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Direct and Indirect Effects of White-Tailed Deer (*Odocoileus virginianus*) Herbivory on Beetle and Spider Assemblages in Northern Wisconsin

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DIRECT AND INDIRECT EFFECTS OF WHITE-TAILED DEER (*Odocoileus virginianus*) HERBIVORY ON BEETLE AND SPIDER ASSEMBLAGES IN NORTHERN WISCONSIN

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By

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Elizabeth Jo Sancomb ENTITLED Direct and indirect effects of white-tailed deer (*Odocoileus virginianus*) herbivory on beetle and spider assemblages in Northern Wisconsin BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science

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ABSTRACT

Sancomb, Elizabeth Jo. M.S. Department of Biological Sciences, Wright State University, 2014. Direct and indirect effects of white-tailed deer (*Odocoileus virginianus*) herbivory on beetle and spider assemblages in Northern Wisconsin

White-tailed deer directly impact vegetation structure and species composition through selective foraging, and indirectly impact other species by altering habitat, food-web interactions, and microclimate. I examined the direct effects of deer exclusion on vegetation communities, and indirect effects on beetle, spider, and web-building spider (WBS) assemblages. Forb and woody plant percent cover were higher in exclosures, while graminoid cover was higher in controls. There were no differences in beetle and spider assemblages between browsed and protected areas. The absence of differences could be attributed to legacy effects, or alternatively high vagility of individuals. WBS assemblages were more abundant and diverse in protected areas, reflecting differences in web site availability and litter depth. This suggests indirect effects of deer alter arthropod assemblages. Through selective feeding, deer act as ecosystem engineers. They are indirectly changing the WBS assemblages in this area, and may be changing beetle and spider assemblage composition.

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I. INTRODUCTION

The ecological community historically assumed that direct interactions are more important than indirect interactions in community dynamics. More recently, however, the importance of these indirect effects (when the direct interaction of species 1 with species 2 indirectly impacts species 3) in community complexity and structure has been increasingly acknowledged (Menge 1997). Three main types of indirect effects have been recognized: numeric (change in abundance through predation, competition, or facilitation), behavioral (change in behavior or morphology independent of abundance), and environmental (change in abundance through changes in quality or structure of an abiotic resource) (Miller & Kerfoot 1987; Strauss 1991). These three indirect effect types can be manifested in a community by the actions of a keystone species or ecosystem engineer: a species that can indirectly affect a co-occurring species by altering their habitat and modifying resources available to other species (Jones et al. 1994; Pringle 2008). Ecosystem engineers can increase the abundance or richness of a co-occurring species if they create or maintain novel habitat (Nasseri et al. 2010; Pringle 2008). They can also decrease abundance or richness of co-occurring species if they lower habitat quality, or destroy existing habitat (Parsons et al. 2013). Ecosystem engineers can also change behaviors of co-occurring species through habitat modifications (Pringle 2008). Overall, indirect interactions account for ~40% of the change in community structure after

manipulations (Menge 1995) and these indirect effects occur either simultaneously or shortly after direct effects are seen (Menge 1997). Because of the large and immediate nature of the community changes, indirect effects of a keystone species or ecosystem engineer on community dynamics are important to examine.

White-tailed deer (*Odocoileus virginianus*, hereafter deer) populations in North America have increased greatly since pre-colonial times, reaching and maintaining densities above 10/km^2 throughout temperate zones (Bressette et al. 2012). Deer were once rare or absent from most of the United States, with overabundant populations restricted to small patches in Wisconsin, New York, Michigan, and Utah (Leopold et al. 1947). Now, deer overabundance is a very widespread problem in much of the United States (Cote et al 2004; Rooney 2009; Warren 1997; Waller & Alverson 1997) including Wisconsin. In 2012, the state reported a total population of approximately 1.3 million deer (8.8/km^2) (Rolley 2012). Deer overabundance has measurable direct effects on forest communities through the manipulation of vegetation (Rooney & Waller 2003; Rooney 2001; Wiegmann & Waller 2006). Deer directly affect the vegetation upon which they feed. Abundant populations are able to suppress local regeneration of specific tree species and cause a shift in understory herb composition. Deer herbivory causes a transition from broad-leafed herb and shrub dominated plant communities to fern and graminoid dominated plant communities (Rooney & Waller 2003; Rooney 2009; Wiegmann & Waller 2006). As a result, deer herbivory fuels biotic impoverishment of forest communities:

sites that have high deer densities support more similar vegetation communities than do sites with no deer grazing (Rooney 2009; Rooney et al. 2004; Begley-Miller et al. 2014). Deer engineer the forest vegetation community through selective feeding. These direct manipulations of the vegetation community have the potential to indirectly alter co-occurring species in communities.

White-tailed deer, as ecosystem engineers, can change co-occurring animal assemblages. Grazing by deer can indirectly affect other forest inhabitants through changes in food-web interactions and the structure of habitats. Competition between deer and other herbivores for food can negatively affect the smaller herbivore communities (i.e. arthropods; small mammals). In 2000, McShea observed that in years of low food (acorn) abundance, deer reduced the abundance of two common rodent species. Therefore, the indirect removal of a food source (acorns) through the direct reduction of the producers (oak trees) by deer negatively affects the abundance of co-occurring species (McShea 2000). Additionally, herbivory by deer can alter resource quality for other herbivores by increasing secondary metabolites of plants, making these plants a less suitable food source (Vourc'h et al. 2001). A reduction in vegetation cover and vertical complexity can alter the microclimate of the forest floor (soil moisture, humidity, temperature, and light) and limit habitat for vegetation dwelling organisms (Rooney & Waller 2003). Also in 2000, Mcshea and Rappole observed that the removal of deer led to the increase of vertical structure, habitat, and cover for ground and low-canopy nesting birds. The increase in habitat corresponded to increases in abundance and richness of these bird communities (McShea &

Rappole 2000). A similar trend was seen by Parsons and colleagues in the interaction between elk (*Cervus elaphus*) and several small mammal species. The presence of elk reduced the abundance of woodrats, voles, and two mouse species because of a reduction in vegetation cover, and habitat quality (Parsons et al. 2013). Therefore, the direct effects of white-tailed deer and other large ungulates on vegetation can induce indirect effects on associated co-occurring animal communities.

Although there is a broad body of work on how deer and other ungulates indirectly affect bird and small mammal communities, much less work has been done on the indirect effects of deer on arthropod assemblages. Many arthropod species are direct competitors with deer for vegetation as food, and an even greater number of species rely on this same vegetation for habitat (Stewart 2001). Arthropods are also very sensitive to small changes in the microclimate; and therefore, deer may easily indirectly alter arthropod assemblages. Baines and colleagues observed in Scotland that the abundance of arthropods was over two times higher in areas relieved of ungulate browsing. This was attributed to less competition for food and more suitable habitat in areas with no browsing pressure (Baines et al. 1994). Allombert and colleagues observed the same pattern in 2005 in the Pacific Northwest (arthropod abundance increased with decreasing browsing pressure) (Allombert et al. 2005). Conversely, the removal of plant biomass benefits some arthropods. Suominen has extensively studied the affect of multiple ungulate species on ground-dwelling arthropods in many areas of the world. Overwhelmingly, Suominen and his colleagues observed that

diversity and abundance of ground-dwelling arthropods was higher in grazed areas than non-grazed areas. As previously mentioned, ungulates preferentially feed on broad-leaved plants and leave grazed areas dominated by graminoid species (Begley-Miller et al. 2014). This change in vegetation structure produces a more favorable microhabitat for ground-dwelling predatory species (Suominen et al. 1999; Suominen et al. 2003). Therefore, ungulates can indirectly positively or negatively impact associated arthropod assemblages through herbivory.

Deer grazing reduces the three dimensional structure of the ground and shrub layers of forest habitats (Rooney 2009; Wiegmann & Waller 2006; Rooney 2001). Vegetation structure is important for web building spiders, which use this structure as web scaffolding. Therefore, ungulate grazing has the potential to greatly affect web-building spider assemblages (Stewart 2001). This relationship was examined by Miyashita and colleagues in 2004 on the Boso Peninsula in eastern Japan (Miyashita et al. 2004). They reported that the abundance and species richness of web spiders was reduced in areas with deer grazing. This was attributed to a lower availability of web sites (less vertical habitat). Four years later, Takada along with Miyashita and other colleagues expanded the study completed in 2004 by including both vegetation and ground habitats (Takada et al. 2008). They examined web-weaving, large orb weaving, small orb weaving, and web invading spiders separately in both the vegetation and ground habitats. In vegetation, web building, large orb weaving, and web-invading spiders were all reduced in abundance and richness in grazed areas. This was likely due to the reduction in the availability of web sites (physical structures to

anchor webs to). Small orb weaving spiders were unaffected because they do not rely on varied and extensive vegetation structure for web weaving. Only the web-weaving spiders were reduced in abundance and richness by deer browsing in the ground habitat. The research suggests that the effect of deer herbivory on spider assemblages is variable and depends on the guild (web-building or not) and habitat (vegetation or ground).

The interaction between deer and forest arthropods is complex and largely understudied. Deer have the potential to benefit some species while greatly reducing others through their role as ecosystem engineers in forested areas. The goal of this study was to determine whether white-tailed deer herbivory has an effect on beetle and spider assemblages. I focused on three main objectives using data collected from four 23 year-old deer exclosures and paired unexclosed control sites in northern Wisconsin. First, I surveyed the vegetation in exclosures and paired controls to determine if deer reduce vegetation cover and structure, and change composition. Second, I surveyed the beetle assemblages in exclosures and controls to examine if deer increase total beetle and ground beetle abundance, diversity, and biomass and/or reduce these in the herbivorous beetle assemblage. I also examined the spider assemblages in exclosures and controls to determine if deer reduce overall spider abundance, diversity, and biomass, but increase these measures in the ground spider assemblage. Third, I surveyed web-building spiders and environmental variables in exclosures and controls to determine if deer reduce web-building spider abundance, diversity, biomass, and alter assemblage composition and to identify possible

environmental predictor variables that explain these differences. Comparisons between areas with and without deer browsing pressure are important in understanding direct and indirect impacts of deer overabundance. These comparisons provide insight into how deer populations will impact complex forest communities.

II. METHODS

STUDY AREA AND SITES

I conducted this study in the Northern Highlands region of northern Wisconsin in Vilas County (46°9' N, 89°51' W) on a 2,500 ha property owned by Dairymen's, Inc. (a membership organization that combines low-impact land use with land stewardship). The regional climate is continental and Pleistocene glacial deposits form moraines and outwash plains. The property contains oligotrophic drainage lakes, forests, and wetlands (Rooney 2009).

In 1990, four deer exclosures were constructed in an old-growth hemlock-hardwood stand (predominantly hemlock, sugar maple, and yellow birch) on the Dairymen's property. Exclosures are 1.8m tall and constructed of wire mesh, and are of varying sizes and names. Big Gap covers 644m^2, Dark Hollow covers 720 m^2, Ovenbird covers 169m^2, and Loner covers 720m^2. Each exclosure has an adjacent control plot of the same area which allows the ambient grazing pressure. The exclosures are separated from

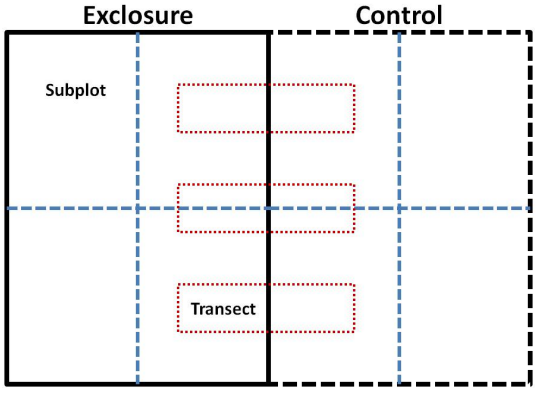

Diagram 1: Schematic of each exclosure/control plot; each block contains the three historically established transects and four sampling subplots

one another by a mean distance of 195 ± 15 m (Rooney 2009). Each exclosure and control pair contains three permanent 10m transects separated from one another by 5m. The transects are at right angles to one edge of the exclosure with 5m of the transect contained within the exclosure and 5m contained within the adjacent control plot (Diagram 1).

