, 2011; Waller, 2014) and more heavily rely on woody browse in the winter. In our

study area with relatively low forest land cover available, deer may select for areas that have more forest land cover to meet their browse requirements in winter. This could explain the observed increase of browse on intermediate species with increase forest land cover. One other possible explanation is that other available winter food sources in Indiana, such as waste grain and hay provide alternate food sources to woody browse in the winter. Having less of these alternate food sources in areas with higher forest land cover could lead to higher browsing on woody stems in forests.

We observed significant interactions between the proportion of forest land cover and both the total density of Amur honeysuckle saplings and the density of browsed honeysuckle saplings. (Fig. 2.7 and 2.8). When the density of Amur honeysuckle (total or browsed) was high, browse pressure on intermediate species decreased with an increase in the proportion of forest. We suggest that in areas with high honeysuckle densities, native intermediate browse may be concealed by the myriad of Amur honeysuckle. The high density of Amur honeysuckle also provides an alternative browse source.

2.5.3 Browse on Amur honeysuckle

Counter to our hypothesis, we did not observe an increase in the proportion of browse of Amur honeysuckle twigs with any level of urban landcover and to the contrary, we observed a significant decrease of the proportion of Amur honeysuckle twigs browsed with increased urban 2 and urban 3 land cover. While the overall chi-squared post-hoc analysis revealed higher browse on Amur honeysuckle in woodlots in urban forest patches combined compared to rural forest patches, deer browse on honeysuckle did not scale down to the level of land cover around individual forest patches in our analysis which could be due to a biological difference in the scale of observation or because we lacked necessary replication at the individual forest patch scale. Thus, it is possible that the observed browse of honeysuckle is part of a larger-scale pattern than we observed with our generalized linear mixed model. Wright et al. (2019) found no relationship between land cover surrounding forest sites and the proportion of Amur honeysuckle twigs browsed. Perhaps the negative relationship in our model is because deer avoid browsing in forest patches surrounded by urban 2 and urban 3 land cover, due to moderate to high amounts of impervious surfaces and increased anthropogenic interactions. While not significant ($p = 0.505$), urban 1 land cover showed a positive relationship with deer browse on Amur honeysuckle. Urban

1 land cover had low amounts of impervious surfaces ($< 20\%$) and is composed of more open green space, which were likely more suitable habitat for deer in an urban interface.

In addition, the significant interaction between the proportion of twigs browsed of neutral and preferred species and the proportion of urban 2 and urban 3 land cover counters our hypothesis that browse on Amur honeysuckle would be higher in urban areas. When urban land cover was high, deer browse on Amur honeysuckle decreased as the proportion browse of neutral and preferred species increased, indicating deer in forest patches surrounded by urban land cover were browsing on other available species instead of Amur honeysuckle. This contrasts the results of Wright et al. (2019) who did not find a negative relationship between the availability of twigs of preferred species and the proportion of Amur honeysuckle twigs browsed or a relationship between land cover surrounding forest patches and deer browse of Amur honeysuckle. Deer and other ungulates expand their diets in response to high densities driving high browsing pressure (Brown and Doucet, 1991; Kie and Bowyer, 1999; Stewart et al., 2011). However, we did not observe heavy overall browsing in our urban forest patches, and it is possible that deer in our study system have a low degree of intraspecific competition, allowing them to preferentially browse on other species. In other systems with higher browse pressure and correspondingly higher competition, deer may expand browsing selection and forage more on Amur honeysuckle.

2.5.4 Conclusions

We observed differences in browse availability and browse preferences in urban and rural forest patches. Browse pressure did not respond to urban land cover but did respond to an interaction of forest land cover and Amur honeysuckle densities, showing that both landscape context (e.g. land cover) and non-native species interact to influence deer browse. The proportion of Amur honeysuckle twigs browsed was affected by a significant interaction of urban land cover and availability of neutral and preferred browse species. Browse pressure in urban forest patches was not severe and deer seemed to browse preferentially on other species when they cooccurred with Amur honeysuckle. In other urban settings with high browse pressure, managers should be aware that deer could preferentially browse and deplete native species, allowing non-native species like Amur honeysuckle to become dominant relative to heavily-browsed natives.

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Table 2.1 Average proportion of urban and agricultural land cover in 500 m buffers around forest patches by county in central Indiana, 2019 – 2020.

Mean urban land cover (Urban 1-4 combined) in forest patch buffers in Tippecanoe County, Indiana was 60.2%, while 75.4-91.6% of the land cover in rural forest patch buffers was agriculture. For definitions and further description of land cover data, see Table 2.3.

County	Number of Forest patches	Urban 1 Land Cover (%)	Urban 2 Land Cover (%)	Urban 3 Land Cover (%)	Urban 4 Land Cover (%)	Urban 1-4 Land Cover (%)	Agriculture Land Cover (%)
Tippecanoe	28	22.1	24.0	11.1	3.0	60.2	17.6
Newton	7	2.3	2.5	0.1	0	4.9	75.4
White	21	3.0	2.4	0	0	5.4	84.0
Carrol	3	3.5	0.2	0.1	0	3.9	87.7
Warren	4	3.0	3.0	0.1	0	6.1	83.3
Montgomery	5	4.6	0.4	0	0	5.1	91.6
Benton	1	2.4	2.0	0	0	4.3	84.8

Table 2.2 Number of vegetation sampling transects assigned to forest patches in central Indiana, 2019 – 2020.

Number of vegetation sampling transects assigned to forest patches in central Indiana to sample herbaceous and sapling-layer vegetation.

Forest Patch Size (ha)	Number of Transects
0-7.99	2
8-17.99	3
18-31.99	4
32-49.99	5
50-71.99	6
72-97.99	7
98-127.99	8
128-161.99	9

Table 2.3 Reclassified National Land Cover (NLCD) 2016 land cover types in 500 m buffers surrounding forest patches in central Indiana, 2019 – 2020.

Land cover classes that were reclassified into 9 categories for our landscape analyses. Categories denoted with an asterisk (*) were left as their own original NLCD class during our reclassification however, we still refer to them by the new reclassified category name.

Reclassified Category for Analyses	NLCD Legend Number	NLCD Name
Forest	41	Deciduous Forest
Forest	42	Evergreen Forest
Forest	43	Mixed Forest
Forest	90	Woody Wetlands
Water	11	Open Water
Forage	52	Shrub/Scrub
Forage	71	Grassland/Herbaceous
Forage	72	Sedge/Herbaceous
Forage	95	Emergent Herbaceous Wetland
Agriculture	81	Pasture/Hay
Agriculture	82	Cultivated Crops
Urban 1	21	Developed Space, Open
Urban 2	22	Developed, Low Intensity
Urban 3	23	Developed, Medium Intensity
Urban 4	24	Developed, High Intensity
Other		All Other Classes

Table 2.4 NMS ordination of available twigs in central-Indiana forest patches axes correlations with environmental variables in 2019 – 2020.

Environmental variable correlations with the three axes from NMS ordination of twigs available for browse in forest patches in west-central Indiana, 2019 -2020. Land cover represents the proportion of that respective land cover in a 500 m buffer around each sampled forest patch. For land cover descriptions see Table 2.3.

Environmental Variable	Axis 1	Axis 2	Axis 3
	<i>r</i>	<i>r</i>	<i>r</i>
Proportion forest land cover	0.004	-0.215	-0.142
Proportion forage land cover	-0.012	0.145	-0.312
Proportion agricultural land cover	-0.187	-0.207	0.688
Urban 1 land cover	0.175	0.141	-0.615
Urban 2 land cover	0.211	0.226	-0.542
Urban 3 land cover	-0.082	0.032	-0.234
Urban 4 land cover	-0.098	0.006	-0.172
Forest patch area	0.181	-0.127	-0.187
Forest patch shape	0.072	0.018	-0.352
Non-native sapling density	-0.363	-0.15	-0.555
Overstory basal area	0.112	0.083	0.008
Proportion of neutral and preferred twigs browsed	-0.35	0.13	-0.051

Table 2.5 Models for browse pressure on intermediately browsed species by white-tailed deer in forest patches in central Indiana, 2019 – 2020.

Best models of the response of proportion browse on intermediately browsed species using generalized linear mixed models with a binomial family. All models included cluster as a random intercept term. Coefficient estimates appear in the same respective order as the model fixed effects are listed. Significant coefficients ($p \leq 0.05$) are bolded. The following are fixed effects variable definitions, all of which (except land cover variables) were averaged within each forest patch: pel_tran - number of deer pellet groups detected per transect, forest - the proportion of forest landcover in a 500 m buffer around each forest patch (see Table 2.3 for detailed description of forest land cover), C2_seed - the density (seedlings/m²) of class 2 seedlings, sap_molar - the density of saplings (saplings/50m²) with branches in the molar zone (20 – 180 cm), Honey_browsed - the density of browsed Amur honeysuckle saplings (saplings/50m²), All_hon - the density of Amur honeysuckle saplings (saplings/50 m²). Variables were not transformed.

Model Group	Fixed Effects	Coefficient estimate	AIC	ΔAIC	Residual Degrees of Freedom	AUC	H measure
Land cover	forest + pel_tran	2.40 , -0.004	2041.2	0	2875	0.633	0.105
Patch-scale	C2_seed + sap_molar + pel_tran	-0.152 , -0.060 , 0.004	2026.5	539.4	2874	0.544	0.022
	Honey_browsed + pel_tran	-0.277 , 0.139	1230.2	43.1	1535	0.672	0.147
	All_hon + pel_tran	-0.038 , 0.148	1187.1	0	1535	0.715	0.171
Interaction	pel_tran + forest:sap_molar	0.019, -1.12	1998.5	826.6	2873	0.692	0.136
	pel_tran + forest:All_hon	0.185 , -0.305	1168.9	0	1533	0.746	0.202
	pel_tran + forest:Honey_browsed	0.340, -6.73	1169.8	0.9	1533	0.751	0.208

Table 2.6 Models for browse on Amur honeysuckle by deer in forest patches in central Indiana, 2019 – 2020.

Models of the response of proportion browse of Amur honeysuckle using generalized linear mixed models with a binomial family. All models included cluster as a random intercept term. Coefficient estimates appear in the respective order as the model fixed effects are listed. Significant coefficients ($p \leq 0.05$) are bolded. We only included AUC and H measure for models showing significant predictors. The following are fixed effects variable definitions, all of which (except land cover variables) were averaged for each forest patch, while land cover variables were calculated in a 500 m buffer around each forest patch: pel_tran - number of deer pellet groups detected per transect, urban 1 - the proportion of urban 1 (see Table 2.3 for more detailed descriptions of land cover definitions), urban 2 - the proportion of urban 2 landcover, urban 3 - the proportion of urban 3 landcover, urban 4 - the proportion of urban 4 landcover, agriculture - the proportion of agricultural land cover, forest - the proportion of forest landcover, forage - the proportion of forage land cover, pref_TA - the count of available twigs of neutral and preferred browse species, pref_prop_b - the proportion of twigs of neutral and preferred species browsed. Variables were not transformed.

Model Group	Fixed effects	Coefficient Estimate	AIC	Δ AIC	Residual Degrees of Freedom	AUC	H measure
Land cover	urban1 + pel_tran	0.370, 0.004	3643.0	12.2	5526		
	urban2 + pel_tran	-2.849 , 0.005	3630.8	0	5526	0.701	0.123
	urban3 + pel_tran	-5.437 , 0.006	3631.0	0.2	5526	0.700	0.129
	urban4 + pel_tran	-1.181, 0.003	3643.1	12.3	5526		
	agriculture + pel_tran	0.689, 0.002	3642.1	11.3	5526		
	forest + pel_tran	1.722, -0.002	3641.1	10.3	5526		
	forage + pel_tran	5.098 , 0.002	3639.2	8.4	5526	0.690	0.120
Patch-scale	pref_TA + pel_tran	-0.0200, 0.002	3640.8	295.2	5526		
	pref_prop_b + pel_tran	-3.030 , 0.058	3345.6	0	5242	0.714	0.138
Interaction	pel_tran + urb2:pref_prop_browse	0.076 , -26.001	3336.7	0	5241	0.714	0.141
	pel_tran* + urb3:pref_prop_browse	0.435 , -24.153	3356.6	19.9	5241	0.710	0.141

* Variable was standardized to improve model convergence

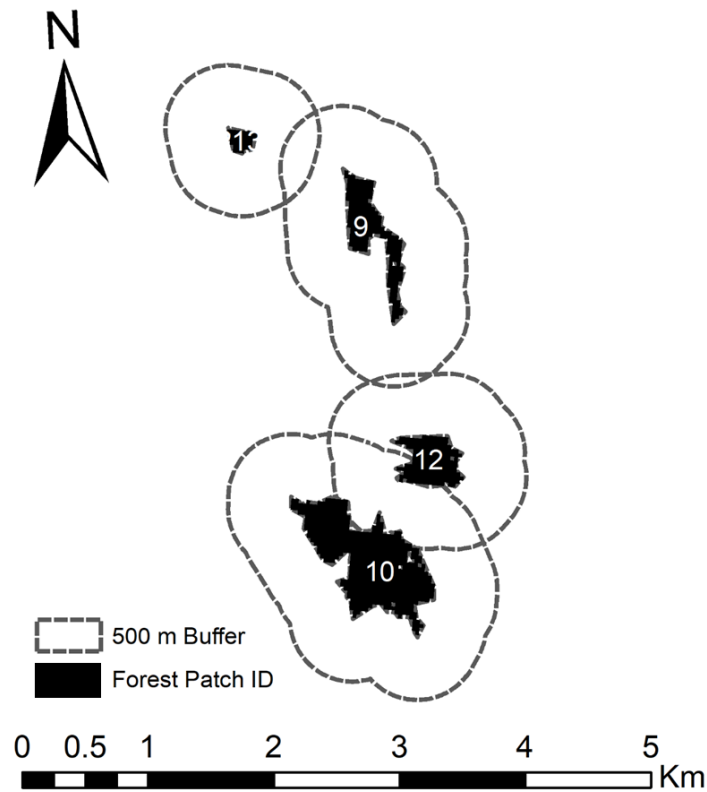


Figure 2.1 Map of forest patches with overlapping buffers in central Indiana, 2019 –2020.

Example of forest patches in central Indiana with overlapping 500 m buffers. Any forest patches with overlapping buffers were clustered. In cases like this where buffers of several forest patches overlap, all forest patches included in any part continuous overlap were clustered.

