CHANGES TO SPIDER COMMUNITY ECOLOGY MEDIATED BY

ALTERED FOREST UNDERSTORY VEGETATION

by

Andrew P. Landsman

A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology and Wildlife Ecology

Spring 2016

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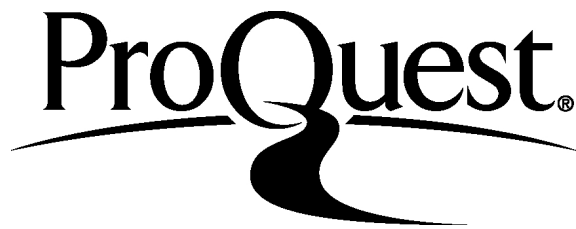
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My loving wife and daughter, whose support and patience helped me immensely throughout this endeavor.

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ABSTRACT

Despite the broad implications and the long history of research on the impacts of dense ungulate populations and invasive plant species on native vegetation, work involving indirect effects to the spider community is explicitly lacking. Forest spiders are dependent upon the abundance of palatable insect prey and habitat structure, both of which can be negatively affected by herbivory and invasive vegetation. To examine the indirect interactions between spiders and factors that may influence forest vegetation, I investigated comprehensive changes to spider communities resulting from altered habitat structure and prey availability. I sampled spider communities, insect prey, and vegetation in central Maryland within paired exclusion plots to prevent white-tailed deer herbivory. I used generalized linear models to analyze spider richness and abundance, and several multivariate models to assess overall effects to the spider community. I also measured stable isotopic ratios of an orb-weaving species (Tetragnathidae: *Leucauge venusta*) to examine potential physiological stress in altered habitats. Greater prey density increased the abundance and richness of all spider functional groups, and nearly all spider families. Increased habitat structure from deer exclusion influenced some spider families with responses discordant within each functional group. More complex habitat structure also decreased overall species richness. Habitat structural complexity and insect prey abundance both influenced the composition of the spider community. Isotopic nitrogen enrichment decreased in spatially complex habitats, suggesting physiological stress and/or altered diet in structurally homogeneous forests. In habitats dominated

by an invasive C_4 plant, spider isotopic carbon signatures closely resembled those of C_3 plants, indicating avoidance of the exotic species by the herbivorous and saprophagous insect community. This work identifies the importance of both habitat structure and insect prey in defining the composition, abundance, and richness of forest spider communities. A history of heavy browsing pressure in the area has resulted in a local spider fauna consisting largely of species that are able to thrive in low-growing vegetation and an open forest understory. Such changes to vegetative structure resulting from dense deer populations and invasive plants have the potential to affect these important primary predators as well as araneophagic birds and the overall nutritional dynamics of the forest food web. Future work should focus on a finer scale and include further examination of changes in insect genera or families, potential changes in taxonomic composition of individual spider diet using stable isotope mixing models, and additional components of spider body condition such as individual biomass and fecundity.

Chapter 1

INDIRECT INTERACTIONS BETWEEN FOREST SPIDERS, WHITE-TAILED DEER, AND INVASIVE PLANTS

Throughout the eastern United States, forested land has generally decreased over the past several decades, in great part due to urban and suburban development (Drummond & Loveland 2010). With an overall reduction in forest cover, the habitat quality of remaining forest patches is often strongly influenced by pressures typically associated with fragmented habitats (Hunter, Jr. & Gibbs 2007). In many regions of the mid-Atlantic U.S., two prevalent factors that influence the ecology of these forest patches are invasive, exotic plant species and large herbivores, particularly white-tailed deer (*Odocoileus virginianus*). The negative ecological impacts from both invasive plant species and white-tailed deer herbivory are relatively well studied, though significant gaps in the scientific literature still exist.

White-tailed Deer Impacts to Vegetation and Vertebrate Wildlife

Although typical forests of the eastern U.S. can sustainably support white-tailed deer populations with the regeneration of palatable, above-ground plant biomass and the production of mast, the negative impacts of deer herbivory become pervasive when populations exceed the capacity of the forest to sustain them. Despite nearing extirpation in the late 19th and early 20th centuries, white-tailed deer populations since rebounded, becoming overabundant throughout much of the mid-Atlantic U.S. (McShea et al. 1997; Côté et al. 2004). Responding positively to hunting restrictions, habitat restoration, and the lack of natural predators, deer populations also benefited

from agriculture and suburban development, which increased favorable edge habitat as well as available forage (Shrauder 1984). The high level of urban and suburban development and forest fragmentation in the mid-Atlantic has allowed deer populations to expand dramatically and become problematic and difficult to manage in forests protected and managed by the U.S. National Park Service and other land management agencies (Porter et al. 1994; Porter & Underwood 1999). Herbivory associated with such large deer populations decreases the ability of land managers to protect and conserve native floral and faunal communities, including the successful regeneration of native tree seedlings (National Park Service 2006; Stewart et al. 2007; Hatfield & Krafft 2009; McShea & Bourg 2009; Abrams & Johnson 2012; Landsman 2013).

The wide-ranging influence that dense white-tailed deer populations may have in forest communities started to become apparent in the late 20th century, with much research focused on impacts to native understory vegetation (Côté et al. 2004; Habeck & Schultz 2015). Causing changes in the herbaceous vegetative community, seedling and sapling survival, and the animal groups that depend on them, white-tailed deer at high densities are considered keystone species that may cause cascading and indirect influences to an entire natural system (Waller & Alverson 1997; Sinclair et al. 2006; Royo et al. 2010). Preferential browsing of palatable native plants decreases the density of many seedling species (Russel et al. 2001; Horsley et al. 2003) while allowing for increasing densities of unpalatable species, often those that may be invasive or exotic (Duguay & Farfaras 2011). In addition, a decreased density of native seedlings lowers recruitment rates to below levels necessary for sufficient forest regeneration (Tilghman 1989). Browsing associated with dense deer populations may

also decrease the abundance, size, and ability of palatable herbaceous plants and species of management concern to successfully flower and germinate (Knight 2003; Furedi & McGraw 2004). Thus, long-term overabundant deer populations can alter the entire vegetative community, creating a new dominant vegetation type that may be more susceptible to future disturbances and pests (Stromayer & Warren 1997; Rooney 2001; Eschtruth & Battles 2008). Alterations to understory and forest floor vegetative structure and composition from herbivory may also subsequently affect preferred habitat for vertebrate species such as forest-obligate birds (deCalesta 1994; McShea & Rappole 2000; Tymkiw et al. 2013) and small mammals (Byman 2011).

Invasive Plant Impacts to Vegetation and Vertebrate Wildlife

In addition to herbivory from white-tailed deer, mid-Atlantic forests also often experience a great number of non-native plant species invasions, particularly in urban and suburban regions. Though it has been well documented that most species introduced into novel geographic regions do not become invasive, increases in global trade and economic activity have resulted in a concurrent increase in the introduction of new species to areas from which they have not been previously established (Mack et al. 2000). Such increases in the human-mediated movement of species, whether deliberate or unintentional, has resulted in a more homogenized flora and fauna across the world and has added over 3,400 naturalized plant species to documented U.S. flora (Mack et al. 2000; Qian & Ricklefs 2006). The abundance and species richness of exotic and invasive plant species are correlated with human populations and urban development, and as such, the fragmented forests surrounding population centers of the mid-Atlantic U.S. are extremely susceptible to plant invasion (Luken & Thieret 1996; Qian & Ricklefs 2006). Land managers and conservation biologists are

particularly concerned about invasive vegetative species in forested habitats, as known invasive species have the capacity to cause drastic changes to ecological systems, including the evolutionary trajectory of native biota (Mack et al. 2000; Mooney & Cleland 2001; Simberloff 2011). As the scientific literature likely underestimates the extent and prevalence of ecosystem impacts from invasive species, it remains an important endeavor to fully understand the resultant changes to ecosystem processes and components after invasion (Simberloff 2011; Davidson & Hewitt 2014).

Although effect size is variable across invasive taxa studied, the wide-ranging and comprehensive negative impacts from invasive plant species can be seen throughout the literature (Mack et al. 2000; Simberloff 2011). With exotic species invasion, resultant native plant communities become modified, with decreased species richness, diversity, and fitness of individual plant species (Vilá et al. 2011). The most conspicuous impact of invasive forest plant species is competition with native plants for space, nutrients, light, and water, which typically reduces species richness, abundance, recruitment, and growth rates for forest plants (Collier et al. 2002; Marshall et al. 2009). The unpalatability of many invasive species also increases this competitive advantage, as herbivores may preferentially forage on palatable native plants (Trisel 1997). The showy and attractive inflorescences of many species, for which they are prized in ornamental landscaping practices, may also alter plant-pollinator relationships, reducing successful insect pollination, flower visitation, and seed production (Brown et al. 2002; McKinney & Goodell 2011). Certain invasive plant species have also been shown to alter the abiotic environment, either through alterations in soil nutrient composition and cycling or via allelopathic exudates (Evans

et al. 2001; Prati & Bossdorf 2003; McGrath & Binkley 2009; deMeester & Richter 2010).

Though some argue for the utility of specific invasive plants in providing food and habitat for wildlife, many studies have found a reduction in both abundance and overall fitness for animal species in invaded habitats (Vilá et al. 2011). For shelter and oviposition, nesting birds may often require dense vegetative structure, a characteristic common to many species of invasive and non-native shrubs. The relationship between nesting birds, invasive plant substrates, and nestling success, however, may be more complicated and influenced by a combination of factors, including prevalence of the invasive cover, proximity to habitat edge, food availability, and the species of bird in question (Borgmann & Rodewald 2004; Tallamy 2004; Schlossberg & King 2009; McChesney & Anderson 2015; Meyer et al. 2015).

Effects to Cursorial Arthropods

Although the impacts of overabundant deer populations and invasive, exotic plant species on vegetative communities are relatively well studied, the relationship between deer browsing, invasive plant cover and cursorial arthropod communities are less clear. In deciduous and coniferous forests, vegetative composition and structural changes from deer browsing have been documented to cause either adverse or positive effects on arthropods, depending on trophic guild and height of vegetative habitat. While forest floor arthropod habitat is not directly affected, several studies have illustrated the complexity of indirect interactions that browsing herbivores may have on the ground-dwelling arthropod community. Due to their dependence on detrital food webs and the contributing influence of additional variables such as litter depth and complexity, ground-dwelling predatory communities may not be as affected by an

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overabundance of large herbivores (Shimazaki & Miyashita 2005). Duguay & Farfaras (2011) found a negative correlation between cervid browsing and insect biomass in leaf litter; however, results from other studies often show wide variations in the species richness and abundance of cursorial insects when comparing browsed and unbrowsed habitats (Suominen et al. 1999; Suominen et al. 2003; Allombert et al. 2005). Compositional changes in the ground-dwelling spider community have resulted from sheep and elephant herbivory (Bonte et al. 2000; Haddad et al. 2010), while reduced vegetative cover from browsing of sika deer (*Cervus nippon*) has shown to increase suitable habitat for linyphiid and amaurobiid spiders that exploit spatial openings in the litter for web placement (Takada et al. 2008). Due to the importance of microclimate (Suominen et al. 1999; Duguay & Farfaras 2011) and ground habitat structure and complexity (Bultman & Uetz 1982, 1984; Gibson et al. 1992; Langellotto & Denno 2004) in shaping ground-dwelling arthropod communities, herbivory likely influences these invertebrates indirectly through the manipulation of these important habitat components.

The correlation between invasive plant cover and ground-dwelling arthropod communities is also unclear as results vary depending on taxa studied and methodology (Litt et al. 2014). In a recent meta-analysis, Litt et al. (2014) found that, despite variability, most non-predatory arthropods decrease in richness and abundance in invaded habitats with the exception of detritivorous species, which often benefit from increased plant litter. Despite often significant increases in ground habitat structural complexity resulting from plant invasion, spider communities often respond negatively to invasive plants, possibly due to reduced capacity for web-building near the ground. Ground covers that may form dense mats in non-native regions such as

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Japanese stiltgrass (*Microstegium vimineum*) and common periwinkle (*Vinca minor*) in the Eastern United States and non-native European grasses in California, may reduce species diversity of spiders and other ground-dwelling arthropods (Bultman & DeWitt 2008; McGrath & Binkley 2009; Wolkovitch et al. 2009). In contrast, spiders that hunt on the ground and do not rely on webs for prey capture may respond positively to invasive plant cover, ultimately changing this predatory community in an invaded habitat (Bultman & DeWitt 2008; DeVore & Maerz 2014).

Factors Influencing Forest Spider Ecology

As an almost exclusively carnivorous group, interactions between forest spider communities and both deer herbivory and invasive vegetation are intuitively indirect, mediated by their insect prey and the structure of vegetation in the forest understory. Web-building spiders are highly dependent upon the vegetative architecture to which they attach their webs, while many active hunting spiders that do not utilize webs for prey capture still require vegetative structure upon which to hunt for prey (Uetz 1991; Foelix 2011). Increased structural heterogeneity of vegetation has shown to increase the diversity and abundance of web-building, hunting, and ground spiders in grasslands, fields dominated by shrubs (Hatley & MacMahon 1980; Gibson et al. 1992; McNett & Rypstra 2010; Malumbres-Olarte et al. 2013), and agro-ecosystems (Balfour & Rypstra 1998; Rypstra et al. 1999; Schmidt & Rypstra 2010). Populations of potential spider prey also respond similarly, with the species richness and abundance of phytophagous, predatory, and parasitoid insects decreasing with herbivory that reduces vegetative structural complexity (Kruess & Tscharntke 2002; Langellotto & Denno 2004). Much of the recent work involving spider communities and forest vegetative structure has occurred in Japanese evergreen forests, with results

relatively concordant among studies: forest understory structure increases spider species richness, density, and abundance (Miyashita et al. 2004; Miyashita & Takada 2007; Takada et al. 2008). Greater vegetative structure is also influential to spider communities when considering the architecture of an individual plant or branch, resulting in an increase of spider diversity, density, and abundance (de Souza 2005; de Aquino Ribas et al. 2011; Marín et al. 2015).

In addition to structural diversity in the vegetation, the availability and abundance of suitable insect prey is another critical component for spider habitat selection and retention, as well as diversity, richness, and abundance (Hodge 1987a; Wise 1993). Both the density and abundance of insect prey are correlated with spider density, as well as individual biomass, age, and fecundity (Wise 1979; Fritz & Morse 1985; Vollrath 1987; Adams 2000; Leborgne & Pasquet 2005; Bucher & Entling 2011). In a New Jersey salt marsh invaded by common reed (*Phragmites australis*), Gratton & Denno (2006) used stable carbon and nitrogen isotopes to show interruptions to natural trophic webs. The authors discovered that with plant invasion, spiders shifted diet to feed on mostly detrital and algal feeders and predators, as opposed to mostly herbivorous insects in native smooth cordgrass (*Spartina alterniflora*) salt marsh habitats. As the individual success of a spider is closely related to its nutritional intake, any change in the available prey base may significantly reduce or increase the viability of a species' population.

Though considered passive predators, spiders, including those that build webs, capture and feed on specific prey items that satisfy their nutrient requirements and their capacity to subdue a potential prey item (Olive 1980; Toft 1999; Mayntz et al 2005; Hénaut et al. 2006; Wilder 2011). Non-native and invasive vegetation may alter

insect prey communities, potentially changing the abundance and diversity of taxa and subsequently affecting the nutritional dynamics of forest spider populations. Whether through incongruent evolutionary history, altered habitat structure, or displaced native plants necessary for food or oviposition, invasive plant species generally cause negative effects to various metrics of insect population health (Tallamy 2004; Langellotto & Denno 2004; Litt et al. 2014). In experimental plots, native plants supported higher biomass, abundance, and diversity of lepidopteran larvae and other insects than non-native plant species (Tallamy & Shropshire 2009; Ballard et al. 2013), even when compared species are congeners (Burghardt et al. 2010; Burghardt & Tallamy 2015). Consecutive studies within riparian forests of the southeastern United States showed correlations between invasive species removal and increased richness, diversity, and abundance of beetles, Lepidoptera, and bee populations (Ulyshen et al. 2010; Hanula & Horn 2011a, 2011b). Carvalheiro et al. (2010) also found a reduced abundance of specialist herbivore and parasitoid insects, particularly when invasive shrub cover exceeded 50%. Changes to the available prey community and subsequent nutritional intake may ultimately result in reduced biomass and fecundity of individual spiders, and a reduced diversity, density, and abundance of the spider community as a whole.

Potential Impacts to Forest Spiders Mediated by Habitat Structure and Prey Availability

In the suburban and agrarian landscapes surrounding the urban population centers of the eastern United States, white-tailed deer populations often reach unsustainable densities and the small, remaining forest fragments are subjected to both browsing and the oppressive propagule pressure from neighboring ornamental and

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invasive plants. Resultant forest habitats, albeit the last remaining fragments in a landscape otherwise inhospitable for forest taxa, have changed in plant species composition and abundance, understory physiognomy, and in their capacity to support native biota. Vegetative architectural complexity and the abundance of suitable prey are two critical components of forest spider communities, both of which are significantly altered by deer browse and invasive plants. In recent work in a managed, Japanese evergreen forest, Katagiri & Hijii (2015) studied the interconnected relationships between ungulate browsing, vegetation structure, prey abundance, and spider populations. Both prey abundance and vegetation structure were important predictors for spider abundance with overall results varying by spatial scale. Browsing sika deer improved structure on an individual plant by increasing lateral branching and abundance of twigs and leaves, which in turn increased both abundance of insects and spiders; however, when examined at the scale of the 9 m^2 plot, browsing decreased total number of individual plants, producing a net loss in both spider and insect prey abundance. Throughout the scientific literature, it is apparent that the relationship between spiders and these other factors are complex and intertwined.

Despite incongruities in the use of the term "trophic cascade" (Strong 1992), direct effects of white-tailed deer browse on forest vegetation conclusively have secondary, indirect impacts on herbivores, with the strong potential for tertiary impacts to primary predators. Because of their reliance on vegetative structure for web attachment, spider communities may be primarily affected by changes to vegetation, resulting in further impacts to insects: the addition of artificial structure in an evergreen forest with high density populations of sika deer allowed web-building spider populations in the low forest understory to increase and subsequently reduce the

abundance of insect populations emerging from the detrital layer (Miyashita & Takada 2007). Similarly, invasive plant species that outcompete and displace native vegetation also have the capacity to indirectly alter the herbivorous insect community and their predators and parasitoids. Populations of *Dictyna* species in a grassland invaded by spotted knapweed (*Centaurea maculosa*) contained over 40 times more individuals than in the native habitat, maintained larger webs, included a greater proportion of fecund females, and were able to capture twice the abundance of insect prey per spider, likely altering overall insect population size (Pearson 2009). Recent evidence for the strength of indirect interaction pathways up the trophic levels was reported by DeVore & Maerz (2014) in forests of the southeastern U.S.: forest floor habitat invaded by Japanese stiltgrass reduced insect prey but provided favorable habitat and microclimate for American toads (*Anaxyrus americanus*). However, overall toad survival decreased, as predatory wolf spider (*Hogna* spp.) populations also increased in abundance and fed on the metamorphosed toads.

