Discordant response of spider communities to forests disturbed by deer herbivory and changes in prey availability

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Abstract. Despite the breadth of research on impacts of dense ungulate populations and invasive plants on native vegetation, work involving indirect effects on spider communities is explicitly lacking. Forest spiders depend on palatable insect prey and habitat structure, both of which are affected by herbivory and invasive vegetation. To examine the indirect interactions between spiders and these influential factors, we sampled spider communities, insect prey, and vegetation in paired deer exclusion plots in central Maryland. Spider abundance and richness increased with greater prey density, while increased habitat structure from deer exclusion reduced species richness and the abundance of a dominant web-building species. Multivariate analyses of spider families also demonstrated the importance of both prey availability and structural complexity to spider community composition. This work identifies the importance of both habitat structure and insect prey in defining the composition, abundance, and richness of forest spider communities. A long history of heavy browsing pressure has resulted in local spider fauna consisting of many species that are able to thrive in low-growing vegetation and open forest understories. Such changes to vegetative structure from dense deer populations and invasive plants have the potential to affect these important primary predators as well as araneophagic birds and the nutritional dynamics of forest food webs.

Key words: Araneae; habitat structure; indirect effects; Odocoileus virginianus; white-tailed deer.

INTRODUCTION

The abundance of palatable insect prey and habitat structural complexity are two of the most significant predictors of spider abundance, density, and habitat selection (Rypstra 1983, Langelotto and Denno 2004). Web-building spiders are highly dependent on vegetative architecture for web attachment, while many active hunting spiders that do not utilize webs for prey capture still require vegetative structure upon which to hunt for prey. 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. Such spatially complex habitats create a more suitable landscape upon which spiders may track down potential prey and can serve as effective refugia from araneophagic and intraguild predators (Schmidt and Rypstra 2010). Across geographic regions, increased structural complexity of vegetation concomitantly increases the diversity and abundance of spiders in all habitat types (Gibson et al. 1992, McNett and Rypstra 2000). Much of the recent work involving understory spider communities and vegetative structure has
occurred in Japanese evergreen forests, with results relatively concordant among studies: Forest understory structure increases spider richness, density, and abundance (Miyashita et al. 2004).

Non-predatory insects are the main source of energy and nutrients for most spiders; therefore, the availability and abundance of suitable insect prey is also an essential component of preferred habitat for spiders (Katagiri and Hijii 2015). 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, Leborgne and Pasquet 2005). 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. Significant changes to the abundance and nutrient dynamics of this predatory group resulting from altered habitat structure or prey base may have substantial ecological and trophic implications on any natural system, particularly as spider communities may influence the density of insect populations and provide critical nutritional contributions to araneophagic predators such as forest birds (Moulder and Reichle 1972, Gunnarsson 2007).

Two common and widespread influences to both vegetative structural complexity and insect populations in the eastern United States are invasive plants and browsing from white-tailed deer (*Odocoileus virginianus*). 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. Herbivory from dense deer populations 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 and Hijii 2015). Extensive deer browsing may also reduce the abundance and diversity of both predatory insects and their phytophagous insect prey (Allombert et al. 2005), as well as vertebrates that rely on understory structure browsed by deer, such as forest-obligate birds and small mammals (Byman 2011, Tymkiw et al. 2013). Beyond the physical structure of forest vegetation that may affect spider habitat, browsing from dense deer populations also reduces the density of native tree seedlings and other understory plants, ultimately altering entire forest plant communities (Rooney 2001, Eschtruth and Battles 2008). Certain invasive plant species also have the capacity to alter vegetative structure, leading to the potential for latent, secondary impacts on multiple trophic levels and taxa (Crooks 2002). Further obfuscating these interactions, deer browse may also facilitate the growth of some exotic species in this area of the country (Shen et al. 2016).