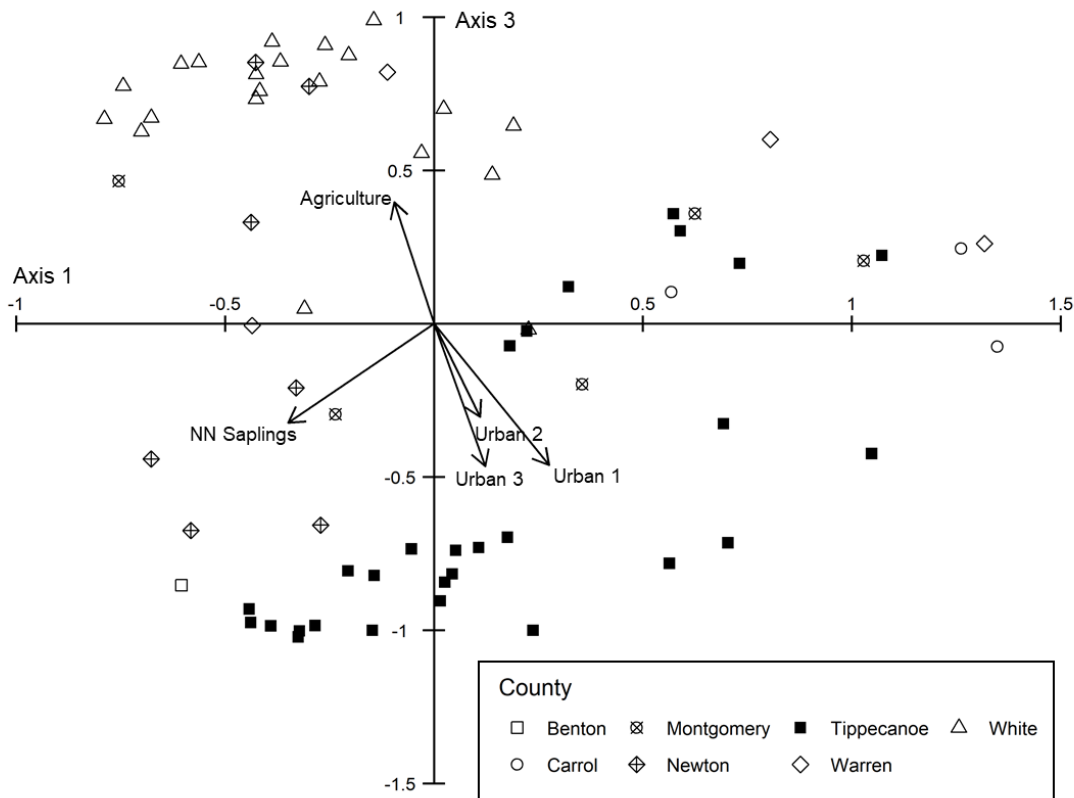


Figure 2.2. NMS ordination of browse availability of forest patches in central Indiana, 2019 –2020.

Nonmetric multidimensional scaling (NMS) ordination of woody forest white-tailed deer browse availability in 69 forest patches by Indiana county with the two dominant axes; axis 1 ($r^2 = 0.174$) and axis 3 ($r^2 = 0.407$). Each point represents a forest patch and the symbols representing the county location. The majority of urban forest patches (all of Tippecanoe County; filled symbols) and rural forest patches (all other counties; hollow symbols) differed on axis 3, demonstrating differences in browse availability between forest patches in different landscape contexts. Environmental variables (displayed as vectors) of proportion of urban 1, urban 2, and urban 3 land cover were negatively correlated with axis 3, while agricultural land cover was positively correlated with axis 3. The density of non-native saplings (NN Saplings) was negatively correlated with both axes 1 and 3.

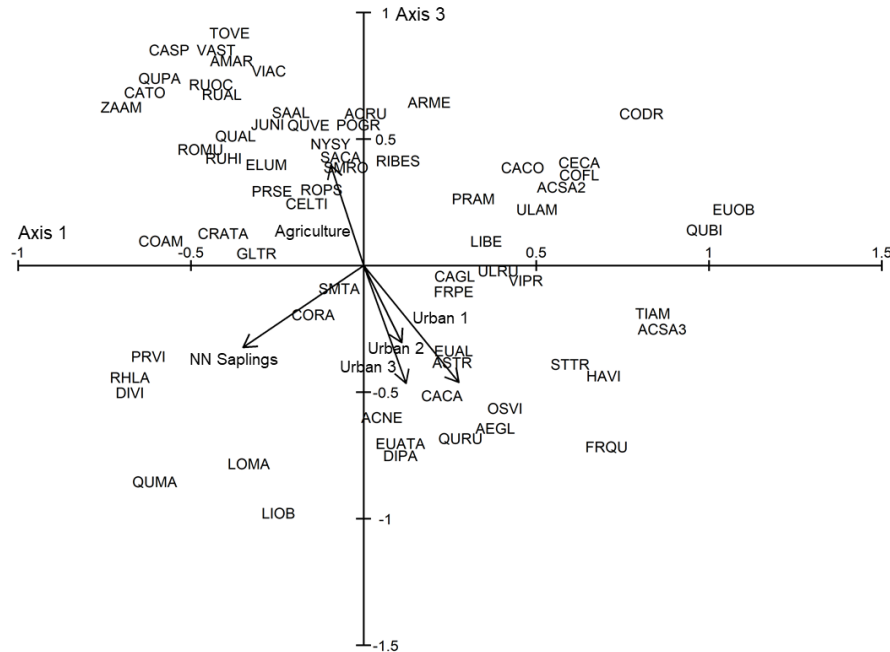


Figure 2.3 NMS ordination of available twig species in central Indiana, 2019 –2020.

Nonmetric multidimensional scaling (NMS) ordination of white-tailed deer browse species available in 69 forest patches in central Indiana with the two dominant axes; axis 1 ($r^2 = 0.174$) and axis 3 ($r^2 = 0.407$). Species codes follow the USDA Plants Database and are provided later in the figure caption. Environmental variables (displayed as vectors) of proportion of urban 1, urban 2, and urban 3 land cover were negatively correlated with axis 3, while agricultural land cover was positively correlated with axis 3. The density of non-native saplings (NN Saplings) was negatively correlated with both axes 1 and 3. The common and scientific name for each species code are as follows: ACNE – boxelder (*Acer negundo*), ACRU – red maple (*Acer rubrum*), ACSA2 – silver maple (*Acer saccharinum*), ACSA3 – sugar maple (*Acer saccharum*), AEGL – Ohio buckeye (*Aesculus glabra*), AMAR – downy serviceberry (*Amerlanhier arborea*), ARME – chokeberry (*Aronia melanocarpa*), ASTR – pawpaw (*Asimina triloba*), CACA – musclewood (*Carpinus caroliniana*), CACO – bitternut hickory (*Carya cordiformis*), CAGL – pignut hickory (*Carya glabra*), CASP – northern catalpa (*Catalpa speciosa*), CATO – mockernut hickory (*Carya tomentosa*), CECA – eastern redbud (*Cercis canadensis*), CELTI – hackberry (*Celtis occidentalis*), COAM – hazelnut (*Corylus americana*), CODR – roughleaf dogwood (*Cornus drummondii*), COFL – flowering dogwood (*Cornus florida*), CRATA – hawthorn (*Crataegus* spp.), DIPAL – leatherwood (*Dirca palustris*), DIVI – persimmon (*Diospyros virginiana*), ELUM – Autumn olive (*Elaeagnus umbellata*), EUAL – winged burningbush (*Euonymus alatus*), EUOB – running strawberry bush (*Euonymus obovatus*), FRPE – green ash (*Fraxinus pennsylvanica*), FRQU – blue ash (*Fraxinus quadrangulata*), GLTR – honeylocust (*Gleditsia triacanthos*), HAVI – witchhazel (*Hamamelis virginiana*), JUNI – black walnut (*Juglans nigra*), LIBE – spicebush (*Lindera benzoin*), LIOB – border privet (*Ligustrum obtusifolium*), LOMA – Amur honeysuckle (*Lonicera maackii*), NYSY – blackgum (*Nyssa sylvatica*), OSVI – ironwood (*Ostrya virginiana*), POGR – bigtooth aspen (*Populus grandidentata*), PRAM – American plum (*Prunus americana*), PRSE – black cherry (*Prunus serotina*), PRVI – chokecherry (*Prunus virginiana*), QUAL – white oak (*Quercus alba*), QUBI – swamp white oak (*Quercus bicolor*), QUMA – bur oak (*Quercus macrocarpa*), QUPA – pin oak (*Quercus palustris*), QURU – northern red oak (*Quercus rubra*), QUVE – black oak (*Quercus velutina*), RHILA – lanceleaf buckthorn (*Rhamnus lanceolata*), RUHI – swamp dewberry (*Rubus hispidus*), RUOC – black raspberry (*Rubus occidentalis*), SAAL – sassafras (*Sassafras albidum*), SACA – elderberry (*Sambucus canadensis*), SMRO – roundleaf greenbrier (*Smilax rotundifolia*), SMTA – bristly greenbrier (*Smilax tamnoides*), STTR – bladdernut (*Staphylea trifolia*), TIAM – American basswood (*Tilia americana*), TOVE – poison sumac (*Toxicodendron vernix*), ULAM – American elm (*Ulmus americana*), ULRU – slippery elm (*Ulmus rubra*), VAST – deerberry (*Vaccinium stamineum*), VIAC – mapleleaf viburnum (*Viburnum acerifolium*), VIPR – blackhaw (*Viburnum prunifolium*), ZAAM – prickly ash (*Zanthoxylum americanum*).

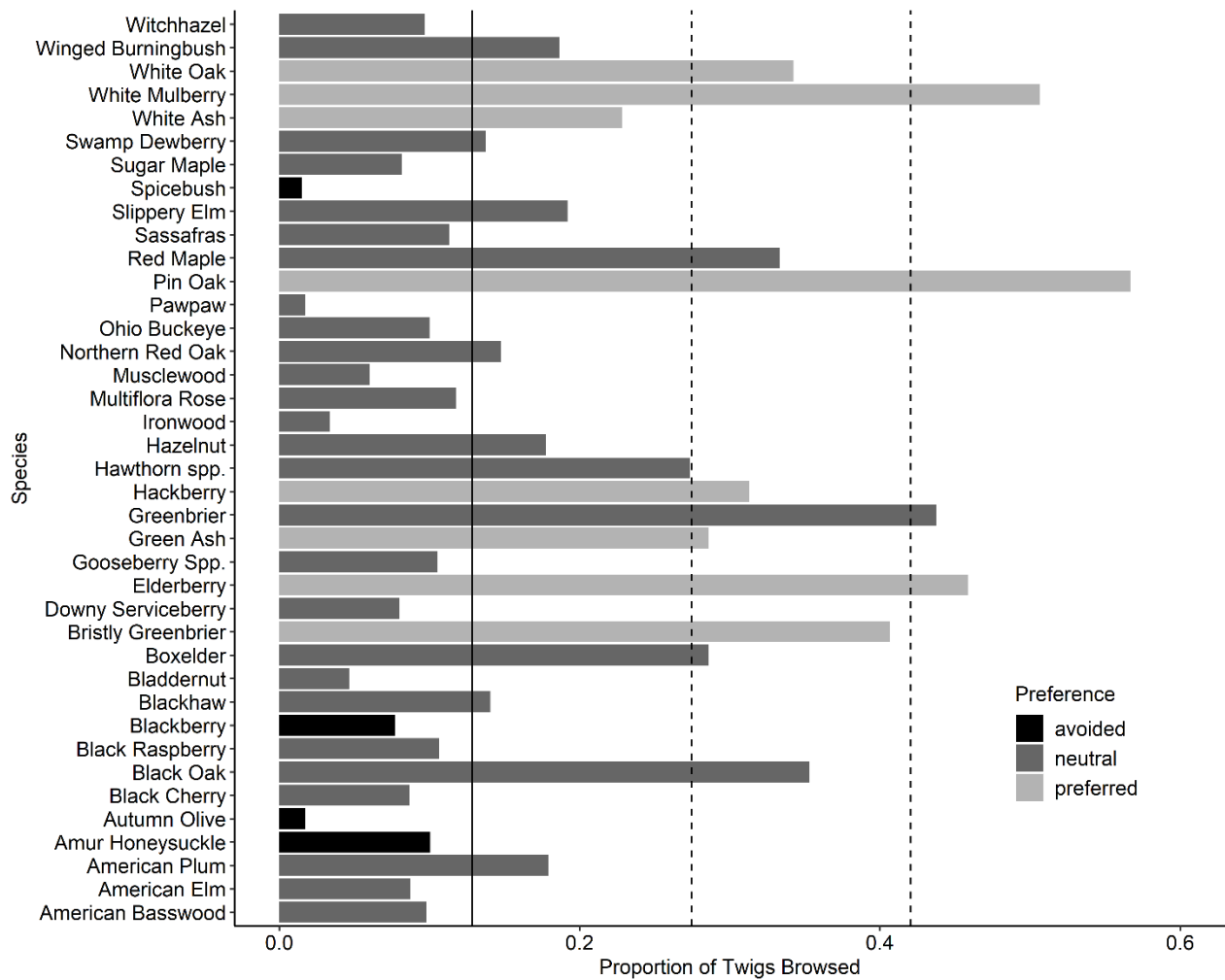


Figure 2.4 Overall species browse preferences of forest patches in central Indiana, 2019 –2020.

White-tailed deer browse preference by species from a chi-square post hoc test of observed and expected twigs browsed by species in all forest patches combined (rural and urban) in Indiana in 2019-2020. The solid black line indicates the mean browse rate of all twigs. The dashed lines indicate standard deviations of the mean browse rate between species. Some neutral species had a higher total proportion of twigs browsed than some preferred species, which is due to some species having a smaller sample size and lower ability to statistically detect a difference.

