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Herbivore Abundance in Simple and Diverse Habitats: The Direct and Indirect Effects of Plant Diversity and Habitat Structure

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HERBIVORE ABUNDANCE IN SIMPLE AND DIVERSE HABITATS - THE
DIRECT AND INDIRECT EFFECTS OF PLANT DIVERSITY AND HABITAT
STRUCTURE

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
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Herbivore abundance in simple and diverse habitats – the direct and indirect effects of
plant diversity and habitat structure

Laura F. Altfeld

ABSTRACT

Herbivore abundances are determined by a set of interacting factors that vary among different habitat types. Specifically, herbivore abundances in monocultures and polycultures may be governed by the same set of factors but with varying influences in the different habitats. In addition, monophagous and polyphagous herbivores may respond differently to the same set of influencing factors. I examined several abiotic and biotic factors in manipulated monocultures and polycultures of *Borrchia frutescens* in a west central Florida salt marsh. The experimental plots differed in both plant diversity and aboveground habitat structure to see how each component of diversity contributed to variability in the abiotic and biotic factors and how those factors were related to differences in herbivore abundances. The monoculture treatment involved clipping all above ground non-host plant material to achieve a host plant monoculture. The polyculture treatments involved pinning all non-host plant material to achieve a polyculture with reduced above ground habitat structure. The second polyculture treatment was a control in which the naturally diverse plots were unmanipulated. Two monophagous and one polyphagous herbivores were chosen for this study because of

their abundance and availability in the field. The two monophagous herbivores on the host plant *Borrchia frutescens* were *Pissonotus quadripustulatus* (Homoptera:Delphacidae) and *Asphondylia borrichiae* (Diptera: Cecidomyiidae) both of which have been well studied in the field where the current experiment took place. The polyphagous herbivore was *Cyarda acutissima* (Homoptera: Flatidae), a poorly known invasive from Cuba. Soil salinity and host plant leaf nitrogen content were the abiotic factors measured. Herbivore abundances, percent egg and gall parasitism by parasitoids, spider abundances on host plant stems and ground spider abundances were the biotic factors measured. Both salinity and host plant leaf nitrogen were significantly different among the different treatments with clipped plots having the highest salinity and leaf nitrogen content. Population densities of both of the monophagous herbivores were not significantly different between treatments. The polyphagous herbivore had significantly higher abundances in the pinned and control plots than in the clipped plots. Stem spider abundances were not significantly different among treatments. Ground spiders, however, were significantly more abundant in control and pinned plots than clipped plots. Parasitism of both monophagous herbivores was not significantly different between treatments but was generally higher in the control plots. The results suggest that for monophagous herbivores bottom-up and top-down factors act antagonistically in monocultures but for the polyphagous herbivore, the presence of multiple host plants is more influential in diverse plots even given the higher abundances of generalist predators.

Introduction

Herbivore abundance is determined by a myriad of factors. Abiotic conditions, such as temperature, humidity and light, and biotic conditions such as nutritional quality and quantity of host resources, and the presence and abundance of natural enemies are some of the major factors considered important in determining the density of herbivores in a given habitat. Naturally, abiotic and biotic factors vary among different habitats. As a result, patterns of herbivore abundance vary among different habitats. However, comparisons between habitat types have revealed interesting patterns in herbivore abundances, especially between monoculture and polyculture habitats. It has been commonly observed that herbivore abundances are increased in monocultures, especially in large-scale agroecosystems, relative to polycultures. This observation has generated much interest among ecologists.

Two hallmark theories that attempt to generalize the patterns of herbivore abundance in monoculture and polyculture habitats come from Root (1973). These are the Resource Concentration Hypothesis and the Enemies Hypothesis. The resource concentration hypothesis states that in monocultures numerical dominance of one or a few specialist herbivore species results from an increased concentration of the host plant and these specialists, whose entire life histories are met by the plant species in said habitat, are better able to persist, thereby remaining dominant. Given the above explanation, it seems reasonable to assume that specialist herbivores will tend to be more abundant in monocultures than in polycultures and more abundant in monocultures than

generalist herbivores. The Enemies Hypothesis holds that diverse plant habitats provide a wide variety of resources to both herbivores, particularly generalists, and predators, the latter of which exerts a suppressing force on the abundance of individuals in any of the herbivore species. In this way, dominance by any or a few species of herbivores, regardless of their eating habits, is prevented in polyculture communities.