Despite near ubiquitous pressure from dense deer populations and invasive and exotic vegetation throughout forest patches in the eastern United States, knowledge of the impacts on spider communities and invertebrate trophic webs is explicitly lacking. We studied the comprehensive effects of deer herbivory and invasive plant species on forest spider and insect prey communities, mediated by their effects on understory vegetation. Utilizing long-term deer exclusion plots in three National Park Service (NPS) units in central Maryland, we examined forest spider abundance, species richness, community composition, and prey availability in habitats including and excluding deer herbivory. Densities of white-tailed deer in our study area ranged from 46 to 66 deer/km², a density similar to other protected, urban/suburban areas in the eastern United States (e.g., Lovallo and Tzilkowski 2003), yet well above the density recommended for successful forest regeneration (Tilghman 1989, Horsley et al. 2003). Our objectives were to (1) analyze changes to plant structural complexity and species composition caused by dense deer populations and invasive plant species; (2) elucidate variations in insect prey availability; and (3) illustrate indirect effects of deer herbivory on understory spider communities mediated through forest vegetation and insect densities. This provides 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**

We studied impacts of altered vegetative structure on spider communities in three NPS units in
central Maryland: Antietam and Monocacy National Battlefields (Antietam; Monocacy) and the C&O Canal National Historical Park (C&O Canal; Fig. 1). These parks were located in a mosaicked landscape consisting of urban and suburban development, small forest fragments, and agriculture. In addition to providing habitat for dense populations of white-tailed deer, forests in all parks were heavily influenced by invasive, exotic vegetation including Japanese stiltgrass (*Microstegium vimineum*), multiflora rose (*Rosa multiflora*), and garlic mustard (*Alliaria petiolata*). Dominant woody vegetation included native maples (*Acer negundo* and *Acer saccharinum*) and hickory species (*Carya* spp.), with an understory of mostly northern spicebush (*Lindera benzoin*) and paw-paw (*Asimina triloba*). To monitor changes in vegetation resulting from white-tailed deer populations, paired exclusion plots were installed in 2003 by NPS and Smithsonian Institution staff throughout forests in the parks. Each plot was 25 m² with fenced plots consisting of 2.4 m tall, 10 × 10 cm woven wire fencing. All fenced plots were open from above and permitted entry to birds and small mammals. A random number generator 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. In total, 25 paired plots in nine forest patches were sampled. We sampled 11 paired plots in four forest sites at Antietam (Cunningham, Sherrick, Snavely, and West Woods), five paired plots in two forest sites at Monocacy (Brooks Hill and Lewis), and nine paired plots in three forest sites at C&O Canal (North Potomac, Snyders, and Taylors).
Vegetation sampling

We sampled vegetation in all paired plots in July 2013 using four subplots, each 1 m² in size and located 0.75 m from the edges of each of the four plot sides. Though vegetative response to deer exclusion was measured only during 2013, these data were included in the long-term monitoring dataset maintained by the NPS. Within subplots, we identified all plants and 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. To assess the structural complexity of understory vegetation, we constructed a vegetative profile board from 0.64 cm plywood, 2.0 m in height and 35.0 cm wide. We placed the board in the center of each plot and used a 12-megapixel digital camera (Nikon COOLPIX S3100; Nikon Corporation, Tokyo, Japan) to take photographs of the board from each square plot edge at a height of 1.0 m. For analyses, we imported images as non-georeferenced raster files in ArcGIS (ArcMap 10.0; ESRI, Redlands, California, USA). Using only the spatial extent of the board within the photograph, we then used maximum-likelihood estimation to assign each pixel to one of 15 multivariate classes based on red, blue, and green pixel coloration. For a structure metric, we calculated the proportion of pixels obscured by dead and live vegetation to total number of pixels in the clipped photograph (Fig. 2). We averaged the four structure estimates of vegetative structure between 0.5 and 2.0 m for each plot and used the mean value in analyses.