GENERAL SAMPLING

I conducted the study using a block design framework. Each block consisted of an exclosure and adjacent control plot (four blocks in total). I completed sweep-net, pitfall, and web-building spider sampling for five days during the months of June (03, 04, 06, 07, 08), July (09, 10, 11, 12, 13), and August (03, 04, 06, 07, 08). I recorded all vegetation composition and percent cover measurements once in the months of June (05), July(11), and August (07) and all vegetation height measurements once in the months of July (12) and August (04). I sampled approximately during 0800 to 1200 daily, with the exception of 06 June when I sampled from 1300 to 1700 due to poor weather. To ensure I removed time dependent environmental variables (time of day, sunlight, temperature, etc.) from the sampling procedure, I sampled the exclosures in a random order. I assigned each exclosure a number 1-4 and for each day of sampling, and chose these numbers in a random order. This represented the order in which I sampled the exclosures.

VEGETATION SAMPLING

Forage type composition, percent cover, and vegetation structure could influence the abundance and diversity of both beetle and spider assemblages. To measure composition and percent cover, I used the line-intercept method along each of the historically established transects. I placed a measuring tape on the ground marking each transect length-wise. Each time a stem or leaf crossed the tape, I recorded the vegetation type (forb, graminoid, woody, or fern) and the length of the tape covered.

I calculated percent cover of each vegetation type (composition) using $\sum n_i/1{,}500$ where *n* is the length of the tape covered by each occurrence of type *i* along the transect. The denominator is the total transect length (cm) for each of the plots (5m X 3 transects). I calculated total percent cover using the same formula but n_i is the total length of tape covered (Rooney 2009; Begley-Miller et al. 2014).

To compare vegetation structure differences between controls and exclosures, I used a meter stick to measure the height of the vegetation up to 2m at five points along each 10m transect (two in each exclosure, two in each control, and one at the fence separating the two). I combined all measurements and calculated an average vegetation height for exclosure, control, and transition.

SWEEP NET SAMPLING

To collect vegetation dwelling-beetles and spiders, I used sweep-net sampling along each of the established transects. I walked slowly along each transect making two sweeps in each meter (for a total of 10 sweeps per transect). At the end of each transect, I emptied the sweep-net, placing all beetles and spiders into a vial containing 70% EtOH labeled with the date, exclosure name, and transect number. After each sampling week, I sorted and identified each individual in the lab. I conducted identifications in 70% EtOH using a Nikon SMZ-1B dissecting scope. I identified all beetles to genus (Eaton & Kaufman 2006; White 1983) and spiders to species (Bradley 2013). I entered all identifications into a community matrix along with numbers of individuals per taxa and placed the individuals back into the labeled EtOH vials.

After I completed all identifications, I sorted the samples for biomass calculations. I created a “master sweep-net sample” for each exclosure or control by combining all samples that I collected that corresponded to the plot. I then sorted the “master samples” by family, placed each family into a metal soil tin and then into a drying oven (Quincy Lab, Inc. Model 40 GC Lab Oven) at 60°C for 24 hours. I weighed each family sample to the nearest 0.1mg (Sartorius TE214S), recorded the measurement, and placed the sample into a vial for long-term storage.

PITFALL SAMPLING

To sample ground dwelling beetles and spiders, I used pitfall traps. Each trap consisted of two plastic cups stacked inside one another placed flush to the ground. Each was filled with a 50/50 mixture of water and ethylene glycol (to preserve arthropods) with a bittering agent to deter small mammals, and a small amount of detergent to break the surface tension of the liquid to facilitate drowning. Each trap had a plastic cover with openings to allow the movement of arthropods into the trap while preventing rain and other debris from clogging the traps. I placed five pitfall traps in each plot using a systematic approach to ensure that the greatest proportion of habitat types was sampled. With the help of two field assistants, I divided each of the plots into a 3X3 grid of equally sized sections. I installed a pitfall trap at the four interior grid vertices and one in the middle of the center grid section. For each sampling day, I removed all beetles and spiders from the traps and placed them into a vial containing 70% EtOH labeled with the date, exclosure name, and trap number.

I used the same identification and biomass measurement procedures outlined above for the pitfall samples.

WEB-BUILDING SPIDER SAMPLING

To sample web-building spiders, I used stratified random sampling. I divided each plot into a 2X2 grid containing four equal sections. For each section, I assigned a sampling distance (1m-distance to next section) and angle (0-90) using a random number generator. Using a 30m tape measure, I walked the assigned distance at the assigned angle (Diagram 2). If I was within 1.5m of the fence due to the distance/angle combination, I adjusted the sampling area inward.

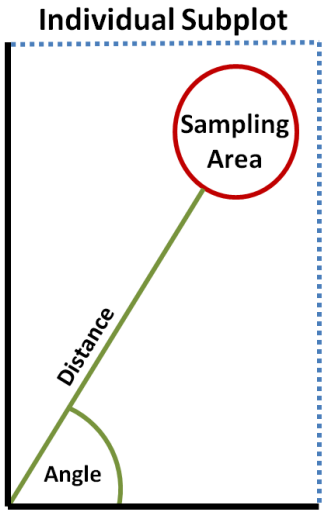

Diagram 2: Schematic of the web-building spider sampling method

Once I reached the assigned point, I established a 1m diameter by 2m high cylinder sampling area. I then misted the entire area with water to increase the visibility of all webs. I identified all web-building spiders to species in the field with the help of a field guide (Bradley 2013) and recorded the abundance of each. If a web contained no spider, I recorded the family and indicated that no spider was found in the web.

After I recorded all of the spiders, I measured two environmental variables that could affect the abundance and/or composition of the web-building spider assemblage. I measured the litter depth at the middle of the sampling area to the nearest 0.1cm using a meter stick. To examine height composition of the vegetation, I used the Web Site Availability Index outlined in Miyashita et al. 2004. This method uses the point intersect method. At the center of the sampling area, I rotated a 1m stick at 0.5m and 1m above the ground. I counted every time

a scaffolding point (branch, twig, leaf, etc.) touched the stick. The total number of recorded scaffolding points at 0.5m and 1.0m represent the WSA 0.5m and WSA 1.0m (Miyashita et al. 2004). To examine prey available of web-building spiders, I used sticky traps. The traps were constructed using 23cmX33cm sheets of clear plastic coated with an adhesive. These sticky sheets were attached to 1m high wooden poles. I deployed one sticky trap in each of the established sections within the 2X2 grid using the same randomization method outlined above. I set up the traps 24 hours before the first sampling day and they were continuously run for 5 days. After the sampling period, I removed each sticky sheet, covered them with clear plastic wrap and placed them on ice. Once in the lab, I counted all insects captured and measured the total body length.

DATA ANALYSIS

VEGETATION

To examine differences in percent cover, I first pooled percent cover measurements from all sampling months I then computed the average total percent cover, and average percent cover for each forage type for each exclosure/control plot. I tested for differences in total percent cover between exclosures and controls using a paired t-test. I ln transformed all forage type measurements to achieve normality of the distributions. I tested for differences in the percent cover for each forage type (woody, graminoid, forb, and fern) using four paired t-tests (R software, R Core Team 2013).

I square-root transformed and pooled vegetation structure data from all sampling months and computed an average vegetation height for each exclosure/control/transition. I tested for differences in vegetation structure between controls, exclosures, and transitions using three paired t-tests (R software, R Core Team 2013).

BEETLES AND SPIDERS

I tested for differences in diversity, abundance, and genus richness pooling pitfall and sweep-net samples from all sampling units and months. I used Shannon's *H'* to estimate diversity, the total number of individuals to estimate abundance, and the total number of represented genera to estimate richness (vegan R package; Oksanen et al. 2013). I compared differences between control and exclosure plots using paired t-tests. To correct for differences in overall sample abundance, I used rarefaction analysis to compute a more reliable measure of diversity (Analytic Rarefaction 2.0, Holland 2009). I plotted number of individuals against genus richness and calculated 95% confidence intervals. I repeated all analyses for herbivorous beetles and ground beetles (Family: Carabidae). For herbivorous and ground beetles, I also calculated the relative abundance of these groups. To do this, I divided the abundance of herbivorous/ground beetles in each plot by the total abundance in each plot. I compared the differences in relative abundance using a paired t-test.

To examine differences in the total biomass of beetles in controls and exclosures, I first pooled all pitfall and sweep-net "master samples" for each

exclosure/control. I then separated the master samples into family biomass samples for each exclosure/control. I tested for differences in total beetle biomass between exclosures and controls using a paired t-test. In addition, I computed the average per beetle biomass by dividing the combined biomass samples by the number of individuals in each sample. I tested for differences between exclosure and controls by using a paired t-test. I repeated these analyses for herbivorous and ground beetles.

I tested for differences in beetle assemblage composition using analysis of similarity (ANOSIM), a non-parametric multivariate test that uses a distance matrix to compare two groups (Clarke 1993). I first combined pitfall and sweep-net abundance data for each sampling month and unit to create an assemblage matrix consisting of a total abundance count for each beetle genus encountered in each exclosure/control (eight sites). I used PRIMER 6 (Clarke & Gorley 2006) to create a distance matrix and then run ANOSIM.

I examined differences in the beetle assemblages of exclosures/controls visually using nonmetric multidimensional scaling (NMDS, PRIMER 6 software, Clarke & Gorley 2006), an ordination method that maximizes the goodness of fit between dissimilarity measures and distance in ordination space to reduce the "stress" of the ordination (Kruskal 1964). Once I computed the coordinates of each point (each exclosure or control), I used R (R Core Team 2013) and the package 3dScatterPlot (Ligges & Mächler 2003) to plot the points in three-dimensional space.

All analyses were repeated for spider data collected with the use of pitfall traps and sweep-nets. The spider analysis was run on species data, not genus. I repeated these analyses for the web-building and non-web-building spiders collected in the samples. Average per spider biomass was calculated for “all spiders”, “web-building spiders”, and “non-web-building spiders”.

To examine if treatment or site had a greater affect on assemblage composition, I first combined the beetle and spider assemblage matrices. I then used PRIMER 6 (Clarke & Gorley 2006) to create a distance matrix and then ran an ANOSIM for both treatments and sites. I examined the results of the ANOSIM visually using the same methods described above.

WEB-BUILDING SPIDERS

All spider, web-site availability, prey availability, and litter data were combined over all sampling months/days for each sampling subplot and natural log transformed. This reduced pseudo-replication and increased the normality of the data, respectively.

I compared differences in abundance, WSA, and litter depth between exclosure and control plots using nested ANOVA, with treatment as an independent variable. To measure differences in prey availability, I used the log response ratio method outlined in Rooney (2009). I used rarefaction analysis to examine the differences in diversity between exclosures and controls (Analytic Rarefaction 2.0, Holland 2009). I plotted number of sampled individuals against

expected family richness and calculated 95% confidence intervals. I then ran the same rarefaction analysis above on spider species instead of family.