Significant changes to the community structure and nutrient dynamics of this predatory group may have substantial ecological and trophic implications on any natural system. Spider communities may exert strong influences on phytophagous insect populations across many habitats, including forests, grasslands, and agroecosystems (Moulder & Reichle 1972; Nyffeler and Benz 1989; Marc et al. 1999; Miyashita & Takada 2007). As a group, spiders also play a critical, intermediary role as a link between various food webs: riparian web-building spiders capture great quantities of emerging aquatic insects while being subject to predation from forest birds (Waters et al. 2011); spiders in the low understory transfer energy out of detrital food webs into higher trophic levels (Miyashita & Takada 2007); and forest spiders

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preying on flying invertebrates may provide significant nutritional contributions to the diet of vertebrate predators such as araneophagic birds and reptiles (Spiller & Schoener 1988; Philpott et al. 2004; Gunnarsson 1996, 2007; Waters et al. 2011). The loss of structural complexity in understory vegetation and concomitant alterations to insect prey availability caused by dense herbivore populations and invasive plant species may ultimately impact spider ecology, individual spider predation and reproductive success, and trophic interactions in the forest understory.

I aim to better understand the dynamic relationships between habitat structure, insect prey and spiders and how indirect impacts from herbivory and invasive plants, mediated through changes in vegetation, ultimately alter spider communities. In Chapter 2, I will analyze the structural complexity and composition of forest vegetation and how the influence of dense white-tailed deer populations and invasive plant species can affect the physiognomy of deciduous forests of the eastern United States. I will also examine changes to the herbivorous and predatory insects that directly result from alterations in vegetative structure and taxonomic composition. Finally, I will also illustrate the relationships between spider communities and the habitat structure and prey upon which they depend. Examining the system beyond the community or taxonomic family level, in Chapter 3 I will use a representative spider species to investigate physiological and nutritional stress resulting from altered habitat structure. This study will better elucidate the depth and complexity of the indirect interactions between forest invertebrate communities and ecosystem-engineering factors such as ungulate herbivory and introduced plant species.

Chapter 2

ECOSYSTEM-ENGINEERING EFFECTS FROM HERBIVORES AND INVASIVE PLANTS ALTER SPIDER COMMUNITIES

Introduction

The abundance of palatable insect prey and habitat structural complexity are likely two of the most significant predictors of spider abundance, density, and habitat selection (Langellotto & Denno 2004; Rypstra 1983). Web-building spiders are highly dependent upon the vegetative architecture to which they attach their webs, while many active hunting spiders that do not utilize webs for prey capture still require vegetative structure upon which to hunt for prey (Uetz 1991; Foelix 2011). Structurally complex vegetation may also support increased densities of herbivorous insect prey if the increased structure results from greater palatable plant tissue or inflorescence density (de Aquino Ribas et al. 2011). Such spatially complex habitats create a more suitable landscape upon which spiders may track down potential prey (Huffaker 1958; Huffaker et al. 1963) and can serve as effective refugia from araneophagic and intraguild predators (Langellotto & Denno 2006; Schmidt & Rypstra 2010). Non-predatory insects are the main source of energy and nutrients for most spiders (Foelix 2011); therefore, the availability and abundance of suitable insect prey is also an essential component of preferable habitat for spiders.

Across geographic regions and habitat types, increased structural heterogeneity and complexity of vegetation has been shown to concomitantly increase the diversity and abundance of spiders. Web-building, hunting, and cursorial spiders in grasslands,

old fields, and pastures all respond positively to increased plant structure (Gibson et al. 1992; McNett & Rypstra 2010; Malumbres-Olarte et al. 2013). Similarly, experimental work in agro-ecosystems has shown increased densities of web-building and ground spiders in more architecturally complex vegetation (Balfour & Rypstra 1998; Schmidt & Rypstra 2010). Much of the recent work involving understory spider communities and vegetative structure have occurred in Japanese evergreen forests, with results relatively concordant among studies: forest understory structure increases spider species richness, density, and abundance (Miyashita et al. 2004; Miyashita & Takada 2007; Takada et al. 2008).

In addition to structural diversity in the vegetation, the availability and abundance of suitable insect prey are strongly correlated with spider habitat selection and retention, as well as diversity, richness, and abundance of the community (Hodge 1987a; Wise 1993; Adams 2000). Increased densities of insect prey often support an increased density of spiders, as has been found in Japanese evergreen forests and plantations (Miyashita et al. 2004; Miyashita & Takada 2007; Takada et al. 2008). In addition, such elevated densities of palatable insect prey also result in improved individual spider health as measured by increased biomass, longevity, and fecundity (Wise 1979; Fritz & Moore 1985; Vollrath 1987; Leborgne & Pasquet 2005; Bucher & Entling 2011). As the individual success of a spider is closely related to its nutritional intake, any change in the available prey base may significantly reduce or increase the viability of a species' population.

Two common and widespread influences to both vegetative structural complexity and insect populations are invasive plants and browsing from large ungulates. Protected forest fragments in the eastern U.S., found interspersed among

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human population centers and suburban development, often experience extensive herbivory from dense white-tailed deer populations and may become inundated with invasive and exotic plant species. As an almost exclusively insectivorous group, interactions between forest spider communities and both deer herbivory and invasive vegetation are intuitively indirect, mediated by their insect prey and the structure of vegetation in the forest understory. White-tailed deer, through the browsing activity of dense populations, are able to alter vegetative structure of the forest understory (Waller & Alverson 1997). Such herbivory can decrease the complexity of plant architecture by reducing stem and individual plant abundance, but may also increase individual plant structure by stimulating lateral stem and leaf development (Katagiri & Hijii 2015). Extensive deer browsing may decrease the abundance and diversity of both predatory insects and their phytophagous insect prey in the understory (Allombert et al. 2005). Certain invasive plant species also have the capacity to alter vegetative structure, either through an increase in structure from shrubs and vines or a decrease in woody plant structure from non-native grasses. Latent, secondary impacts from such ecosystem-engineering species can ultimately alter multiple trophic levels and taxa (Jones et al. 1997; Crooks 2002). As such, these non-native, invasive plants may alter insect prey communities, potentially changing the abundance and diversity of available prey taxa. Whether through incongruent evolutionary history, altered habitat structure, or displaced native plants necessary for food or oviposition, invasive plant species generally cause negative effects to various metrics of insect population health (Tallamy 2004; Litt et al. 2014). Changes to the available prey community and subsequent nutritional intake may ultimately result in reduced biomass and fecundity

of individual spiders, and a reduced diversity, density, and abundance of the spider community as a whole.

Significant changes to the community structure and nutrient dynamics of this predatory group may have substantial ecological and trophic implications on any natural system. Spider communities may exert strong influences on phytophagous insect populations within many habitats, including forests, grasslands, and agroecosystems (Moulder & Reichle 1972; Nyffeler and Benz 1989; Marc et al. 1999; Miyashita & Takada 2007). As a group, spiders also play a critical, intermediary role as a link between various food webs. Riparian web-building spiders capture great quantities of emerging aquatic insects and comprise a large proportion of prey for some forest birds (Waters et al. 2011), while spiders in the low understory transfer energy out of detrital food webs into higher trophic levels (Miyashita & Takada 2007). Additionally, forest spiders preying on flying invertebrates provide significant nutritional contributions to the diet of vertebrate predators such as araneophagic birds and reptiles (Spiller & Schoener 1988; Philpott et al. 2004; Gunnarsson 2007). The loss of structural complexity in understory vegetation and concomitant alterations to insect prey availability caused by dense herbivore populations and invasive plant species may ultimately impact spider ecology, individual spider predation and reproductive success, and trophic interactions in the forest understory.

Despite near ubiquitous pressure from dense deer populations and invasive and exotic vegetation throughout forest patches in the eastern U.S., knowledge of the impacts to spider communities and invertebrate trophic webs is explicitly lacking. I studied the comprehensive effects of deer herbivory and invasive plant species on forest spider communities, mediated by their effects on understory vegetation.

Utilizing long-term deer exclusion plots in forest patches on National Park Service (NPS) lands in the mid-Atlantic U.S., I was able to compare forest spider abundance, species richness, community composition, and prey availability in habitats including and excluding deer herbivory. In addition, as ecosystem-engineering invasive plant species such as Japanese stiltgrass (*Microstegium vimineum*) and multiflora rose (*Rosa multiflora*) may respond negatively and positively to deer exclusion, respectively (pers. obs.), I was also able to evaluate the influence these species have on habitat structure and herbivorous insects. My objectives were to 1) analyze changes to the vertical structural complexity, species composition and nativity of vegetation caused by dense white-tailed deer populations and invasive plant species; 2) elucidate variations in insect prey availability that may result from changes in the plant community; and 3) illustrate indirect effects of deer herbivory and invasive vegetation to understory spider communities mediated through forest vegetation and subsequent changes in insect densities. This work has provided a better understanding of the depth and complexity of these indirect interactions, particularly as this system is poorly studied despite the ubiquity of ecological pressures from deer browse and invasive plants.

Methods

Study Area

As both dense white-tailed deer populations and invasive, exotic vegetation are common threats to public lands near human development, I studied their impacts to spider communities in 3 NPS units in Washington and Frederick Counties, Maryland: Antietam National Battlefield (ANTI), Chesapeake and Ohio Canal National

Historical Park (CHOH), and Monocacy National Battlefield (MONO) (Figures 1, 2). These parks were all located in a mosaicked landscape consisting of urban and suburban development, small forest fragments, and agricultural lands. Densities of white-tailed deer at the study sites ranged from $46 - 66$ deer/km^2, as estimated by annual density sampling (Distance 6.0; Thomas et al. 2010). Forest fragments in all parks are also heavily influenced by invasive, exotic vegetation including Japanese stiltgrass, multiflora rose, and garlic mustard (*Alliaria petiolata*). Dominant canopy trees included native maples (*Acer negundo* and *A. saccharinum*), white ash (*Fraxinus americana*), and hickory species (*Carya* spp.), with an understory that consisted of mostly northern spicebush (*Lindera benzoin*), paw-paw (*Asimina triloba*), and slippery elm (*Ulmus rubra*).

To monitor changes in vegetation resulting from white-tailed deer populations, paired exclusion plots were installed throughout forest fragments in the parks in 2003 (McShea 2004). Each plot was 25 m^2 with fenced plots consisting of 2.4 m tall woven wire cattle fencing with 10 x 10 cm mesh. All fenced plots were open from above and permitted entry and herbivory from birds and small mammals. Random numbers selected between 0 and 359 defined the azimuth for direction of open control plots, established a distance of 10 m from fenced plots. All paired plots were located at least 20 m from the forest edge. A total of 25 paired plots in 9 forest patches was sampled (Table 1).

Vegetation Sampling

I sampled vegetation in all paired plots in July of 2013. To measure abundance and diversity of vegetation, I established 4 subplots, each 1 x 1 m in size. Subplots were located 0.75 m from the plot edges along each of the 4 plot sides. Within

subplots, I identified all plants to species. I also measured the height of all seedlings, saplings, and shrubs up to 2.0 m. Trees taller than 2.0 m were identified but not measured.

I constructed a modified vegetative profile board to assess structural complexity of the understory vegetation (Nudds 1977). The profile board was composed of lightweight 0.64 cm plywood, 2.0 m in height and 35.0 cm wide. To facilitate analysis, I painted the profile board white with divisions separating each 0.5 m height class. To measure the vegetative structure within a plot, I placed the board in the center of each plot and used a 12-megapixel digital camera (Nikon COOLPIX S3100) to take a photograph of the board at a distance of 2.5 m and at a height of 1.0 m from the ground. Photographs were taken facing each edge of the plot for a total of 4 images per plot. I imported images as raster files in ArcGIS (ESRI 2011, ArcMap 10.2., California) and used maximum likelihood estimation to assign each pixel to one of 15 classes based on red, blue, and green pixel coloration. I then used binary reclassification to assign each of the defined classes to a value of 1 for live and dead vegetation and a value of 0 for all non-vegetation. To estimate structure in each of the height classes, I calculated the proportion of pixels obscured by vegetation to total number of pixels within each height class. I averaged the $0.5 - 2.0$ m structure readings for each plot for analyses (Figure 3).

Arthropod Sampling

To leverage the time period of greatest likelihood for capturing adult web-building spiders, I sampled both insect and spider communities in August of 2013 (Levi 2005). I collected arthropods using vacuum sampling methodology (Craftsman 25cc gasoline-powered blower/vacuum with 5-gallon paint strainer bag) for a period

of 10 minutes within each plot. I randomly sampled all vegetative surfaces throughout

the plot for herbivorous insects and hunting spiders, as well as interstitial spaces for

flying insects and web-building spiders (Gibson et al. 1992; Burghardt et al. 2010). I

sampled all structural surfaces, spatial openings, and visible webs between 0.5 and 2.0

m, as white-tailed deer generally browse at or below 2.0 m in height (Bressette et al.

2012). Larger spiders that were not effectively collected using a vacuum sampler

(mature *Neoscona* species and Pisauridae) were collected by hand. As ground spider

fauna have exhibited varied responses to deer browsing, this specific group was

avoided by sampling only above 0.5 m. After the 10-minute vacuuming period, the

paint strainer bag was tied off and specimens were immediately euthanized using ethyl

acetate. I placed the entire sample in 95% ethyl alcohol and removed larger leaves

and debris after rinsing adhered specimens into the sample (Carolina Biological

Supply Company). I identified spiders to the lowest taxonomic ranking possible

following generic taxonomy in Ubick et al. (2005) with recently published and widely

accepted taxonomic revisions (e.g., Yoshida 2008). Insects were identified to

phylogenetic order (Triplehorn & Johnson 2005) and I grouped spiders in each plot to

obtain family-level dry biomass. All specimens were dried for 24 h at 60 degrees C

(Lindberg/Blue M Gravity Oven) and weighed (Sartorius Research Scale).

Statistical Analyses

I used functional group designations modified from Cardoso et al. (2011) to

classify spiders into 5 groups based on prey capture method for analyses (Table 2).

The orb web weaving spider group included species that weave typical, round orb

webs while the space web weaving spiders included those spiders that weave modified

orbs and are typically more three-dimensional in shape. The active hunting group

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included spiders that hunt for prey on vegetative surfaces. Ground spiders included those cursorial species that hunt for prey on the forest floor, and the remaining group included spiders that are either kleptoparasitic or araneophagic, almost exclusively utilizing other spiders for prey. Collected only incidentally in understory vegetation, ground spiders were identified but excluded from all analyses. As the kleptoparasitic and araneophagic species represented such a small portion of overall spiders collected, I did not include them in multivariate analyses of the community. Insects were classified by order or by functional group when great differences existed in more refined phylogenetic groups: Hymenoptera was divided into ants and parasitic wasps, Hemiptera was divided into predatory families (Reduviidae and Nabidae) and phytophagous families, and Lepidoptera was divided into larvae and adults. For relevant analyses, I separately classified insects palatable to forest understory spiders (Diptera, non-predatory Hemiptera, Psocodea, and Thysanoptera) (Nentwig 1985; Nentwig 1987; Bardwell & Averill 1997; Hénaut et al. 2001). Coleoptera and Hymenoptera were excluded from this group as weevils were the dominant beetle group collected, and neither weevils nor parasitic wasps comprise a large portion of diet for small web-building spiders (Nentwig 1983; Uetz & Hartsock 1987; González et al. 2009).

I performed all statistical analyses in Program R 3.2.3 (R Core Team 2015). I used generalized linear models (GLM) with a negative binomial probability distribution in package 'MASS' for analyzing spider abundance in response to habitat structure and prey availability, and package 'car' to produce analysis of deviance tables (Venables & Ripley 2002; Fox & Weisberg 2011). I also used GLM with a Poisson probability distribution in package 'lme4' to model changes in spider species

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richness as well as abundance of kleptoparasitic and araneophagic species (Bates et al. 2015). I used linear mixed-effect models with package 'nlme' for analyses of vegetative response to deer exclusion and insect-vegetation relationships (Pinheiro et al. 2016). I visually assessed adherence to parametric testing assumptions using quantile-quantile plots, standardized residual plots, and by plotting residuals against predicted values. I used package 'vegan' for obtaining the Shannon-Weiner diversity index for woody vegetation, Jaccard dissimilarity index for vegetative communities, and the Bray-Curtis dissimilarity metric for spider communities (Faith et al. 1987; Oksanen et al. 2016). All figures were produced using 'ggplot2' (Wickham 2009). Diversity indices for spider communities were not calculated as too few adults were captured and indices would be irrelevant and poorly representative of the community as a whole. I performed permutational multivariate analysis of variance (ANOVA) for vegetative structural dissimilarity between forest patches to ensure the appropriate strata for the random effect (McArdle & Anderson 2001). In order to comprehensively assess changes to spider community structure across the study area, I used multiple analytical techniques. I used multivariate linear regression to model effects of vegetative structure, insect abundance, and forest patch on the abundances of spider functional groups and families. I then performed *post-hoc* univariate linear regression on the relative abundance of functional groups and used GLM with a Poisson distribution for further analyzing the raw abundance of individual families. I also used permutational multivariate ANOVA tests on the relative and raw abundances of the functional groups to assess variations in spider communities in response to the environmental variables. Though the permutational models are less sensitive to heterogeneity, I assessed multivariate homogeneity of variances using 'betadisper' in

statistical package 'vegan' (Oksanen et al. 2016). For models with a Poisson distribution, I used the canonical log link function and I used the identity link for models with a negative binomial probability distribution. I used Wilk's Λ test statistic and the likelihood ratio test statistic with chi-squared distribution to determine *P*-values for multivariate regression models and generalized linear models, respectively (Fox 2015). The likelihood ratio test statistic was calculated by:

$$G^2 = -2log_e\left(\frac{L(reduced)}{L(full)}\right)$$

where *L(full)* represents the likelihood function for the model with all explanatory variables included and *L(reduced)* represents the likelihood function for a model without the specific variable.

Results

Vegetative Diversity and Structure

Throughout all plots, I identified a total of 26 tree and shrub species, as well as 2 graminoid, 4 vine, and 34 herbaceous species (Appendix A). 13 of these species are considered introduced to the eastern United States while 10 have invasive growth habits and have been targeted for management in forests within the study area (USDA 2016). Overall vegetative communities were dissimilar between forest patches ($F_{8,41}$=2.707, *P*=0.001) (Table 3).