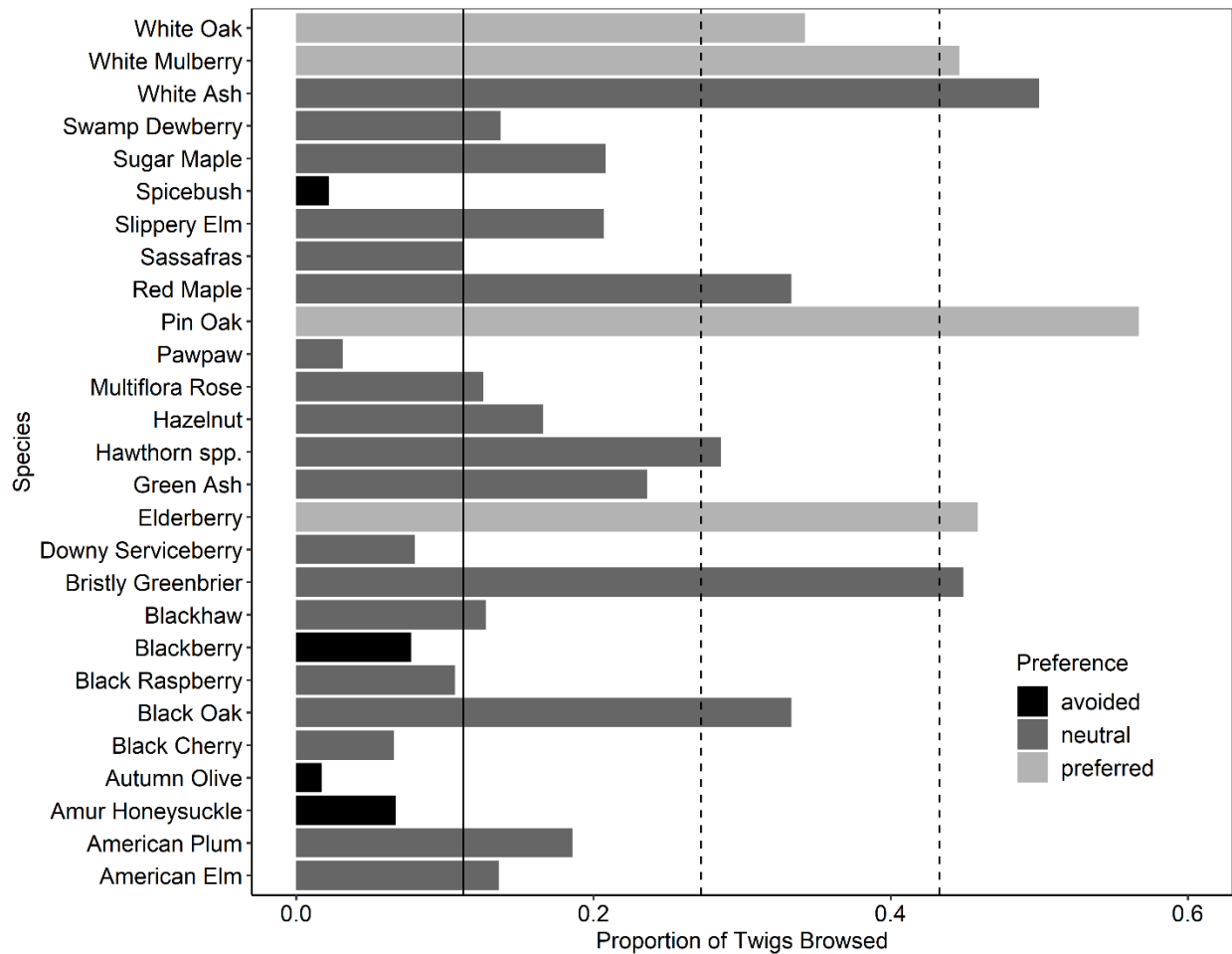


Figure 2.5 Rural forest patch species browse preferences in central Indiana, 2019 – 2020.

White-tailed deer browse preference by species from a chi-square post hoc test of observed and expected twigs browsed by species in rural forest patches in Indiana in 2019-2020. The solid black line indicates the mean browse rate of all twigs. The dashed lines indicate standard deviations of the mean browse rate between species. Some neutral species had a higher total proportion of twigs browsed than some preferred species, which is due to some species having a smaller sample size and lower ability to statistically detect a difference.

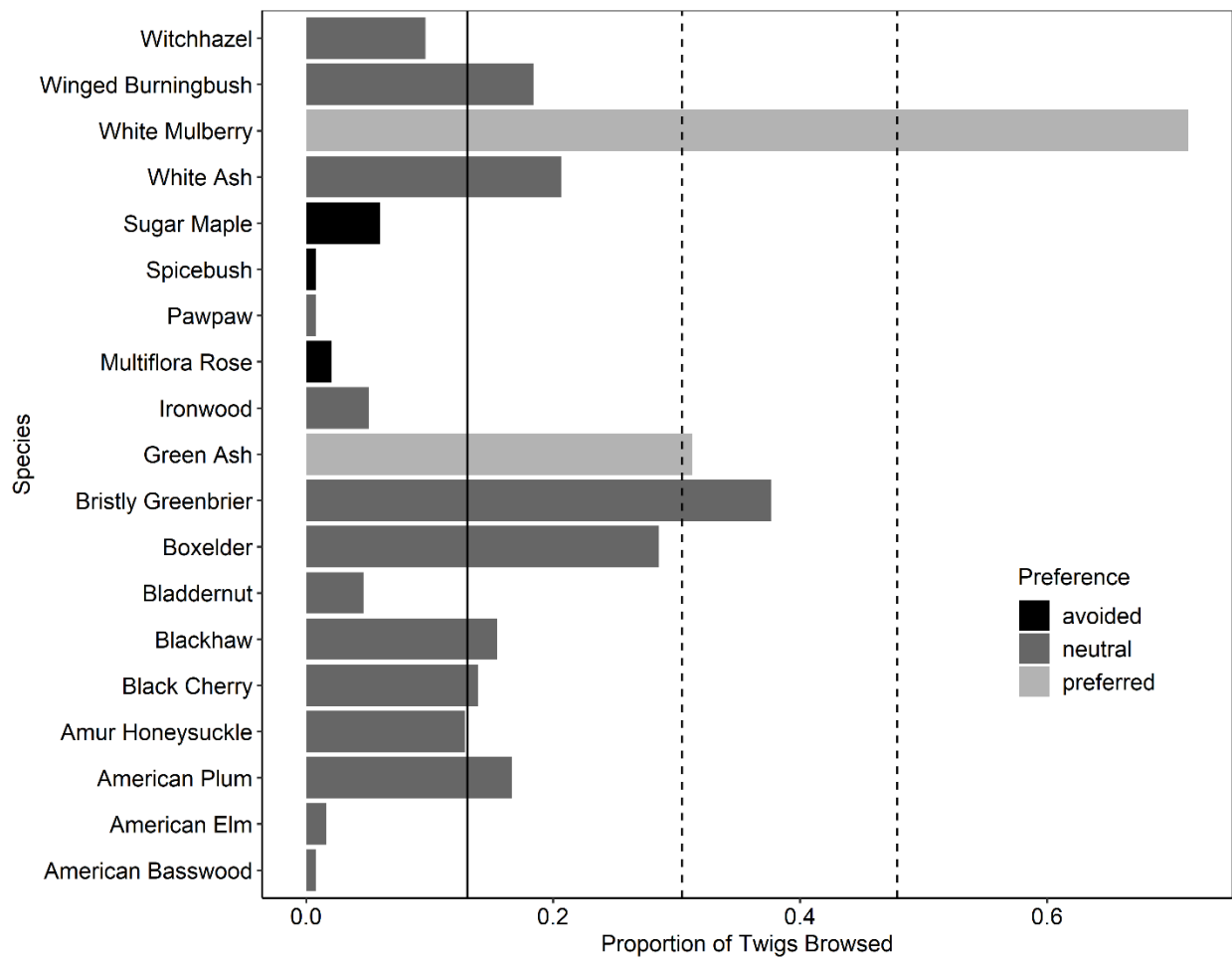


Figure 2.6 Urban forest patch species browse preferences in central Indiana, 2019 –2020.

White-tailed deer browse preference by species from a chi-square post hoc test of observed and expected twigs browsed by species in urban forest patches in Indiana in 2019-2020. The solid black line indicates the mean browse rate of all twigs. The dashed lines indicate standard deviations of the mean browse rate between species. Some neutral species had a higher total proportion of twigs browsed than some preferred species, which is due to some species having a smaller sample size and lower ability to statistically detect a difference.

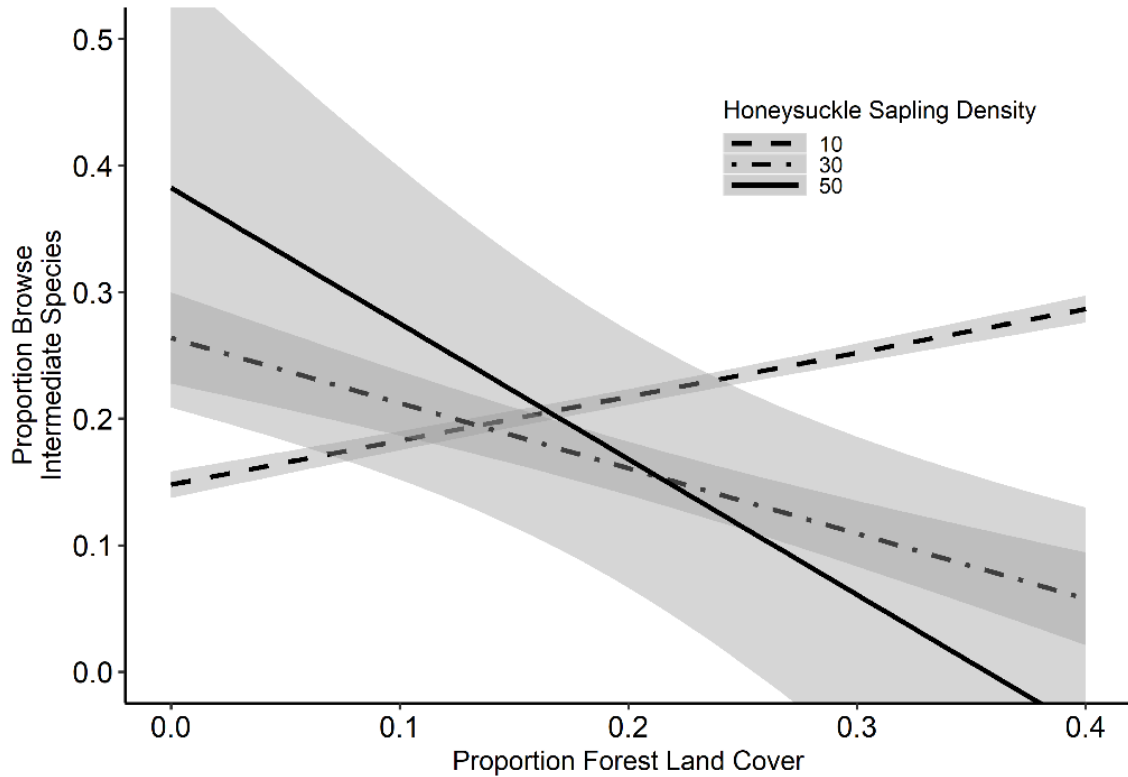


Figure 2.7 Interaction of forest land cover and Amur honeysuckle sapling density on browse pressure by white-tailed deer in forest patches in central Indiana, 2019 – 2020.

The proportion of twigs browsed of intermediately browsed species in response to the interaction of the density of Amur honeysuckle saplings (saplings/50 m²) and the proportion of forest land cover surrounding central-Indiana forest patches in a 500 m buffer. When Amur honeysuckle sapling densities are low, the browse of intermediate species increases with forest land cover. However, when Amur honeysuckle sapling densities are high, browse of intermediate species decreases with forest land cover.

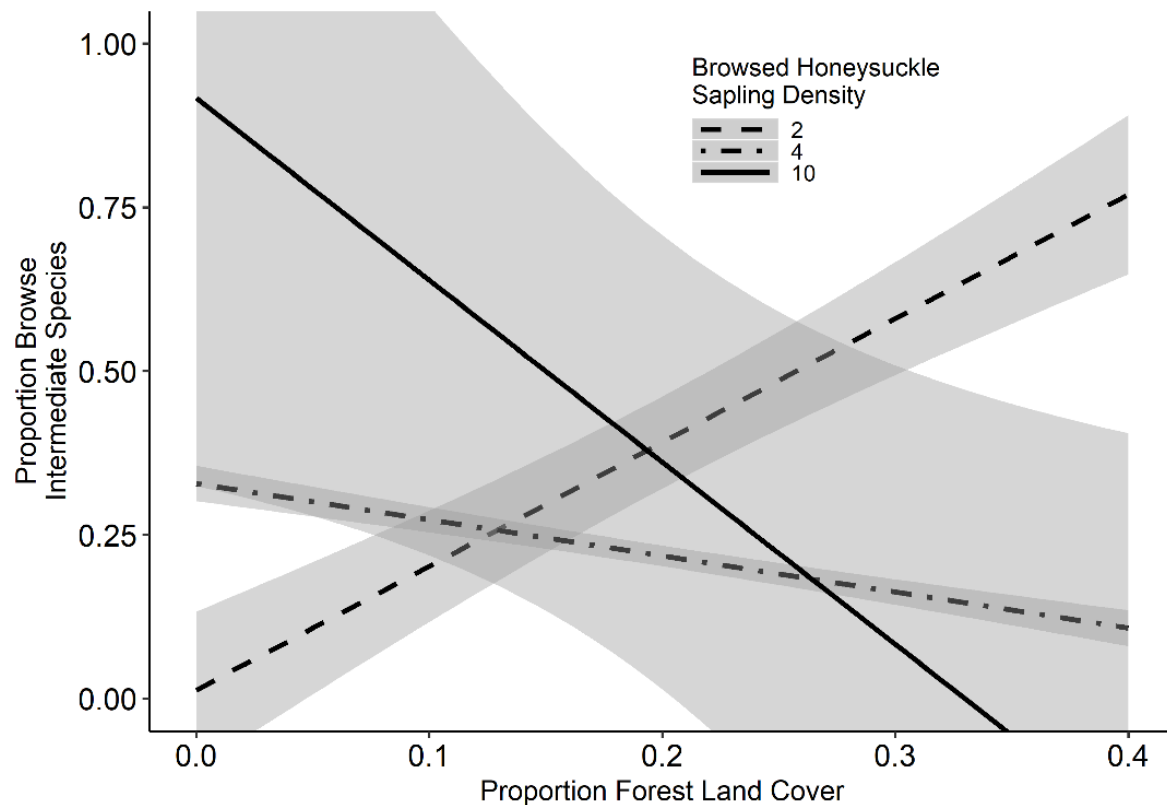


Figure 2.8 Interaction of forest land cover and browse Amur honeysuckle sapling density on browse pressure by white-tailed deer in forest patches in central Indiana, 2019 – 2020.

The proportion of twigs browsed of intermediately browsed species in response to the interaction of the density of browsed Amur honeysuckle saplings (saplings/50 m²) and the proportion of forest land cover surrounding central-Indiana forest patches in a 500 m buffer. When browsed Amur honeysuckle sapling densities are low, the browse of intermediate species increases with forest land cover. However, when browsed Amur honeysuckle sapling densities are high, browse of intermediate species decreases with forest land cover.