To examine the differences in assemblage composition between exclosures and controls, I first combined all abundance data from all sampling months/days and subplots to create a community matrix for each plot. I used PRIMER 6 (Clarke & Gorley 2006) to create a distance matrix and then run an ANOSIM. I used NMDS to compute the coordinates of each plot and graphed them using R (R Core Team 2013) and the package 3dScatterPlot (Ligges & Mächler 2003).

I examined differences in relative abundance of the web-building spider families by first combining all web-building spider data from all dates and subplots to get two “master measurements”, one for controls and one for exclosures. These master measurements contained the total number of encountered individuals in each family and in total. I then divided each family total by the total number of individuals for controls/exclosures. Then, I graphed these relative abundances using R (R Core Team 2013).

I used analysis of covariance (ANCOVA) to examine the relationship between web-building spider abundance/family richness and treatment/predictor variables. ANCOVA is a hybrid between linear regression and analysis of variance (ANOVA) used for data with both a categorical and continuous independent variable. The analysis can separate and examine significance of the variance contributed by both variable types (Gotelli & Ellison 2004). By computing the significance of both treatment (categorical) and predictor variables

(Website availability at 0.5 and 1.0m, litter depth, prey availability; continuous), I was able to examine both direct and indirect effects of deer herbivory on spider assemblages.

III. RESULTS

VEGETATION

Average total percent cover was nearly three times higher in exclosure plots (62.3 ± 2.5% SE) as compared to controls (22.4 ± 0.7% SE; df = 3; paired t = 7.56; P = 0.005) (Fig. 1). Forage type composition also differed between exclosures and controls.

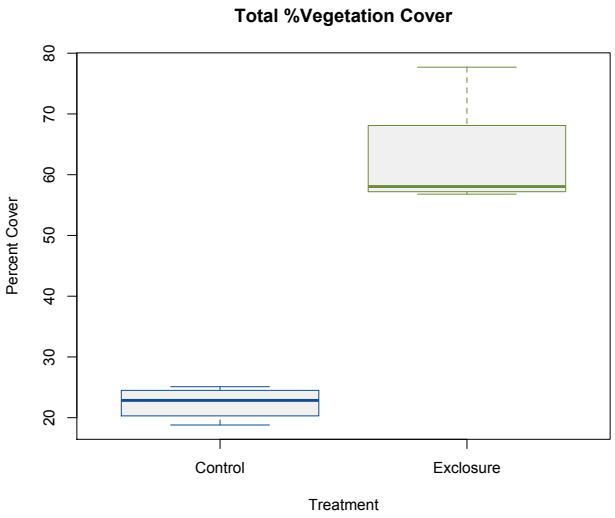

Fig. 1: Average total vegetation percent cover; Control = 22.4 ± 0.7%, Exclosure = 62.7 ± 2.5%; paired t = 7.56; df = 3; P = 0.005

Woody browse percent cover was over fifty times greater in exclosures (37.9 ± 4.5% SE) than in controls (0.73 ± 0.22% SE; df = 3; paired t = 4.31; P = 0.02). Forb percent cover was also significantly higher in exclosures (16.6 ± 3.1% SE in exclosures, 1.2 ± 0.4% SE in controls; df = 3; paired t = 5.26; P = 0.01). Control plots had a significantly higher graminoid percent cover (17.7 ± 0.9% SE) as compared to exclosures (3.0 ± 0.6% SE; df = 3; paired t = 8.93; P = 0.003). Fern percent cover was higher in exclosures (5.1 ± 0.6% SE) than in controls (2.75 ± 0.6% SE; df = 3; paired t = 1.39; P = 0.26), but not significantly so (Fig. 2).

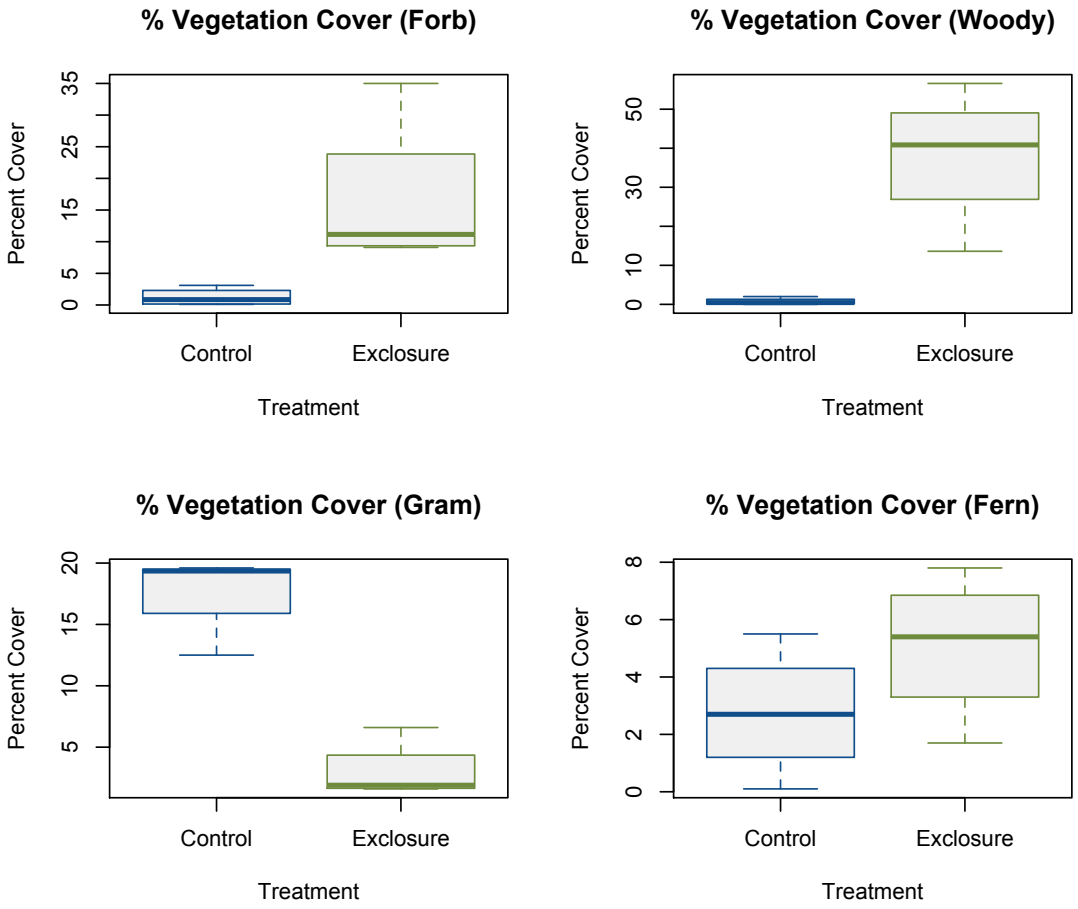

Fig. 2: Average percent cover of each sampled forage type; Forb: paired t = 7.56, P = 0.005; Woody: paired t = 4.31, P = 0.011; Graminoid: paired t = 8.93, P = 0.003; Fern: paired t = 1.39, P = 0.26

Vegetation height was significantly greater in exclosures (1.52 ± 0.20m SE) when compared to both controls (0.18 ± 0.03m SE; df = 3; paired t = 8.50; P = 0.003) and transitions (0.39 ± 0.06m SE; df = 3; paired t = 7.30; P = 0.005). Transitions also had significantly greater vegetation height than controls (df = 3; paired t = 3.93; P = 0.03) (Fig. 3).

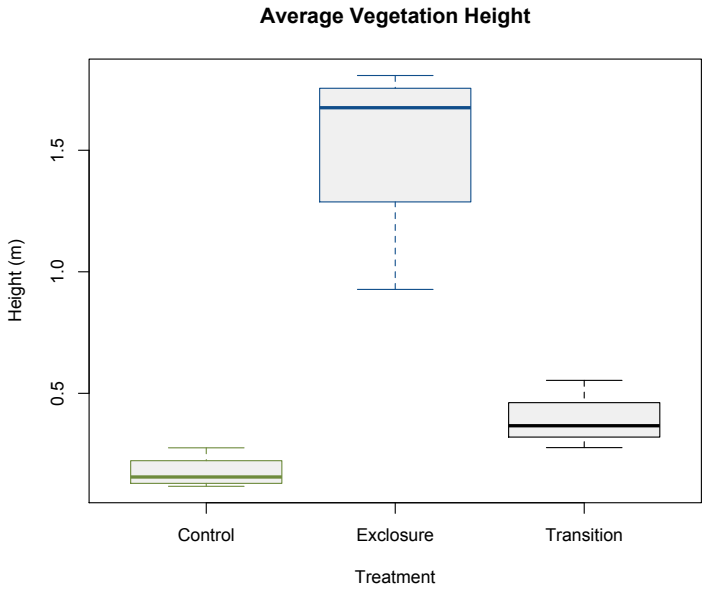

Fig. 3: Average vegetation height at three measured areas; Control = 0.18 ± 0.03m, Exclosure = 1.52 ± 0.20m, Transition = 0.39 ± 0.06m; *C v E*: paired t = 8.50, df = 3, P = 0.003; *C v T*: paired t = 3.93, df = 3, P = 0.029; *E v T*: paired t = 7.30; df = 3, P = 0.005

Table 1: Summary of vegetation results

Vegetation Results					
Comparison	Control	Exclosure	df	paired-t	P-value
Total % Cover	22.4 ± 0.7%	62.3 ± 2.5%	3	7.56	0.005
Woody % Cover	0.73 ± 0.22%	37.9 ± 4.5%	3	4.31	0.02
Forb % Cover	1.2 ± 0.4%	16.6 ± 3.1%	3	5.26	0.01
Graminoid % Cover	17.7 ± 0.9%	3.0 ± 0.6%	3	8.93	0.003
Fern % Cover	5.1 ± 0.6%	2.75 ± 0.6%	3	1.39	0.26
Height	0.18 ± 0.03m	1.52 ± 0.2m	3	8.5	0.003

BEETLES

Total beetle Shannon's *H'* diversity was not significantly higher in controls (2.4 ± 0.09 SE) when compared to exclosures (2.3 ± 0.09 SE; df = 3; paired t = 0.46; P = 0.67). Beetle abundance was also not significantly higher in controls (72 ± 14 SE compared to 58 ± 15 SE; df = 3; paired t = 1.35; P = 0.27). The same was true for genus richness (controls: 17 ± 1 SE, exclosures: 16.3 ± 2 SE; df = 3; paired t = 0.57; P = 0.61). Total beetle biomass was close to two times higher in controls (2.84 ± 0.53g SE) when compared to exclosures (1.51 ± 0.23g SE; df = 3, paired t = 2.87; P = 0.064), although not significant. Average per beetle biomass was higher in controls (0.039 ± 0.002g SE) when compared to exclsoures (0.030 ± 0.006g SE; df = 3; paired t = 1.45; P = 0.24), but this was not significant. Rarefaction analysis revealed that exclosures reach a genus richness of 29 genera at 232 sampled individuals while controls reach 26 genera at 288 individuals. However, the 95% confidence intervals overlapped until 232 individuals were sampled (Fig. 4).