Richness of native species and all plant species did not differ in fenced and control plots (*t*=0.3046, *P*=0.7623; *t*=0.052, *P*=0.9588, respectively), with a mean of 8.26 ± 0.41 total species per plot and 5.66 ± 0.38 native species per plot. However, diversity of woody plant species increased with deer exclusion (*t*=2.6849, *P*=0.0105) as fenced plots contained a higher degree of evenness. Vegetative structure was

positively correlated with deer exclusion (t=4.0210, P=0.0002), though trends were not significant in plots at CHOH (Figure 4). Too few plots contained ground cover of Japanese stiltgrass or multiflora rose stems to analyze the effects of these invasive plants on vegetative structure; however, habitat structure was increased by the presence of multiflora rose shrubs (t=2.4578, P=0.0185) and field observations indicated their impact to understory physiognomy.

<center>Insect Prey Abundance and Biomass</center>

I collected a total of 11,298 insects and related taxa, including 3 non-spider arachnid groups (Acari, Opiliones, Pseudoscorpiones), as well as millipedes (Diplopoda), isopods (Isopoda), and springtails (Collembola). Insects from 15 orders were found, with flies, true bugs, and parasitic Hymenoptera the most abundant taxa. I collected an average of 225.96 ± 13.48 insects per plot, with 145.75 ± 10.48 palatable insects. Insect orders exhibited various responses to changes in vegetation, depending on order and typical diet. Overall insect abundance decreased with exotic plant species richness (t=-2.3451, P=0.0251). In regard to spiders, both palatable species abundance and biomass decreased with exotic plant species richness (P=0.0369; P=0.0719), and increased with native species richness (P=0.1344; P=0.0697). As strictly phytophagous taxa, the dry biomass of collected beetles decreased with exotic plant species richness (t=-2.1841, P=0.0366) and increased with native plant richness (t=1.9167, P=0.0645). Correspondingly, non-predatory true bugs also increased in biomass and abundance with greater native plant species richness (P=0.0391; P=0.1130). Predatory insect abundance was correlated with insect prey abundance, with higher predatory hemipteran and parasitic hymenopteran abundance associated with increasing numbers of prey (P=0.0516; P<0.0001). More complex vegetative

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structure was not correlated with the abundance of spider prey taxa or non-spider arthropods ($P>0.1$). However, the abundance of parasitic Hymenoptera decreased with more complex vegetative structure ($t=-3.4494$, $P=0.0017$) and the exclusion of deer browsing ($t=-3.4436$, $P=0.0088$). Beetles, consisting mostly of weevils (Curculionidae) and some leaf beetles (Chrysomelidae), increased in density in response to greater rose stem abundance ($t=2.2553$, $P=0.0313$), though the response was only evident in a single forest patch at CHOH. Conversely, several insect taxa increased in abundance in response to the presence of Japanese stiltgrass, including wasps ($t=3.0953$, $P=0.0041$), adult Lepidoptera ($t=1.8101$, $P=0.0800$), caterpillars ($t=2.0298$, $P=0.0510$), and flies ($t=1.7945$, $P=0.0825$).

Spiders

I identified a total of 7,653 individual spiders in 17 families, comprising 56 species (Appendix B). I collected 170.94 ± 17.28 spiders per plot at CHOH, 178.68 ± 11.53 at ANTI, and only 64.5 ± 13.58 spiders per plot at MONO. Sexually mature adult spiders constituted only 5.07% of individuals collected, and newly hatched, first instar spiders represented 36.18% of individuals and 54.92 mg or 1.94% of total spider biomass. Hunting spider species were the most abundant with 2,163 individuals, while orb weaving spiders and space web weaving spiders were also commonly collected, with 1,790 and 858 individuals, respectively. I collected only 13 ground spiders from 4 species, and the remaining group included 60 individuals from a single araneophagic species (Mimetidae: *Mimetus* sp.) and 2 kleptoparasitic species (Theridiidae: *Argyrodes elevatus*, *Rhomphaea fictilium*).

Overall spider abundance was best explained by the abundance of palatable insect prey (Table 4). Increased prey availability was positively correlated with the

abundance of all spiders (G^2=36.213, P<0.0001), as well as each functional group independently (P<0.005). Vegetative structure was positively correlated with the abundance of all spiders only at α=0.1 (G^2=2.896, P=0.0888); however, the abundance of individual functional groups and structure were not correlated. Relying on web-building spiders as opposed to the availability of insect prey, the abundance of the kleptoparasitic and araneophagic spider group was positively correlated with the abundance of space web spiders in the Theridiidae and Linyphiidae (G^2=8.147, P=0.0043), but not with orb weaving spiders (G^2=0.547, P=0.4594). Deer exclusion increased overall spider abundance (G^2=13.868, P=0.0002) but was not correlated with individual functional groups. Overall spider species richness decreased with vegetative structure (G^2=3.015, P=0.0825) and increased with insect abundance (G^2=7.753, P=0.0054). In contrast, habitat structure and prey availability did not affect the richness of any functional group: considering the predictor variables, the full and null models were not significantly different in explanatory power (P>0.1). Similarly, deer exclusion decreased overall species richness (G^2=4.502, P=0.0339), yet did not increase or decrease the richness of any spider functional group.

Habitat structure, palatable insect density, and forest patch were all predictors of spider community composition. Multivariate regression models showed that vegetative structure did not affect the relative abundance of spider functional groups (Table 5). Subsequent univariate analyses revealed that habitat structure was positively correlated with the relative abundance of hunting spiders, but only at α=0.1 (Table 6; P=0.0789). Mirroring results from the generalized linear models, both prey abundance and forest patch influenced the raw abundance of the 3 functional groups (P<0.01). Dependent on the natural history of species collected, individual taxonomic

families responded differently to habitat structure, prey, and forest site (Table 7). Though most taxonomic families were collected too infrequently to be included in analyses, the more abundant taxa exhibited various responses to habitat structure. Hunting spiders in the Anyphaenidae increased in abundance with greater habitat complexity (P=0.0092), while in contrast, the orb weaving Araneidae responded negatively (P=0.0529). The other common web building families, the Tetragnathidae and the Theridiidae, were not significantly correlated with vegetative structure (P>0.1). All family-level analyses of abundance showed a positive response to insect prey availability (P<0.05), with the exception of the Salticidae (P=0.3290). Results from permutational multivariate ANOVA of community dissimilarity based on functional group relative and raw abundances illustrated the significant effects of both habitat structure and insect prey on the community (Tables 8 & 9; P<0.05). Family-level composition of the spider community, assessed by community dissimilarity of abundances, was also influenced by all 3 variables (P<0.05). Deer exclusion was only significant in explaining family relative abundance as assessed by the non-parametric ANOVA of dissimilarity (P=0.0132).

Discussion

Deer herbivory, through both direct and indirect impacts to understory vegetation, changes forest spider communities in central Maryland through its influence on dominant families such as the Araneidae and Anyphaenidae. Lower than mean spring and summer temperatures prior to sampling resulted in mostly juvenile spiders collected which prevented accurate calculation of appropriate diversity indices. However, I was still able to detect correlations between my measures of the spider community and both habitat structure and insect prey availability. As I sampled

spiders above the ground floor, these results cannot be extrapolated to cursorial spiders, particularly as these taxa have been shown to exhibit varying responses to ungulate browsing (Shimazaki & Miyashita 2005; Takada et al. 2008). With deer population densities likely to be higher than that of landscapes outside these NPS units, reductions in habitat structure from deer browse and subsequent effects to spiders may be more pronounced in this study than would be found in other forest patches in the region.

The structural complexity of understory vegetation increased with deer exclusion, though no difference in structure within paired plots at CHOH was detected. Certain forested areas within CHOH are occasionally subjected to inundation from the Potomac River, which may preclude some woody plant growth and partially negate effects of browsing on understory shrubs and trees. Several of the CHOH forest patches are surrounded by steep, rocky topography and are located within narrow strips of federally-owned lands which may have reduced browsing pressure from both restricted deer access and adjacent hunting on private lands. Exclusion of deer herbivory, while increasing native plant species richness, diversity, and evenness, subsequently increased exotic plant species richness as well. Such increases in exotic plant species after deer exclusion implicate the management difficulties of establishing and restoring a functional forest after ungulate management. Insect response to deer exclusion was relatively discordant and heterogeneous depending on taxa studied, with some herbivorous insect groups weakly correlated to plant species nativity. Insect communities may be more strongly influenced by the landscape surrounding these plots, particularly as 25 m^2 plots may not be large enough to fully support and maintain vagile insect prey. Unfortunately,

the location of the extant exclusion plots precluded a thorough examination of the impacts of Japanese stiltgrass and other invasive plants on insects and spiders as these species were present in fewer than half of the plots. More strategically placed plot locations, in conjunction with an accurate estimate of ground cover, will allow for a better examination of the insect-plant relationship for such locally abundant species as Japanese stiltgrass. The apparent rise in Lepidoptera in conjunction with stiltgrass prevalence was explained by just 2 plots within the Cunningham forest patch at ANTI, which contained a single species of tortricid caterpillar and moth (*Acleris* sp.) in great density. As these caterpillars feed on foliage in the canopy and drop to the forest floor when ready to pupate, their presence in stiltgrass-dominated areas should be considered incidental and more indicative of canopy tree species than the understory habitat (Beadle & Leckie 2012). Contrary to prediction, parasitic wasp abundance responded strongly and negatively to vegetative structure and deer exclusion, while predatory Hemiptera were not correlated. In a comprehensive meta-analysis, Langellotto & Denno (2004) found that predatory and parasitic insect taxa are often the most positively correlated groups in terms of habitat structure. Further investigation into the specific wasp species that were collected would clarify whether the wasps consisted of species that utilize spiders as prey.

Increased palatable insect prey resulted in a higher abundance of all spider functional groups and nearly all families. These findings are consistent with similar work on the critical importance of insect prey availability in various aspects of the life history of a spider, including reproductive health and fecundity (Wise 1979; Fritz & Morse 1985; Leborgne & Pasquet 2005), body condition and biomass (Bucher & Entling 2011), and spider web residence (Hodge 1987a, Adams 2000). Greater insect

prey densities also increased overall spider species richness, likely a simple response from the increased quantity of ingestible nutrients available and able to support a diversified predatory assemblage. The inability of my explanatory variables to predict species richness of the individual spider functional groups is more plausibly an artefact of low diversity habitats or inter-group variation and not an indicator of the importance of habitat structure and insect density.

Both understory habitat structure and exclusion of deer browse were also important correlates of overall spider species richness; however, increased vegetation structure resulted in decreased spider richness. These findings are in stark contrast with the large body of literature indicating the positive correlation between habitat structure and spider richness in meadows and fields (Greenstone 1984) and in coniferous forest canopy branches of the northwestern U.S. (Halaj et al. 1998; 2000). In some of the only published, similar work in this field, Miyashita et al. (2004) and Takada et al. (2008) found increased spider species richness in response to increased habitat structure and the exclusion of herbivory in Japanese coniferous and evergreen forests and plantations. Differences in species richness response could in part result from overall habitat differences, the specific metrics used for estimating structure, and ecological differences in cervid behavior. Both aforementioned works studied effects of sika deer browsing at heights of less than 1 m: sika deer are more likely to feed on grasses and low vegetation as opposed to white-tailed deer, which often feed on branches up to 2.0 m in height (Bressette et al. 2012; Kalb 2015).

Structural diversity in deciduous forest understories should provide both increased substrate for web supports and a greater prevalence of branches and leaves upon which hunting spiders may find prey (Huffaker 1958; Huffaker et al. 1963).

More structurally complex habitats should also provide a greater variability in the size of interstitial spaces between branches and leaves, ultimately providing greater niche availability for webs of different sizes and configurations. The specific reason why species richness remained higher in browsed plots with less vegetative complexity is unclear, though the increases may be attributed to increases in common species that prefer open understories and disturbed habitats (e.g., *Micrathena gracilis* and *Neoscona domiciliorum*; Berman & Levi 1971; Hodge 1987b). Given the correlation between the presence of multiflora rose and vegetative structure, such a decline in spider species richness could possibly result from increased abundance of the structurally complex rose. Increased individual plant structure, as seen on invasive rose bushes, may decrease available spaces for web-spinning spiders, ultimately reducing overall available habitat or shelter (Gonçalves-Souza et al. 2011). Paired plots were relatively close to the forest edge and much of the herbaceous layer consisted of plant species common in ruderal habitats: spider assemblages are known to increase in richness and diversity at ecotones as compared to the forest interior, as the habitat intergradation permits the existence of spiders common to both habitat types (Downie et al. 1996; Rodrigues et al. 2014). Several of the dominant species collected are often found in low-growing vegetation and tall grasses, and the long history of this study area supporting herbivory from dense deer populations could have effectively removed source populations for forest interior spider species and those that require denser understory vegetation. As relatively immobile predators whose dispersal is limited by epigeic movement or airborne ballooning, larger geographic regions with similar, depauperate native understory vegetation may not so readily be recolonized by forest habitat specialist species.

Though positively correlated with overall spider abundance, likely caused by the strong correlation between structure and Anyphaenidae, vegetation structure was not related to the abundance of any individual functional group. This lack of correlation between functional groups and vegetative architecture likely arose from within-group differences that were evident when examined at the taxonomic family level. Predominant orb web weaving spider families included the Araneidae, which decreased in abundance with greater structure, and the Tetragnathidae, which was not correlated with structure. Such complex responses to environmental changes are likely in part due to the local taxonomic composition of these families. Within the orb web weaving group, the collected Araneidae consisted mainly of *Mangora* species, relatively small spiders nearly 3.6 mm in total length at sexual maturity (Levi 1965). *Mangora* webs are often placed in low vegetation, including tall grasses, herbaceous plants, and low tree branches (Kaston 1948). Due to the preferred height of *Mangora* webs and their ability to utilize tall grasses, this species increased in abundance in browsed habitats with less complex woody plant structure. Conversely, the most commonly collected spider in this functional group was *Leucauge venusta* (Tetragnathidae), which reaches a total length of nearly 6.0 mm at maturity. This species maintains an approximately 20 cm viscid web but can have supporting anchor strands up to 2.0 m, allowing for greater flexibility in selecting web sites in both browsed and un-browsed habitats (Levi 1980; Foelix 2011). The space web weaving group and the Theridiidae were also not correlated with habitat structure. The Theridiidae comprised nearly 82% of individual spiders in this functional group and were dominated by *Theridion* species, reaching approximately 4.3 mm total length at maturity (Kaston 1948; Levi 1957; Paquin & Dupérré 2003). These spiders utilize tall

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grasses and tight spaces between leaves and stems of low vegetation for their irregular, three-dimensional webs (Kaston 1948). Similar to *L. venusta*, *Theridion* species are likely more flexible in exploiting available spaces in grasses and low vegetation within both browsed and un-browsed habitats. The Anyphaenidae were strongly correlated with habitat structure and were the only family to increase in abundance with greater structure. Comprising species that are dependent upon structure for substrate upon which to hunt, these species could respond greater to structure than do web-building species that require the spaces between vegetative surfaces within which to build webs.

The lack of a cohesive response of spider families and groups to greater habitat structure may be caused by the current depauperate condition of the resident spider community. The species selecting these forest patches likely resulted from a history of deer browsing and spatially homogeneous habitats, and as such, these results are contrary to much of the related work in this field. Congruent with work in agro-ecosystems (Balfour & Rypstra 1998; Schmidt & Rypstra 2010) and fields and meadows (McNett & Rypstra 2010; Malumbres-Olarte et al. 2013), research in Japanese forests and plantations has shown similar results: more complex habitat structure increases individual spider abundance (Miyashita et al. 2004; Miyashita & Takada 2007; Takada et al. 2008). Throughout the literature, there exists conflicting evidence regarding the relative importance of prey availability and habitat structure in forming spider community structure and population density (Greenstone 1984; Rypstra 1983; McNett & Rypstra 2000). In recent work in a managed, Japanese evergreen forest, Katagiri & Hijii (2015) studied the interconnected relationships between ungulate browsing, vegetation structure, prey abundance, and spider

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populations and how they varied by spatial scale. Browsing sika deer improved structure on an individual plant by increasing lateral branching and abundance of twigs and leaves, which in turn increased both abundance of insects and spiders; however, when examined at the scale of the 9 m^2 plot, browsing decreased total number of individual plants, producing a net loss in both spider and insect prey densities. In this work, it is apparent that insect prey availability is an extremely significant predictor for both spider abundance and species richness, while habitat structure significantly, yet negatively, correlates with spider species richness. As mentioned above, many of the forest-dwelling species typically associated with more complex forest understory vegetation may have already been extirpated from these forest patches, with local landscape heterogeneity preventing prompt recolonization from adjacent, suitable habitats. These species may also be found higher in the forest understory, above my targeted sampling area. I sampled spiders in the space within which a white-tailed deer would be likely to browse ($\leq$2.0 m); however, my sampling methods may have effectively missed species higher in the branches of understory shrubs and trees. A larger spatial sampling scale may also allow for a more efficient snapshot of understory spider community response to structural changes, particularly as larger web building spiders will not be sampled in such great densities due to more patchy distributions. Abundance of the 3 kleptoparasitic and araneophagic species closely tracked densities of space web weavers and not orb weaving spiders, implicating the likely source of their prey.

In terms of spider assemblages in forest fragments, prey availability, habitat structure, and forest patch all influenced the community composition when assessed at both the taxonomic family and spider functional group designation. Deer exclusion

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was not as significant of a predictor of community structure as was the direct measure of vegetation, likely in part resulting from the lack of effect of deer browse on structure at CHOH. These findings are in line with past research in fields and meadows (Greenstone 1984, Gibson et al. 1992; Bonte et al. 2000), and coniferous (Halaj et al. 1998, 2000) and Brazilian forests (de Aquino Ribas et al. 2011), which all found changes to spider assemblages from habitat structure, large herbivores, or insect prey. Community structure analyses showed significant turnover of spider families across gradients of prey availability and habitat structure, indicating the importance of these variables in defining assemblages of spiders in mid-Atlantic forests. Such changes to composition of spider communities may result from replacement of forest interior spiders and habitat specialists to species that may thrive in open, ruderal habitats or low-growing vegetation. Long-term herbivory from large deer populations may lead to local extirpation of forest taxa in areas that do not contain sufficient vegetative substrate. Nursery web spiders (Pisauridae) were represented in spider communities of many forest patches. The relative abundance of Pisauridae was predicted by specific forest patch: the family consisted of *Pisaurina* and *Dolomedes* species, which prefer grassy meadows and riparian habitats, respectively, and likely responded more to the geographic location and adjacent habitat type than other considered variables. A different metric that better measures the spatial variability of understory habitats instead of the vegetation itself may provide a clearer understanding of species' response to habitat structure.