The implications for the behavior of monophagous and polyphagous herbivores as predicted by Root's theories are interesting. Monophagous herbivore species are predicted to be less abundant in polycultures regardless of the influences of natural enemies because of the importance of host plant concentration; polyphagous herbivore species are predicted to be less abundant in polyculture when (a) the effects of natural enemies is most important but (b) more abundant in polyculture when food resources are most important (Risch et al. 1983). In the field, the behavior of many herbivore species agree with the predictions made by Root's theories. As suggested in a review by Andow (1991), monophagous species were less abundant in polyculture in 60.8% of the studies reviewed while polyphagous species were less abundant in polyculture in only 47.1% of the studies reviewed. This latter result suggests that food resources may be more important than natural enemies are for polyphagous species. However, there are some herbivore species that have unique and unpredicted responses to plant diversity that result from specific ecological interactions within a habitat (Letourneau 1986, Letourneau 1995). For example, Hacker and Bertness (1995) studied salt marsh aphids and found that they were more abundant on lower quality, short form *Iva frutescens* in mixed stands than on healthy tall form *I. frutescens* in pure stands despite the insects' improved growth on the tall form plants. Such a result was due to significantly higher predation rates by

ladybird beetles in monoculture, an example of a complex interaction between a host plant and natural enemies.

The great complexity of ecological interactions among plants, herbivores and natural enemies has made predicting herbivore abundance difficult (Andow 1991). Plant diversity can change herbivore growth directly through host plant nutritional quality and/or indirectly by altering the efficiency or abundance of natural enemies. Plant chemical cues can help parasitoids find their prey; nectaries may provide alternative resources to natural enemies, and plant structures can obstruct parasitoid movement yet provide habitat for spiders and other generalist predators (Price et al. 1980). These and other factors can act in concert or antagonistically to produce differing, and perhaps otherwise unpredicted effects on herbivore abundances.

The purpose of this study was to investigate the independent effects of plant diversity and habitat structure on a host plant, the abundance of two monophagous and one polyphagous herbivore species common on the host plant, and the abundance/rate of attack of natural enemies. The two monophagous herbivore species in this study have been extensively examined in natural monocultures of the host plant (Stiling et al. 1992, Rossi and Stiling 1995, Moon et al. 2000, Moon and Stiling 2000, Moon and Stiling 2001). While much is known about the relative influences of bottom-up and top-down factors on the monophagous herbivores in natural monocultures this study will examine the relative influences of the same factors in diverse habitats. The polyphagous herbivore species in this study has not been previously documented as occurring at this study site. In addition to providing information on the abundance of herbivores in relation to plant

diversity and habitat structure, this study will also serve to document an invasive insect's presence and abundance on the host plant in a central Florida salt marsh.

Study System

This study examined the effects of plant diversity and habitat structure on the different levels of a tri-trophic system. The main thrust of the experiment was to examine selected abiotic and biotic factors for their degree of influence in affecting changes in herbivore abundances in monoculture versus polyculture. Soil salinity and host plant leaf nitrogen were the abiotic factors examined. Biotic factors were rates of parasitism and spider abundances. Three insect herbivore species, two monophagous and one polyphagous, were monitored for changes in monthly abundances on a single host plant in both simple (monoculture) and diverse (polyculture) habitats. Changes in herbivore abundances were related to the biotic and abiotic conditions in the different habitat types.

Habitats within the park range from salt marsh at the bay's edge to upland scrub habitat further inland.

The vegetation in this area of the marsh is a mosaic of several plant species and matches what has been previously termed a *Distichlis* meadow (Rey and McCoy 1982). The plant community is predominantly comprised of *Distichlis spicata* Linnaeus (Poaceae), *Borrchia frutescens* L. (Asteraceae), *Batis maritima* L. (Bataceae), and *Avicennia germinans* L. (Avicenniaceae) in varying relative proportions. Tidal flooding of the meadow is infrequent, occurring only during times of strong westerly winds, storms and spring tides. Infrequent tidal flooding and evaporation cause salt accumulation in this back marsh meadow and the increased interstitial salinity results in

stunted growth forms of *Borrchia frutescens* (Antlfinger 1981), the targeted host plant in this study.

Borrchia frutescens Linnaeus is a succulent perennial of the family Asteraceae. Commonly known as the sea oxeye daisy, it is abundant in salt marshes along the southeastern U.S. Typically less than 1 m in height *B. frutescens* produces yellow ray florets, spreads through the use of rhizomes and is found in areas of both high and low salinities along the marsh (Antlfinger 1981). Specimens in areas of high relative salinity on the marsh, especially around the salt pans, are usually stunted in height (less than 30 cm in Upper Tampa Bay, Altfeld, personal observation) compared to specimens in pure stands closer to the water's edge (60 – 100 cm). At the study site these stunted forms grow in close association with, primarily, *Distichlis spicata* and *Batis maritima* although there are also occasionally encountered young *Avicennia germinans* shrubs throughout the meadow.