Arthropod sampling

We sampled both insect and spider communities in August 2013, the time at which most web-building spiders are mature. Although
invertebrate population densities often vary between years, we were interested in relationships with environmental parameters and not temporal differences. Spiders generally develop later in the season and will similarly respond with an increase or decrease in the insect population, so we did not expect annual fluctuations to alter our effect sizes or any correlative relationships. We collected arthropods using vacuum sampling methodology (Craftsman 25 cc blower/vacuum with 5-gallon paint strainer bag; Sears Brands, LLC, Hoffman Estates, Illinois, USA) for 10 min within each plot. We randomly sampled all vegetative surfaces for insects and hunting spiders, as well as interstitial spaces for flying insects and web-building spiders, between 0.5 and 2.0 m to encompass the browsing area for white-tailed deer. Larger spiders that were not effectively collected using a vacuum sampler (e.g., adult Neoscona spp.) were collected by hand. As ground spider fauna have exhibited varied responses to deer browsing, this specific group was avoided by sampling above 0.5 m. After the vacuuming period, we tied off the paint strainer bag, euthanized specimens with ethyl acetate, and placed samples in 95% EtOH. We identified insects to order and spiders to the lowest taxonomic ranking possible, then grouped spiders in each plot to obtain family-level dry biomass.

Statistical analyses

Vegetative diversity and structure.—We calculated Shannon–Wiener diversity of woody plant species and used the Jaccard dissimilarity metric to compare both woody and herbaceous species between plots and forest patches. We then used linear mixed-effect models to assess the impacts of deer exclusion on vegetative diversity, species richness, and structure. To account for broad differences in vegetative communities between forest patches, individual patch was included as a random effect in mixed models. We utilized the Jaccard index to perform permutational multivariate analysis of variance (MANOVA) of plant community dissimilarity between forest patches to ensure the appropriate strata for the random effect (McArdle and Anderson 2001). Though these permutational models are less sensitive to heterogeneity, we used “betadisper” in package “vegan” to ensure multivariate homogeneity of variances (Oksanen et al. 2016).

Insect prey abundance and biomass.—Insects were classified by order or 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, we separately classified insects palatable to the forest understory spiders we collected (Diploperenidae, non-predatory Hemiptera, Psocidea, and Thysanoptera) (Nentwig 1983, Bardwell and Averill 1997). We used mixed-effect models in package “nlme” for analyzing relationships between insect abundance and biomass, native and exotic plant richness, and the exclusion of deer herbivory (Pinheiro et al. 2016). We used a logarithmic transformation to obtain normality for insect groups that were non-normally distributed.

Spider communities.—We classified spiders into five functional groups based on prey capture method, namely orb web-weaving spiders, space or cobweb weavers, active hunting species, ground-dwelling spiders, and species that almost exclusively utilize other spiders for prey. Collected only incidentally in understory vegetation, ground spiders were identified but excluded from analysis and the kleptoparasitic and araneophagic species were excluded from multivariate analyses as they represented only a small portion of overall spiders collected. As mixed-effect models with spider counts exhibited non-constant error variance, we used generalized linear models (GLM) in packages “lme4” and “MASS” to analyze the response of spider abundance and richness to deer exclusion, insect prey abundance, and forest patch (Venables and Ripley 2002, Bates et al. 2015). We also incorporated our metric of vegetative structure into subsequent models, but did not include deer exclusion and vegetative structure in the same models due to their covariance. Depending on model overdispersion, as tested using function “dispersiontest” in R package “AER,” we used either a Poisson or negative binomial probability distribution (Kleiber and Zeileis 2008). Species diversity indices for spider communities were not used in analysis as too few adults were captured to effectively represent the community at the species or genus level. To comprehensively assess changes to spider community structure, we used multivariate linear regression to model
effects of deer exclusion, insect prey, and forest patch on the relative abundance of spider functional groups and families. We also performed post hoc univariate linear regression on the relative abundance of functional groups and used Poisson GLM for analyzing the raw abundance of individual families. Bray-Curtis ecological dissimilarity of spider communities was used in permutational MANOVA tests for both functional groups and taxonomic families to assess variations in spider community response to deer exclusion, prey abundance, and forest patch. Analogous to the permutational MANOVA, we used distance-based as well as traditional redundancy analysis (RDA) to plot ordination figures for spider communities. For all multivariate tests, we used a factorial variable derived from our measure of insect density by splitting the variable distribution into seven classes in increments of 50 individuals. All statistical analyses were completed in Program R 3.3.1 (R Core Team 2016).