Habitat structure and insect prey density conclusively influence the community structure and composition of spider assemblages in mid-Atlantic forests, yet individual functional group abundance did not respond to structural changes despite the

significant relationship when examined with all groups. As changes in abundance were evident when examining individual spider families, it is likely the functional group designation was too coarse to capture the diverse responses. It is also possible that species turnover to more resilient taxa occurs along with such habitat changes: depending on the physiological similarity of such replacement species, the proteinaceous biomass and overall energy dynamics of this component of invertebrate-vertebrate food webs may drastically change the nutritional composition of forest birds and other araneophagic predators (Wilder 2011). As yet unknown changes to the nutritional dynamics of the spider community maintain the capacity to alter the trophic movement of important macro- and micro-nutrients to higher-level predators. Published literature on forest bird diet generally includes a single category for spiders, which may or may not include multiple families or functional groups. Spider genera within a functional group or family may differ in susceptibility and palatability to higher predators as well as opisthosomal nutritional content, ultimately causing changes to the energy dynamics of the invertebrate-vertebrate food webs. Changes in habitat structure could also have altered proportions of the taxonomic components of palatable prey and subsequent spider dietary composition, particularly as insect prey was characterized by order and did not represent diversity. Spiders are capable of shifting diet depending on prey availability, though with likely consequences to individual reproductive health and nutritional content for higher level predators (Gratton & Denno 2006; Wilder 2011). Further work identifying potential shifts in diet and effects to individual fecundity and body condition in such structurally-reduced habitats is necessary to elucidate physiological trends beyond the community or family level.

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Serving as powerful ecosystem engineers in eastern deciduous forests, white-tailed deer browsing conclusively alters forest vegetation, with the capacity to indirectly influence various trophic levels within the arthropod community, potentially including both herbivores and primary predators and parasitoids. Because of their reliance on vegetative structure for web attachment and hunting substrate, spider communities may be affected by changes to vegetation, resulting in further impacts to insects: the addition of artificial structure in an evergreen forest with high density populations of sika deer allowed web-building spider populations in the low forest understory to increase and subsequently reduce the abundance of insect populations emerging from the detrital layer (Miyashita & Takada 2007). Similarly, invasive plant species that outcompete and displace native vegetation also have the capacity to indirectly alter the herbivorous insect community and their predators and parasitoids. Populations of a space-web weaving species (Dictynidae: *Dictyna* sp.) in a structurally complex grassland invaded by spotted knapweed (*Centaurea maculosa*) contained over 40 times more individuals than in the native habitat, maintained larger webs, included a greater proportion of fecund females, and were able to capture twice the abundance of insect prey per spider, likely altering overall insect population size (Pearson 2009). Recent evidence for the strength of indirect interaction pathways up the trophic levels was also reported by DeVore & Maerz (2014) in forests of the southeastern U.S.: forest floor habitat invaded by Japanese stiltgrass reduced insect prey but provided favorable habitat and microclimate for American toads (*Anaxyrus americanus*). However, overall toad survival decreased as predatory wolf spider (Lycosidae: *Hogna* spp.) populations also increased in abundance and fed on the metamorphosed toads.

Throughout the scientific literature, it is apparent that the relationship between spiders and these environmental correlates are complex and intertwined. These results illustrate how changes in above-ground forest vegetation, mediated by white-tailed deer browsing and coupled with changes in insect prey abundance, have the capacity to alter various aspects of the forest understory spider community. The history of heavy browsing pressure on these forests has resulted in a spider community that consists of many species that thrive in the low understory and in tall grasses. These results largely reflect the depauperate condition of spider communities in these habitats and do not necessarily indicate that white-tailed deer browsing is beneficial or benign to forest spiders. Controlling herbivory from white-tailed deer may result in unknown long-term impacts to spiders through facilitating the growth of structurally complex invasive plants such as multiflora rose. Such invasive plant species, only tangentially studied within this paired plot design, may play a more prominent role in defining spider community composition and abundance due to its complex architecture and the capacity for certain invasive plants to alter herbivorous insect densities. Despite their integral role in both affecting herbivorous insect populations and transferring energy and nutrients from invertebrate to vertebrate trophic webs, these organisms are often overlooked in studies of ecological interactions. Particularly when considering the prevalence of dense deer populations and invasive plants throughout mid-Atlantic forests, this work indicates the need for further investigation into effects on forest spider communities.

TABLES

Table 1   Geographic locations of forest patches within study area. Coordinates represent approximate centroid of paired plots per forest fragment. Latitude is listed as decimal degrees North and Longitude listed as decimal degrees West. All coordinates reported in North American Datum of 1983 (NAD 1983).

Park	Forest Site	Latitude	Longitude
ANTI	Cunningham	39.474378	-77.796222
	Snavely	39.442561	-77.731927
	Sherrick	39.458262	-77.730632
	West Woods	39.481561	-77.753472
CHOH	North Potomac	39.562053	-77.849102
	Taylors	39.492298	-77.796152
	Snyders	39.459046	-77.796152
MONO	Brooks Hill	39.355087	-77.408140
	Lewis	39.352379	-77.388352

Table 2   Classification of spider families into functional groups used in analyses. Groups are based on predominant prey capture method and natural history. Functional group designations were modified from Cardoso et al. (2011).

Orb web spiders	Space web spiders	Hunting spiders	Ground spiders	Araneophagic & kleptoparasitic spiders
Araneidae	Dictynidae	Anyphaenidae	Agelenidae	Mimetidae
Tetragnathidae	Linyphiidae	Clubionidae	Corinnidae	Theridiidae[a]
Theridiosomatidae	Theridiidae	Oxyopidae	Lycosidae	
Uloboridae		Philodromidae		
		Pisauridae		
		Salticidae		
		Thomisidae		

[a]   Includes only the genera *Argyrodes* and *Rhomphaea*

Table 3   Jaccard community dissimilarity for herbaceous and woody vegetation throughout study area in July, 2013. Presence of vegetative species was pooled within forest patches and compared between each patch.

Park	Forest Site	Cunning -ham	Snavely	Sherrick	West Woods	North Potomac	Taylors	Snyders	Brooks Hill
ANTI	Snavely	0.5517							
	Sherrick	0.6667	0.5000						
	West Woods	0.6286	0.5625	0.6667					
CHOH	North Potomac	0.5806	0.5517	0.6667	0.6667				
	Taylors	0.6207	0.5517	0.6207	0.6286	0.5806			
	Snyders	0.4167	0.4000	0.5385	0.6471	0.6452	0.4800		
MONO	Brooks Hill	0.7632	0.6389	0.7632	0.6905	0.7561	0.7297	0.7143	
	Lewis	0.8750	0.7333	0.7586	0.7059	0.7879	0.8387	0.8276	0.6563

Table 4   Spider species richness and raw abundance in response to habitat
structure and prey availability in August, 2013. Functional group
abundances were analyzed using GLM with negative binomial
probability distribution to account for overdispersion. Richness was
analyzed using GLM with Poisson distribution. Likelihood ratio test
statistic G^2 was used to determine P-value.

Parameter	Group	Vegetative Structure		Insect Abundance	
		G^2	P	G^2	P
Abundance	Orb weaver	0.563	P=0.4530	13.445	P=0.0003** (+)
	Space web	0.072	P=0.7879	7.911	P=0.0049** (+)
	Hunter	1.933	P=0.1644	19.344	P<0.0001** (+)
	Spiderlings	0.001	P=0.9753	8.842	P=0.0029** (+)
	All spiders	2.896	P=0.0888* (+)	36.213	P<0.0001** (+)
Richness	All spiders	3.015	P=0.0825* (-)	7.753	P=0.0054** (+)

*   Statistically significant at α=0.1
**   Statistically significant at α=0.05

Table 5   Multivariate linear regression results for raw and relative abundance of spider functional groups in response to environmental variables. The orb web weaving, space web weaving, and hunting spider functional groups were included in analysis. Wilk's Λ test statistic was used to assess significance. Spider data were collected in August, 2013.

	Vegetative Structure		Insect Prey Abundance		Forest Site	
	Λ	P	Λ	P	Λ	P
Relative Abundance	0.9136	0.3356	0.9921	0.9603	0.1910	<0.0001**
Raw Abundance	0.9162	0.35018	0.7180	0.0061** (+)	5.2988	<0.0001**

*   Statistically significant at α=0.1
** Statistically significant at α=0.05

Table 6　Univariate linear regression results for relative abundance of individual spider functional groups in response to environmental variables. Spider data were collected in August, 2013.

	Vegetative Structure		Insect Prey Abundance		Forest Site	
	F	*P*	*F*	*P*	*F*	*P*
Orb web	1.0562	0.3104	0.0465	0.8304	5.1616	0.0002**
Space web	0.4666	0.4986	0.0690	0.7942	3.7512	0.0024**
Hunter	3.2561	0.0789* (+)	0.2359	0.6299	6.9829	<0.0001**

*　Statistically significant at α=0.1
**　Statistically significant at α=0.05

Table 7   Univariate analysis of raw abundance of specific individual families in the orb web weaving, space web weaving, and hunting functional groups. Analyses were conducted using GLM with Poisson distribution. Likelihood ratio test statistic G^2 was used to determine P-value. Members of other taxonomic families were identified too infrequently to be included in analyses. Spider data were collected in August, 2013.

	Vegetative Structure		Insect Prey Abundance		Forest Site	
	G^2	P	G^2	P	G^2	P
Anyphaen-idae	6.79	0.0092** (+)	14.78	0.0001** (+)	409.16	<0.0001**
Araneidae	3.747	0.0529* (-)	3.920	0.0477** (+)	57.514	<0.0001**
Pisauridae	2.271	0.1318	4.830	0.0280** (+)	56.020	<0.0001**
Salticidae	1.158	0.2819	0.953	0.3290	25.747	0.0012**
Tetragnath-idea	0.200	0.6543	74.281	<0.0001** (+)	170.54	<0.0001**
Theridiidae	1.015	0.3137	8.240	0.0041** (+)	96.620	<0.0001**

*   Statistically significant at α=0.1
**   Statistically significant at α=0.05

Table 8   Permutational multivariate ANOVA results showing influence of environmental variables on spider communities. Analyses were performed on the Bray-Curtis community dissimilarity of relative abundances, classified by functional group and family. Spider data were collected in August, 2013.

	Vegetative Structure		Insect Prey Abundance		Forest Site	
	F	*P*	*F*	*P*	*F*	*P*
All Functional Groups	10.0906	0.0009**	5.5039	0.0079**	5.1007	0.0001**
All Families	6.6705	0.0003**	3.2764	0.0207**	4.5402	0.0001**

*   Statistically significant at α=0.1

** Statistically significant at α=0.05

Table 9   Permutational multivariate ANOVA results showing influence of environmental variables on spider communities. Analyses were performed on the Bray-Curtis community dissimilarity of raw abundances, classified by functional group and family. Spider data were collected in August, 2013.

	Vegetative Structure		Insect Prey Abundance		Forest Site	
	F	*P*	*F*	*P*	*F*	*P*
All Functional Groups	3.9261	0.0183**	16.7422	0.0001**	4.6994	0.0001**
All Families	5.4005	0.0002**	6.3873	0.0002**	3.9196	0.0001**