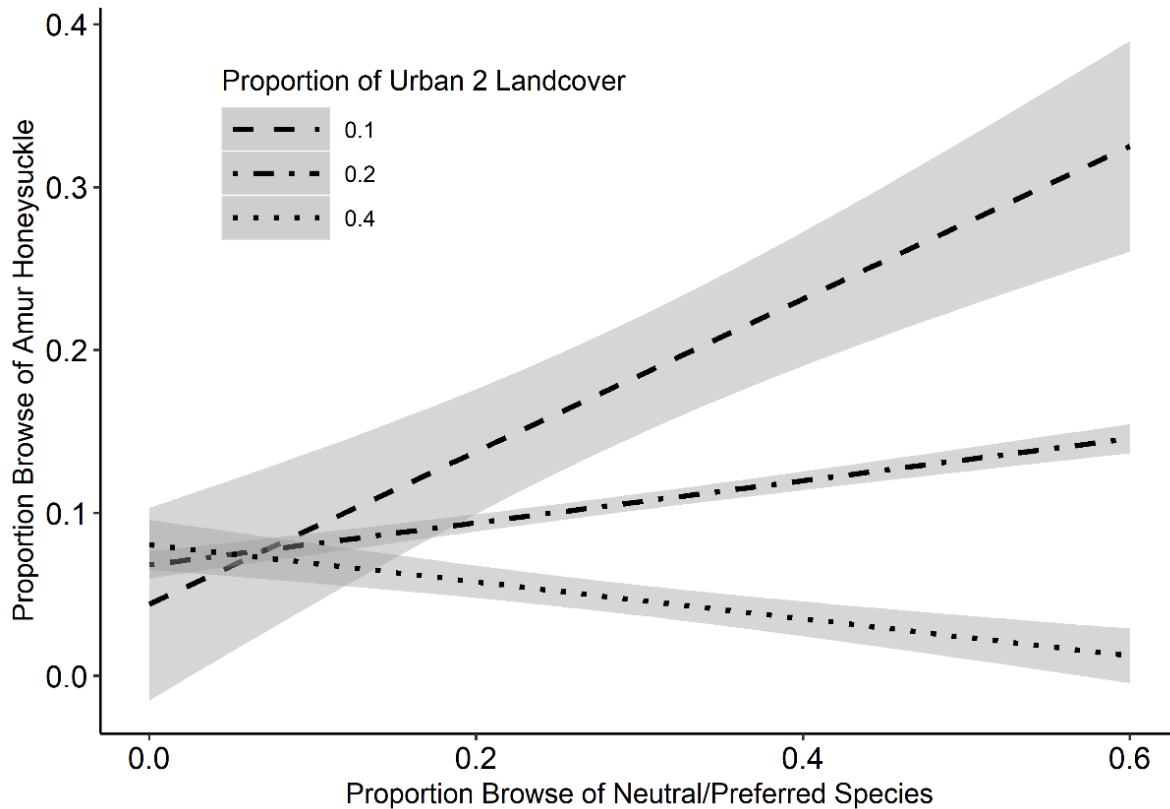


Figure 2.9 Interaction of browse on neutral/preferred species and urban 2 land cover on the browse of Amur honeysuckle by white-tailed deer in forest patches in central Indiana, 2019 – 2020.

The response of the proportion of Amur honeysuckle browsed to the interactive effect of urban 2 land cover (see Table 1 for land cover category definitions) in 500 m buffers around central-Indiana forest patches and the proportion browse of neutral and preferred species. When urban 2 landcover is low, Amur honeysuckle browse increases with browse on neutral and preferred species. However, when urban2 landcover is high, browse on Amur honeysuckle decreases as the proportion browse of neutral and preferred species increases.

CHAPTER 3. THE IMPACTS OF WHITE-TAILED DEER, LANDSCAPE CONTEXT, AND NON-NATIVE SPECIES ON THE DIVERSITY OF HERBACEOUS AND SAPLING LAYERS

3.1 Introduction

Forests of the eastern United States in the last half-century have faced fragmentation and habitat loss (Riitters et al., 2012), high white-tailed deer (*Odocoileus virginianus*; hereafter “deer”) densities (Côté et al., 2004), and non-native plant invasions (Oswalt et al., 2015), which are all associated with decreases in plant species diversity. These factors rarely occur individually, and their combined effects on diversity can be synergistic. Fragmentation of forests can decrease diversity (Munguia-Rosas et al. 2014; Sonnier et al. 2014) by amplifying edge effects and increasing the distance between neighboring patches, which can reduce the occurrence of dispersal-limited and specialist species (Almoussawi et al., 2020; Jamoneau et al., 2011). In addition, urbanization has been linked to decreased forest plant diversity (Burton et al., 2005; Burton and Samuelson, 2008; Pennington et al., 2010) and can impact plant communities through a variety of mechanisms including altered hydrology (Sheldon et al. 2019), increased air pollutants and anthropogenically emitted CO₂ (Bereitschaft and Debbage, 2013), increased temperatures (Bachelet et al., 2001; Karl et al., 1988), and increased introductions of non-native plants (Aronson et al., 2015; Duguay et al., 2007). Urban land cover is not a uniform condition, but often has varying mixtures of built-up urban structures and open space that results in different impacts on plant community diversity (Godefroid and Koedam, 2007; Pennington et al., 2010). Thus, landscape conditions (e.g. size of forest patches, intensity of urban land cover) created by anthropogenic land use and the specific land use, urbanization, impact the diversity of forest plant species.

Deer, a keystone herbivore in many temperate forests, also influence forest plant diversity by impacting plant communities through direct processes (i.e. herbivory) and indirect processes (e.g. competitive release, soil compaction; Rooney 2001, Heckel et al. 2010, Shelton et al. 2014, Pendergast IV et al. 2016). Herbivory directly decreases the cover of palatable plant species and can shift the size structures of browse-sensitive plant populations towards smaller plants (Augustine and Frelich, 1998). Herbivory when deer are not overabundant can increase species richness and diversity by reducing growth and cover of competitively superior species, which

allows less competitive species to persist (Judziewicz & Koch 1993; Royo et al. 2010). However, herbivory by overabundant deer has caused local extinctions of preferred palatable species (Anderson, 1994; Mulligan and Gorchov, 2004). When deer decrease the growth and cover of palatable species, nonpreferred or unpalatable species dominate forest understories because of reduced competition for growing space and resources. This can lead to forests with impoverished “park-like” open understories of unpalatable herbaceous plants like graminoids and ferns (Pedersen and Wallis, 2004; Waller, 2014). As a result, high deer abundances can reduce forest plant diversity (DeCalesta and Stout, 1997; Rooney and Dress, 1997; Rooney and Waller, 2003; Waller, 2014). This is not only a conservation concern for maintaining diverse plant communities, but also for other organisms including mammals, birds, and invertebrates that respond negatively to over-browsed habitats (Allombert et al. 2005*a, b*; Martin et al. 2010; Jirinec et al. 2017).

When examining herbivory impacts on diversity, it is important to consider scale (Brown and Allen, 1989) and landscape context because these factors can influence the effects of deer herbivory. Royo et al. (2017) and Miller et al. (2009) found that damage from deer herbivory decreased in forest understories if enough forage-rich areas, such as recent timber harvests, were present on the landscape. Similarly, Hurley et al. (2012) observed that interspersed non-forest perennial forage in areas outside state parks in Indiana influenced herbivory within the parks. This highlights the need to consider both local-scale deer herbivory and landscape-scale context when examining plant species diversity in forests.

Another important consideration when examining forest plant diversity is non-native plants within forest systems. Non-native plants influence native plant diversity through a variety of mechanisms including allelopathy (Hierro and Callaway, 2003), competition (Gioria and Osborne, 2014), and altered nutrient cycling (Ehrenfeld, 2003). In most cases, native plant richness and diversity are lower in forests invaded by non-native plants compared to forests without non-native plants (Pysek et al., 2012; Vila et al., 2011). When considering non-native plant impacts, it is important to consider that both landscape context and deer impacts can influence the distribution and severity of non-native plants. Non-native plants tend to be associated with forest edges (Honu and Gibson, 2008) and urban landscapes (Aronson et al., 2015; McKinney, 2006). The interactive effects of deer and non-native species (via deer browsing on native plants which reduces competition for non-native plants) can synergistically reduce native plant richness and diversity (Haffey and Gorchov, 2019; Webster et al., 2008). Another possible way that non-native plants

indirectly impact native plants is through apparent competition, where deer populations benefit from browsing on non-native plants and are then able to further browse and negatively impact native plants (Martinod and Gorchov, 2017). The association of non-native plant invasions with urbanization and high deer abundances highlights the question whether non-native species are passengers or drivers of ecosystem change. MacDougall and Turkington (2005) found that non-native plants tend to be passengers of other disturbances within anthropogenically modified ecosystems. However, even if non-native species are passengers rather than drivers of change, their increased dominance is emblematic of reduced plant diversity in urban landscapes. To assess the simultaneous and possibly interactive impacts of landscape, deer, and non-native plants on forest plant diversity, we conducted a study across multiple forest patches in both rural and urban landscapes. We specifically examined the plant diversity of the herbaceous and the sapling layers in response to deer herbivory on woody stems, a proxy for deer abundance (detected pellet groups), fragmentation (forest size and perimeter-area ratio), urban land cover, non-forest forage land cover, agricultural land cover, and non-native plant cover and density. We hypothesized that diversity of both the herbaceous and sapling layers would have a positive relationship with forest size and a negative relationship with perimeter-area ratio and urban landcover. For the herbaceous layer specifically, we hypothesized that plant diversity would be negatively related to non-native plant cover and density, deer browse intensity, and our proxy for deer abundance. We also hypothesized that plant diversity would be negatively related to urban land cover and examined if diversity differed with the intensity of surrounding urbanization (i.e. more green space with less impervious surfaces versus less green space and more impervious surfaces). By studying both rural and urban forests in central Indiana, these results clarify the threats to forest diversity in midwestern landscapes that should be incorporated into conservation and management.

3.2 Methods

3.2.1 Study Area

We sampled the same forest patches described in Pierce et al. (unpublished data) located throughout western-central Indiana. Forest patches were located in Tippecanoe, Warren, Carrol, Montgomery, White, Benton, and Newton Counties situated in the Central Till Plain and Grand Prairie Natural Regions (Homoya et al., 1985). Forests in these regions contain overstories with

oak (*Quercus*), hickory (*Carya*), black walnut (*Juglans nigra*), sassafras (*Sassafras albidum*), black cherry (*Prunus serotina*), and American basswood (*Tilia americana*). Bottomland forests often include American sycamore (*Platanus occidentalis*), eastern cottonwood (*Populus deltoides*), and silver maple (*Acer saccharinum*). Forest patches in Warren County were within the Entrenched Valley Section which has steep ravines and cliffs that provide habitat to plants not found in other parts of the Central Till Plain. However, the general composition of most forests in the Entrenched Valley Section is similar to forests in the rest of the Central Till Plain Region (Homoya et al. 1985). Tippecanoe County contains a large area of urban land use; the Greater Lafayette area has a population of approximately 122,717 people (US Census Bureau, 2018; US Census Bureau 2019).

3.2.2 Site Selection and Study Design

We sampled a total of 69 forest patches in 2019 and 2020. We collected all vegetation data between late May and the end of July and deer pellet data in March and early April. We sampled 41 rural forest patches that were within a regional Indiana deer management unit defined by Swihart et al. (2020). These large regional units were created based on land cover, mortality of deer, the density of hunters, and feedback from natural resource managers within the state. Rural forest patches were located within 10 randomly located 3.22×3.22 km (2×2 miles) areas within the regional unit. Urban forest patches included publicly accessible properties (i.e. local parks) and privately-owned forest patches with landowners that granted us permission to access and were > 0.6 ha.

Distances between patches ranged from < 100 m to several km. Because plant diversity in forests can be influenced at a broad spatial scale (Amici et al., 2015), the diversity of forest patches in close proximity were likely not independent. To account for this lack of independence, we used a spatial cluster analysis to group forest patches into clusters to be used as random intercepts in mixed models. Using a distance matrix calculated from the spatial coordinates of each forest patch centroid, we used a k-means cluster analysis and inspected Ball-Hall and Calinski-Harabes plots to determine the number of clusters to use. The plots revealed that between six and eight clusters were appropriate for our forest patches. We evaluated the outcome of each option (six, seven, or eight clusters) and concluded that seven clusters was the best grouping of forests to account for spatial proximity and similarity of forest patches within clusters and provided sufficient spatial

separation between clusters (> 15 km). The forest patches in each county formed a cluster with two exceptions. White County had two clusters, one near the eastern county edge and the other near the western county edge. Additionally, the cluster analysis grouped our single forest patch in Benton County with forest patches from the western part of White County (Fig. 3.1).

Cluster 1 included all forest patches located in and around the Greater Lafayette Area in Tippecanoe County. We refer to these as “urban” forest patches for our study due to the large cover of developed land in 500 m buffers surrounding forest patches (Table 3.1). Land cover in clusters 2-7 were all dominated by agriculture with very little developed land (Table 3.1), and we refer to forest patches in these clusters as “rural” forest patches. We sampled 28 urban forest and 41 rural forest patches in 2019 and 2020.

3.2.3 Vegetation Sampling

We used 50 m transects to collect vegetation and browse data in forest patches. Using ArcMap (v. 10.8, ESRI Corporation, Redlands, CA, USA), we randomly generated transect locations within forest patches but avoided changes in elevation, placing transects parallel to the contour of any slopes we encountered. To determine the number of transects sampled per forest patch, we determined the minimum number of transects needed to satisfy the inequality $A/t > 2t$, where A is forest patch size (ha) and t is the number of transects assigned to a forest patch. This allowed for more intensive sampling of larger areas, but also restricted the number of transects sampled in forests patches to a feasible number for data collection (Table 3.2).

Within 50×1 m belt transects, we tallied all saplings (diameter at breast height [dbh; 1.37m] < 10 cm; height ≥ 1.37 m) by species. For each sapling, we determined whether a species was native or non-native according to the USDA Plants database (USDA, NRCS 2020). In each forest patch, we calculated the density of non-native saplings per belt transect (saplings/50 m²) and averaged all transects within a forest patch to produce an average, patch-level density value for analysis. We calculated Shannon’s diversity (H') for saplings in each forest patch using the patch-level density of each species in the patch using the program PC-ORD (McCune and Mefford 2011). We calculated this for overall sapling layer diversity (all species), and for native sapling layer diversity.