RESULTS

Vegetative diversity and structure
Throughout all plots, we identified 26 tree and shrub species, as well as two graminoid, four vine, and 34 herbaceous species. Vegetative communities were dissimilar between forest patches ($F_{8,41} = 2.707, P = 0.001$). Richness of native species and all plant species did not differ in fenced and control plots ($P > 0.1$), with a mean of 8.26 ± 0.41 total species and 5.66 ± 0.38 native species per plot. However, diversity of woody plant species increased with deer exclusion ($t = 2.685, P = 0.011$) as fenced plots contained greater evenness. Plant structure was positively correlated with deer exclusion ($t = 4.021, P < 0.001$), though trends were not significant in plots at C&O Canal (Fig. 3). Habitat structure increased with the presence of multiflora rose ($t = 2.458, P = 0.019$). Although habitat structure was visibly reduced in forests with Japanese stiltgrass, too few paired plots contained this species to include in models.

Insect prey abundance and biomass
We collected 11,298 insects and related taxa, including three non-spider arachnid groups. Insects from 15 orders were found, with flies, true bugs, and parasitic Hymenoptera the most abundant taxa. We 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 nativity and structure of vegetation, depending on order and typical diet (Table 1). Overall insect abundance decreased with exotic plant species richness ($t = -2.327, P = 0.025$). Palatable insect prey abundance and biomass also decreased with exotic plant species richness ($P = 0.031; P = 0.036$). Though deer exclusion was not a significant predictor of either insect prey or overall invertebrate abundance, removal of deer herbivory did increase both the abundance and biomass of insect herbivores ($P = 0.040; P = 0.045$). Vegetative structure increased insect prey abundance only at $P = 0.1$ ($t = 1.693, P = 0.099$). Native plant species richness increased the abundance or biomass of several insect orders, including flies ($P = 0.097$), beetles ($P = 0.074$), and caterpillars ($P = 0.060$). Conversely, greater exotic plant species richness decreased the abundance of flies ($P = 0.009$), beetles ($P = 0.043$), and overall insect prey ($P = 0.031$), as well as true bug biomass ($P = 0.038$). Beetle abundance and biomass increased with deer exclusion ($P < 0.001; P < 0.001$); however, the abundance of parasitic
wasps decreased in fenced plots \( (P = 0.002) \). Both predatory Hemipterans and parasitoid wasps were positively correlated with available prey \( (P = 0.067; P < 0.001) \).

**Spider communities**

We identified 7653 spiders in 17 families, comprising 56 species. We collected 170.9±17.28 spiders per plot at C&O Canal, 178.6±11.53 at Antietam, and 64.5±13.58 spiders per plot at Monocacy. Sexually mature spiders constituted only 5.07% of individuals collected, and newly hatched, first-instar spiders represented 36.18% of individuals and 1.94% of total spider biomass. Hunting spider species were the most abundant group, while orb web-weaving spiders and space web-weaving spiders were also commonly collected. We collected 13 ground spiders from four species, and the remaining group included 60 araneophagic *Mimetus* sp. and two kleptoparasitic species (*Argyrodes elevatus*, *Rhomphaea fictilium*).