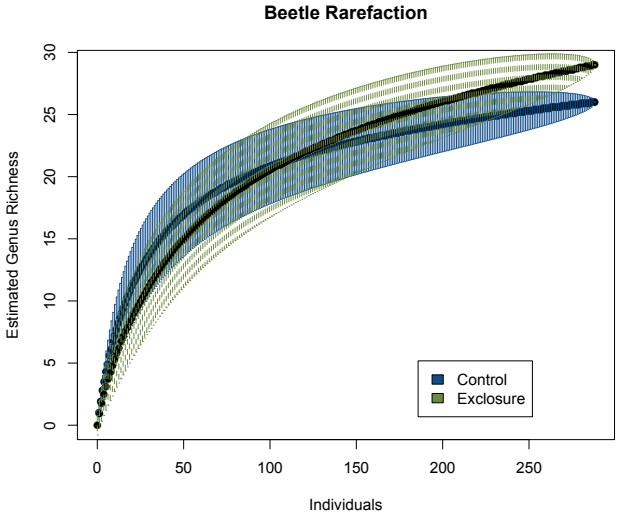

Fig. 4: Exclosures reach a genus richness of 29 genera at 232 sampled individuals while controls reach 26 genera at 288 individuals

According to the analysis of similarity (ANOSIM), there is no statistical difference between the composition of the beetle assemblages of controls and exclosures (Global R = -0.073; P = 0.69) (Fig. 5).

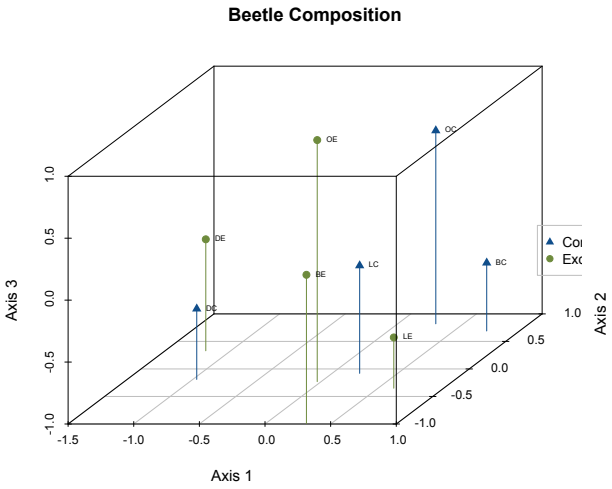

Fig. 5: NMDS ordination; no statistical difference between the composition of the beetle assemblages of controls and exclosures; Global R = -0.073; P = 0.69

Herbivorous beetle Shannon's *H'* diversity was not significantly higher in controls (0.92 ± 0.13 SE) than in exclosures (0.87 ± 0.11 SE; df = 3; paired t = 0.21; P = 0.84). Abundance was higher in exclosures (29 ± 10.7 SE compared to 21.3 ± 6.9 SE; df = 3; paired t = 1.29; P = 0.29), but not significantly. Genus richness was not statistically higher in controls (3.75 ± 0.48 SE compared to 3.5 ± 0.5 SE; df = 3; paired t = 0.52; P = 0.63). The relative abundance of herbivorous beetles was 1.5 times higher in exclosures (45.3 ± 6.9% SE) than controls (29.8 ± 7.0% SE; df = 3; paired t = 2.02; P = 0.14). The total herbivorous beetle biomass was two times higher in exclosures (0.16 ± 0.04g SE) compared to controls (0.08 ± 0.03 SE; df = 3; paired t = 3.09; P = 0.054), and the average per herbivorous beetle biomass was also higher in exclosures (7.5 ± 3.5mg SE compared to 3.9 ± 1.3mg SE; df = 3; paired t = 1.63; P = 0.20), although both were not significant.

Rarefaction analysis revealed that controls reach a genus richness of seven at 85 sampled individuals while exclosures reach this same richness at 116 sampled individuals (Fig. 6).

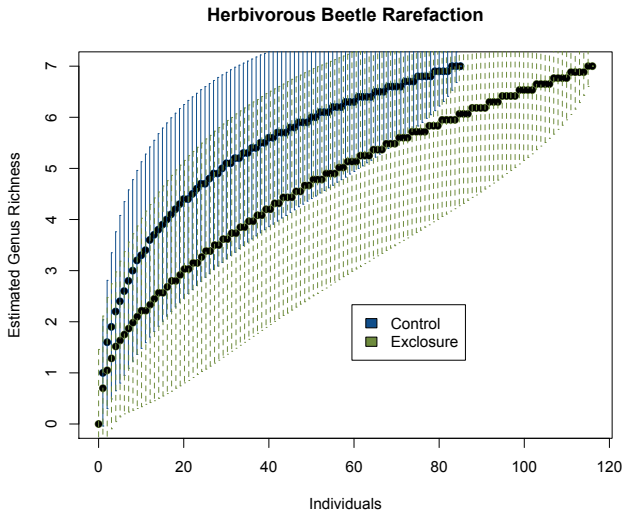

Fig. 6: Herbivorous beetle rarefaction; Controls reach a genus richness of seven at 85 sampled individuals while Exclosures reach this same richness at 116 sampled individuals

Ground beetle Shannon's H' diversity was significantly higher in exclosures (1.40 ± 0.08 SE) than in controls (1.28 ± 0.07 SE; df = 3; paired t = 5.40; P = 0.012) (Fig. 7). Abundance was almost two times higher in controls (19.75 ± 5.51 SE compared to 11 ± 1.29 SE; df = 3; paired t = 1.23; P = 0.31), although this was not significant. Genus richness was not significantly higher in exclosures (4.5 ± 0.29 SE) than in controls (4.25 ± 0.25 SE; df = 3; paired t = 1.00; P = 0.39). The relative abundance of carabid beetles was higher in controls (27.6 ± 5.5% SE) than in exclosures (24.2 ± 7.9% SE;

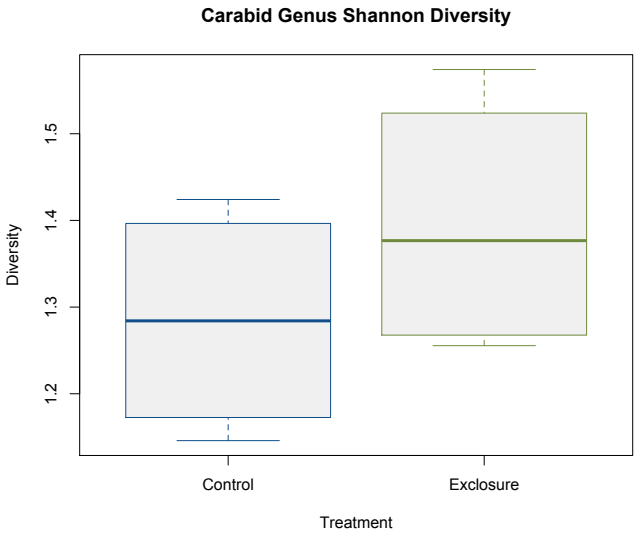

Fig. 7: Ground beetle Shannon's H' diversity; Exclosures = 1.40 ± 0.08, Controls = 1.28 ± 0.07; df = 3; paired t = 5.40; P = 0.012

df = 3; paired t = 0.40; P = 0.70), although not significantly. The total carabid beetle biomass was two times higher in controls (1.54 ± 0.48g SE) compared to exclosures (0.79 ± 0.08g SE; df = 3; paired t = 1.73; P = 0.18), and the average per carabid beetle biomass was also higher in controls (78.14 ± 0.6mg SE compared to 72.62 ± 5.5mg SE; df = 3; paired t = 0.50; P = 0.65), although both were not significant. Rarefaction analysis revealed that controls reach a genus richness of five at 51 sampled individuals while exclosures reach a genus richness of six with only 44 sampled individuals (Fig. 8).

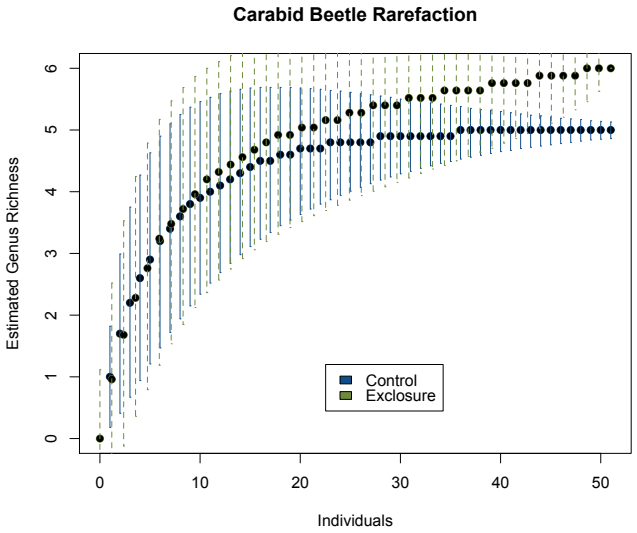

Fig. 8: Ground beetle rarefaction; Controls reach a genus richness of five at 51 sampled individuals while Exclosures reach a genus richness of six with only 44 sampled individuals

Table 2: Summary of beetle results

Beetles					
Comparison	Control	Exclosure	df	paired-t	P-value
Shannon's H' Diversity	2.3 ± 0.09	2.4 ± 0.09	3	0.46	0.67
Abundance	72 ± 14	58 ± 15	3	1.35	0.27
Genus Richness	17 ± 1	16.3 ± 2	3	0.57	0.61
Total Biomass	2.84 ± 0.53g	1.51 ± 0.23g	3	2.87	0.064
per Individual Biomass	0.039 ± 0.002g	0.030 ± 0.006g	3	1.45	0.24
Herb. Shannon's Div	0.92 ± 0.13	0.87 ± 0.11	3	0.21	0.84
Herb. Abundance	21.3 ± 6.9	29 ± 10.7	3	1.29	0.29
Herb. Genus Richness	3.75 ± 0.48	3.5 ± 0.5	3	0.52	0.63
Herb. Rel. Abundance	29.8 ± 7.0%	45.3 ± 6.9%	3	2.02	0.14
Herb. Total Biomass	0.08 ± 0.03g	0.16 ± 0.04g	3	3.09	0.054
Herb. per Ind. Biomass	3.9 ± 1.3mg	7.5 ± 3.5mg	3	1.63	0.2
Gr. Shannon's Div	1.28 ± 0.07	1.4 ± 0.08	3	5.4	0.012
Gr. Abundance	19.75 ± 5.51	11 ± 1.29	3	1.23	0.31
Gr. Genus Richness	4.25 ± 0.25	4.5 ± 0.29	3	1	0.39
Gr. Rel Abundance	27.6 ± 5.5%	24.2 ± 7.9%	3	0.4	0.7
Gr. Total Biomass	1.54 ± 0.48g	0.79 ± 0.08g	3	1.73	0.18
Gr. per Ind. Biomass	78.14 ± 0.6mg	72.62 ± 5.mg	3	0.5	0.65

SPIDERS

Total spider Shannon's *H'* diversity was not significantly higher in controls (2.81 ± 0.07 SE) when compared to exclosures (2.77 ± 0.07 SE; df = 3; paired t = 0.94; P = 0.42). Spider abundance was significantly higher in controls (66 ± 5 SE) as compared to exclosures (55 ± 6 SE; df = 3; paired t = 3.24; P = 0.048) (Fig. 9). Species richness was also higher in controls (23 ± 1 SE compared with 22 ± 1 SE; df = 3; paired t = 2.05; P = 0.13), although not statistically significant. Total spider biomass was not significantly higher in controls (0.25 ± 0.03g SE) when compared to exclosures (0.24 ± 0.06g SE; df = 3, paired t = 0.112; P = 0.92). Average per spider biomass was higher in exclosures (7.9 ± 3.0mg SE) compared to controls (5.0 ± 0.7mg SE; df = 3; paired t = 1.37; P = 0.26). Rarefaction analysis