B. frutescens is host to two monophagous herbivores at the study site. These are *Pissonotus quadripustulatus* (Homoptera:Delphacidae) and *Asphondylia borrichiae* (Diptera: Cecidomyiidae). Both monophagous species are found year-round on the marsh. Also commonly present on *B. frutescens* is a polyphagous herbivore, *Cyrtoda acutissima* (Homoptera: Flatidae). *C. acutissima* has been observed to be present throughout the year.

Pissonotus quadripustulatus is a monophagous phloem feeder on *B. frutescens* (Denno 1978). Adults are typically brachypterous and multivoltine with the females laying their eggs under the epidermis of *B. frutescens* stems, usually just above the nodes (Stiling, 1994). *P. quadripustulatus* eggs are parasitised by the fairy fly *Anagrus sp. nr.*

armatus (Moon et al. 2000). Previous studies conducted at Upper Tampa Bay Park indicate that in pure stands of *B. frutescens*, *A. armatus* is considered the primary natural enemy of *P. quadripustulatus* with rates of parasitism of 60% or higher (Moon and Stiling 2001). Rates of parasitism in diverse stands, however, (i.e. *Distichlis* meadow) have been found to be somewhat higher (Altfeld, personal observation). Although previously undocumented, predation by spiders may also be important for *P. quadripustulatus* particularly because the planthoppers feed at the base of the leaves where spiders have often been found (Altfeld, personal observation). Spiders have also been documented as important predators for other salt marsh planthoppers, namely *Prokelisia* on *Spartina alterniflora* in mid-Atlantic marshes (Finke and Denno 2002).

Asphondylia borrichiae is a gall making fly found on *B. frutescens* (Stiling et al. 1992). Galls are made on the apical meristem of non-flowering stems and can contain 1 to 8 fly larvae that are parasitised by four species of Hymenoptera, *Rileyia cecidomyiae*, *Tenuipetiolus teredon*, *Torymus umbilicatus* and *Galeopsomyia haemon* (Stiling et al. 1992). As with *P. quadripustulatus*, parasitism of the gallfly is considered to be the main mortality factor in pure stand *B. frutescens* with rates ranging from 60-100% (Stiling et al. 1992). Parasitism rates for *A. borrichiae* in mixed stands are not yet known. Mortality by spiders is less likely as the gallfly only alights on the apical meristems during oviposition.

Cyarda acutissima Metcalf and Bruner is a planthopper species of the family Flatidae (Homoptera, Fulgoroidea). This Cuban species has been documented in South Florida by Wheeler and Hoebeke and has been abundant at the field site during 2000-2003. *C. acutissima* is thought to have a very broad host range. In South Florida, the

planthopper was found to be present on *Batis maritima* (saltwort, Bataceae), *Suaeda linearis* (sea blite, Amaranthaceae), *Sesuvium portulacastrum* (shoreline seapurslane, Aizoaceae), *Flaveria linearis* (narrowleaf yellowtops, Asteraceae), *Bidens pilosa* (Spanish needles, Asteraceae), *Cynanchum scoparium* (leafless swallowwort, Apocynaceae); nymphs were also observed on *Coccoloba uvifera* (seagrape, Polygonaceae), *Lippia nodiflora* (capeweed, Verbenaceae), *Pteris longifolia* (ladder brake, Pteridaceae), *Mikania scandens* (climbing hempweed, Asteraceae), *Brysonima lucida* (locustberry, Malpighiaceae), *Conocarpus erectus* (buttonwood, Combretaceae), and *Ambrosia artemisiifolia* (common ragweed, Asteraceae) (Wheeler and Hoebeke 1982). Personal observations working at the current field site from 2000-2003 have identified *C. acutissima* as commonly occurring on *Borrchia frutescens* (sea oxeye daisy, Asteraceae), *Distichlis spicata* (salt grass, Poaceae), *Batis maritima* (saltwort, Bataceae) and *Salicornia virginica* (glasswort, Amaranthaceae). Although nothing is known about their egg-laying habits, nymphs have been associated with *Salicornia virginica*, the potential host in the Florida Keys (Wheeler and Hoebeke 1982). Adult specimens collected at the study site on *B. frutescens* stems were identified as *C. acutissima*. In the *Distichlis* meadows of Upper Tampa Bay Park adults of this species have been observed on *D. spicata*, *B. frutescens* and *B. maritima* (Altfeld, personal observation). Because nothing specific is known about host use for developing larva and investigations of the like are beyond the scope of this study, estimates of parasitism cannot be made for this species. However, adults are much larger than *P. quadripustulatus* and they congregate both on the stems and leaves of *B. frutescens* making them potentially easier and more satisfying targets for spider predators.