We used a 1 m² quadrat placed every 10 m in the belt transect (total of 5 quadrats per transect) to visually estimated the percent cover of herbaceous and woody species < 1 m tall. We

also tallied seedlings (woody stems < 1.37 m tall) inside quadrats by species in two height classes: (1) 0 – 20 cm, and (2) 20 – 137 cm. To summarize quadrat data for each forest patch, we calculated percent cover and seedling density (seedlings/m²) of non-native species in each quadrat in a forest patch. We then averaged these values between quadrats within each forest patch to have patch-level averages for analysis. We calculated H' for the herbaceous layer overall and for native species using the patch-level average percent cover of each species in a forest patch in the program PC-ORD. We classified understory plant species into seven functional groups similar to Jenkins et al. (2014): herbs, non-native (exotic), trees, shrubs, lily species, ferns, and graminoids.

We sampled the overstory with variable radius plots using a 2.296 m²/ha basal area factor prism. We conducted an overstory plot at the midpoint of each belt transect and identified trees to species. To summarize overstory data, we calculated basal area per species and total basal area for each forest patch.

3.2.4 Deer Impacts

To develop an index of deer abundance, we conducted 200 m pellet transects using a distance sampling framework (Marques et al., 2001) in late winter/early spring before leaves flushed for the spring. An observer walked each transect and scanned both sides of the transect to visually search for pellet groups. Whenever the observer detected a pellet group, they recorded the perpendicular distance from the centroid of the pellet group to the transect and counted the number of pellets in the group. Rural forest patches were part of a larger integrated deer project, which had a research objective of estimating deer abundance in large spatial areas. As a result, some rural forest patches did not contain pellet transects while others had multiple transects (Z. Delisle, unpublished data). In each urban forest patch sampled for our study, we sampled one pellet transect due to logistical constraints. Pellet density estimates at the forest patch scale were not reliable statistically, nor conceptually, because in some cases we calculated a density in an area smaller than a deer home range. To estimate a forest patch-level predictor, we used the average number of pellets detected per transect in each forest patch as a proxy for deer abundance. Because a given deer abundance can have different impacts on forest vegetation depending on forest structure and landscape context, we also calculated a proxy for deer browsing pressure with data from Pierce et al. (unpublished data). This browsing proxy consisted of the proportion of twigs browsed in each forest patch of species that were neutral or preferred by deer, based on a chi-squared analysis done

in the same forest patches. Thus, the proxy of browse pressure (proportion of neutral and preferred twigs browsed) was at a forest patch level like the other variables for our analyses.

3.2.5 Land Cover and Landscape Metrics

We reclassified land cover data from the 2016 national land cover database (NLCD; Dewitz 2019) into nine classes for our analyses (Table 3.3) that described agriculture, land cover rich with deer forage, and varying levels of urban development. We then calculated the proportions of each reclassified land cover group within a 500 m buffer around each forest patch. We used a raster layer of forests patches sampled in our study and calculated the patch level-characteristics of forest patch area, perimeter-area ratio and shape index (the perimeter of a patch divided by the minimum possible perimeter of a patch with that area) with the FRAGSTATS program (McGarigal et al. 2012).

3.2.6 Statistical Analysis

We also conducted non-metric multidimensional scaling (NMS) ordinations of forest patches based on the herbaceous and sapling layer composition. We then used PC-ORD on autopilot mode with 250 runs with real data and 250 runs of randomized data using the Sørensen distance measure and a 0.00001 stability criterion. We used correlation analysis between NMS axes and environmental vectors of proportion land cover of forest, agriculture, urban 1, urban 2, urban 3, urban 4, as well as overstory basal area, density of non-native species in the midstory, and for the herbaceous layer NMS the percent cover of non-native species.

We constructed linear mixed models with H' of forest patches as the response variable in R (R Core Team 2019) using the package lme4 (Bates et al., 2015). We examined H' of the herbaceous and sapling layer (separately) in response to landscape-scale metrics including the proportions of land cover types surrounding forest patches, patch-scale metrics including forest patch area, forest patch shape, and forest patch perimeter-area ratio of the forest patch. We also examined the response of H' to within-patch metrics such as percent cover of non-native plants in the understory, density of non-native seedlings and saplings, overstory basal area, a proxy for deer abundance, and deer browsing pressure. We standardized all predictor variables to have a mean of 0 to improve model convergence. After examining H' responses to these landscape- and patch-

scale metrics, we built models with significant landscape- and patch-scale predictors and tested for interaction terms. Each model included cluster as a random intercept. We performed this model-building procedure for the sapling and herbaceous layers with two response variables for each layer: overall species diversity and native species diversity. We ranked models using corrected Akaike's information criterion (cAIC) for lme4 (Saefken and Ruegamer 2018).

3.3 Results

3.3.1 Functional Group Cover and NMS Ordinations

Herbs had the highest cover of the seven functional groups in each cluster, except cluster 2 in which non-native cover was the highest (Table 3.4). Non-native species had the second highest cover in five clusters. Ferns exhibited the lowest cover in all clusters and lily group cover was second lowest in all clusters, except cluster 5. Trees and shrubs were generally intermediate in cover, except for cluster 5 which had low shrub cover (Table 3.4).

The NMS ordination of herbaceous layer composition resulted in a three-dimensional solution and had a final stress equal to 16.07. Axes 1, 2, and 3 explained 72.5% of total variance with axes 2 and 3 accounting for 21.9 and 33.1%, respectively. Two environmental variables, non-native cover and sapling density positively correlated with axis 2 ($r = 0.523$ and $r = 0.404$ respectively) while urban 1 land cover ($r = -0.543$), proportion of urban 2 landcover ($r = -0.284$), and proportion of agricultural land cover ($r = 0.402$) correlated with axis 3 (Fig. 3.2; Table 3.5). The NMS displayed a differentiation between urban and rural forest patches with 89% of urban forest patches having negative axis 3 values, and 85% of rural forest patches having positive axis 3 values. The correlations of non-native cover and non-native sapling density with axis 2, which did not differentiate urban and rural forest patches, demonstrated that non-native plants were not associated exclusively with urban or rural forest patches (Fig. 3.2). The majority of forest patches in clusters 2, 3, and 4 had positive axis 2 values, exhibiting an association with non-native plants (Fig. 3.2).

The NMS ordination of sapling layer composition resulted in a three-dimensional solution and had a final stress equal to 19.81. Axes 1, 2, and 3 explained 62% of total variance, with axes 1 and 3 explaining 18.1 and 27.5% respectively. Environmental variables positively correlated with axis 1 including proportion of urban 1 land cover ($r = 0.287$) and proportion of urban 2 land

cover ($r = 0.377$), while the proportion of agricultural land cover ($r = -0.344$) was negatively correlated with axis 1 (Fig. 3.3; Table 3.6). Positive correlations with axis 3 included proportion of urban 1 land cover ($r = 0.534$), proportion of urban 2 land cover ($r = 0.431$), forest patch shape ($r = 0.345$), and non-native sapling density ($r = 0.539$; Table 3.6). The sapling-layer NMS showed a separation of urban and rural forest patches with respect to the two dominant axes, 1 and 3. All urban forest patches exhibited positive scores on one or both axes (Fig. 3.3), while only three rural forest patches (7%) scored positively on both axes and the remaining 93% of rural forest patches scored negatively with one or both axes (Fig. 3.3).

3.3.2 Overall Herbaceous-layer Diversity

We could not use the proportion of urban 1, urban 2, or urban 3 land cover as predictor for overall (all species) herbaceous-layer diversity due to models having a singular fit. Significant positive predictors included one landscape-scale variable, the proportion of forest land cover ($p < 0.001$), and two patch-scale variables forest patch area ($p = 0.014$) and forest patch shape ($p = 0.033$; Table 3.7). We observed one significant negative patch-scale predictor, forest patch perimeter-area ratio ($p = 0.001$). Significant within forest patch predictors included, the proportion of twigs browsed of neutral and preferred species ($p = 0.012$), non-native seedling density ($p = 0.001$), non-native sapling density ($p = 0.004$), and percent cover of non-native plants ($p = 0.006$; Table 3.7), which were all negatively related to overall herbaceous-layer diversity.

We observed three significant two-way interactions between non-native seedling density and perimeter-area ratio ($p = 0.016$), non-native sapling density and perimeter area ratio ($p = 0.022$), and non-native species cover and forest patch area ($p = 0.01$). For interactions of both non-native seedling and sapling with perimeter-area ratio, whenever forest patch perimeter-area ratio was low, herbaceous-layer diversity did not respond to changes in non-native seedling or sapling densities. However, when perimeter-area ratios were high, and the density of non-native saplings or seedlings increased, herbaceous-layer diversity decreased (Fig. 3.4). The interaction between forest patch area and non-native cover revealed that when forest patch area was small, increased non-native cover was associated with decreased herbaceous-layer diversity. However, when forest patch area was large, increased non-native cover was associated with increased herbaceous-layer diversity. We also observed a marginally significant two-way interaction between non-native sapling density and the proportion of forest landcover ($p = 0.076$; Table 3.7). In this marginal

interaction, when the proportion of forest land cover was small, an increase in non-native sapling density was related to a decrease in herbaceous-layer diversity. However, with high proportions of forest land cover, non-native sapling density did not reveal a relationship with overall herbaceous-layer diversity (Fig. 3.5).

Within models with landscape-scale and patch-scale predictors, the proportion of forest land cover was the best model, with the next best model having a $\Delta\text{cAIC} > 4$. Models including within-patch predictors were all very closely ranked in ΔcAIC (Table 3.7). After comparing the cAIC of all models, the model with the marginal interaction between the proportion of forest land cover and density of non-native saplings had the lowest cAIC. The next best model was the interaction of non-native seedling density and perimeter-area ratio, which had a $\Delta\text{cAIC} = 3.9$ (Table 3.7).

3.3.3 Native Herbaceous-layer Diversity

In our models for response of native herbaceous-layer diversity, significant predictors included the proportion of forest land cover ($p = 0.001$), proportion of forage land cover ($p = 0.024$), and forest patch perimeter-area ratio ($p = 0.009$; Table 3.7). Forest and forage land cover had a positive relationship with native herbaceous-layer diversity while the perimeter-area ratio had a negative relationship. We were unable to use urban 2 and urban 3 land cover as predictors due to model singularity. Urban 1 and urban 4 land cover were marginally significant predictors ($p = 0.051$ and $p = 0.097$, respectively) and negatively related to native herbaceous-layer diversity (Table 3.7). The only significant forest patch-scale predictor of native herbaceous-layer diversity was the proportion of twigs browsed of neutral and preferred species ($p = 0.045$).

There were no interactions between the significant predictors of native herbaceous-layer diversity. However, we tested for an interaction between the significant predictors of native herb cover and non-native cover and observed one significant interaction between non-native cover and the proportion of forest land cover ($p = 0.037$). In this interaction, when non-native cover was low, the proportion of forest land cover did not affect native herbaceous-layer diversity. When non-native cover was high, as the proportion of forest land increased, the diversity of native herbaceous species also increased (Fig. 3.6).

3.3.4 Overall Sapling-layer Diversity

Urban 3 land cover ($p = 0.042$) was the only significant landscape-scale predictor for the overall (all species) diversity of the sapling layer and had a negative relationship (Table 3.8). We did observe one other marginally significant landscape-scale predictor, proportion of forest land cover ($p = 0.069$), which displayed a positive relationship to overall sapling diversity. We also observed one marginally significant patch-scale predictor, perimeter-area ratio ($p = 0.075$), which displayed a negative relationship to overall sapling-layer diversity. One within-patch predictor, the density of non-native saplings, was marginally significant ($p = 0.0504$) and negatively related to overall sapling-layer diversity. We observed no significant interactions between significant and these marginally significant predictors.

We constructed two additive models, one with non-native sapling density and proportion of forest landcover as predictors, and one with non-native sapling density and perimeter-area ratio as predictors. We then compared cAIC values for each model with significant and marginally significant predictors, and our additive models. No model had strong support as the best model, as all models had $\Delta\text{cAIC} < 4$ (Table 3.8).

3.3.5 Native Sapling-layer Diversity

We were not able to use the density of non-native saplings as a predictor due to model singularity. The proportion of forest land cover was the only significant predictor ($p = 0.035$) and had a positive relationship with native sapling-layer diversity (Table 3.8). Two predictors were marginally significant, forest patch area ($p = 0.063$), which was positively related to native sapling-layer diversity, and urban 3 land cover ($p = 0.051$), which was negatively related to native sapling-layer diversity (Table 3.8). No within-patch predictors were significant.

While the proportion of twigs browsed of neutral and preferred species was not a significant predictor of native sapling-layer diversity, we tested for interactions between it and the proportion of forest land cover, forest patch area, and the proportion of urban 3 land cover but did not detect any significant interactions. We compared the ΔcAIC of the three landscape and patch-scale models with significant and marginally significant predictors. There was no clear separation among the models, with each having $\Delta\text{cAIC} < 2$ (Table 3.8).

3.4 Discussion

3.4.1 Herbaceous and Sapling-layer Composition

Both sapling and herbaceous-layer NMS ordinations revealed different compositions of plant communities in urban landscapes compared to rural/agricultural landscapes. Similarly, Templeton et al. (2019) found composition differed between rural and urban forests in Maryland and Godefroid and Koedam (2007) reported that densely built-up urban areas (industrial areas and areas with high building densities and impervious surface) impacted plant species compositions in Belgium. The notable separation of urban and rural forest patches in our NMS ordinations demonstrates that even within a relatively small region consisting of seven counties, plant communities in urban forest patches can be distinct from rural forest patches. In areas where urbanization is increasing, these differences could be consequential not only for plant species, but also for the wide variety of other taxa that rely on the habitat characteristics plant communities provide. We expected to observe a strong association of non-native species with our urban forest patches, however, our NMS results from the herbaceous and sapling layers demonstrated that both rural and urban forest patches were associated with non-native species. One possible explanation is that one particular invasive shrub species, Amur honeysuckle, which comprised 84% of non-native saplings and 36% of non-native cover in our study, was found in both urban and rural forest patches. However, Amur honeysuckle was more common in urban forest patches, while other non-native species like multiflora rose and Autumn olive were more common in rural forest patches. Additionally, many of our rural forest patches were privately-owned land near roads with houses located on the property. Gavier-Pizarro et al. (2010) found that houses in rural areas and the distance of forests to roads were linked to the cover and richness of non-native species, which offers additional explanation of why rural forest patches contained non-native species and our environmental vectors of non-native species did not distinguish between rural and urban forest patches in the NMS.