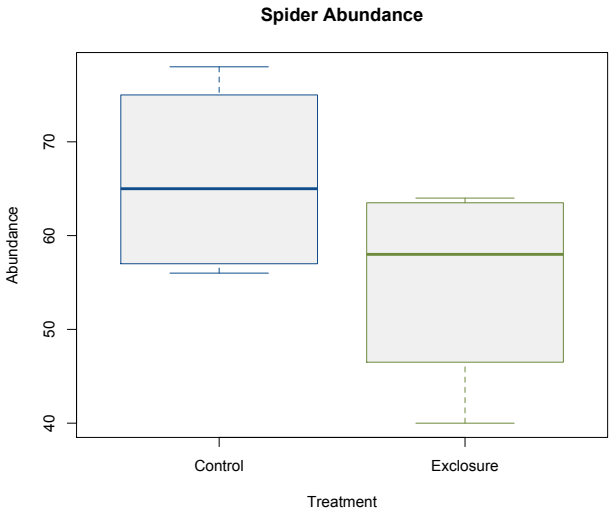

Fig. 9: Total spider abundnace; Controls = 66 ± 5, Exclosures = 55 ± 6; df = 3; paired t = 3.24; P = 0.048

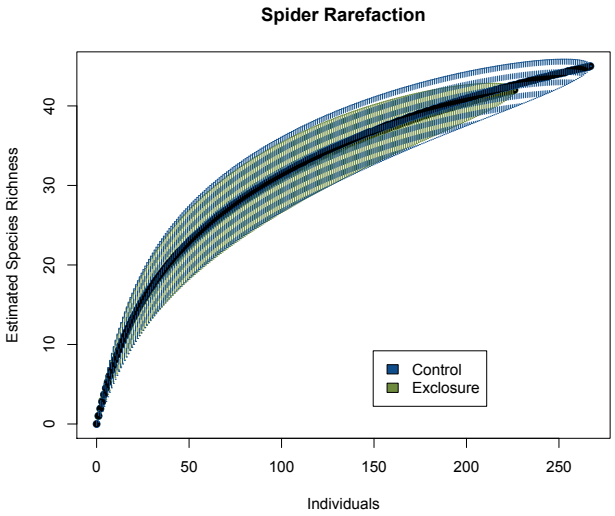

Fig. 10: Total spider rarefaction; Controls reach a species richness of 45 at 267 sampled individuals while Exclosures reach 42 species at 226 individuals

revealed that controls reach a species richness of 45 at 267 sampled individuals while exclosures reach 42 species at 226 individuals (Fig. 10).

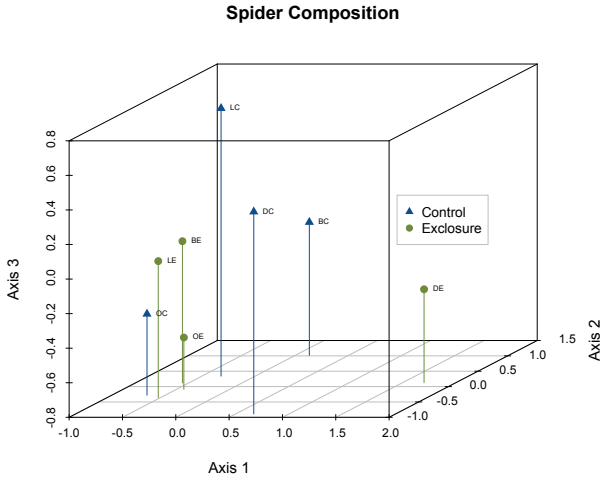

Fig. 11: Non-metric multidimensional scaling (NMDS) ordination analysis; no statistical difference between the composition of the spider assemblages of controls and exclosures; Global R = -0.177; P = 0.91

ANOSIM revealed that there is no statistical difference between the composition of the spider assemblages of controls and exclosures (Global R = -0.177; P = 0.91) (Fig. 11).

Web spider Shannon's *H'* diversity was not statistically higher in controls (2.15 ± 0.11 SE) than in exclosures (2.11 ± 0.04 SE; df = 3; paired t = 0.29; P = 0.79). Abundance was also higher in controls (35 ± 2.3 SE compared to 32 ± 3.8 SE; df = 3; paired t = 0.61; P = 0.58) as was species richness (11.8 ± 0.95 SE compared to 11.5 ± 0.5 SE; df = 3; paired t = 0.2; P = 0.85), although both were not significant. The web spider biomass was not significantly higher in exclosures (0.06 ± 0.01g SE) compared to controls (0.04 ± 0.01 SE; df = 3; paired t = 0.95; P = 0.41) as was average per web spider (2.1 ± 0.8mg SE compared to 1.4 ± 0.9mg SE; df = 3; paired t = 0.91; P = 0.43). According to rarefaction analysis, exclosures reach a maximum species richness (23 species) at 130 sampled individuals. Controls reached maximum species richness (20 species) at 156 sampled individuals (Fig. 12).

Non-web spider

Shannon's *H'* diversity was higher in controls (2.20 ± 0.09 SE) than in exclosures (2.16 ± 0.06 SE; df = 3; paired t = 0.46; P = 0.68); however, this result was not significant. Abundance was higher in controls (31 ± 7.39 SE compared to 23.75 ± 4.61 SE; df = 3; paired t = 2.13; P = 0.12), as was richness (11.75 ± 0.95 SE compared to 10.5 ± 0.96 SE; df = 3; paired t = 1.67; P = 0.19). The non-web spider biomass was higher in controls (0.22 ± 0.04g SE) when compared to exclosures (0.20 ± 0.06g SE; df = 3; paired t = 0.23; P = 0.8345), although not significantly so. Average per non-web spider biomass was higher in exclosures (8.6 ± 1.7mg SE) compared to controls (7.6 ± 1.7mg SE; df = 3; paired t = 0.26; P = 0.81), but not significantly.

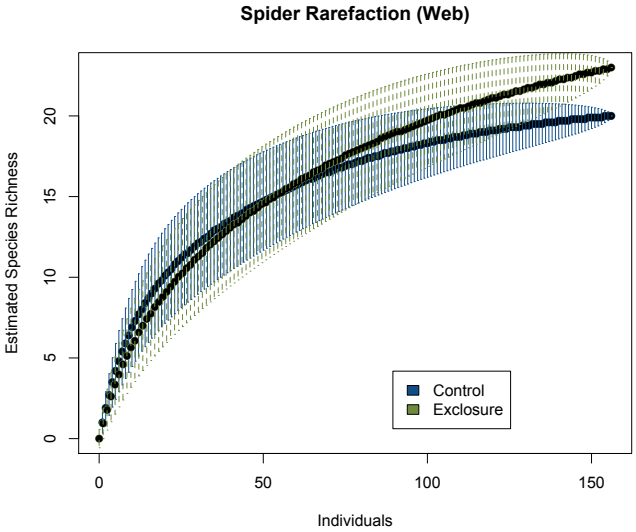

Fig. 12: Web spider rarefaction; Exclosures reach a maximum species richness (23 species) at 130 sampled individuals, Controls reached maximum species richness (20 species) at 156 sampled individuals

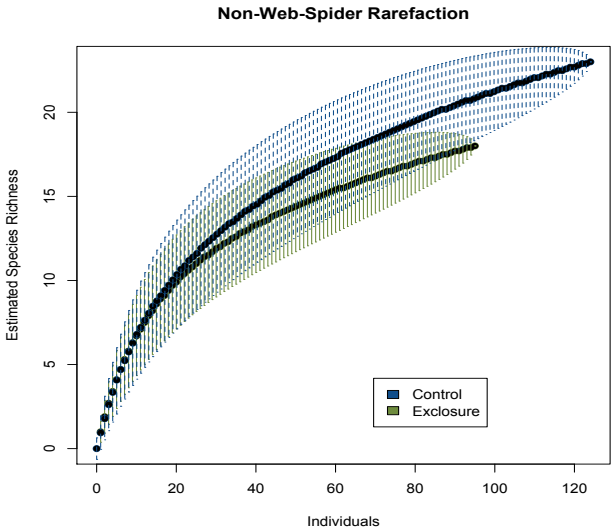

Fig. 13: Non-Web spider rarefaction; Exclosures reach a maximum species richness (18 species) at 95 sampled individuals, Controls reached maximum species richness (23 species) at 124 sampled individuals

Rarefaction analysis revealed that exclosures reach a maximum species richness (18 species) at 95 individuals, while controls reached a maximum species richness (23 species) at 124 sampled individuals (Fig. 13).

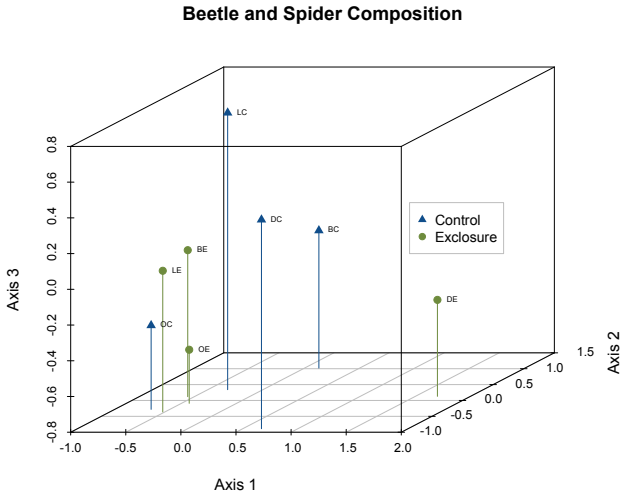

Fig. 14: NMDS Ordination of Beetles and Spiders combined; No statistical difference between the total assemblages in controls and exclosures (Global R = -0.177; P = 0.91; Beetle/Spider assemblage in each exclosure/control pair is statistically similar (Global R = 0.85; P = 0.01)

When beetles and spiders were combined, ANOSIM revealed that there is no statistical difference between the total assemblages in controls and exclosures (Global R = -0.177; P = 0.91. However, the similarity analysis did reveal that the beetle/spider assemblage in each exclosure/control pair is statistically similar (Global R = 0.85; P = 0.01) (Fig. 14).