Overall spider abundance was best explained by the abundance of palatable insect prey (Table 2). Increased prey availability was positively

Table 2. Relationships between deer exclusion, insect prey abundance, and spider community parameters throughout the study area.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Group</th>
<th>Insect abundance</th>
<th>Deer exclusion</th>
<th>Model fit</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( G^2 )</td>
<td>( P )</td>
<td>( G^2 )</td>
</tr>
<tr>
<td>Abundance</td>
<td>Orb weaver</td>
<td>11.278</td>
<td>0.0008 (+)***</td>
<td>1.004</td>
</tr>
<tr>
<td></td>
<td>Space web</td>
<td>9.370</td>
<td>0.0022 (+)*</td>
<td>0.225</td>
</tr>
<tr>
<td></td>
<td>Hunter</td>
<td>12.045</td>
<td>0.0005 (+)***</td>
<td>1.129</td>
</tr>
<tr>
<td></td>
<td>Spiderlings</td>
<td>9.861</td>
<td>0.0017 (+)*</td>
<td>2.883</td>
</tr>
<tr>
<td></td>
<td>All spiders</td>
<td>32.327</td>
<td>&lt;0.0001 (+)***</td>
<td>13.583</td>
</tr>
<tr>
<td></td>
<td>Anyphaenidae</td>
<td>8.534</td>
<td>0.0035 (+)*</td>
<td>1.315</td>
</tr>
<tr>
<td></td>
<td>Araneidae</td>
<td>0.045</td>
<td>0.8317</td>
<td>3.983</td>
</tr>
<tr>
<td></td>
<td>Pisauridae</td>
<td>1.882</td>
<td>0.1701</td>
<td>1.876</td>
</tr>
<tr>
<td></td>
<td>Salticidae</td>
<td>1.954</td>
<td>0.1622</td>
<td>2.509</td>
</tr>
<tr>
<td></td>
<td>Tetragnathidae</td>
<td>14.025</td>
<td>0.0002 (+)***</td>
<td>9.873</td>
</tr>
<tr>
<td></td>
<td>Theridiidae</td>
<td>8.227</td>
<td>0.0041 (+)*</td>
<td>1.138</td>
</tr>
<tr>
<td>Richness</td>
<td>All spiders</td>
<td>6.681</td>
<td>0.0097 (+)*</td>
<td>4.502</td>
</tr>
</tbody>
</table>

† Pseudo-\( R^2 = 1 – (\text{residual deviance}/\text{null deviance}) \).
‡ Statistically significant at \( \alpha = 0.1 \)
* \( P < 0.05 \), †* \( P < 0.01 \), ‡* \( P < 0.001 \).
correlated with the abundance of all spiders ($G^2 = 32.237, P < 0.001$), as well as each functional group independently ($P < 0.005$). Deer exclusion increased overall spider abundance ($G^2 = 13.583, P < 0.001$), but was not correlated with individual functional groups. Vegetative structure was positively correlated with the abundance of all spiders ($G^2 = 8.559, P = 0.003$) and hunting spiders ($G^2 = 5.192, P = 0.023$); however, the abundance of other functional groups and structure were not correlated. Relying on web-building spiders as opposed to insect prey, kleptoparasitic spiders were positively correlated with the abundance of space web-weaving spiders in the Theridiidae and Linyphiidae ($G^2 = 8.147, P = 0.004$), but not with orb web-weaving species ($G^2 = 0.547, P = 0.459$). Overall spider species richness decreased with the exclusion of deer browse ($G^2 = 4.502, P = 0.034$) and increased with greater insect abundance ($G^2 = 6.681, P = 0.010$). In contrast, neither deer browse nor prey availability affected the richness of individual functional groups. More complex vegetative structure similarly decreased overall spider species richness ($G^2 = 3.015, P = 0.083$), yet did not increase or decrease the richness of any functional group.