*   Statistically significant at α=0.1

**   Statistically significant at α=0.05

FIGURES

Figure 1   Map of study area in Washington and Frederick Counties, Maryland. Green shading indicates forested land cover and black lines indicate the U.S. National Park Service legislative park boundaries.
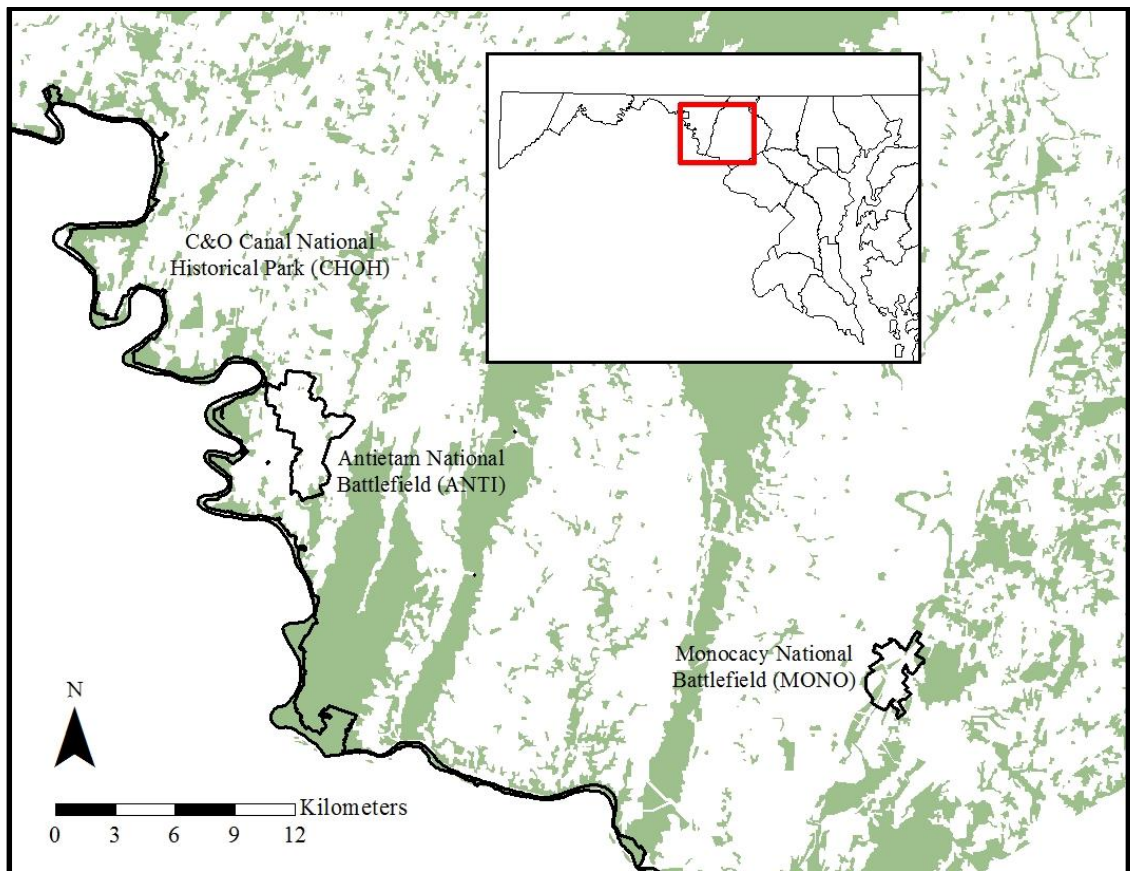
Figure 2   Detailed map of study area. Figure on the left shows study area within Antietam National Battlefield (ANTI) and C&O Canal National Historical Park (CHOH). Figure on the right shows Monocacy National Battlefield (MONO). Approximate centroid of paired plot locations are depicted by points. Green shading indicates forested land cover and black lines indicate the U.S. National Park Service legislative park boundaries.
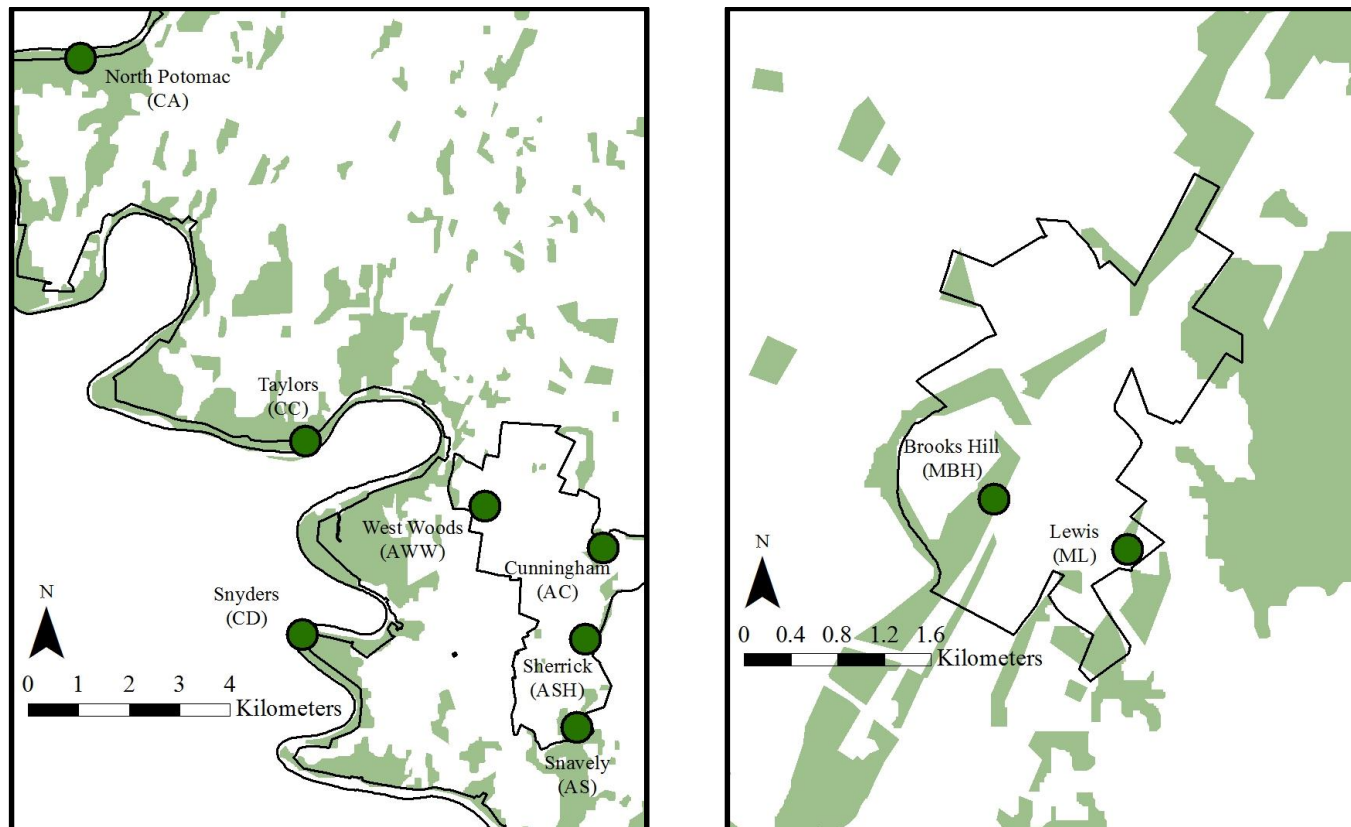
Figure 3   Spatial estimation of vegetative structure using GIS software (ESRI 2011, ArcMap 10.2. California). Pixels of rasterized photographs were classified into 15 color classes using maximum likelihood estimation. Habitat structure was calculated as the proportion of each 0.5 m height class obscured by vegetation.
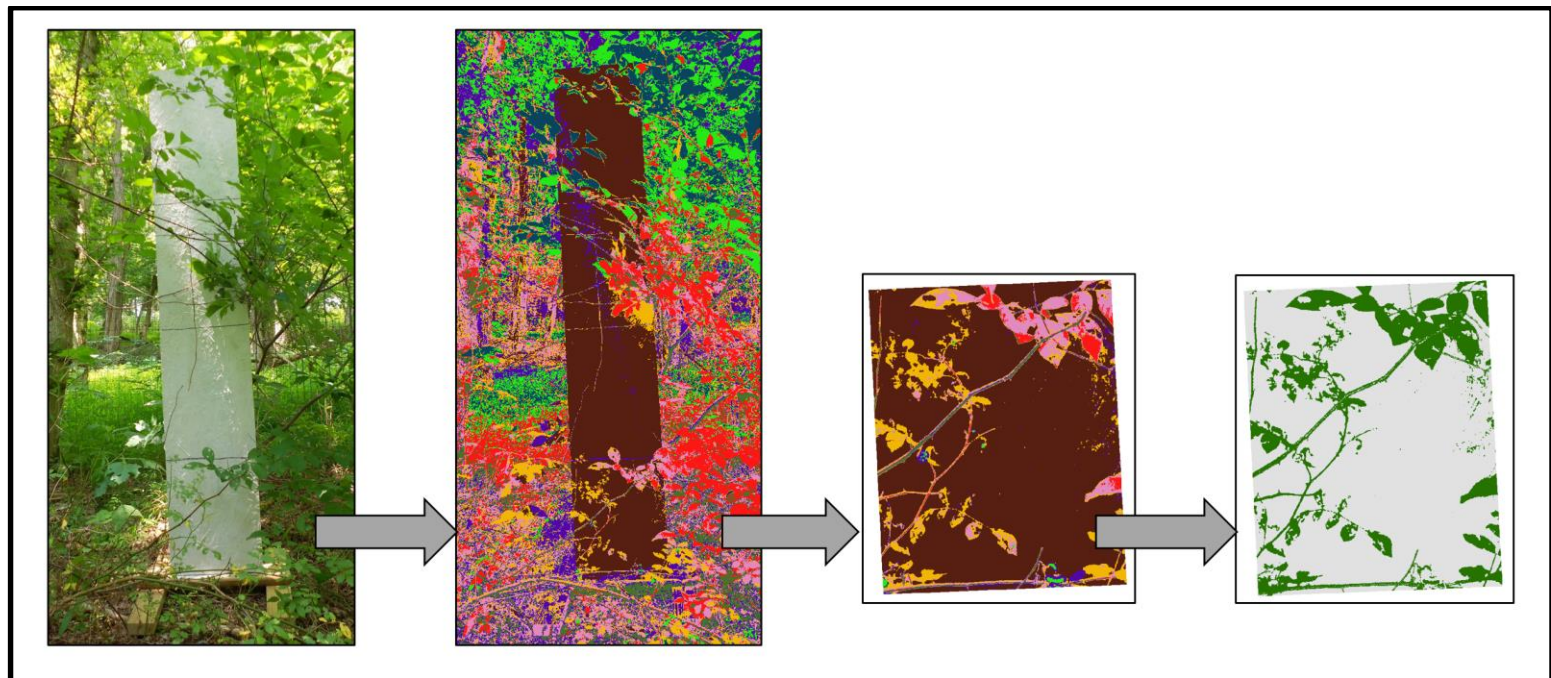
Figure 4   Boxplot showing effect of deer exclusion on habitat structure within plots in July, 2013. Data from individual parks are represented separately, with individual boxes for fenced plots and control or open plots. Boxes represent 1st and 3rd quartiles and median. Points greater than 1.5 times the interquartile range are considered outliers and are shown as individual points.
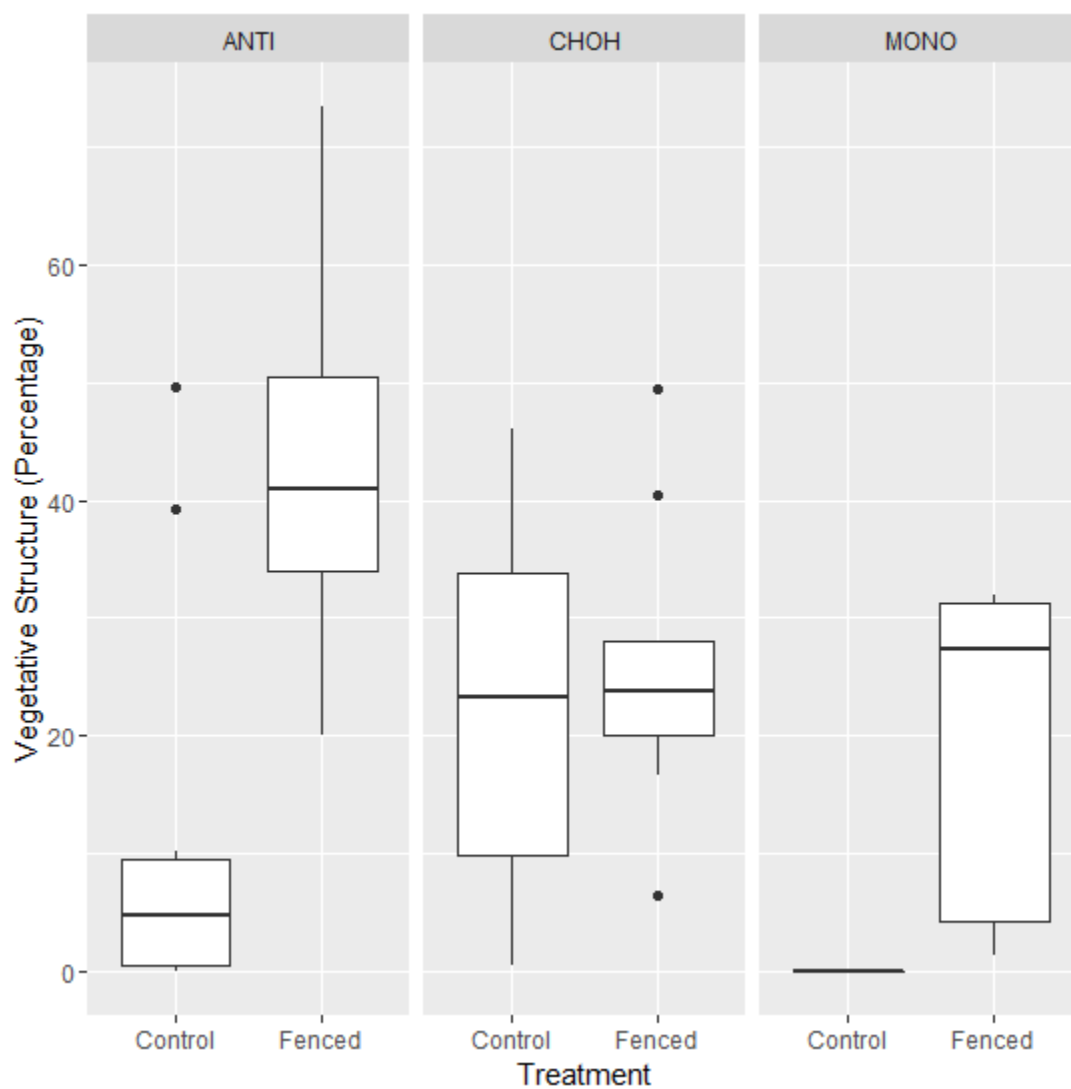
Figure 5   Normalized stacked bar chart showing functional group composition of spider communities sampled in August, 2013. Data from each forest site are represented separately, with individual bars for fenced plots and control or open plots.
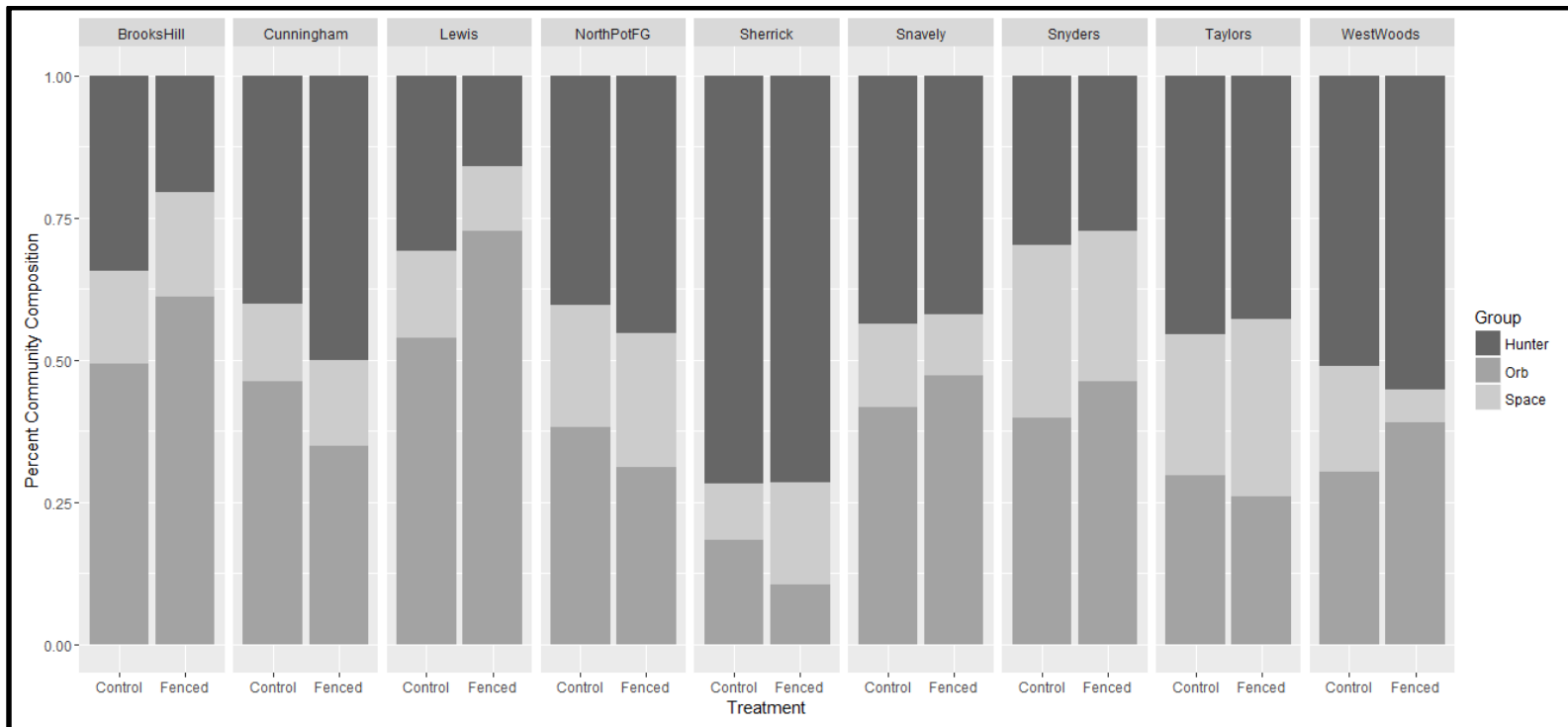
Figure 6   Normalized stacked bar chart showing functional group composition of spider communities sampled in August, 2013 in forest sites at MONO. Data from each forest site are represented separately, with individual bars for fenced plots and control or open plots.
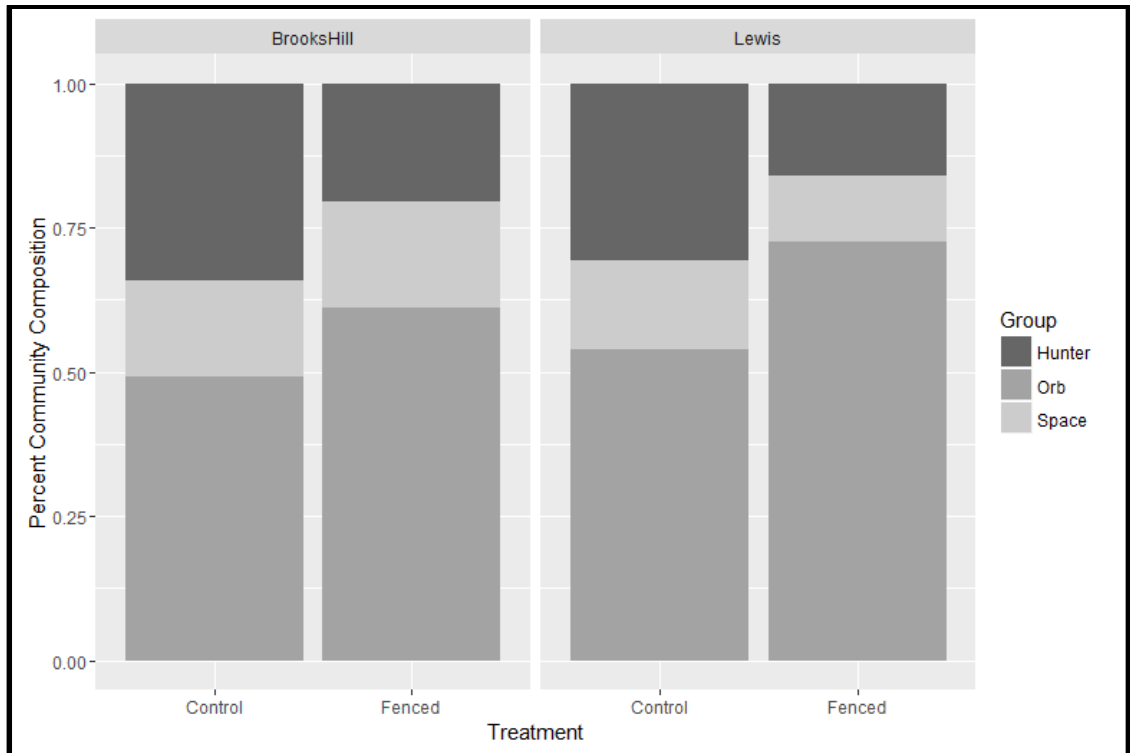
Figure 7   Normalized stacked bar chart showing functional group composition of spider communities sampled in August, 2013 in forest sites at ANTI. Data from each forest site are represented separately, with individual bars for fenced plots and control or open plots.
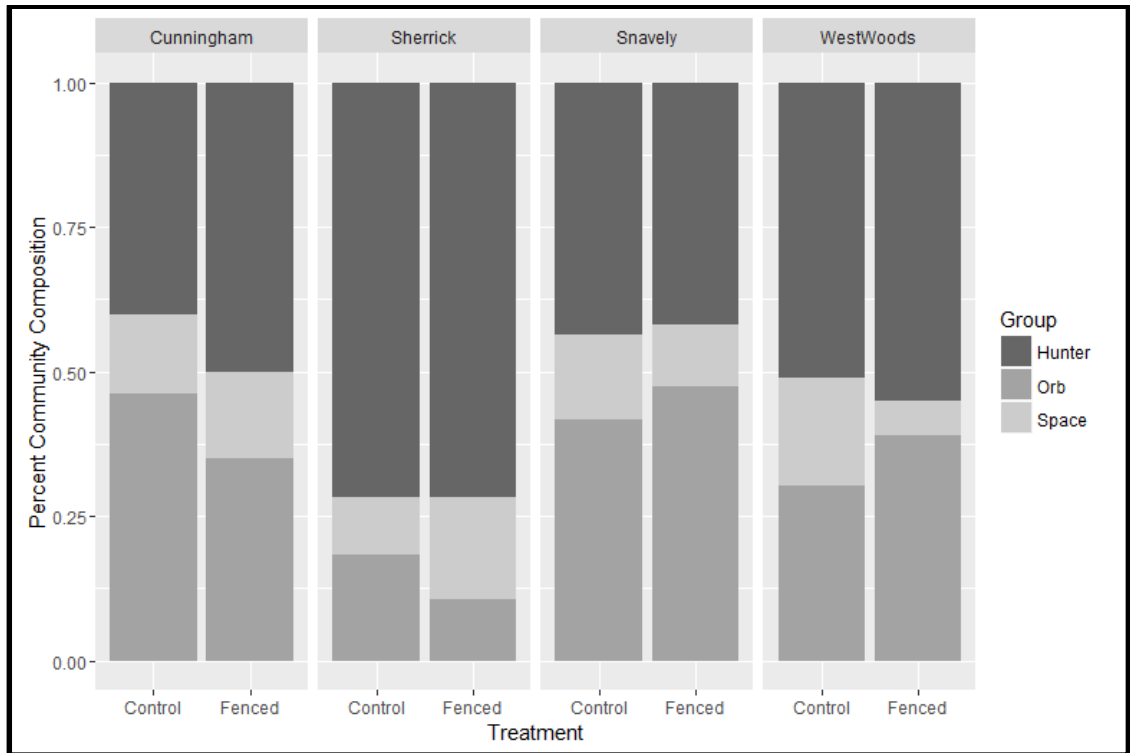
Figure 8   Normalized stacked bar chart showing functional group composition of spider communities sampled in August, 2013 in forest sites at CHOH. Data from each forest site are represented separately, with individual bars for fenced plots and control or open plots.
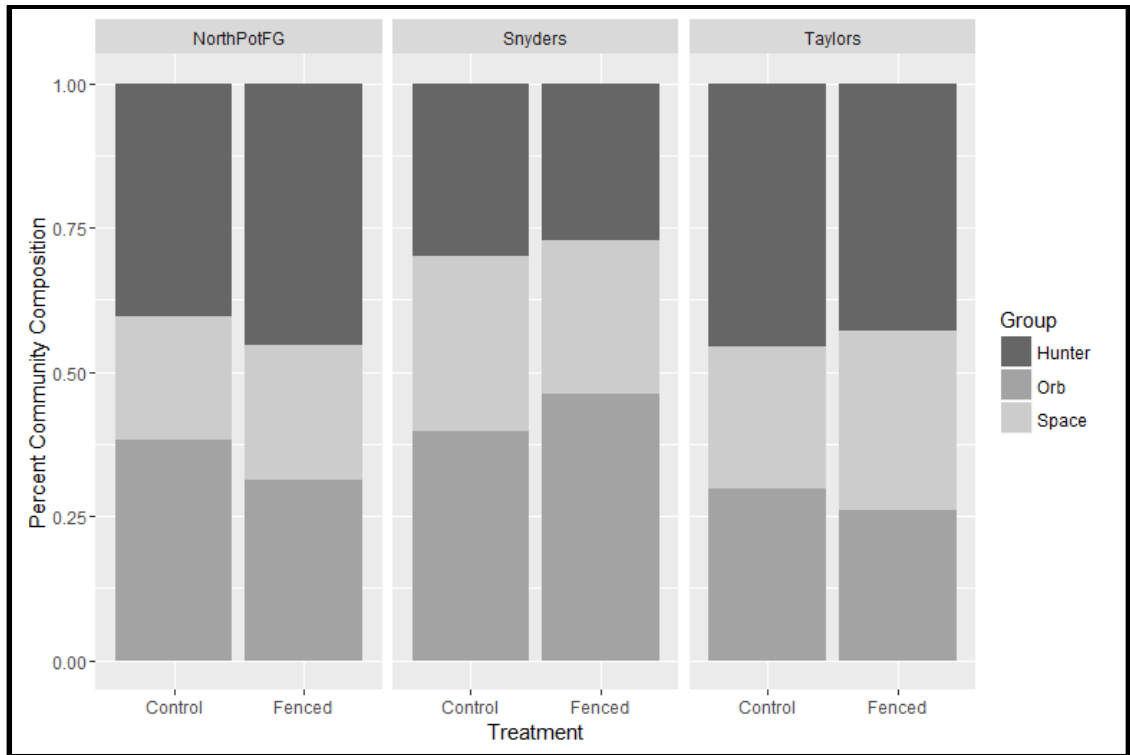
Chapter 3