Methods

The experiment was carried out at Upper Tampa Bay Park (28.0175° North Latitude, 82.6393° West Longitude), Hillsborough County, Florida, USA. Upper Tampa Bay Park is a county maintained park that rests on the northeastern edge of Upper Tampa Bay.

In February 2002, twenty-four 2m x 2m plots were established within a region of the *Distichlis* meadow that contained an ample distribution of *B. frutescens*. Each square plot was marked by a 1.905 cm PVC stake at each of the four corners of the plot, leaving all sides of the plot open to allow for free movement of fauna into and out of plots. Once the plots were initially established, each plot was evaluated for *B. frutescens* stem density. All *B. frutescens* stems were counted in each plot and any plot found to have fewer than 150 stems was replaced with another plot that contained the minimum stem density (150). Plots with a stem density of more than 200 stems were pruned to 200 stems. Throughout the experiment, *B. frutescens* stem density was maintained at 150-200 stems per 4m² plot.

Once the plots were established, three manipulation treatments were randomly applied using 8 replicates. Eight of the 24 plots had all non-host (*B. frutescens* = host plant) vegetation clipped at ground level and removed from plots. Clipping non-host vegetation was found to be a less disruptive technique than pulling because pulling some of the non-host vegetation, particularly *D. spicata*, also resulted in uprooting *B. frutescens* and leaving large holes in the plots. Another eight plots had all non-host

vegetation pinned to the ground with sod staples. Clipping and pinning non-host vegetation served to differentiate between eliminating non-host vegetation (clipping) and maintaining non-host vegetation while eliminating canopy structure (pinning) (Rand 1999). The remaining eight plots were left in their original diverse state (control). Each month new growth of non-host vegetation in clipped and pinned plots was appropriately treated to maintain the integrity of the experimental treatments throughout the study.

The experiment ran from February 2002 – September 2002. Prior to treatment application, the following pre-treatment measures were taken: (1) soil salinity; (2) host plant leaf nitrogen; (3) *P. quadripustulatus* abundance; (4) *P. quadripustulatus* parasitism; (5) *A. borrichiae* gall abundance; (6) *A. borrichiae* gall parasitism; (7) *C. acutissima* abundance; and (8) spider abundance. All of the pre-treatment measures listed above are identical to the monthly post-treatment measures made starting in March 2002 and continuing through September 2002. The measures are described in more detail below.

Monthly soil salinity measurements were made by collecting a 6 cm. deep core (3 cm. diameter.) of sediment from each plot and storing it in a plastic bag for return to the laboratory. At the laboratory, each core was weighed, broken up into a dish and air-dried. Once dry, each sediment sample was weighed again and placed in an Erlenmeyer flask. Distilled water in the amount of 10 ml plus the amount of water originally in the sediment sample (determined by weight differential between wet and dry sample) was added to each flask and swirled. The flasks were left for one day to allow the suspended particles in the water to settle. The salinity of the supernatant was then measured with a

refractometer (Pennings and Moore 2001). This method ensured that each sample, although diluted, provided enough water for a relative salinity reading.

Host plant leaf nitrogen measurements were made by collecting *B. frutescens* leaves in the field. One leaf was collected from the second pair of leaves down from the apical meristem on each of ten randomly selected stems. The collected leaves were stored in plastic airtight bags and kept at -70° C until they could be dried and ground into fine powder. Once ground, a sub sample (5.5 – 6.5 mg) of leaves from each plot was burned in a CN analyzer to determine percent nitrogen.