Table 3: Summary of spider results

Spiders					
Comparison	Control	Exclosure	df	paired-t	P-value
Shannon's H' Diversity	2.81 ± 0.07	2.77 ± 0.07	3	0.94	0.42
Abundance	66 ± 5	55 ± 6	3	3.24	0.048
Species Richness	23 ± 1	22 ± 1	3	2.05	0.13
Total Biomass	0.25 ± 0.03g	0.24 ± 0.06g	3	0.112	0.92
per Individual Biomass	5.0 ± 0.7mg	7.9 ± 3.0mg	3	1.37	0.26
Web Shannon's Div	2.15 ± 0.11	2.11 ± 0.04	3	0.29	0.79
Web Abundance	35 ± 2.3	32 ± 3.8	3	0.61	0.58
Web Species Richness	11.8 ± 0.95	11.5 ± 0.5	3	0.2	0.85
Web Total Biomass	0.04 ± 0.01g	0.06 ± 0.01g	3	0.95	0.41
Web per Ind. Biomass	1.4 ± 0.9mg	2.1 ± 0.8mg	3	0.91	0.43
Non Web Shannon's Div	2.20 ± 0.09	2.16 ± 0.06	3	0.46	0.68
Non Web Abundance	31 ± 7.39	23.75 ± 4.61	3	2.13	0.12
Non Web Species Richness	11.75 ± 0.95	10.5 ± 0.96	3	1.67	0.19
Non Web Total Biomass	0.22 ± 0.06g	0.22 ± 0.04g	3	0.23	0.83
Non Web per Ind. Biomass	7.6 ± 1.7mg	8.6 ± 1.7mg	3	0.26	0.81

WEB-BUILDING SPIDERS

Web spider abundance was significantly higher in exclosures (22.9 ± 2.4 SE) compared to controls (14.9 ± 1.9 SE; df = 31; F = 3.66; P = 0.008) (Fig. 15), as was family richness (4.6 ± 0.2 SE compared to 4.1 ± 0.2 SE; df = 31; F = 14.49; P = 0.0006). Web-site availability at 0.5m was seven times higher in exclosures and WSA at 1.0m was fifty times higher in exclosures (0.5m: exclosure = 127.9 ± 21.4 SE, control = 18.1 ± 3.7 SE; df = 31; F = 7.96; P = <0.0001; Fig. 16; 1.0m: exclosure = 51.5 ± 12.7 SE, control = 1.1 ± 0.3 SE; df = 23; F = 3.29; P = 0.023). Litter depth was 1.5 times higher in exclosures (51.9 ± 1.9mm SE) compared to controls (34.0 ± 2.3mm SE; df = 31; F = 3.58; P = 0.009). Total prey availability was significantly higher in controls (886.8 ± 160.8 SE) compared to exclosures (330.0 ± 55.4 SE; effect size = -0.90 ± 0.13; 95%CI = -1.49, -0.43). Average prey size was higher in exclosures (2.80 ± 0.16mm SE) compared to controls

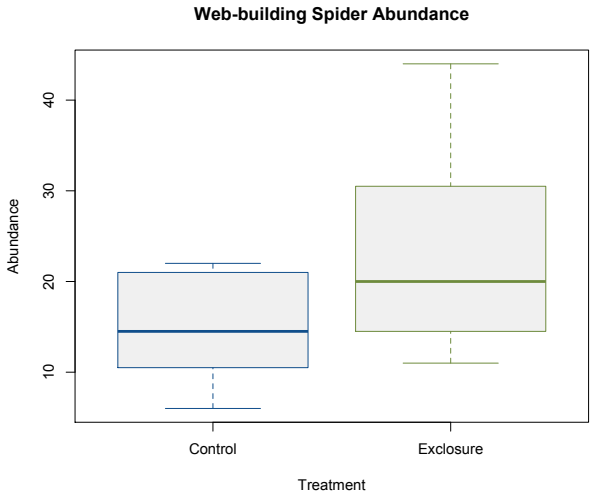

Fig. 15: Web-building spider abundance; Exclosures = 22.9 ± 2.4, Controls = 14.9 ± 1.9; df = 31; paired t = 3.66; P = 0.008

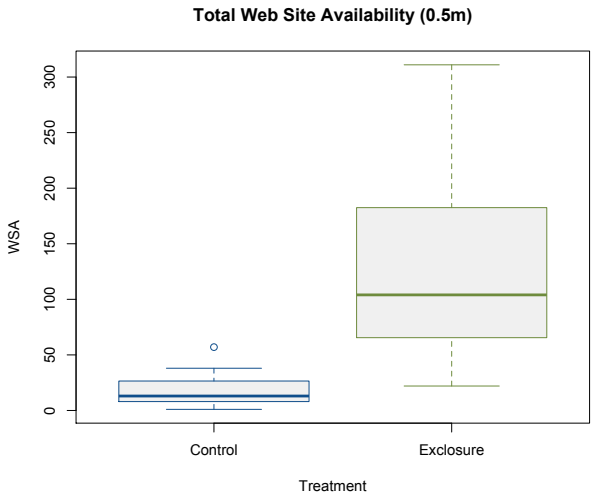

Fig. 16: Web site availability at 0.5m; Exclosures = 127.9 ± 21.4, Controls = 18.1 ± 3.7; df = 31; paired t = 7.96; P < 0.0001

(2.61 ± 0.10mm SE; effect size = 0.08 ± 0.04; 95%CI = -0.11, 0.25), although not significantly so.

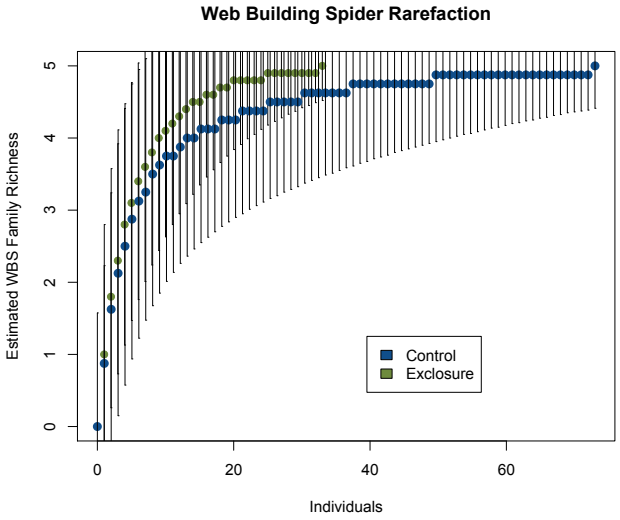

Fig. 17: Web spider family rarefaction; Exclosures reach a maximum family richness (5 families) at 33 sampled individuals, Controls reached maximum family richness (5 families) at 73 sampled individuals

According to rarefaction analysis, exclosures reach a maximum family richness (5 families) at 33 sampled individuals. Controls reached maximum family richness (5 families) at 73 sampled individuals (Fig. 17). Rarefaction analysis revealed that exclosures reach a maximum species richness (24 species) at 131 sampled individuals. Controls reach maximum species richness (22 species) at 143 sampled individuals (Fig. 18).

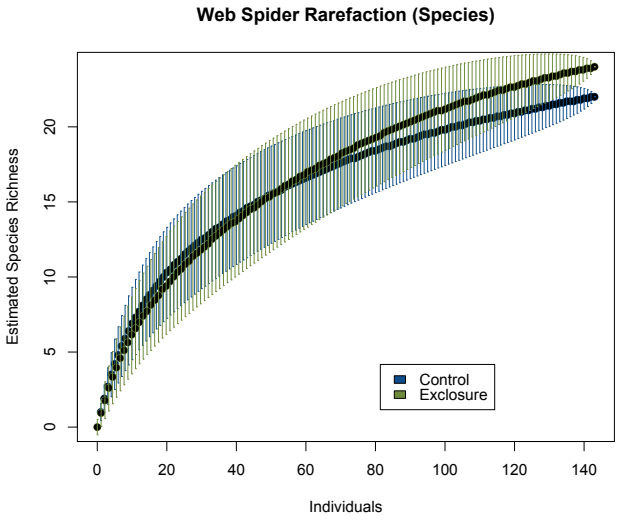

Fig. 18: Web spider species rarefaction; Exclosures reach a maximum species richness (24 species) at 131 sampled individuals, Controls reach maximum species richness (22 species) at 143 sampled individuals

The web-building spider family assemblage composition may differ between controls and exclosures, revealed by ANOSIM analysis (Global R = 0.344; P = 0.057); (Fig. 19).

The relative abundance of all five families encountered differed between controls and exclosures. Aranaeidae (vertical orb weavers) comprised 3.4% of the control assemblage and 10.4% of the exclosure assemblage; Tetragnathidae (horizontal orb weavers) made up 10.5% of the control assemblage and 10.4% of the exclosure assemblage; Theridiidae (tangle/cob weavers) comprised 23.9% of the control assemblage and 31.7% of the exclosure assemblage; Linyphiidae (sheet weavers) made up 34.9% of the control assemblage and 32.8% of the exclosure assemblage; Angelenidae (funnel weavers) comprised 27.3% of the control assemblage and 14.6% of the exclosure assemblage (Fig. 20).

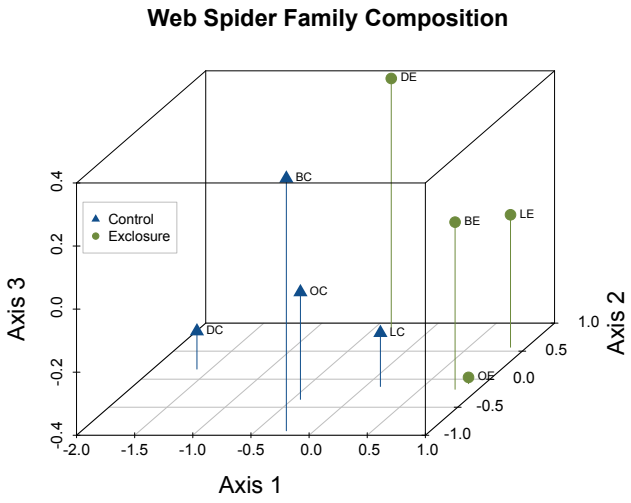

Fig. 19: Web-building spider family NMDS ordination; Assemblage composition may differ between controls and exclosures; R = 0.344; P = 0.057

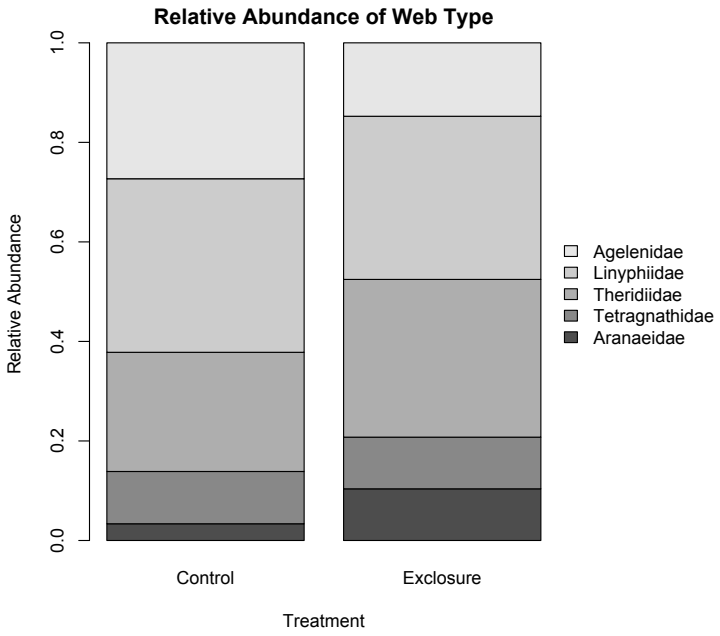

Fig. 20: Relative abundance of web-building spider families; Aranaeidae: control = 3.4%, exclosure =10.4%; Tetragnathidae: control = 10.5%, exclosure = 10.4%; Theridiidae: control = 23.9%, exclosure = 31.7%; Linyphiidae control = 34.9%, exclosure = 32.8%; Angelenidae: control = 27.3%, exclosure = 14.6%

ANCOVA analysis was used to determine if the treatment (control or exclosure) or the predictor variables (WSA0.5m, WSA1.0m, and litter depth) explained a significant portion of the variance in the data. When compared across WSA at 0.5m, web-building spider abundance was significantly related to treatment (df = 1; F = 7.09; P = 0.012), not WSA at 0.5m (WSA0.5m; df = 1; F = 2.32; P = 0.14) (Fig. 21). When compared across WSA at 1.0m, web-building spider abundance was neither significantly related to treatment (df = 1; F = 3.59; P = 0.072) nor WSA at 1.0m (WSA1.0m; df = 1; F = 1.22; P = 0.28). Additionally, abundance was significantly related to litter depth (df = 1; F = 9.61; P = 0.004), not treatment (df = 1; F =