Though most families were collected too infrequently to be included in individual analyses, the more abundant taxa exhibited various responses to habitat structure, prey, and forest site (Table 2). Orb web-weaving spiders in the Araneidae responded negatively to both deer exclusion ($P = 0.046$) and increased habitat complexity ($P = 0.033$). Conversely, the abundance of Tetragnathid orb web-weaving spiders increased with the exclusion of deer ($P = 0.002$). Space web-building spiders in the Theridiidae and hunting spiders in the Anyphaenidae, Pisauridae, and Salticidae were not significantly correlated with deer exclusion or habitat structure. Analyses of abundance for the Tetragnathidae, Theridiidae, and Anyphaenidae showed a positive response to insect prey availability ($P < 0.005$). Multivariate and subsequent univariate linear regression models showed that vegetative structure, deer exclusion, and insect prey density did not affect the relative abundance of spider functional groups. Permutational MANOVA and redundancy analyses illustrated the importance of forest patch to spider functional community structure ($P < 0.001; P < 0.001$), while insect prey abundance and exclusion of deer browse were not significant predictors (Fig. 4A). However, distance-based family analyses indicated that deer exclusion ($P = 0.041$), insect prey ($P = 0.016$), and forest patch ($P < 0.001$) all affected community structure (Fig. 4B). Similarly, the RDA of spider families showed that forest patch significantly influenced family structure ($P < 0.001$), while deer exclusion ($P = 0.074$) and insect prey abundance ($P = 0.055$) were significant at $\alpha = 0.1$.

**DISCUSSION**

Deer herbivory, through both direct and indirect impacts on understory vegetation, changes forest spider communities in central Maryland through its influence on dominant families such as the Araneidae, Tetragnathidae, and Anyphaenidae (Fig. 5). With deer densities likely to be higher than that of surrounding privately owned land, reductions in habitat structure from deer browse and subsequent effects on the spider community may be more pronounced than would be found in other forested areas. Despite increasing native plant diversity in this study, deer exclusion has also been documented to subsequently increase prevalence of certain exotic plants (Shen et al. 2016). Such increases in exotic species after deer exclusion implicate the logistical difficulties in restoring a functional forest after ungulate management. Regrettably, the patchy distribution of the more prevalent invasive plant species in this study area prohibited robust analysis of their impacts on the insect community. Of the herbivorous insects, beetles and true bugs responded positively to plant nativity, while caterpillar abundance decreased with greater native species richness. This is likely attributed to the relative prevalence of canopy-feeding Tortricid caterpillars (Acleris sp.) in some forest patches, a genus not influenced by understory plant richness. We had hypothesized a stronger response from herbivorous insects to the geographic origin of the plant community; however, a more appropriate metric representing available plant food may better elucidate these relationships. Exclusion of deer herbivory and increased structural complexity did increase the abundance and dry biomass of phytophagous insects as a group, a finding substantiated by
Fig. 4. Ordination plots showing (A) RDA results for spider functional groups and (B) distance-based RDA results for spider families. Red points represent individual plots, green points represent spider functional groups, and blue arrows depict correlations with independent variables.
Fig. 5. Normalized bar chart depicting spider community composition of most abundant taxonomic families within and outside of fenced plots at (A) Antietam National Battlefield, (B) Monocacy National Battlefield, and (C) C&O Canal National Historical Park.
much of the previous literature on the boon of greater habitat structure on insect communities (Langellotto and Denno 2004).

Increased insect prey resulted in a higher abundance of all spider functional groups and several families, which is consistent with similar work on the critical importance of prey availability to fecundity, body condition, and spider web residence (Wise 1979, Leborgne and Pasquet 2005). Greater 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. Both deer browse and understory habitat structure were also important correlates of spider species richness; however, reduced structure from deer herbivory increased spider richness. These findings are in stark contrast with past literature that indicates the positive correlation between habitat structure and species richness (Miyashita et al. 2004, Takada et al. 2008). Differences in species richness response could result from overall habitat differences, specific metrics for estimating structure, and ecological differences in cervid behavior. Both aforementioned works studied effects of sika deer browsing below 1 m: Sika deer are more likely to feed on grasses and low vegetation as opposed to white-tailed deer, which feed on branches up to 2.0 m in height. Greater richness in browsed plots may be attributed to common species that prefer open understories and disturbed habitats (e.g., Micrathena gracilis). Given the correlation between the presence of multiflora rose and vegetative structure, such a decline in spider richness could also result from increased abundance of the structurally complex rose. Increased individual plant structure as seen in rose may decrease available spaces for web-spinning spiders and ultimately reduce overall available habitat (Gonçalves-Souza et al. 2011).