P. quadripustulatus and *C. acutissima* abundance measurements were made by counting the number of individuals of each species found on 20 randomly selected *B. frutescens* stems. Stem spider abundances were also determined by noting the number of individuals found on the same 20 stems measured for herbivore abundances. In addition, at the end of the summer when ground-dwelling spider abundances have been observed to be highest at this field site (Altfeld, personal observation) a visual census of each plot was made at ground level for total number of ground-dwelling spiders. *A. borrichiae* abundance measurements were made by counting the number of galls found on 100 randomly selected *B. frutescens* stems. Each gall was then inspected for emergence holes. *A. borrichiae* produce relatively large, somewhat ragged emergence holes often with attached puparia (Stiling et al. 1992). Gall fly parasitoid emergence holes, however, are very small, clean and pin-like. Comparing gallfly versus parasitoid emergence hole abundances produced an estimate of parasitism rates for *A. borrichiae*. *Pissonotus quadripustulatus* parasitism rates were measured by dissecting *B. frutescens* stems collected from the field. Five randomly selected *B. frutescens* stems were clipped at

ground level from each experimental plot and placed in water to prevent dehydration. The stems were then left in the laboratory for two days to allow recently parasitised larva time to develop. The epidermis of each stem was then carefully removed under a dissecting microscope to reveal *P. quadripustulatus* larva. Health larvae are milky white in color. Parasitised larvae are orange, brown or even black, depending on the stage of the developing parasitoid (for review of method see Moon and Stiling 2000).

Single factor analyses of variance (ANOVA) tests were used to assess between- and within-group differences for all of the variables measured under the three treatment regimes. The underlying assumption of normality of the data set for each ANOVA was tested at $\alpha=0.05$ using t tests on the skewness and kurtosis values obtained from SYSTAT (version 9.0). For test details see Appendix A. Homogeneity of variance among treatments was tested at $\alpha=0.01$ using the Burr Foster Q test. For test details see Appendix B. In those cases where the data were not normal and/or heteroscedastic, transformations were used to meet proper ANOVA assumptions. Data analyzed were totaled among all months as overall effects of treatments and not time effects were of prime interest to this study. Significant results from ANOVA tests were further examined using the Bonferroni pair wise comparison test. Bonferroni was chosen because treatment number is small (3) and the test is sensitive to small treatment numbers. Each pair wise comparison was made at $\alpha=0.05$. The procedure for Bonferroni is not presented as it is computed through SYSTAT™. Variable correlations were computed on SYSTAT 9™.

Results

Abiotic factors

Average salinity values ranged from 6.25 to 27.75 ppt with a mean of 13.3 ± 1.01 SE in all plots (Figure 1). Data points were square root ($x+1$) transformed prior to analysis in order to meet normality and homoscedasticity assumptions of ANOVA. Salinities were highest in the clipped monocultures and lowest in the control plots (Figure 1). Salinity was significantly ($P < 0.001$) different between treatments (Table 1). The clipped monocultures differed from the control polycultures at $P < 0.001$ and from the pinned polycultures at $P = 0.01$. The pinned and control plots did not differ significantly from one another, $P = 0.478$ (Table 2).

Mean percent leaf nitrogen ranged from 1.44 to 1.94 with a mean value of 1.65 ± 0.027 SE (Figure 2). Treatments differed significantly ($P = 0.003$, Table 3). The difference was only significant between the clipped and control plots ($P = 0.002$, Table 4). Clipped and pinned plots did not differ from one another ($P = 0.176$) nor did pinned and control plots ($P = 0.207$).

Table 1. Analysis of variance, mean salinity values. Data square root (x+1) transformed to meet assumption of normality. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	4.908	2	2.454	11.989	<0.001
Error	4.299	21	0.205		

Table 2. Bonferroni matrix of pairwise comparison probabilities, mean salinity values.

Treatments	clipped	pinned	control
clipped	1.000		
pinned	0.010**	1.000	
control	0.000***	0.478	1.000

Figure 1. Mean monthly salinity values. Bars represent standard error.