3.4.2 Herbaceous-layer Diversity

In support of our hypotheses, deer browse and non-native plant densities/cover were negatively associated with herbaceous-layer diversity. We were unable to assess how three of our urban land cover categories were related to overall herbaceous-layer diversity and were unable to

support or counter our prediction that urban land cover would be negatively related to overall herbaceous-layer diversity. Regarding native herbaceous-layer diversity, we found negative relationships between urban 1 and urban 4 land cover and diversity although these were only marginally significant (Table 3.7). This shows limited support of our hypothesis that urban land cover would be negatively associated with diversity. Our results differed from those of Godefroid and Koedam (2007) where densely built up urban areas were associated with reductions in diversity, while less-dense urban areas with greater vegetation cover were associated with increases in plant species diversity. In our study both urban 1 land cover (mostly open space) and urban 4 land cover (highly developed impervious surface) were negatively related to native herbaceous-layer diversity. This difference could be due to the rural to urban gradient we examined compared to the low urban development to high urban development gradient examined by Godefroid and Koedam (2007). Additionally, we had very low amounts of urban 4 land cover, our highest intensity level of urbanization, around forest patches and it is possible that our data are not suitable to capture this trend.

We found a positive association between the proportion of forage land cover and native herbaceous-layer diversity, similar to Hurley et al. (2012) reporting a positive association between interspersed forage and native herb cover in nearby forests, which suggests that the availability of non-forest forage for deer within a landscape could reduce deer impacts on forest understories. The proportion of forest land cover was positively associated with overall and native herbaceous-layer diversity, supporting the habitat amount hypothesis which states that patch-level metrics, such as patch size, are not important in determining species richness, but rather that species richness is better explained by the total amount of a habitat (sum of all patches) in a given landscape (Fahrig, 2013). However, contrary to the habitat amount hypothesis, we did find that forest patch area and perimeter-area ratio were important in predicting diversity, especially with respect to non-native plant species due to significant interactions.

The negative association of overall herbaceous-layer diversity with non-native seedling and sapling densities was context dependent. Non-native seedling density interacted with forest patch perimeter-area ratio and non-native sapling density interacted with both perimeter-area ratio and the proportion of forest landcover. These interactions suggest that forest patches that are small and, consequently, have a relatively high amount of edge relative to the amount of interior, are more susceptible to negative impacts from non-native plants. These results are consistent with other

research that identified an association between forest edges and the richness and cover of non-native species (Honu and Gibson, 2008), and found that small forest patches are more susceptible invasion by non-native plant species (Predick and Turner, 2008). Our results support the hypothesis that non-native plant species are passengers, rather than drivers of change (MacDougall and Turkington, 2005) because larger forest patches in landscapes with a greater proportion of forest land cover (i.e. less human modification to forest systems) had greater diversity of native plants species.

When only considering native herbaceous species diversity, non-native plants as individual predictors did not significantly impact diversity (Table 3.7). However, the interaction between non-native species cover and the proportion of forest land cover demonstrates that when non-native cover is high, having more forest land cover in the surrounding landscape can help maintain native herbaceous-layer diversity. This interaction is consistent with the biotic resistance hypothesis. The biotic resistance hypothesis predicts that diverse plant communities are more difficult for non-native plant plants to invade due to limited niche space available for the non-native plants to exploit (Beaury et al., 2020). Indeed, a broad review found strong evidence for biotic resistance in ecosystems across the United States (Beaury et al., 2020). Our observed positive association with the proportion of forest land cover and herbaceous-layer diversity and the subsequent interaction between the proportion of forest land cover and non-native plant cover demonstrates that conditions of high herbaceous-layer diversity in our study system also were not associated with reductions in herbaceous-layer diversity due to the cover of non-native plants, even when non-native plant cover was high.

Our proxy of deer abundance (pellet groups) was not a significant predictor of overall or native herbaceous-layer diversity, although deer browse of neutral and preferred species was negatively related to both metrics, which is not surprising considering the well-documented evidence that deer herbivory can reduce richness and diversity of native plant species (Côté et al., 2004; Habek and Schultz, 2015; Nuttle et al., 2014; Pendergast IV et al., 2016; Rooney, 2001; Rooney and Waller, 2003; Waller, 2014). However, contrary to our hypothesis, we did not observe any interactions between predictors of deer impacts and land cover or deer impacts and non-native plant densities and cover. We expected deer to synergistically interact with non-native plants in reducing diversity, which has been documented in multiple studies (Haffey and Gorchov, 2019; Heberling et al., 2017; Morrison, 2017; Webster et al., 2008). We also expected to observe an

interaction between deer abundance and urban land cover where a given deer abundance would decrease herbaceous-layer diversity more in forest patches surrounded by urban land cover because deer in urban landscapes do not have alternate food sources provided by agriculture. One limitation of our study was the lack of fenced control plots to observe plant responses in the absence of deer impacts. Therefore, our inference was limited to the various levels of deer impacts and densities naturally occurring within our study system. The relatively low browsing rate of deer in our urban forest patches was another possible reason we did not observe interactions between deer impacts and land cover. Approximately 14% of all available twigs in urban forest patches were browsed (Pierce et al, unpublished data), while one study of an urban forest reserve with high deer abundances documented 60% of available twigs browsed (Hygnstrom et al., 2011). Thus, deer browsing may not have been high enough in our urban forest patches to observe interactions between deer and urban land cover.

3.4.3 Sapling-layer Diversity

Deer browse was not a significant predictor of overall or native sapling-layer diversity. It is possible that current and past levels of deer browse in our study system were not high enough to impact sapling diversity. One within-patch variable, non-native sapling density was significant when combined with forest land cover in an additive model and was negatively related to overall sapling-layers species diversity. The absence of impacts from deer browse and the negative impact of non-native saplings on overall sapling-layer diversity implies that either non-native saplings in our system are able to directly compete with native saplings and reduce diversity, or that another impact besides deer herbivory such as land cover (Burton and Samuelson, 2008; Pennington et al., 2010), increased forest edge (Yates et al., 2004), or nearby roads (Gavier-Pizarro et al., 2010) is facilitating the spread of non-native saplings and reducing overall sapling-layer diversity.

In support of our hypothesis that urban land cover would decrease sapling-layer diversity, urban 3 land cover was negatively related to overall sapling-layer species diversity. Urban 3 land cover contains 50-80% impervious surface (Dewitz, 2019) further supporting the relationship between increased impervious surface and decreased woody species diversity (Pennington et al., 2010). Similarly, Burton and Samuelson (2008) found lower plant species diversity closer to the urban center in Columbus, Georgia. However, support for the decrease of plant diversity with urbanization is not unanimous, as Templeton et al., (2019) found higher alpha diversity in urban

forest patches compared to rural forest patches, and (Cameron et al., 2015) did not observe declines in herb diversity with increasing urbanization. The mechanisms through which urbanization can impact plant communities are numerous, such as alterations to hydrology (Sheldon et al. 2019), increased air pollution (Bereitschaft and Debbage, 2013; Bytnerowicz et al., 2007), and increased temperatures (Bachelet et al., 2001; Karl et al., 1988). Detailed consideration of these mechanisms may improve understanding of how urbanization decreases plant diversity in some cases, and not in others. While not significant predictors in our analyses, urban land cover was negatively associated with herbaceous-layer plant diversity and was significantly related (negatively) to sapling layer diversity. Thus, our research supports other results showing decreases in plant diversity with increasing urbanization (Burton and Samuelson, 2008; Godefroid and Koedam, 2007; Pennington et al., 2010; Schwoertzig et al., 2016)

Similar to the herbaceous layer, the proportion of forest land cover was positively associated with sapling-layer species diversity (Table 3.8). This supports the habitat amount hypothesis which claims that the total amount of habitat in a landscape determines species richness (Fahrig, 2013). One point to account for in the habitat amount hypothesis is the assumption that colonization/dispersal can occur from one patch to the next. Depending on dispersal ability, some species may not be able to cross the matrix between two forest patches. If the matrix functioned as an impermeable barrier between patches, the amount of habitat would be irrelevant. Furthermore, slow-migrating species can be negatively impacted by fragmentation and anthropogenic landscapes (Matlack, 2005), emphasizing that dispersal between patches may not always be assumed.

3.4.4 Conclusions

The results of both our herbaceous and sapling-layer models suggest that human modification of the landscape through alterations to the size and number of forest patches, as well as the composition of surrounding land cover, impacts plant species diversity. Interactions between non-native plant cover/density and land cover, as well as forest patch area and perimeter-area ratio, demonstrate the complexity of processes impacting forest plant diversity in fragmented landscapes. We recommend that forest herbaceous and sapling-layer species diversity be considered with regard to landscape context (i.e. rural with agriculture, urban, forested), patch-level effects (forest size and shape), deer herbivory, and non-native plants in the management of forests within

fragmented landscapes. Managers should be aware that forests with a high perimeter-area ratio and/or in landscapes with little forest land cover may be especially susceptible to decreases in native plant diversity, and these forests may be especially vulnerable to decreases in diversity in response to non-native plants dominances. Additionally, future studies should address mechanisms through which urbanization decreases plant diversity and examine how the different plant communities in these urban landscapes impacts other taxa.

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Table 3.1 Urban and agricultural land cover averages in 500 m buffers around forest patches in central Indiana in 2019-2020.

Average proportion of urban land cover and agriculture land cover in 500 m buffers around forest patches located in central Indiana, 2019-2020. Cluster 1 contained all urban forest patches, while clusters 2-7 contained rural forest patches. For further land cover definitions see Table 3.3.

Cluster	Urban 1	Urban 2	Urban 3	Urban 4	Urban 1-4	Agriculture
1	21.44	22.85	11.11	2.98	58.39	17.97
2	2.32	2.52	0.08	0.00	4.92	75.42
3	4.14	1.34	0.02	0.00	5.49	84.11
4	2.06	3.18	0.05	0.00	5.29	83.11
5	3.53	0.25	0.08	0.00	3.88	87.73
6	3.0	3.02	0.10	0.00	6.11	83.31
7	4.62	0.43	0.01	0.00	5.07	91.65

Table 3.2 Transect assignment for vegetation sampling based on forest patch size in central Indiana, 2019 – 2020.

Adapted from Pierce et al. (unpublished data). Number of vegetation sampling transects assigned to forest patches in central Indiana to sample herbaceous and sapling layer vegetation.

Forest Patch Size (ha)	Number of Transects
0-7.99	2
8-17.99	3
18-31.99	4
32-49.99	5
50-71.99	6
72-97.99	7
98-127.99	8
128-161.99	9

Table 3.3. National Land Cover Database land cover reclassification for land cover surrounding forest patches in central Indiana, 2019 – 2020.

Adapted from Pierce et al. (unpublished data). National land cover database (NLCD) 2016 land cover types that were reclassified into 9 categories for our analyses. Categories denoted with an asterisk (*) were left as their own original class during our reclassification however, we refer to them by the reclassified category name.

Reclassified Category for Analyses	NLCD Legend Number	NLCD Name
Forest	41	Deciduous Forest
Forest	42	Evergreen Forest
Forest	43	Mixed Forest
Forest	90	Woody Wetlands
Water	11	Open Water
Forage	52	Shrub/Scrub
Forage	71	Grassland/Herbaceous
Forage	72	Sedge/Herbaceous
Forage	95	Emergent Herbaceous Wetland
Agriculture	81	Pasture/Hay
Agriculture	82	Cultivated Crops
Urban 1	21	Developed Space, Open
Urban 2	22	Developed, Low Intensity
Urban 3	23	Developed, Medium Intensity
Urban 4	24	Developed, High Intensity
Other		All Other Classes

Table 3.4 Herbaceous layer cover by functional group for forest patches in central Indiana, 2019 – 2020.

The mean percent cover by plant functional groups in the herbaceous layer (< 1 m tall) averaged between forest patches in each of seven clusters. Cluster 1 is composed of forest patches in Tippecanoe County and that were defined as “urban” forest patches for our study. Clusters 2-7 were in high agricultural landscapes and defined as “rural” forest patches. Averages of all urban forest patches are provided by cluster 1 averages and the averages of all rural forest patches are included.

	Mean Percent Cover of Plant Functional Group						
	Non-native	Fern	Graminoid	Herb	Lily	Shrub	Tree
Cluster 1	7.76	0.09	0.68	24.23	0.12	0.98	4.51
Cluster 2	13.23	0.30	2.38	11.76	1.57	6.94	5.31
Cluster 3	9.02	0.01	2.99	35.43	0.15	4.52	3.85
Cluster 4	12.11	0.26	0.78	24.75	0.48	6.35	3.65
Cluster 5	0.06	0.10	1.27	16.16	1.32	1.27	3.38
Cluster 6	8.50	0.02	2.19	18.85	0.01	4.14	1.95
Cluster 7	5.11	0.04	3.35	41.17	0.42	2.66	3.49
All Rural Patches	9.54	0.15	2.03	25.7	0.60	5.01	3.77

Table 3.5 Herbaceous layer NMS environmental variable correlations for forest patches in central Indiana, 2019 – 2020.

Correlations of environmental variables with three axes of a non-metric multidimensional scaling (NMS) of herbaceous layer composition of 69 forest patches in central Indiana. See Table 3.3 for landcover variable descriptions. Other variable definitions are: PTB - proportion of twigs browsed by deer of neutral and preferred species, Area – forest patch area, Shape – forest patch shape index from FRAGSTATS, non-native cover – the average percent cover of non-native plant cover in the herbaceous layer (< 1 m tall), non-native sapling density – density of non-native saplings, basal area – average basal area of trees overstory trees (diameter at 1.37 m > 10 cm) in forest patches.

Environmental Variables	Axis 1	Axis 2	Axis 3
	<i>r</i>	<i>r</i>	<i>r</i>
Forest	0.133	-0.085	-0.106
Forage	-0.139	-0.033	-0.192
Agriculture	-0.066	0.142	0.716
Urban 1	0.232	-0.059	-0.72
Urban 2	0.103	-0.154	-0.63
Urban 3	0.029	0.152	-0.214
Urban 4	0.034	0.157	-0.151
PTB	-0.284	0.173	0.082
Area	0.06	-0.233	-0.165
Shape	-0.023	-0.197	-0.33
Non-native Cover	-0.113	0.628	-0.04
Non-native Sapling Density	0.025	0.421	-0.462
Basal Area	-0.063	-0.172	-0.01

Table 3.6 Sapling layer NMS environmental variable correlations for forest patches in central Indiana, 2019 – 2020.

Environmental variable correlations with three axes from non-metric multidimensional scaling of sapling-layer composition of 68 forest patches in central Indiana. For variable descriptions see Table 3.5.