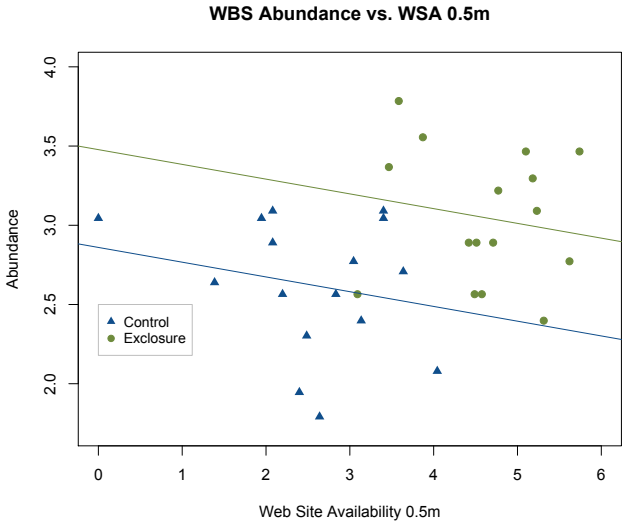

Fig. 21: ANCOVA of Web-building spider abundance compared across WSA at 0.5m; significantly related to treatment (df = 1; F = 7.09; P = 0.012), not the predictor variable (df = 1; F = 2.32; P = 0.14)

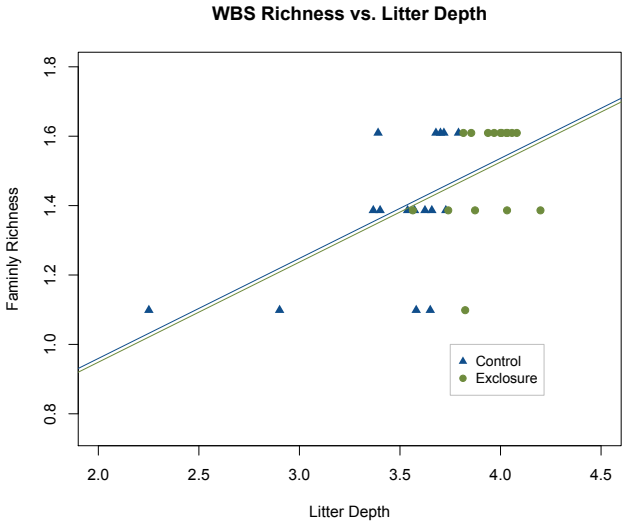

Fig. 22: ANCOVA of Web-building spider family richness compared across litter depth; significantly related to the predictor variable (df = 1; F = 14.02; P = < 0.0001) and not the treatment (df = 1; F = 0.023; P = 0.88)

1.61; P = 0.21). Web-building spider family richness, when compared across WSA0.5m, was neither significantly related to treatment (df = 1; F = 1.81; P = 0.19) or WSA at 0.5m (WSA0.5m; df = 1; F = 2.04; P = 0.16). When compared across WSA at 1.0m, however, family richness was significantly related to the predictor variable, WSA at 1.0m, (df = 1; F = 7.41; P = 0.013) and not the treatment (df = 1; F = 0.19; P = 0.67). The same was true when family richness was compared across litter depth (Treatment: df = 1; F = 0.023; P = 0.88; Litter Depth: df = 1; F = 14.02; P = < 0.0001) (Fig. 22). When compared across total prey availability, web-building spider abundance was significantly related to treatment, not prey availability (Treatment: df = 1; F = 5.05; P = 0.033; Prey Availability: df = 1; F = 3.12; P = 0.087) (Fig. 23). However, richness was neither related to treatment nor prey availability (Treatment: df = 1; F = 0.87; P = 0.35; Prey Availability: df = 1; F = 3.32; P = 0.079).

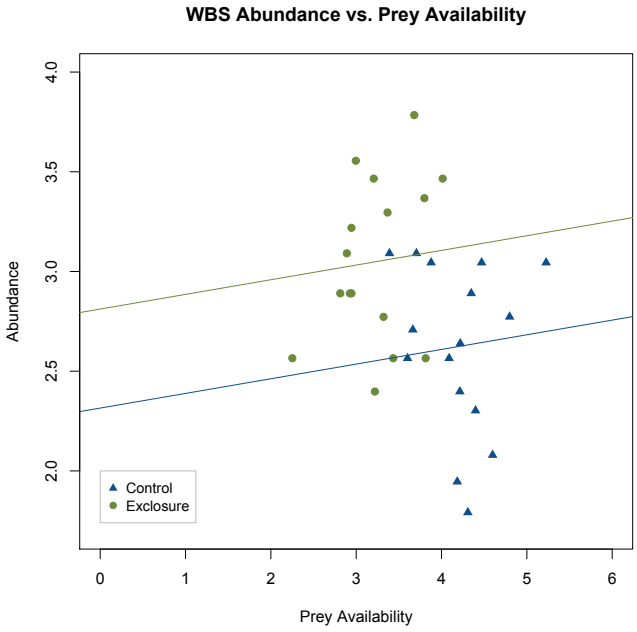

Fig. 23: ANCOVA of Web-building spider abundance compared across prey availability; significantly related to treatment (df = 1; F = 5.05; P = 0.033), not the predictor variable (df = 1; F = 3.12; P = 0.087)

Table 4: Summary of Web-building spider results

Web-Building Spiders					
Comparison	Control	Exclosure	df	F	P-value
Abundance	14.9 ± 1.9	22.9 ± 2.4	31	3.66	0.008
Family Richness	4.1 ± 0.2	4.6 ± 0.2	31	14.49	0.0006
WSA at 0.5m	18.1 ± 3.7	127.9 ± 21.4	31	7.96	<0.0001
WSA at 1.0m	1.1 ± 0.3	51.5 ± 12.7	23	3.29	0.023
Litter Depth	34.0 ± 2.3mm	51.9 ± 1.9mm	31	3.58	0.009
	Control	Exclosure		Effect Size	95% CI
Total Prey Availability	886.8 ± 160.8	330.0 ± 55.4		-0.90 ± 0.13	-1.49, -0.43
Avg. Prey Size	2.61 ± 0.1mm	2.8 ± 0.16mm		0.08 ± 0.04	-0.11, 0.25

POWER

Many of the results in this study, especially those comparing that beetle and total spider assemblages were not significant. This likely is due to the small sample size that using historically established exclosures entailed (my data collection was limited to a sample size of four). To examine if small sample size could be a reason for low effect detection, I completed a power test on beetle abundance using the pwr package in R (Champely 2012). The power test determines the sample size required to detect an effect given an effect size and degree of confidence or calculates the probability of detecting an effect given a sample size. According to the power test, there is a 43.3% chance that I will detect a difference in beetle abundance between controls and exclosures using a paired t-test with a sample size of four and a significance level of 0.05. Additionally, in order to detect a difference between beetle abundance in controls and exclosures 95% of the time with a significance level of 0.05, I would require a

sample size of 9.83 (almost ten exclosures). Therefore, at least for beetle abundance, there could be differences between the assemblages in controls and exclosures that cannot be detected due to small sample size.

IV. DISCUSSION

VEGETATION

Differences in the vegetation community between exclosures and controls were visually striking. Both percent cover and vegetation height were significantly higher in areas without ungulate browsing pressure. The removal of browsing pressure allows and promotes plant growth. Forage type composition also differed significantly between areas affected and un-affected by deer (Begley-Miller et al. 2014). Woody and forb forage types were both significantly higher in areas protected from deer (nearly 52 and 14 times greater respectively) while graminoid forage type percent cover was almost 6 times higher in areas with deer browsing. Deer have engineered these areas through selective feeding. They prefer woody and herbaceous species and are able to completely eliminate tree regeneration and extirpate some herbaceous species from an area (Waller and Alverson 1997). Graminoid species dominate in areas of high deer populations because they are browse-tolerant and not selectively fed upon by deer. This creates biotic impoverishment of the forest vegetation and a movement toward graminoid dominated areas. This pattern has been observed in many areas (Rooney 2009, same area; Wiegmann & Waller 2003, all over WI; Waller and Alverson 1997, PA; Stockton et al. 2005, British Columbia, Canada). Selective feeding may also help to explain the percent cover differences between

exclosures and controls. Woody and forb plant species (which dominated exclosed areas) have greater leaf area and therefore contribute more to the total percent cover than graminoid species (which dominated control areas exposed to deer browsing). Overall, deer browsing reduces vegetation percent cover, changes and simplifies forage type composition, and reduces vegetation height. This has the potential to homogenize microclimates (fewer vegetation types, less height structure, less litter, less humid, more sunlight) (Rooney& Waller 2003) and affect beetle and spider assemblages (Stewart 2001).

BEETLES AND SPIDERS

There were not many statistically significant results when comparing the beetle and total spider assemblages of deer impacted areas and those areas relieved from browsing pressure. I expected exclosed areas to provide a greater diversity of habitats, greater food abundance for herbivorous beetles, and greater structural diversity, and therefore boast a higher diversity, abundance, and richness of herbivorous beetles and web-building spiders (Baines et al. 1994; Allombert et al. 2005; Takada et al. 2008; Miyashita et al. 2004; Chips et al. 2014). I expected the opposite for predatory beetles and non-web spiders because control areas provide more open area for hunting (Suominen et al. 1999; Suominen et al. 2003). It is important to remember, however, that exclosed areas represent a relief from grazing, not an ungrazed area. Deer densities have been extraordinarily high for over 50 years in the entire state of Wisconsin (Rolley 2012; Leopold et al. 1947). There are no refugia for beetles and spiders

that require low deer browsing within which to persist close to the sampling area. Therefore, even though the exclosures protected forest area from grazing for twenty-three years, beetle and spider species associated with ungrazed or lightly grazed areas may have not yet returned to this area. More specifically, deer have reduced the abundance of forb and woody forage types to almost zero in this area (Rooney 2009; Wiegmann & Waller 2003). Beetle species that are monophagous or rely on a habitat with structural variability (specific plants or parts of plants for reproduction) will have been extirpated from the area. With no refugia within a reasonable distance, the recolonization of these species may not yet have, or may never happen. Additionally, we are not able to compare the assemblages of grazed areas to their historical baseline and therefore might not be detecting the changes that deer have caused in these assemblages.

In addition to limited differences in beetle and spider abundance, diversity, and richness between exclosures and controls, the composition of these assemblages also did not differ between sampled areas. Even though abundance, diversity, and richness did not differ between areas with and without deer pressure, I did expect the assemblage compositions to differ. The microclimates and microhabitats are very different (exclosures have higher percent cover, structural diversity, and a greater percentage of forb/woody species, and therefore are more shaded, have greater litter depth, and cooler temperatures) and I therefore expected the composition of species inhabiting these areas to differ. However, the lack of difference between the assemblages observed in these areas could, again, be attributed to the lack of close refugia.