**HABITAT STRUCTURE ALTERS INVERTEBRATE NUTRITIONAL
DYNAMICS AS INDICATED BY CHANGES IN STABLE ISOTOPES**

The structural complexity and physiognomy of forest vegetation is an
extremely important determinant of preferred habitat for many taxa. For those species
that require vegetation for nesting, oviposition, food, or shelter, changes in the
architecture and spatial diversity of vegetation may result in reduced body condition,
decreased reproductive success, or even local extirpation. Communities of forest
interior birds and small mammals that use understory vegetation for nesting and
protection from predators are responsive to habitat structural changes as sensitive taxa
are replaced by more resilient species (Byman 2011; Chollet et al. 2015). Often less
vagile and more restrictive in selecting preferred habitat, invertebrate populations may
exhibit stronger correlations with changes to vegetative structure and composition.
Increased structure may provide a preferable microclimate for insects, additional
shelter from predators, and while indirectly related, habitats with greater structure may
contain more plant biomass and food for phytophagous invertebrates. Structurally
complex vegetative habitats may also benefit invertebrate predators through the
creation of more suitable hunting landscapes while also providing refugia and shelter
from intraguild predators and cannibalistic interactions (Langellotto & Denno 2004,
2006; Schmidt & Rypstra 2010).

Habitat structure and complexity is known to be a strong correlate and critical
determinant for multiple parameters of spider communities. Web-building and

hunting spiders are highly dependent on vegetative architecture, both for stable web attachment sites as well as a substrate upon which they may hunt (Uetz 1991; Foelix 2011). In general, habitat complexity is positively correlated with spider richness, diversity, and density when considered in agro-ecosystems (Balfour & Rypstra 1998; Schmidt & Rypstra 2010), fields and meadows (McNett & Rypstra 2010; Malumbres-Olartes et al. 2013), and individual plants or branches (de Souza 2005; Marín et al. 2014). Extensive work in Japanese evergreen vegetation has shown concordant results, with increased structure resulting in more abundant and diverse spider communities (Miyashita et al. 2004; Miyashita & Takada 2007; Takada et al. 2008). Vegetative structure also contributes to the overall composition and relative abundances of the taxonomic components of the spider community (Greenstone 1984; Gibson et al. 1992; Halaj et al. 1998, 2000). The importance of vegetative structure can be seen in a structurally complex grassland: populations of a small, dictynid spider contained over 40 times more individuals than in the homogenous habitat, maintained larger webs, included a greater proportion of fecund females, and were able to capture twice the abundance of insect prey per spider (Pearson 2009).

In deciduous forests of the populous eastern United States, understory vegetative communities are often impacted by both ungulate herbivory and invasive plants. Browsing from large herbivores and invasive plant populations are manageable, albeit at times infeasible, threats to natural systems which have the capacity to produce ecosystem-engineering impacts to multiple trophic levels (Jones et al. 1997; Crooks 2002). Through browsing activity in U.S. forests, white-tailed deer (*Odocoileus virginianus*) are capable of altering the structure of the forest understory, drastically reducing palatable woody and herbaceous native plant species (Waller &

Alverson 1997; Côté et al. 2004). In heavily browsed deciduous forests, understory vegetation may become structurally simplified and homogenous, consisting largely of unpalatable or non-native plant species (Horsley et al. 2003). Certain invasive plant species now present in this geographic region also have the capacity to alter vegetative structure throughout the forest understory. Through their growth habit, invasive plant species such as Japanese stiltgrass (*Microstegium vimineum*) are able to change habitat structural complexity throughout the forest understory. Despite the preponderance of work investigating effects of deer browsing on forest vegetation, research into indirect impacts to the spider community in deciduous forests is explicitly lacking. Much of the work in this area has been done in Japanese evergreen vegetation, which has shown that sika deer (*Cervus nippon*) browse decreases structure, which in turn reduces diversity and abundance of spiders (Miyashita et al. 2004; Miyashita & Takada 2007; Takada et al. 2008).

Despite the importance of habitat structure in determining spider densities and assemblages, the abundance of suitable insect prey is likely as critical in affecting spiders (Greenstone 1984; Rypstra 1983; McNett & Rypstra 2000; see Chapter 2). Availability of insect prey is positively correlated with spider fecundity and body condition (Wise 1979; Fritz & Morse 1985; Leborgne & Pasquet 2005). Within Pennsylvanian forests, Rypstra (1983) found that prey densities and habitat structure were both important in defining web-building spider densities. Similarly, in recent work by Katagiri & Hijii (2015), both vegetative structure and insect prey were important predictors for spider abundance. Cascading impacts from ungulates (Den Herder et al. 2004; Allombert et al. 2005) and invasive plants (Ballard et al. 2013; Burghardt & Tallamy 2015) evidently reduce densities of available prey for spiders,

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concurrently altering the relative abundance of each insect order. Changes to habitat

structure, coupled with reduced prey densities, will likely cause subsequent losses in

spider diversity and density. Beyond reduced fecundity and biomass, changes to

habitat structure and prey availability also modify web residence and abandonment

(Hodge 1987a; Adams 2000), increasing individual vulnerability to predation.

Compositional dietary changes may also alter the availability of required nutrients for

successful survival and reproduction, as well as the dynamics and transfer of

proteinaceous biomass to higher order predators (Wilder 2011; Wilder et al. 2013).

Stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) are often used to assess

spider diet composition, trophic structure, and physiological stress (Akamatusu et al.

2004; Kato et al. 2004; Hood-Nowoltny & Knols 2007; Walters et al. 2010),

particularly as extra-oral digestion and a generalist diet may otherwise prove difficult

to investigate (Belivanov & Hambäck 2015). In animals under physiological stress

from lack of sufficient nutrition, δ^{15}N levels become enriched as the lower-energy

molecular bonds of ^{14}N preferentially break during deamination and transamination

processes (Ambrose & DeNiro 1986; Hobson & Clark 1992; Hobson et al. 1993;

Oelbermann & Scheu 2002). Although enriched δ^{15}N may indicate nutritional stress

or sub-optimal diets, changes in isotopic nitrogen may also indicate compositional

differences in dietary composition (Webb et al. 1998; Adams & Sterner 2000). δ_{13}C,

though not effective in detecting trophic structure, can discern the base of food webs

as values change depending on photosynthetic pathway (Smith 1972). I used stable

carbon and nitrogen isotopes to assess changes in dietary composition and/or

nutritional deficiency in a common orb-weaving spider species in mid-Atlantic forests

of the U.S. Through this work, my objectives were to 1) utilize stable isotope ratios to

investigate whether changes in habitat structure may alter the nutritional dynamics of invertebrate food webs in these habitats, mediated by the availability and relative abundance of insect prey and 2) asses how structurally-influential invasive plants may contribute to the dietary energetics of forest understory spiders.

Methods

Study System

I utilized 11 existing paired plots established in 2003 in 4 forest patches within Antietam National Battlefield (ANTI) and the Chesapeake and Ohio Canal National Historical Park (CHOH), units of the U.S. National Park Service located in Washington County, Maryland (McShea 2004). Each paired plot was 25 m^2, with a fenced plot excluding deer herbivory paired with an open control plot 10 m away that permitted browsing. Fenced plots were used to increase understory structural complexity and to provide comparison with heavily browsed habitat. Forest patches existed in a fragmented landscape and contained multiple invasive plant species and are heavily browsed by white-tailed deer populations ranging from $46 - 66$ deer/km^2. Common invasive plant species included multiflora rose (*Rosa multiflora*), Japanese stiltgrass, and garlic mustard (*Alliaria petiolata*). The forest canopy was dominated by maples (*Acer negundo* and *A. saccharinum*), white ash (*Fraxinus americana*), and hickory (*Carya* spp.), with an understory consisting mostly of northern spicebush (*Lindera benzoin*) and paw-paw (*Asimina triloba*).

To evaluate the extent that deer herbivory and invasive plants influence spider nutritional dynamics via habitat structure, I sampled a long-jawed orb weaving spider common to eastern deciduous forests (Tetragnathidae: *Leucauge venusta* Walckenaer

1841). *L. venusta* spins a relatively horizontal orb web with attachment points in low shrubs and trees of wooded areas (Kaston 1948; Levi 1980; Hénaut et al. 2001) (Figures 9 & 10). Though the viscid portion of the web is approximately 20 cm (Kaston 1948; Levi 1980), supporting anchor strands of *L. venusta* webs may span up to 2.0 m in the study area (pers. obs.). With a maximum total length of 5.9 mm (Levi 1980), *L. venusta* and other orb-weaving spiders of this size prey mostly on flies (Diptera), leaf-hoppers (Hemiptera: Cicadellidae) and other small, alate true bugs (Nyffeler & Benz 1989; Bardwell & Averill 1997; Hénaut et al. 2001).

I collected sexually mature female spiders from all sampled plots in late June of 2015. This time period was selected as I was able to collect adult spiders prior to fertilization by males and subsequent oviposition, as physiological stress causes increased isotopic fractionation (Hobson et al. 1993). Spiders were collected by hand into 2.0 mL microcentrifuge tubules (Carolina Biological Supply) and immediately frozen to prevent further metabolic activity in the gut. Samples were individually dried for 24 h at 60 degrees C, then ground, homogenized, and encapsulated. Individual spiders were analyzed for $\delta^{15}N$ and $\delta^{13}C$ using a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Germany) with an elemental analyzer (ECS 4010, Costech Analytical, California). Isotopic carbon results were expressed in parts per mille relative to Vienna PeeDee Belemnite, with isotopic nitrogen reported in parts per mille relative to atmospheric nitrogen. I used univariate mixed effect models in package 'nlme' in Program R 3.2.3 to assess impacts of habitat structure to $\delta^{15}N$ and $\delta^{13}C$ independently (Pinheiro et al. 2016; R Core Team 2015). All figures were produced using 'ggplot2' (Wickham 2009). Differences in isotopic nitrogen and carbon were analyzed at the paired plot level, as isotopic levels differed

between plots, and differences in vegetative structure were analyzed at the forest patch level, according to previous work which illustrated vegetation community dissimilarity between forest fragments (see Chapter 2). Stem abundance of multiflora rose shrubs was analyzed using generalized linear models with a Poisson probability distribution to account for heterogeneity of variances.

Habitat Structure

I measured habitat structure using a 2.0 m tall vegetative profile board separated into 0.5 m vertical increments (see Chapter 2). Placing the board in the center of each plot, I took digital photographs of the board at the 4 plot edges at a height of 1.0 m (Nikon COOLPIX S3100). I imported images as raster files in ArcGIS (ESRI 2011, ArcMap 10.2., California) and used maximum likelihood estimation to assign each pixel to one of 15 classes based on red, blue, and green pixel coloration. I then used binary reclassification to assign each of the defined classes to a value of 1 for live and dead vegetation and a value of 0 for all non-vegetation. To estimate structure in each of the height classes, I calculated the proportion of pixels obscured by vegetation to total number of pixels within each height class, using the average 0.5 – 2.0 m structure reading for analyses (Figure 3). All structure measurements were collected in late June of 2015. In addition to metrics of structure, I recorded the abundance of multiflora rose stems in each plot as well as the presence or absence of Japanese stiltgrass in four 1 m^2 subplots, arranged as previously described (see Chapter 2).

Results

The best model to explain changes in habitat structure included the presence of Japanese stiltgrass and deer herbivory. The exclusion of deer browse increased habitat structure in the understory ($t=2.2703$, $P=0.0374$), though the effect of deer exclusion on structure was more pronounced in forest patches at ANTI than CHOH (Figure 11). The presence of Japanese stiltgrass as a ground cover decreased habitat structure by over 26% compared to plots without the species ($t=-3.0751$, $P=0.0072$). The Cunningham forest patch at ANTI was the only site with consistently heavy ground cover: for the 3 paired plots, Japanese stiltgrass maintained 100% cover in control plots and 0% cover in plots excluding deer herbivory. Conversely, exclusion of deer herbivory increased the stem abundance of multiflora rose shrubs ($P<0.0001$).

I collected 77 adult female *L. venusta*, with 40 individuals from CHOH plots and 37 from ANTI plots. $\delta^{15}N$ values varied between plots, with an overall mean of 5.5245 ± 0.1231 (Appendix C). Isotopic nitrogen was negatively correlated with habitat structure, with more structure resulting in reduced $\delta^{15}N$ ($t=-2.3506$, $P=0.0406$) (Figures 12 & 13). Mean isotopic carbon ratios were -25.6983 ± 0.0653. $\delta^{13}C$ values were not correlated with vegetative structure ($t=-1.2717$, $P=0.2323$) (Figures 14 & 15). For the Cunningham forest plots with Japanese stiltgrass comprising the dominant groundcover, mean $\delta^{13}C$ values were -25.6843 ± 0.0822.

Discussion

The structural complexity of vegetation has been documented throughout the literature as an important component of spider habitat selection and retention, and is a positive correlate with individual spider health (Hodge 1987a). As is evident with this work, white-tailed deer herbivory can have a great impact on forest understory

physiognomy depending on geographic location and capacity of the forest to sustain

deer populations and native vegetation. Exclusion of deer herbivory, while increasing

habitat structure at ANTI, subsequently increased exotic plant species including

multiflora rose. Such increases in exotic plant species after deer exclusion implicate

the management difficulties of establishing and restoring a functional forest after

ungulate management. Multiflora rose and Japanese stiltgrass were not prevalent

enough within the extant plot design to provide sufficient information as to the

response of spiders to structure from invasive versus native plant species. The dense

growth habit and thorny stems of multiflora rose may increase structure to the point

that it impairs spider movement and web placement sites, though better inclusion of

this plant species within sampling plots would be necessary (Gonçalves-Souza et al.

2011).

Changes in the nitrogen isotopic ratio of a predator can be indicative of the diet

composition of a consumer, and as such can be used in combination with isotopic

carbon to detect taxonomic components of prey (Hood-Nowotny & Knols 2007;

Hyodo 2015). Isotopic nitrogen levels increase with deamination and transamination

as the lighter ^{14}N is preferentially excreted over the isotopic ^{15}N (Miniwaga & Wada

1984). For sampled spiders, decreased habitat structure resulted in enriched $\delta^{15}N$.

Such isotopic nitrogen enrichment could either indicate a shift in prey composition or

physiological stress from a nutritional deficit (Vanderklift & Ponsard 2003). Poor

quality food with a higher carbon:nitrogen ratio or a lack of sufficient prey has

resulted in enriched $\delta^{15}N$ in birds (Hobson & Clark 1992; Hobson et al. 1993; Cherel

et al. 2005), fish (Bowes et al. 2014), and spiders and other invertebrates (Adams &

Sterner 2000; Oelbermann & Scheu 2002). Certain insect populations may reach

higher densities in response to increased vegetation and structure (Langellotto & Denno 2004; Katagiri & Hijii 2015): as passive predators, *L. venusta* may have captured and ingested more prey in structurally complex habitats, resulting in reduced $\delta^{15}N$ and greater body condition. Spider diet in less complex habitats may also consist of different insects than in more complex plots. Changes in diet composition to include less preferable prey items could result in a lower nutrient quality diet and enriched ^{15}N. Parasitic Hymenopterans are not generally considered a preferred prey item for orb-weaving spiders (Nentwig 1983; Uetz & Hartsock 1987), and ingestion of these small wasps would cause enriched $\delta^{15}N$ due to stepwise enrichment of isotopic nitrogen from herbivore to parasitic wasp to spider (Miniwaga & Wada 1984). Detritivorous flies (Diptera) are common prey taken by orb-weaving spiders, though are often $\delta^{15}N$ enriched, as well (Hyodo 2015). Previous work (see Chapter 2) showed a strong, positive response of Diptera to Japanese stiltgrass ground cover: sampled spiders could have ingested relatively higher amounts of flies in these habitats. Using stationary orb webs for prey capture, *L. venusta* diet should reflect the relative densities of flying insect prey within a desired prey size range. If the relative abundance of nitrogen-rich prey were reduced in less complex habitats, parasitic wasps and/or detritivorous flies may comprise a larger portion of the diet. Spiders excrete much of their nitrogenous waste as guanine and may store additional nitrogen within opisthosomal tissues (Seitz 1987; Foelix 2011). As guanicotelic organisms generally use nitrogen efficiently (Vanderklift & Ponsard 2003), such diet shifts that include a greater component of nitrogen-poor prey may affect individual body condition or fecundity (Toft & Wise 1999), but would surely have subsequent impacts to the diet of higher predators. Forest spiders are an important proteinaceous

component of the diet of araneophagic predators such as nesting birds, and changes in the nitrogenous composition of spiders in habitats with reduced physiognomy may prevent attainment of sufficient micro- and macro-nutrients required for proper development (Ramsay & Houston 2003; Ladin 2015).