Environmental Variables	Axis 1 <i>r</i>	Axis 2 <i>r</i>	Axis 3 <i>r</i>
Forest	-0.096	-0.052	0.142
Forage	0.034	-0.14	0.342
Agriculture	-0.344	-0.184	-0.59
Urban 1	0.287	0.25	0.534
Urban 2	0.377	0.29	0.431
Urban 3	0.069	-0.118	0.198
Urban 4	0.023	-0.133	0.151
PTB	0.176	-0.26	-0.046
Area	-0.012	0.118	0.254
Shape	0.03	0.067	0.345
Non-native Sapling Density	-0.155	-0.449	0.539
Basal Area	0.132	0.174	-0.036

Table 3.7 Mixed model results for herbaceous-layer diversity of forest patches in central Indiana, 2019 – 2020.

Fixed effect predictors, coefficients, t-values, p-values, Satterthwaite's degrees of freedom (df) conditional Akaike Information Criterion (cAIC) and difference in cAIC from the best model (Δ cAIC) for mixed models predicting overall herbaceous-layer diversity and native herbaceous-layer diversity in forest patches in central Indiana. Each model included cluster (spatial grouping variable) as a random intercept. Significant p-values ($p < 0.05$) are bolded. Non-native saplings and non-native cover are abbreviated NNsap, and NNcov respectively in this table. NNseed is the density of non-native seedlings and PARA is the perimeter-area ratio of a forest patch. For remaining variable definitions see Tables 3.3 and 3.5. Predictors variables were standardized to aid model convergence.

Model Response	Fixed Effect Predictor(s)	Coefficient	t	p	Satterthwaite's df	cAIC	Δ cAIC
Overall Herbaceous-layer Diversity	Forest	0.194	3.88	< 0.001	64.84	74.12	11.32
	Area	0.132	2.53	0.014	64.25	82.42	19.62
	Shape	0.120	2.168	0.034	65.10	83.88	21.08
	PARA	-0.164	-3.33	0.001	63.82	78.56	15.76
	PTB	-0.135	-2.60	0.012	64.60	81.18	18.38
	NNseed	-0.178	-3.45	< 0.001	66.61	79.23	16.43
	NNsap	-0.158	-2.96	0.004	66.96	81.46	18.66
	NNcov	-0.145	-2.81	0.006	65.80	81.48	18.68
	NNseed:PARA	-0.103	-2.48	0.016	62.25	66.7	3.9
	NNsap:PARA	-0.120	-2.36	0.022	61.91	69.81	7.01
	NNcov:Area	0.272	2.66	0.010	61.40	72.56	9.76
	NNsap:Forest	0.083	1.81	0.076	60.92	62.8	0
Native Herbaceous-layer Diversity	Forest	0.165	3.42	0.001	65.32	69.29	0.81
	Forage	0.118	2.31	0.024	64.73	75.27	6.79
	PARA	-0.128	-2.67	0.009	63.79	74.39	5.91
	PTB	-0.104	-2.05	0.045	64.40	77.90	9.42
	Forest:NNcov	0.120	2.13	0.037	61.59	68.48	0
	Urban 1	-0.201	-3.94	0.051	2.17	81.55	13.07
	Urban 4	-0.094	-1.69	0.097	64.71	80.70	12.22

Table 3.8. Mixed model results for sapling-layer diversity of forest patches in central Indiana, 2019 – 2020.

Fixed effects, coefficient estimates, t-values, p-values, Satterthwaite's degrees of freedom (df), corrected Akaike's Information Criterion (cAIC), and difference in cAIC from the best model (Δ cAIC) for mixed models predicting overall sapling-layer diversity and native sapling-layer diversity in forest patches in central Indiana. Each model included cluster (spatial grouping variable) as a random intercept. For variable descriptions see Tables 3.3, 3.5 and 3.7. All predictor variables were standardized to aid model convergence. Significant p-values ($p < 0.05$) are bolded.

Model Response	Fixed Effect Predictor(s)	Coefficient	t	p	Satterthwaite's df	cAIC	Δ cAIC
Overall Sapling-layer Diversity	Urban 3	-0.169	-2.153	0.042	22.49	110.89	2.52
	Forest	0.121	1.851	0.069	63.84	108.59	0.22
	PARA	-0.116	-1.813	0.075	61.34	109.78	1.41
	NNsap	-0.133	-1.99	0.0504	63.36	111.25	2.88
	NNsap + Forest	-0.138, 0.126	-2.088, 1.951	0.041 , 0.055	64.0, 63.18	108.37	0
	NNsap + PARA	-0.121, -0.105	-1.834, -1.648	0.071, 0.105	62.59, 60.95	110.26	1.89
Native Sapling-layer Diversity	Forest	0.153	2.154	0.035	64.1	120.96	0
	Urban 3	-0.178	-2.023	0.051	35.1	122.05	1.09
	Area	0.134	1.892	0.063	63.05	122.95	1.99

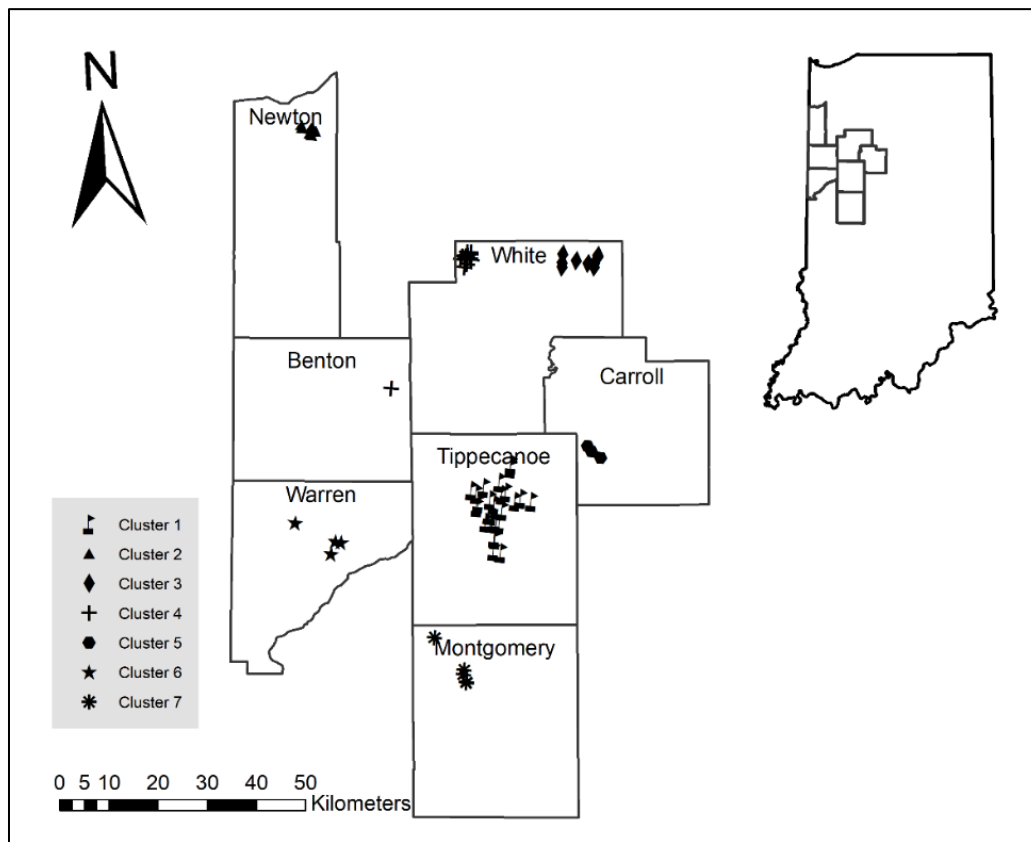


Figure 3.1 Map of forest patches grouped by cluster in central Indiana, 2019 – 2020.

Map of forest patches grouped into clusters for analysis of vegetation diversity in west-central Indiana. Each symbol represents a forest patch.

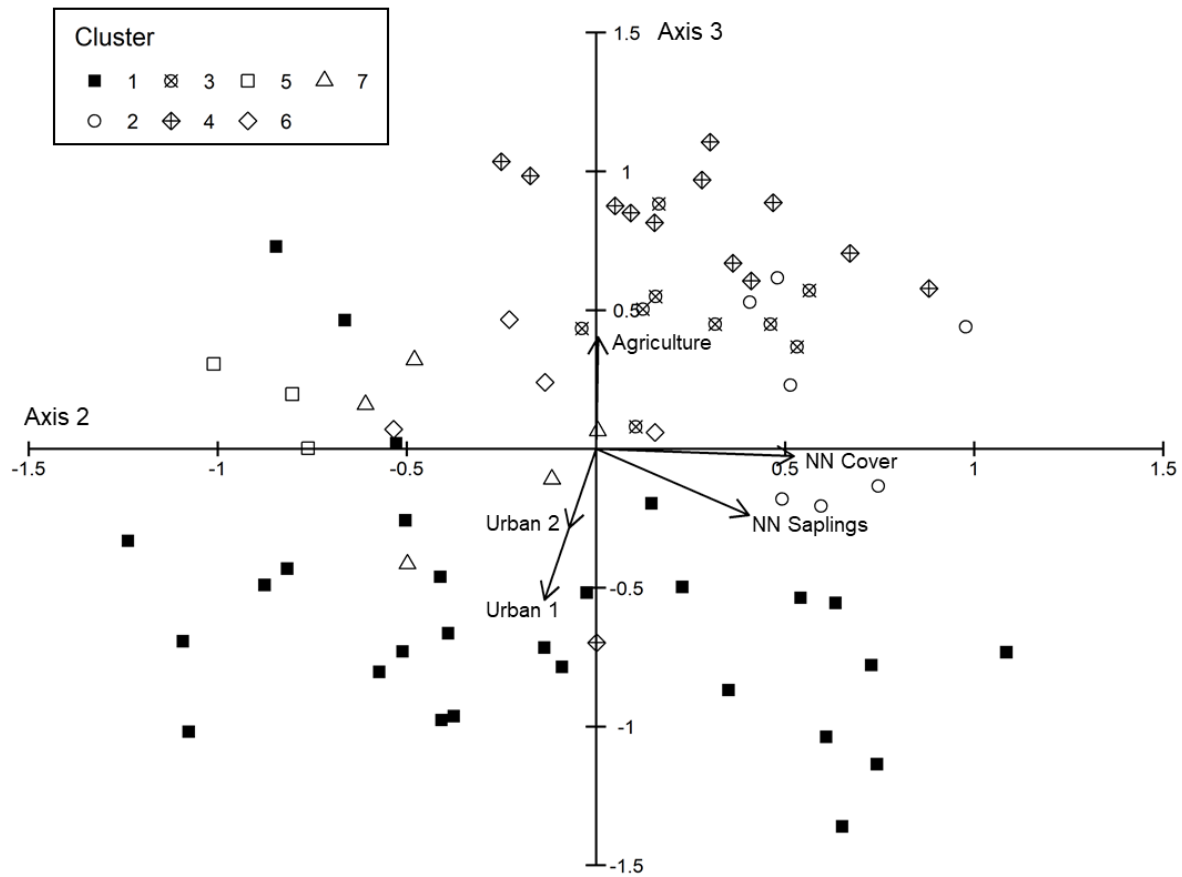


Figure 3.2 NMS ordination of forest patch herbaceous-layer composition in central Indiana, 2019 – 2020.

Non-metric multidimensional scaling ordination of herbaceous-layer composition of 69 central-Indiana forest patches in urban (cluster 1) and rural (clusters 2-7) landscapes on axis 2 ($r^2 = 0.22$) and 3 ($r^2 = 0.33$). Dominant environmental variables are displayed as vectors and include agricultural land cover, urban 1 land cover, urban 2 land cover, non-native cover (NN Cover) and non-native sapling density (NN Saplings). For land cover definitions see Table 3.3. The length of the vector is proportional to the strength of the correlation.

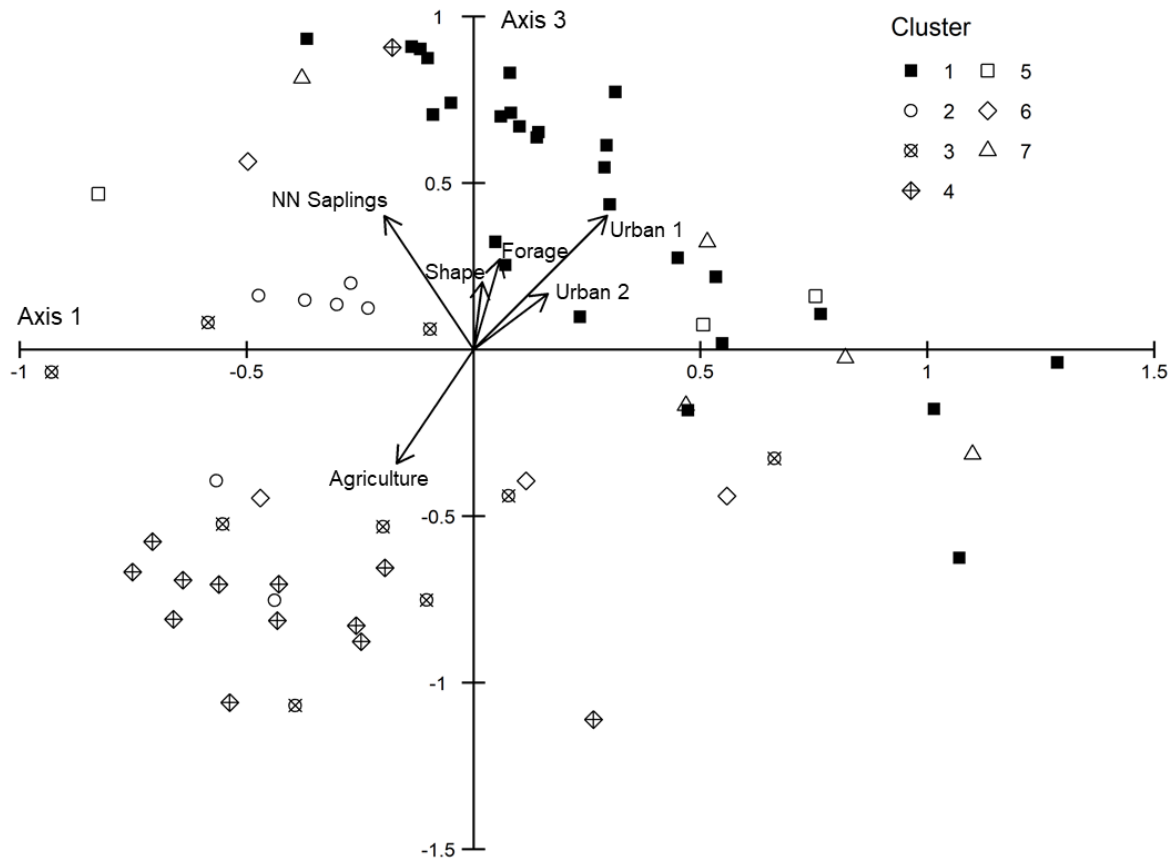


Figure 3.3 NMS ordination of forest patch sapling-layer composition in central Indiana, 2019 – 2020.