Additionally, this could be an artifact of the overall small deer-free area. Since there is so little deer-free space here to support all individuals, even if one area is favorable for some activities (i.e. open hunting area for carabids or ground spiders), individuals must venture into the unfavorable area for others (i.e. prey availability). This could explain why the assemblage composition of exclosures and controls were indistinguishable. Although the assemblages of exclosures and controls were not distinguishable from one another, each exclosure/control pair was statistically similar to one another. This affirms that there is a high rate of flow of species between controls and exclosures (each pair is very close to one another) but not between sampled pairs. There are most likely small local differences in the microclimate (humidity, temperature, light) between sampled a pairs, although these measurements were not recorded. From personal observation, Dark Hollow is dark and relatively lacking in vegetation cover in both the exclosure and control; Ovenbird has extremely dense vegetation in the exclosure, and is sparse in the control; Loner is similar to Ovenbird, but a bit less dense; and Big Gap is similar to Loner, but there is a large light gap in the control. These small differences could change the vegetation composition (vegetation type, height, heterogeneity) and prey availability available at each pair, and therefore the beetle and spider species present.

WEB-BUILDING SPIDERS

Web-building spiders were significantly more abundant and diverse in areas protected from deer herbivory. Additionally, the composition of the spider

community in deer affected areas differed significantly from those areas protected from deer herbivory. These differences corresponded with significantly higher web site availability and litter depth in exclosed compared to control areas. Exclosures, because of the removal of deer herbivory, have a higher percentage of woody and forb species and a greater vegetation height. This provides spiders with more places to anchor their webs on live vegetation and in/on leaf litter. Exclosures had higher relative abundance of vertical orb weavers and cob weavers. Both spider types require many anchor points to construct their webs (Wise 1993; Bradley 2013). Conversely, through the indirect effects of their grazing, deer have engineered the controlled areas in such a way that the environment can no longer support a high abundance of web-building spiders. Those web-building spiders that can be supported the degraded areas construct smaller or more tangled webs that can be supported by few, close together anchor points (funnel-web weavers). Additionally, prey availability was higher in controls, but size did not differ. It is likely, therefore, that web-building spider abundance in controls is limited by web site availability while in exclosures web-building spider abundance is limited by prey availability (Wise 1993).

Deer are indirectly affecting both abundance and richness of web-building spiders through changes in web site availability and litter depth. Changes in the spider community can be attributed to changes in web site availability and litter depth (indirect consequences of deer herbivory) in more cases than the treatment (direct presence or absence of deer) alone. Deer are changing web site availability and litter depth in controlled areas through the removal of plant

biomass. This equates to fewer web sites for spiders and indirectly affects their abundance and richness. It is interesting to note that deer indirectly change the environment for spiders in complex ways. Deer change the vegetation composition of the forest understory through selective feeding (Rooney 2009; Wiegmann & Waller 2003). Over time, this changes the vertical structure because of the suppression of seedling regeneration. Consequently, leaf litter build-up in highly deer populated areas decreases due to the lack of deciduous seedlings and saplings. Additionally, this lack of mid-canopy trees may reduce shade, increase temperature, decrease humidity, and quicken the pace of leaf litter decomposition although these microclimate parameters were not recorded in this study (Rooney & Waller 2003; Stewart 2001). Regardless, deer herbivory reduces available habitat availability and changes the microclimate for web building spiders. Therefore, through selective feeding, deer are engineering forest environments to be graminoid dominated and structurally lacking, and this is negatively affecting web-building spider abundance and richness and is changing the composition of the assemblages in northern Wisconsin.

CONCLUSIONS

These results demonstrate that the indirect consequences of deer overpopulation are complex and far-reaching. Through selective feeding and plant biomass removal, deer are acting as ecosystem engineers, driving this forest ecosystem to one dominated by low-structure, browse-tolerant graminoid plant species. This is indirectly negatively impacting and changing the web-

building spider assemblages in this area and may have changed beetle and total spider assemblages, although we do not have a historical dataset upon which to make comparisons. This study revealed interesting results but additional study of this area could increase the validity and depth of the results.

Future studies using these sample experimental exclosures, overall, need to be more thorough. Differences in mircoclimate were observed but the individual parameters were not recorded. In future studies, I would record temperature, humidity, light, and the state of the leaf litter decomposition at each sampling point so the differences in microclimate could be definitively stated. Additionally, the methods of sampling (sweep-net, pitfall trap, site-counts) left room for missing individuals and whole species such as those that prefer plant heights above 1m or those that are fast moving. To reduce this in future studies, a more complete method of sampling on vegetation (i.e. insecticide application and subsequent invertebrate collection) could be incorporated into the sampling scheme. Also, I expected that the overall size of the webs constructed in control areas was smaller than that in exclosures because controls have fewer web anchor points. However, I did not collect this data. In future studies, I would record the length of the largest portion of each web encountered so this hypothesis could be investigated. It would be interesting to investigate if the spider assemblage differences observed were due to differences in habitat structure alone, rather than the presence or absence of deer. In order to test this, I could construct artificial structures for spiders to use in exclosed and controlled areas and compare the associated spider assemblages. This could help remove

some indirect effects of deer presence or absence and allow for the comparison of structure and deer alone. More importantly, these experiments need to be repeated in an area with a more average deer population history. Wisconsin deer populations are abnormally high and have been high for decades (Rolley 2012; Leopold et al. 1947). Therefore, the results shown in this study may not be indicative of trends seen in more “normal” areas.

In northern Wisconsin, it seems that the indirect effects of deer overpopulation are a more important driver in shaping connected communities than direct effects. Through selective herbivory, deer are acting as an ecosystem engineer in this study area because they alter the abundance or richness of co-occurring species through habitat alterations (Jones et al. 1994; Pringle 2008). These findings may have widespread significance because deer and other large ungulates are overpopulated in many areas of the world (Ward 2005; Gortazar et al. 1998; Alverson et al. 1988; McShea et al. 1997). Although Wisconsin has had unusually high deer populations for an extended period of time and therefore we can cannot draw direct comparisons to other locations, this study can provide us with a picture of what could happen if deer populations in other locations are allowed to reach and maintain these high densities. Therefore, an important challenge for future studies is to understand further how deer and other large ungulates are interacting with co-occurring communities indirectly, at what densities do these herbivores threaten other communities, and how are these ungulate effects best managed.

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VI. APPENDIX

Table A1: Species/Genus List, contains all collected individuals from pitfall traps, sweep-net samples, and web spider site counts. Beetles are organized by family, spiders are organized by functional group.

Sweep-net and Pitfall

Beetles

	Control	Exclosure	Total
Carabidae			
Bradycellus	8	3	11
Calosoma	5	7	12
Carabus	38	14	52
Harpalus	11	8	19
Pterostichus	17	11	28
Stenolophus	0	1	1
Cerabycidae			
Desmocerus	1	3	4
Curcurlionidae			
Attelabus	4	0	4
Hylobius	6	0	6
Otiorhynchus	17	41	58
Sitona	54	65	119
Elateridae			
Ctenicera	1	1	2
Melanotus	2	4	6
Geotrupidae			
Geotrupes	11	6	17
Histeridae			
Xerosaprinus	1	1	2
Lampyridae			
Ellychnia	0	1	1
Lucidota	3	2	5
Leptodiridae			
Catops	13	8	21
Lucanidae			
Platycerus	1	0	1
Lycidae			
Plateros	0	1	1

Meloidae			
Meloe	0	1	1
Scarabaeidae			
Macrodactylus	0	1	1
Onthophagus	1	0	1
Serica	2	1	3
Silphidae			
Necrophilia	28	12	40
Nicrophorus	20	6	26
Oiceoptoma	8	2	10
Staphylinidae			
Eusphalerum	0	2	2
Philonthus	16	11	27
Platydracus	10	8	18
Tachyporus	7	5	12
Tenebrionidae			
Strongylium	0	4	4
Trogidae			
Trox	3	2	5
Total	**288**	**232**	**520**

Spiders

	Control	Exclosure	Total
Orb Weavers			
Araneus marmoreus	4	3	7
Araneus spp.	1	11	12
Araniella displicata	1	0	1
Glenognatha foxi	0	1	1
Hypsosinga rubens	0	1	1
Mangora placida	2	0	2
Pachygnatha furcillata	0	2	2
Tetragnatha spp.	20	21	41
Space-filling Weavers			
Asagena sp.	3	3	6
Cryptachaea porteri	5	3	8
Enoplognatha ovata	18	23	41
Hentziectypus globosus	4	1	5
Neospintharus trigonum	0	1	1
Steatoda borealis	1	0	1
Wolf Spiders			
Allocosa funerea	1	0	1
Geolycosa wrighti	1	0	1
Hogna aspersa	0	1	1
Pardosa saxatilis	19	21	40
Pardosa xerampelina	1	0	1

Pirata insularis	7	6	13
Trabeops aurantiacus	3	0	3
Trochosa terricola	10	7	17
Foliage Hunters			
Anyphaena sp.	4	6	10
Clubiona abboti	11	11	22
Cheiracanthium inclusum	1	2	3
Clubiona canadensis	0	1	1
Drassyllus depressus	1	0	1
Elaver excepta	8	13	21
Titanoeca sp.	1	2	3
Trachelas tranquillus	1	1	2
Ground Hunters			
Castianeira amoena	2	0	2
Dipoena spp.	16	11	27
Scotinella spp.	1	0	1
Funnel Web Weavers			
Callobius bennetti	0	1	1
Coras juvenilis	2	3	5
Sheet Web Weavers			
Hypselistes florens	0	1	1
Microlinyphia mandibulata	3	0	3
Microneta viaria	3	3	6
Neoantistea agilis	17	11	28
Neriene clathrata	8	3	11
Neriene radiata	2	2	4
Pityohphantes costatus	0	2	2
Tenuiphantes tenuis	23	19	42
Crab Spiders			
Mechaphesa asperata	16	9	25
Philodromus rufus	3	1	4
Tibellus oblongus	22	5	27
Xysticus ferox	1	1	2
Surface Hunters			
Dolomedes spp.	7	2	9
Pisaurina mira	1	1	2
Jumping Spiders			
Evarcha spp.	2	2	4
Hentzia mitrata	7	7	14
Pelegrina spp.	3	1	4
Total	**267**	**226**	**493**

Web-building Spiders

	Control	Exclosure	Total
Vertical Orb Weavers			

Empty Web	3	12	15
Hyposisinga rubens	2	2	4
Singa keyserllingi	1	0	1
Araneus saevus	0	1	1
Araneus thaddeus	0	1	1
Araneus marmoreus	0	12	12
Larinoides borealis	2	5	7
Larinoides patagiatus	0	1	1
Araneus diadematus	0	2	2
Metazygia labyrinthea	0	1	1
Neoscona domicilorum	0	1	1
Horizontal Orb Weavers			
Empty Web	3	4	7
Mangora maculata	18	22	40
Glenognatha foxi	2	4	6
Araniella displicata	0	4	4
Tetragnatha sp.	1	4	5
Larinoides cornutus	1	0	1
Cob Web Weavers			
Empty Web	45	99	144
Enoplognatha marmorata	0	1	1
Theridion frondeum	2	4	6
Neospintharus trigonum	3	5	8
Eidmannella pallida	2	0	2
Yunohamella lyrica	1	1	2
Spintharus flavidus	0	2	2
Asagena americana	1	0	1
Platnickina alabamensis	3	4	7
Sheet Web Weaver			
Empty Web	25	21	46
Neriene radiata	35	71	106
Frontinella communis	0	6	6
Pityohyphantes costatus	1	1	2
Hypselistes florens	1	1	2
Helophora insignis	18	18	36
Estrandia grandaeva	0	2	2
Meioneta fabra	1	0	1
Ceratinopsidis formosa	2	0	2
Funnel Web Weaver			
Empty Web	45	27	72
Agelenopsis pennsylvanica	19	27	46
Tegenaria domestica	1	1	2
Cybaeopsis tibialis	0	1	1
Total	**238**	**368**	**606**