Though not as effective in detecting predator dietary changes as isotopic nitrogen, organismal $\delta^{13}C$ is capable of identifying plant producer photosynthetic pathways, as the RuBP enzyme associated with C_3 plants discriminates against isotopic carbon (Smith 1972): C_3 plants generally have $\delta^{13}C$ values near -26 to -27‰ while C_4 plants are nearer to -10 to -13‰ (Kelly 2000; Hyodo 2015). While Japanese stiltgrass, a C_4 grass, has been shown to have $\delta^{13}C$ levels of -13.49 to -14.72‰ (Bradford et al. 2010), spiders collected in plots with a stiltgrass-dominated groundcover maintained $\delta^{13}C$ values of approximately -26‰. When considering a mean stepwise increase of 0.5‰ $\delta^{13}C$ per trophic level (McCutchan, Jr. et al. 2003), it is unlikely that the insects supporting spiders in this invaded habitat are utilizing Japanese stiltgrass. Bradford et al. (2010) found that stiltgrass comprised a significant portion of the diet for Orthoptera and larger Hemiptera; however, overall invertebrate herbivory on stiltgrass is generally very low (Sanders et al. 2004; Morrison et al. 2007) and the insects that Bradford et al. studied are not ingested by most forest web-building spiders. If insect prey had been utilizing the stiltgrass, the spider $\delta^{13}C$ values should be much closer to that of C_4 plant species. The producer species supporting the food web in this forest patch are the less abundant herbaceous and woody C_3 plants.

These findings, albeit preliminary, lay the foundation for a closer examination of spider dietary changes resulting from both habitat structure and invasive species. Further investigation into relative abundances and densities of insect prey taxa is a

crucial next step for examining specific compositional changes for the potential prey base for this spider as well as other forest web-building species. Comprehensive isotopic carbon and nitrogen analyses of spider populations, insect prey communities, and prevalent plant species will also allow for a clearer view of the trophic relationships in such invaded and structurally homogeneous habitats. It is apparent that changes in habitat structure resulting from deer browse and the prevalence of invasive Japanese stiltgrass both have significant impacts on the nutritional dynamics of this system, with subsequent implications for higher level predators that require proteinaceous prey such as forest spiders.

FIGURES

Figure 9   Study species, *Leucauge venusta* Walckenaer 1841 (Tetragnathidae), showing typical web construction and waiting location for hunting spider. Photograph by Gustavo Hormiga, Ph.D., George Washington University.

Figure 10   Study species, *Leucauge venusta* Walckenaer 1841 (Tetragnathidae), showing typical position under web. Photograph by Richard Orr, Mid-Atlantic Invertebrate Field Studies.

Figure 11   Boxplot showing effect of deer exclusion on habitat structure in June, 2015. Data from individual forest sites
are represented separately, with individual bars for fenced plots and control or open plots. Cunningham and
WestWoods forest sites are within ANTI and Snyders and Taylors forest sites are within CHOH. Boxes
represent 1st and 3rd quartiles and median. Points greater than 1.5 times the interquartile range are considered
outliers and are shown as individual points.
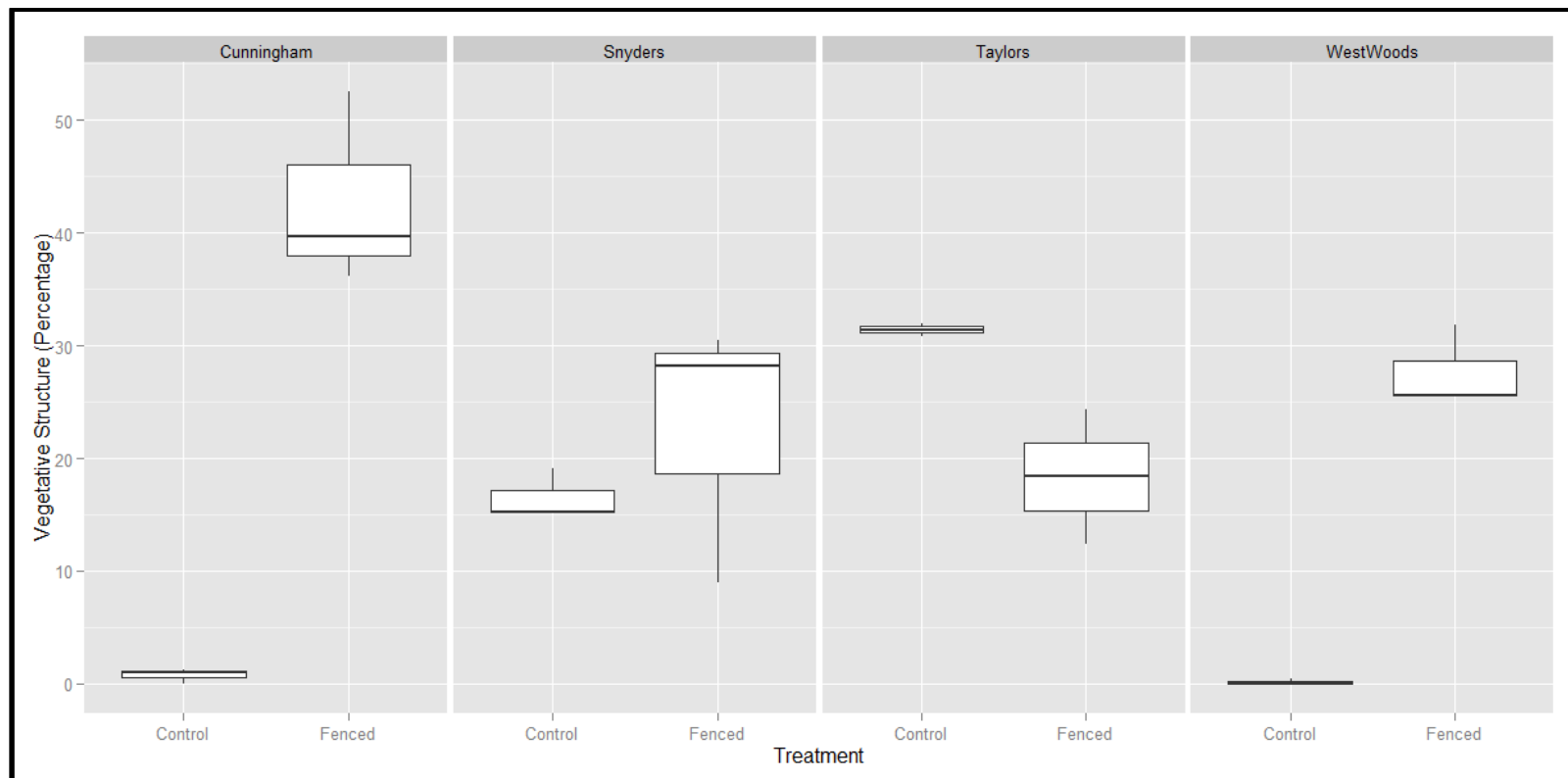
Figure 12   Plot showing spider δ^{15}N in relation to habitat structure in plots within Cunningham (AC1, AC2, AC3) and
West Woods (AWW1, AWW2, AWW3) forest sites at ANTI in June, 2015. Data from paired plots are
represented separately, with individual bars for fenced plots and control or open plots. All fenced plots
contained higher vegetative structure than control plots. Error bars represent ± 1 standard error from the mean.
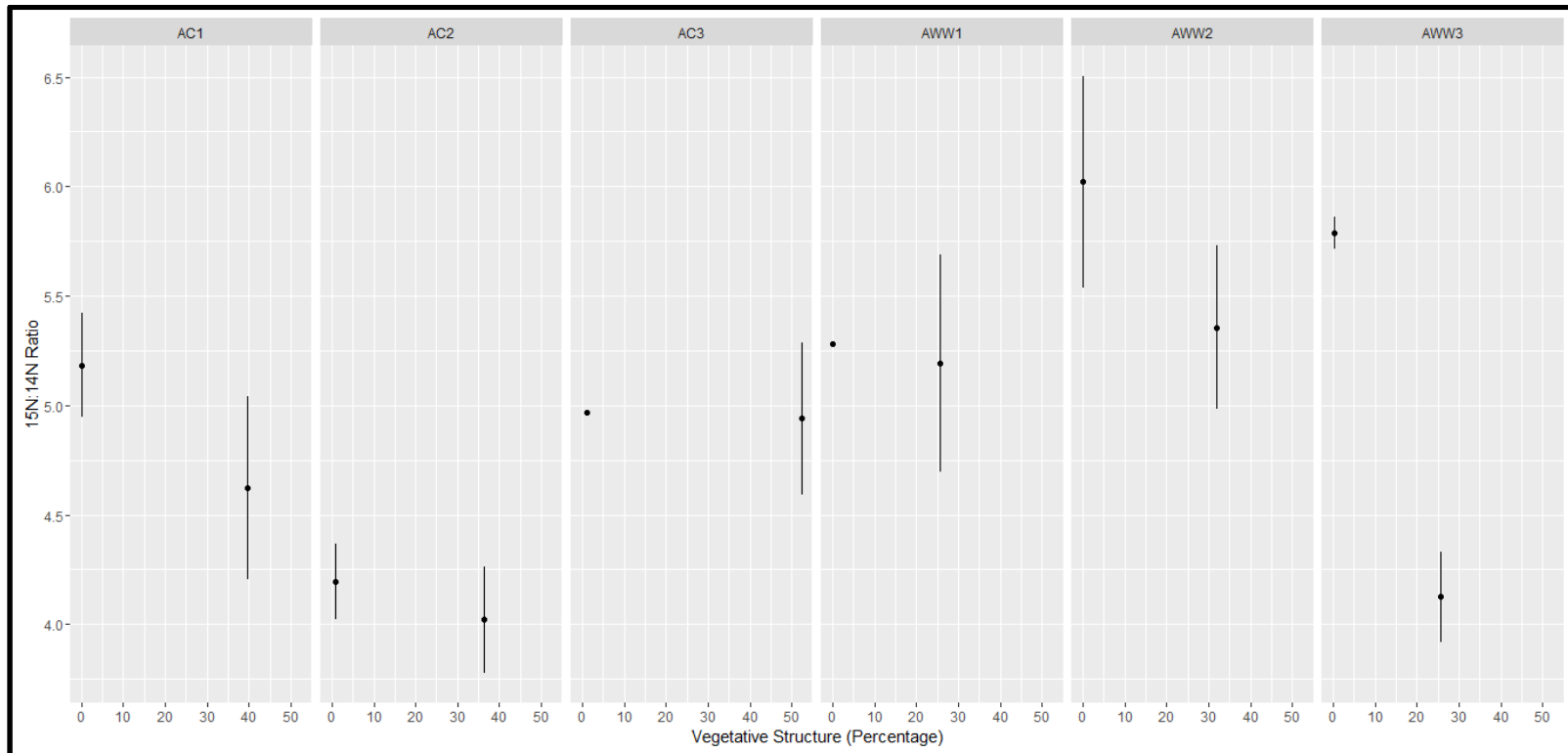
Figure 13   Plot showing spider $\delta^{15}N$ in relation to habitat structure in plots within Taylors (CC2, CC3) and Snyders (CD1, CD2, CD3) forest sites at CHOH in June, 2015. Data from paired plots are represented separately, with individual bars for fenced plots and control or open plots. Control plots in the Taylors forest site had greater structure while control plots in Snyders forest site had less structure than fenced plots. Error bars are ± 1 standard error from the mean.
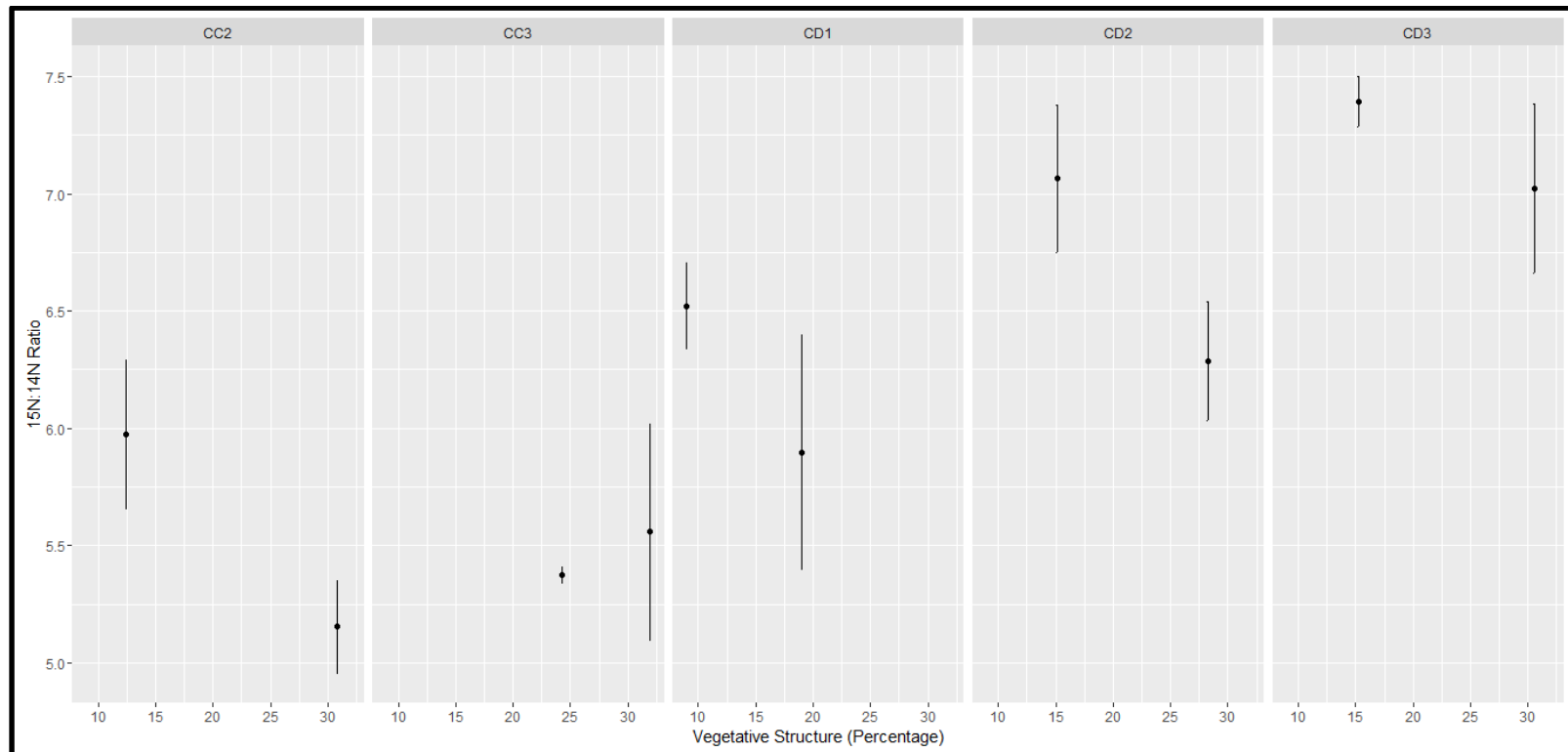
Figure 14   Plot showing spider δ¹³C in relation to habitat structure in plots within Cunningham (AC1, AC2, AC3) and West Woods (AWW1, AWW2, AWW3) forest sites at ANTI in June, 2015. Data from paired plots are represented separately, with individual bars for fenced plots and control or open plots. All fenced plots contained higher vegetative structure than control plots. Error bars are ± 1 standard error from the mean.
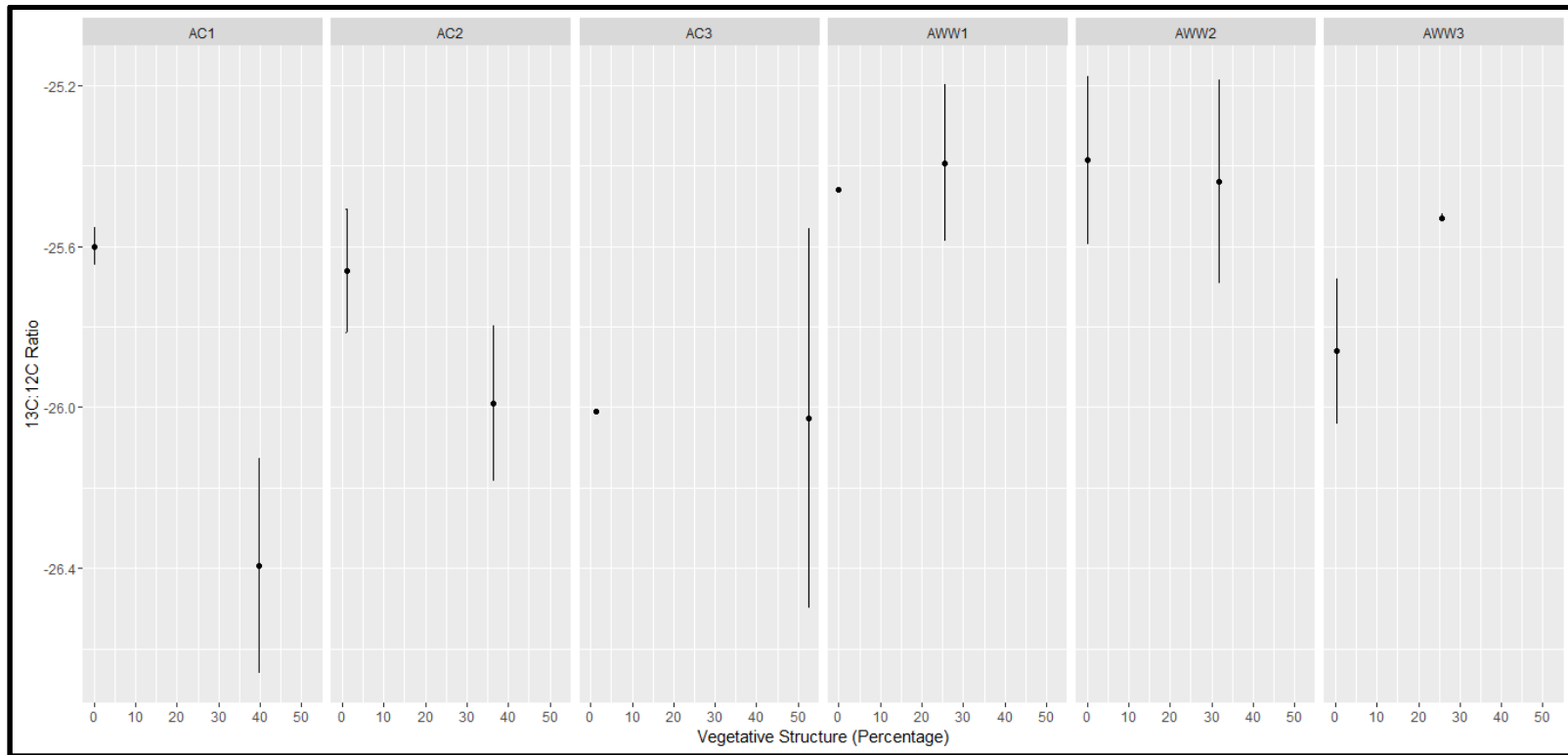
Figure 15   Plot showing spider $\delta^{13}C$ in relation to habitat structure in plots within Taylors (CC2, CC3) and Snyders (CD1, CD2, CD3) forest sites at CHOH in June, 2015. Data from paired plots are represented separately, with individual bars for fenced plots and control or open plots. Control plots in the Taylors forest site had greater structure while control plots in Snyders forest site had less structure than fenced plots. Error bars are ± 1 standard error from the mean.
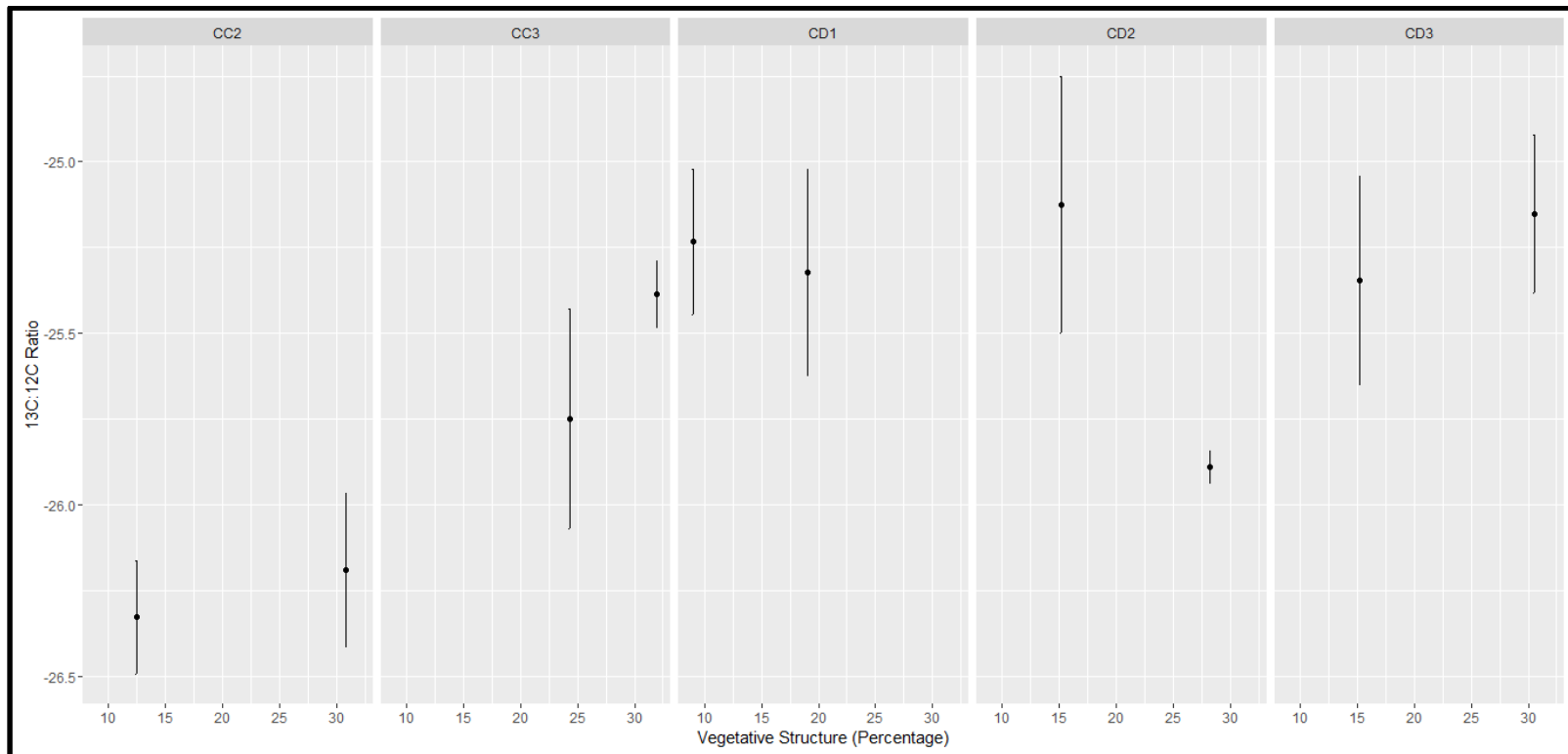
Chapter 4