Non-metric multidimensional scaling ordination of sapling-layer composition in 68 central-Indiana forest patches in urban (cluster 1) and rural (clusters 2-7) landscapes on axis 1 ($r^2 = 0.18$) and 3 ($r^2 = 0.28$). Dominant environmental variables are displayed as vectors and include agricultural land cover, urban 1 land cover, urban 2 land cover, forest patch shape index, and non-native sapling density (NN Saplings). For land cover variable definitions see Table 3.3. The length of the vector is proportional to the strength of the correlation.

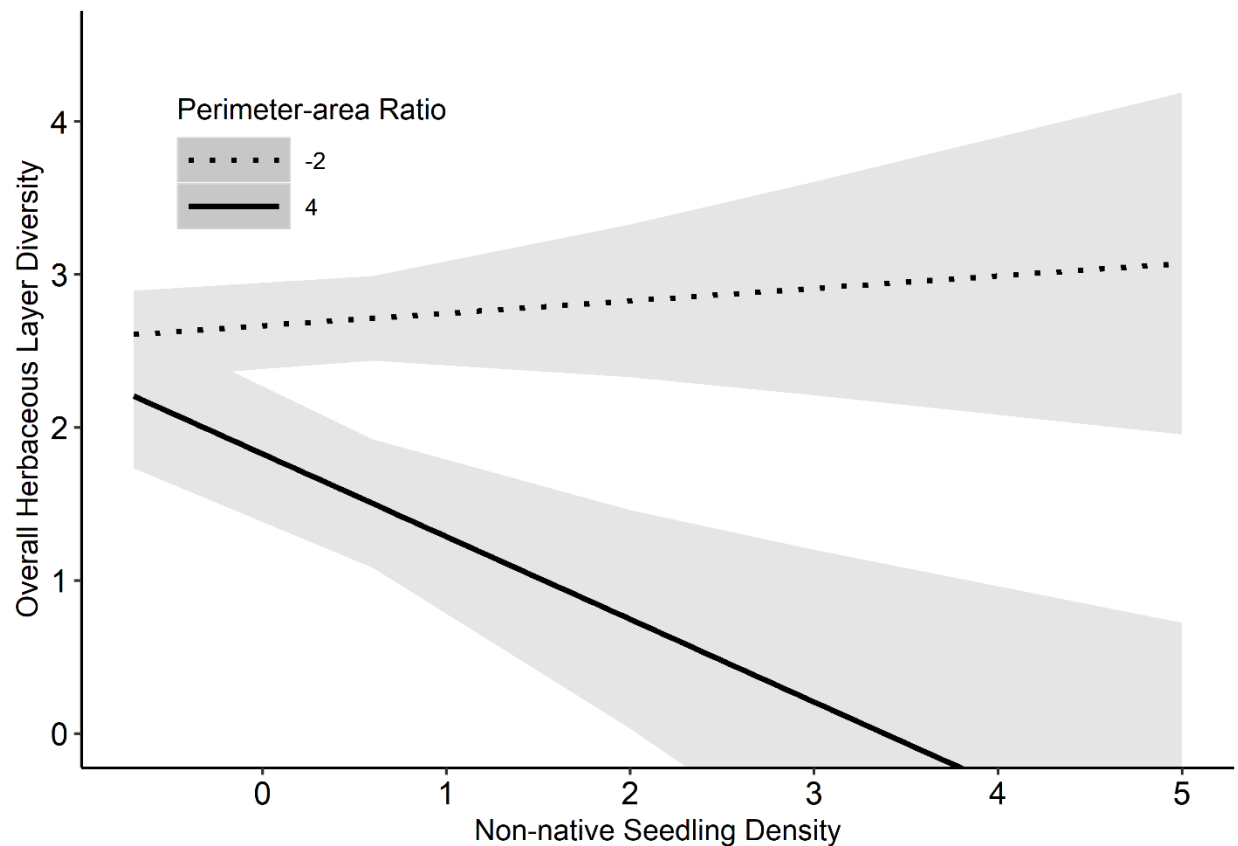


Figure 3.4 Interaction between non-native seedling density and perimeter-area ratio on overall herbaceous-layer diversity in forest patches in central Indiana, 2019 – 2020.

The interactive effects of non-native seedling density and perimeter-area ratio of central-Indiana forest patches on overall herbaceous-layer diversity (Shannon's Diversity Index). When perimeter-area ratio was low, non-native seedlings did not decrease (or increase) overall diversity. However, when perimeter-area ratio was high, non-native seedlings were negatively related to reduced herbaceous-layer diversity. Predictor variables are standardized values. Gray shading around each line represents 95% confidence bands.

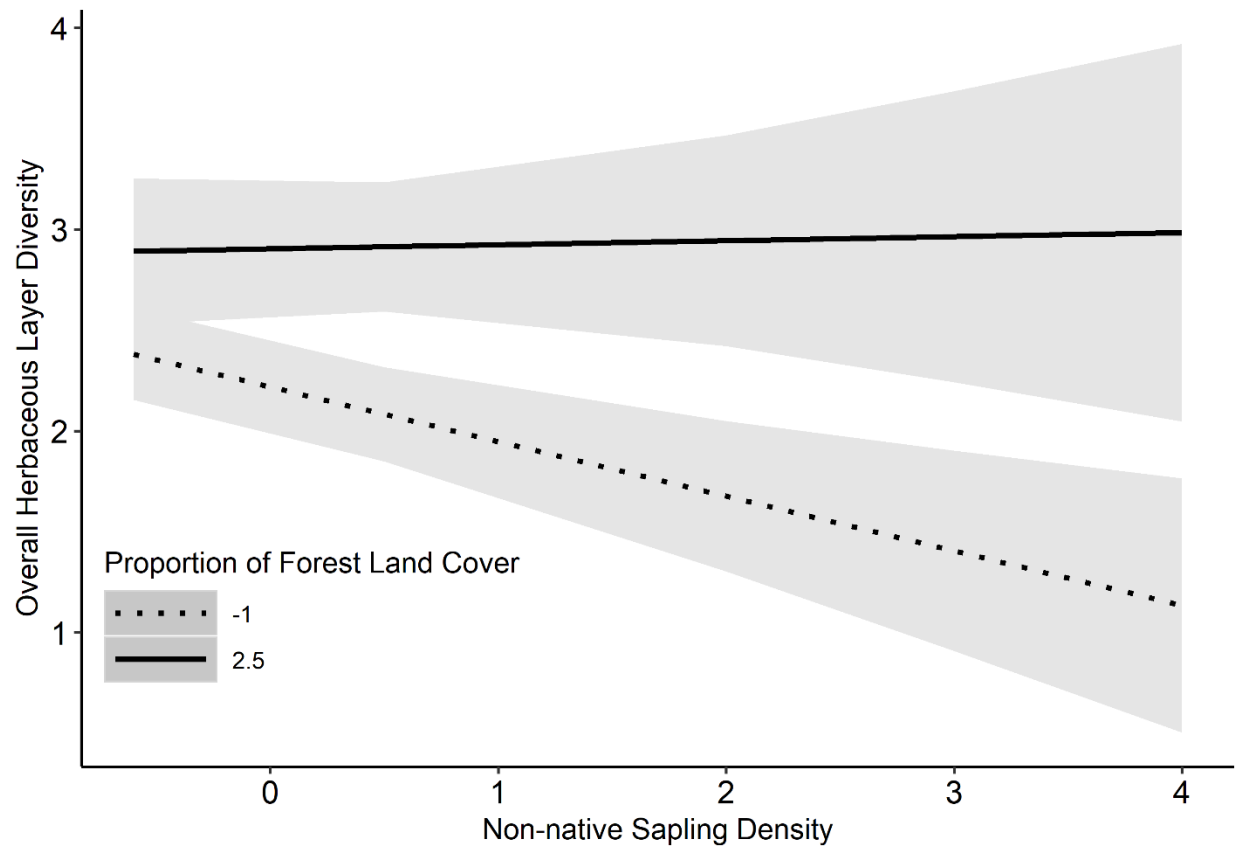


Figure 3.5 Interaction between non-native sapling density and forest land cover on overall herbaceous-layer diversity in forest patches in central Indiana, 2019 – 2020.

Marginally significant ($p = 0.076$) interactive relationships of non-native sapling density and the proportion of forest land cover in 500 m buffers around central-Indiana forest patches on overall herbaceous-layer diversity (Shannon's Diversity Index). When the proportion of forest land cover was low, an increase in non-native sapling density was related to an increase in overall herbaceous-layer diversity. When the proportion of forest was high, there was no clear relationship between non-native sapling density and overall herbaceous-layer diversity. Predictor variables are standardized values and gray shading represents 95% confidence bands.

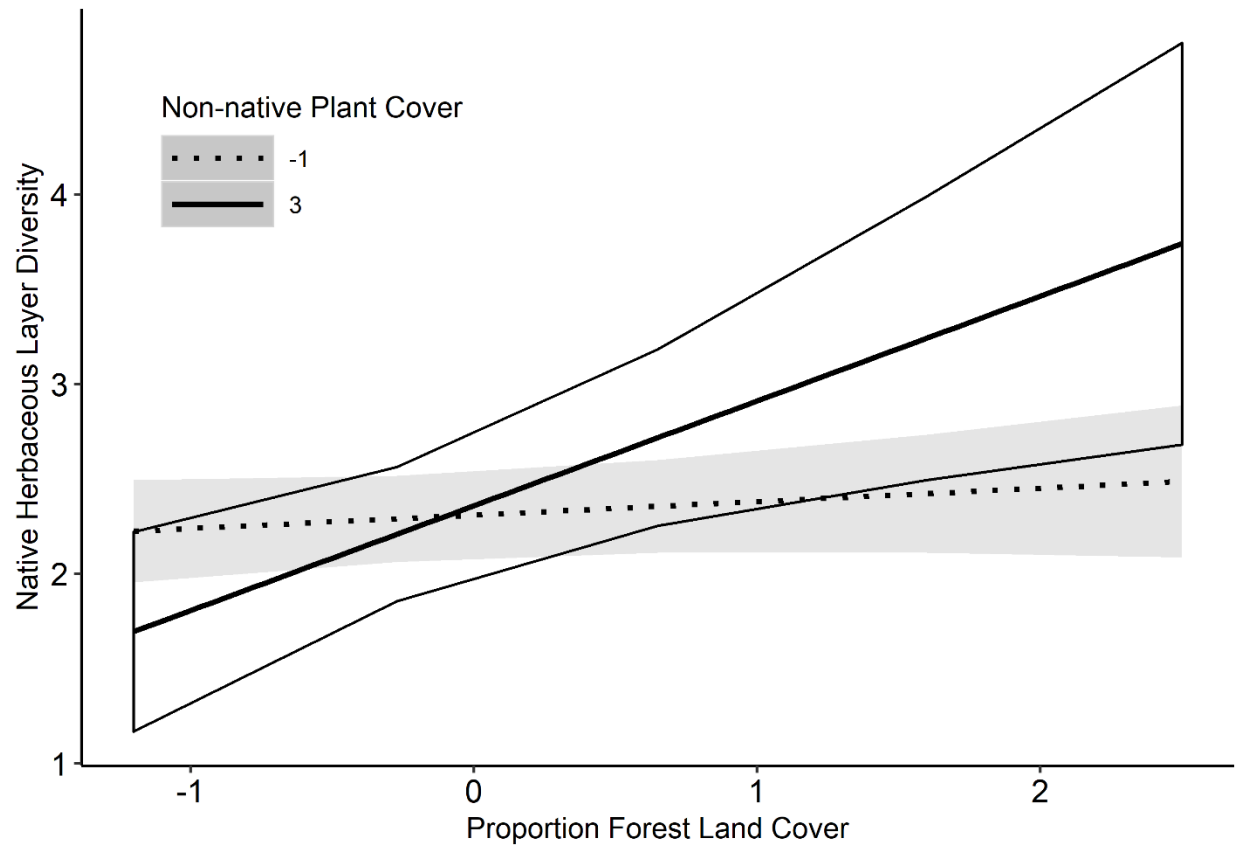


Figure 3.6 Interaction between non-native plant cover and forest land cover on native herbaceous-layer diversity in forest patches in central Indiana, 2019 – 2020.

Interactive effects of the proportion of forest land cover in a 500 m buffer around central-Indiana forest patches and non-native plant cover on native herbaceous-layer diversity (Shannon's Diversity Index). When non-native plant cover was low, we did not observe an impact of forest land cover on native herbaceous-layer diversity. However, when non-native plant cover was high the proportion of forest increased native herbaceous-layer diversity. Predictor variables are standardized values. Gray shading for low non-native cover and solid lines for high non-native cover represents 95% confidence bands.

CHAPTER 4. SUMMARY

4.1 Summary

This thesis demonstrated that landscape context, impacts of white-tailed deer, and non-native plants are all important processes to consider when managing forest plant species diversity in the herbaceous and sapling layers. White-tailed deer herbivory preferences shifted among certain species, notably Amur honeysuckle, in urban versus rural forest patches. However, Wright et al. (2019) did not find an impact of land cover on deer browse of Amur honeysuckle, warranting additional research on this topic. We also observed differences in the composition of browse available for deer in rural versus urban forest patches, emphasizing the importance of landscape context when assessing deer herbivory and plant browse availability.

Landscape context was also important regarding plant species diversity. We found that the increased forest land cover on the landscape around forest patches not only increased diversity but also minimized reductions in diversity from non-native plants. We did not identify any interactions of deer impacts with either landscape context or non-native plants, but we did observe decreased herbaceous-layer diversity where the intensity of deer browsing was greater. Therefore, future research is recommended, especially in urban areas with high deer abundances and greater browse impacts.

Another notable result from this work was the differences in plant community composition between urban and rural forest patches in the same geographic region. This supports results from other studies (Pennington et al., 2010; Templeton et al., 2019) and indicates that as urbanization continues to increase in the United States, forest plant communities may shift in composition. Based on our findings, we recommend, if possible, preserving forest patches that have other forest landcover nearby, which was associated with increased diversity. Additionally, isolated patches may be more likely to suffer decreased plant diversity and countering this trend would require a greater cost, with less return, for managers seeking to allocate finite resources.

4.2 Literature Cited

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