The collected orb web-weaving Araneidae consisted mainly of Mangora species, whose webs are often placed in low vegetation such as tall grasses, herbaceous plants, and low tree branches. Due to the preferred height of Mangora webs and their ability to utilize grasses, this species increased in abundance in browsed habitats with less complex plant structure. The most commonly collected spider in the Tetragnathidae was Leucauge venusta, which increased within fenced plots. This species maintains an approximately 20-cm viscid web but can have much wider supporting anchor strands: As such, greater complexity in the understory provided diverse interstitial spaces for a greater number of webs. Theridion spp., the most commonly collected in the Theridiidae, are more flexible in exploiting tight spaces between tall grasses and low vegetation for their three-dimensional webs, so were not influenced by the presence or absence of deer browse. Though not correlated with deer browse, hunting spiders in the Anyphaenidae increased in response to greater vegetative structure. Comprising species that are dependent on structure for substrates upon which to hunt, these species could respond more strongly to structure than do web-building species that require the spaces between vegetative surfaces to build webs.

The lack of a cohesive response of spider families and groups to deer browse and habitat structure may reflect the current depauperate condition of the resident spider community and does not necessarily indicate that this degree of deer browse is benign or beneficial to forest spiders. The species selecting these forest patches likely resulted from a long history of deer browsing and spatially homogeneous habitats. Many of the forest-dwelling species typically associated with more complex forest understories may already be extirpated from these forest patches, with local landscape heterogeneity and continued heavy deer browse preventing recolonization from nearby suitable habitats. Such changes to the taxonomic and functional 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: Depending on the physiological similarity of replacement species, the proteinaceous biomass and energy dynamics of this component of invertebrate–vertebrate food webs may drastically change the nutritional composition of araneophagic predators such as forest birds (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. Spider genera within a functional group or family may also differ in susceptibility to predation and palatability to higher-level predators as well as nutritional content. Changes in habitat structure could have altered
the relative proportions of suitable prey and subsequent spider dietary composition, particularly as insect prey was characterized only by order. Gratton and Denno (2006) illustrated the capacity of spiders to shift diet depending on prey availability, though such dietary shifts likely hold consequences for spider reproductive health and opisthosomal protein content. Impacts from altered habitat structure may also have cascading effects beyond the spider community and their predators, also reaching detrital communities (Miyashita and Takada 2007).

In addition to a reduction in resident deer density, continued management of invasive plant populations known to affect forest structure and/or insect taxa is a fundamental step in maintaining the stability of invertebrate food webs. Though only tangentially studied here, invasive plants like multiflora rose may play a more prominent role in defining spider community composition, particularly as limiting deer herbivory may facilitate their growth. Long-term management goals should include the enhancement of forest patch connectivity to assist in juvenile dispersion and maintenance of genetic diversity, as well as an overarching incorporation of ecological processes and natural resources into long-range planning: Many national parks in the eastern United States are set aside for their historical importance with little concern for biological conservation. These results represent a brief snapshot in time, yet illustrate how changes in forest vegetation, mediated in part by white-tailed deer browsing, have the capacity to alter understory spider communities. This system is understandably dynamic, with long-term monitoring needed to fully grasp the continued, successive changes that occur as deer populations fluctuate and understory vegetation changes with invasive plant growth and the advent of novel plant species. As national parks in the eastern United States consider and undertake active management of overabundant deer populations, recurrent monitoring of vegetative communities and understory physiognomy is critical in understanding processes of forest regeneration and succession after heavy deer browse is reduced. Continued monitoring of invertebrate communities is also vital in understanding the indirect interactions between deer, vegetation, and invertebrates in these habitats, particularly to examine the mechanisms of species turnover and habitat recolonization by species once extirpated due to habitat loss. 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. 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.

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LITERATURE CITED