MANAGEMENT IMPLICATIONS

As a predator highly dependent on plants for substrate and insects for nutrition, forest spiders are indirectly affected by controllable factors that alter the architecture and capacity of the understory to support a diverse and abundant insect population. Vegetative structure plays a prominent role in helping define spider community composition, as has been illustrated in various habitats, including deciduous forests of the eastern U.S. as documented here. Although structurally complex vegetation resulted in reduced spider species richness overall, isotopic data on a representative orb-weaving spider showed reduced δ^{15}N enrichment in such complex habitats, indicating better body condition and likely higher growth rates. Insect prey availability similarly played an important role in the assemblage of spider families and functional groups, and positively influenced richness and abundance of all groups. Ecosystem-engineering invasive plant species and dense white-tailed deer populations, through their capacity to modify habitat structure and/or insect prey density, can alter the ecology of this important arthropod group, with the potential for shifting energy and nutritional dynamics of forest food webs.

The architects and structural components of forests, as well as the basal source of energy for almost all living organisms on earth, plants are the most important component of any conservation and management action. The negative ecological impacts of deer browse on native vegetation are well understood and thoroughly documented throughout the scientific literature, the most critical impact being a

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prevention of native forest seedling regeneration. Forest wildlife taxa, including birds, small mammals, and invertebrates, all depend on forest vegetation to provide shelter from predators, suitable sites for oviposition, food, and/or structure upon which to find food. In fragmented landscapes such as this study area, small forest patches in protected areas such as national parks may be some of the only remaining habitat available for forest species. With documented lack of native, understory tree seedlings and dense white-tailed deer populations in these 3 national parks, it is apparent that active management of the deer population is overdue. Permitted and recommended by NPS Management Policies (National Park Service 2006), direct ungulate management is an essential action to be taken in order to protect native vegetation as well as native forest wildlife. Despite a long history of high deer densities in the area, native forest seedlings at the neighboring Catoctin Mountain Park have shown a relatively quick, positive response after a reduction in population size via lethal management (NPS unpublished data).

However, as seen here with multiflora rose, reducing deer browse can allow some invasive plants to succeed and compete with native species (Coomes et al. 2003). Due to the effects of herbivore release on invasive plants, it is apparent that a simple reduction in browsing pressure will not restore a native and diverse forest understory. Invasive plant species, particularly those that may greatly alter habitat structure or significantly reduce phytophagous insect populations, should be prioritized for management and controlled in forested areas. Plant species such as Japanese stiltgrass may still support spider prey, though changes to the relative abundance of preferred prey may have detrimental physiological impacts to the individual predator, with potentially substantial effects to higher level consumers such

as forest birds. Gratton & Denno (2006) present a scenario in which the invertebrate food web of a brackish marsh was significantly altered due to the invasive common reed. Dietary composition of spiders was altered to include a greater proportion of detritivores in the presence of the reed; however, in habitats with native smooth cordgrass, spider diet included very little detritivorous prey and instead comprised mostly herbivorous insects. Such changes to the arthropod food web, brought about through replacement of native plants by invasive species, are largely undocumented and potentially pervasive across forest habitats with introduced and invasive plants.

Despite their ecological importance in supporting higher level predators and regulating insect populations, direct conservation and management of spider communities and/or specific taxa is unlikely to ever become a priority for state, local, or federal conservation agencies. However, their small size and home range allow them to benefit from large-scale management designed to conserve other taxa. In small forest fragments, understory spider communities are likely to consist of many common species and those that are resilient to human disturbance and edge habitats. Although forest edges and ecotones generally maintain higher spider diversity due to the intergradation of forest/open habitat species (Downie et al. 1996), forest interior habitats support a greater abundance of spiders (Rodrigues et al. 2014). To provide more suitable habitat for forest spiders, as well as a multitude of other taxa, larger forest patches should be included in conservation areas. Within the study area, many of the state and national protected areas are in part conserved for their historical importance with little to no concern regarding arthropod conservation. Consideration of ecological processes and conservation of natural communities must be included in long-range planning and management efforts to more effectively protect spiders and

other invertebrates, as well as migratory birds, small mammals, and other taxa. Small, disconnected forest patches such as these, amidst human development and agriculture, may not provide sufficient interior area to support wildlife populations nor the habitat connectivity necessary to maintain the genetic diversity of forest obligate species.

Monitoring of spider communities has been recommended as a cost-effective method for assessing habitat health and responses to environmental factors (Gibson et al. 1992; Kremen et al. 1993). Recurrent sampling for spiders is easily standardized, as sampling can be done quickly, adults can be separated into family or morphospecies relatively easily, and some genera and families can exhibit strong ties to specific habitat characteristics and dominant vegetation. However, the difficulty in identifying juvenile spiders as well as many of the small, morphologically similar species (e.g., Linyphiidae) often precludes use of this group for indicator taxa unless taxonomic expertise is available. As an important component of forest bird diet, conservation and monitoring systems should focus on avian species. Mentioned above, reduction in landscape fragmentation and increasing the size of protected forest patches should benefit forest interior obligate species by providing habitat, reducing nest parasitism, and reducing competition with ecotone and synanthropic species (Boulinier et al. 2001; Chalfoun et al. 2002). Protected area managers should select forest interior obligate birds of management concern to enhance research on dietary composition. Research into such diet composition generally pools all spiders sampled into a single order; however, the dietary taxonomic composition is a critical need in identifying potential changes in the availability of preferred prey. Changes in spider community structure could alter the biomass and nutritional content of spiders eaten by birds and fed to altricial young. Reduced protein and nitrogen availability for young birds has

shown to affect proper development and growth (Ramsay & Houston 2003; Ladin 2015).

The current, resultant condition of small forest patches in the populous eastern U.S. is the product of a long history of deer browsing and anthropogenic land development and use without regard to maintenance of ecological processes. With further increases in development and the globalization of trade and commerce, novel invasive plant species are likely to continue to arrive in the region and threaten natural areas. Priority conservation actions should include the immediate management of deer populations and the ongoing, routine maintenance of invasive plant species known to alter habitat structure and/or insect densities in order to keep plants from exceeding a controllable level. Direct management of these factors will provide the opportunity for native vegetation to regenerate, ultimately aiding the restoration of forest habitat throughout the region. Longer term management goals should include the restoration of larger sections of forest habitat and the enhancement of forest connectivity to assist in juvenile dispersal and maintenance of genetic diversity, as well as an overarching incorporation of ecological process and natural resources into long-range planning. Finally, there are also key research and monitoring endeavors necessary to more comprehensively assess potential and realized impacts of these environmental changes to invertebrate-vertebrate food webs.

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Appendix A

PLANT SPECIES FOUND IN STUDY AREA

Table 10   Plant species identified throughout the study area in July, 2013.

Acer negundo	*Carya* sp.	*Maianthemum racemosum*	*Quercus prinus*
Acer rubrum	*Caulophyllum thalictroides*	*Microstegium vimineum**	*Rosa multiflora**
Actaea sp.	*Celastrus orbiculatus**	*Morus* sp.	*Rubus occidentalis*
Ailanthus altissima*	*Celtis occidentalis*	*Nyssa sylvatica*	*Rubus phoenicolasius**
Alliaria petiolata*	*Chenopodium album*	*Oxalis* sp.	*Sanicula canadensis*
Ambrosia artemisiifolia	*Circaea lutetiana*	*Parthenocissus quinquefolia*	*Smilax* sp.
Amphicarpaea bracteata	*Conium maculatum**	*Perilla frutescens**	*Solidago* sp.
Arisaema triphyllum	*Duchesnea indica**	*Phytolacca americana*	*Toxicodendron radicans*
Asarum canadense	*Fagus grandifolia*	*Pilea pumila*	*Trillium cernuum*
Asclepias sp.	*Fraxinus americana*	*Platanus occidentalis*	*Ulmus rubrum*
Asimina triloba	*Galium* sp.	*Poa* sp.	*Urtica dioica*
Aster sp.	*Glechoma hederacea**	*Polygonum persicaria**	*Verbesina alternifolia*
Berberis thunbergii*	*Hedeoma pulegioides*	*Polymnia canadensis*	*Viola* sp.
Boehmeria cylindrical	*Laportea canadensis*	*Prunus serotina*	*Vitis* sp.
Carpinus caroliniana	*Lonicera japonica**	*Quercus alba*	

*   Considered introduced in the study area by the United States Department of Agriculture PLANTS Database (USDA 2016).

Appendix B

SPIDER SPECIES

Table 11   List of spider species collected in August, 2013 throughout study area.
Functional group classification was modified from Cardoso et al. (2011)
and indicates the group within which each species or genus was placed
for analyses.

Family	Species	Functional Group
Agelenidae	*Agelenopsis* sp.	Ground spiders
Anyphaenidae	*Anyphaena* sp.	Hunting spiders
	Wulfila sp.	Hunting spiders
	Acacesia hamata	Orb weaving spiders
	Araneus sp.	Orb weaving spiders
	Araniella displicata	Orb weaving spiders
	Eustala sp.	Orb weaving spiders
	Mangora maculata	Orb weaving spiders
	Mastophora sp.	Orb weaving spiders
Araneidae	*Metepeira labyrinthea*	Orb weaving spiders
	Micrathena gracilis	Orb weaving spiders
	Neoscona arabesca	Orb weaving spiders
	Neoscona domiciliorum	Orb weaving spiders
	Ocrepeira sp.	Orb weaving spiders
	Verrucosa arenata	Orb weaving spiders
Clubionidae	*Clubiona* sp.	Hunting spiders
	Elaver sp.	Hunting spiders
Corinnidae	*Castianeira* sp.	Ground spiders
	Trachelas tranquillus	Ground spiders
Dictynidae	*Dictyna* sp.	Space web spiders
	Ceratinopsidis sp.	Space web spiders
	Ceratinopsis sp.	Space web spiders
Linyphiidae	*Erigoninae*	Space web spiders
	Frontinella communis	Space web spiders
	Linyphiinae	Space web spiders
Lycosidae	Unknown sp.	Ground spiders

Mimetidae	*Mimetus* sp.	Araneophagic/kleptoparasitic
Oxyopidae	*Oxyopes* sp.	Hunting spiders
Philodromidae	*Philodromus* sp.	Hunting spiders
Pisauridae	*Dolomedes* sp.	Hunting spiders
	Pisaurina mira	Hunting spiders
Salticidae	*Neon/Neonella* sp.	Hunting spiders
	Sitticus sp.	Hunting spiders
	Thiodina sylvatica	Hunting spiders
	Zygoballus rufipes	Hunting spiders
Tetragnathidae	*Leucauge venusta*	Orb weaving spiders
	Tetragnatha laboriosa	Orb weaving spiders
Theridiidae	*Argyrodes elevatus*	Araneophagic/kleptoparasitic
	Cryptachaea sp.	Space web spiders
	Dipoena nigra	Space web spiders
	Euryopis funebris	Space web spiders
	Rhomphaea fictilium	Araneophagic/kleptoparasitic
	Steatoda sp.	Space web spiders
	Theridion albidum	Space web spiders
	Theridion frondeum	Space web spiders
	Theridula sp.	Space web spiders
	Thymoites unimaculatus	Space web spiders
	Yunohamella lyrica	Space web spiders
Theridiosomatidae	*Theridiosoma gemmosum*	Orb weaving spiders
Thomisidae	*Misumena* sp.	Hunting spiders
	Misumenops sp.	Hunting spiders
	Synema parvulum	Hunting spiders
	Tmarus sp.	Hunting spiders
	Xysticus sp.	Hunting spiders
Uloboridae	*Hyptiotes cavatus*	Orb weaving spiders

ISOTOPIC ENRICHMENT SAMPLES

Table 12   Mean δ^{15}N and δ^{13}C values ± standard error for sampled *Leucauge venusta* in plots at ANTI in June, 2015. Entire spider bodies were dried, homogenized, and included for analyses. Isotopic nitrogen and carbon are reported in parts per mille relative to Vienna Pee Dee Belemnite (Carbon) and atmospheric nitrogen (Nitrogen).

Site	Plot	Treatment	δ^{15}N (‰) ± SE	δ^{13}C (‰) ± SE
Cunningham	AC1	Control	5.18 ± 0.24	-25.60 ± 0.05
	AC1	Fenced	4.62 ± 0.42	-26.39 ± 0.27
	AC2	Control	4.20 ± 0.17	-25.66 ± 0.15
	AC2	Fenced	4.02 ± 0.24	-25.99 ± 0.19
	AC3	Control	4.97	-26.01
	AC3	Fenced	4.94 ± 0.35	-26.03 ± 0.47
West Woods	AWW1	Control	5.28	-25.46
	AWW1	Fenced	5.19 ± 0.50	-25.39 ± 0.19
	AWW2	Control	6.02 ± 0.49	-25.39 ± 0.21
	AWW2	Fenced	5.36 ± 0.37	-25.44 ± 0.25
	AWW3	Control	5.79 ± 0.07	-25.86 ± 0.18
	AWW3	Fenced	4.13 ± 0.21	-25.53 ± 0.01

Table 13   Mean δ^{15}N and δ^{13}C values ± standard error for sampled *Leucauge venusta* in plots at CHOH in June, 2015. Entire spider bodies were dried, homogenized, and included for analyses. Isotopic nitrogen and carbon are reported in parts per mille relative to Vienna Pee Dee Belemnite (Carbon) and atmospheric nitrogen (Nitrogen).

Site	Plot	Treatment	δ^{15}N (‰) ± SE	δ^{13}C (‰) ± SE
Taylors	CC2	Control	5.15 ± 0.20	-26.19 ± 0.22
	CC2	Fenced	5.98 ± 0.32	-26.33 ± 0.17
	CC3	Control	5.56 ± 0.46	-25.39 ± 0.10
	CC3	Fenced	5.38 ± 0.04	-25.75 ± 0.32
Snyders	CD1	Control	5.90 ± 0.50	-25.32 ± 0.30
	CD1	Fenced	6.52 ± 0.18	-25.23 ± 0.21
	CD2	Control	7.07 ± 0.32	-25.13 ± 0.38
	CD2	Fenced	6.29 ± 0.25	-25.89 ± 0.05
	CD3	Control	7.39 ± 0.11	-25.35 ± 0.30
	CD3	Fenced	7.02 ± 0.36	-25.15 ± 0.23