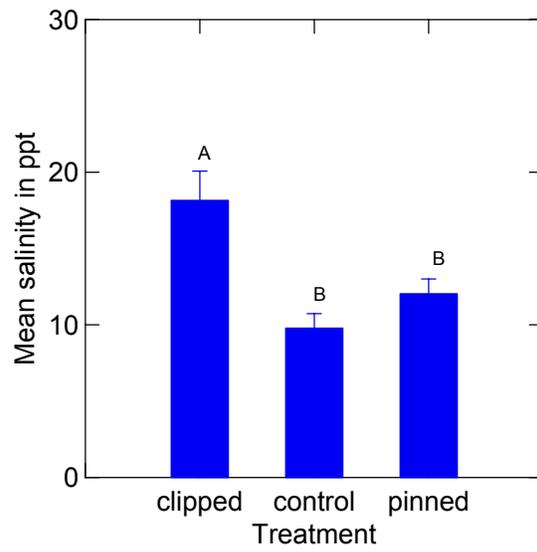


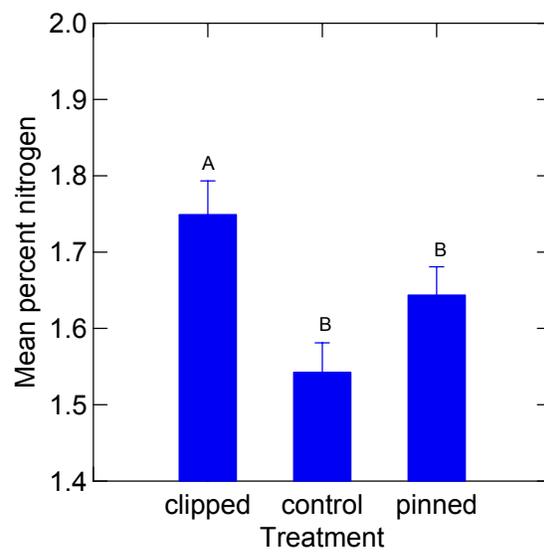
Table 3. Analysis of variance, mean percent leaf nitrogen, *B. frutescens*. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	0.171	2	0.085	7.668	0.003
Error	0.234	21	0.011		

Table 4. Bonferroni matrix of pair wise comparison probabilities, mean percent leaf nitrogen, *B. frutescens*.

Treatments	clipped	pinned	control
clipped	1.000		
pinned	0.176	1.000	
control	0.002**	0.207	1.000

Figure 2. Mean monthly percent leaf nitrogen of *B. frutescens*. Bars represent standard error.



Herbivores

Pissonotus quadripustulatus monthly abundances ranged from 30 individuals to 85 individuals among 20 stems per plot. Mean number of individuals for all months was 54.04 ± 3.14 SE. Abundance values did not differ significantly among treatments ($P=0.598$, Table 5, Figure 3). Total number of *P. quadripustulatus* eggs was insignificant for treatment effect (Figure 4).

Asphondylia borrichiae gall abundance did not statistically differ among treatments ($P=0.229$, Table 6, Figure 5). Generally, gall abundances were very low ranging from 0 to 27, with a mean number of galls at 5.67 ± 1.34 SE. It was necessary to $\log(x+1)$ transform data to meet the assumption of normality.

Mean number of *Cyrtoda acutissima* individuals per 20 stems for the three treatments (clipped, control and pinned) were 57.6 ± 9.96 SE, 100.13 ± 15.16 SE and 120.63 ± 15.32 . Values differed significantly among treatments ($P=0.012$). The only difference among treatments was between the clipped monoculture and pinned polyculture plots ($P=0.011$). Neither the clipped and control nor pinned and control plots were significantly different ($P>0.05$, Table 8). Clipped plots had the lowest abundance of individuals (Figure 6).

Table 5. Analysis of Variance, *Pissonotus quadripustulatus* abundance. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	260.083	2	130.042	0.527	0.598
Error	5178.875	21	246.613		

Figure 3. *Pissonotus quadripustulatus* abundance on *B. frutescens*. Means represent averages of 7 monthly counts of 20 stems per plot, for 8 plots of each treatment, i.e. per 140 stems. Bars represent standard error.

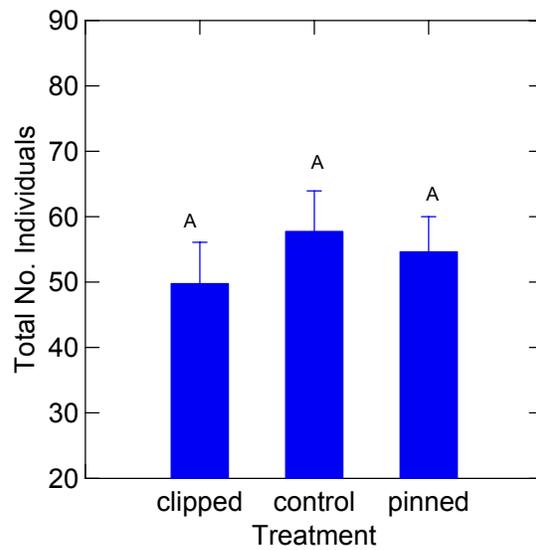


Figure 4. Egg totals for *Pissonotus quadripustulatus*. Means represent averages per 5 stems per plot for 8 plots of each treatment. Bars represent standard error.

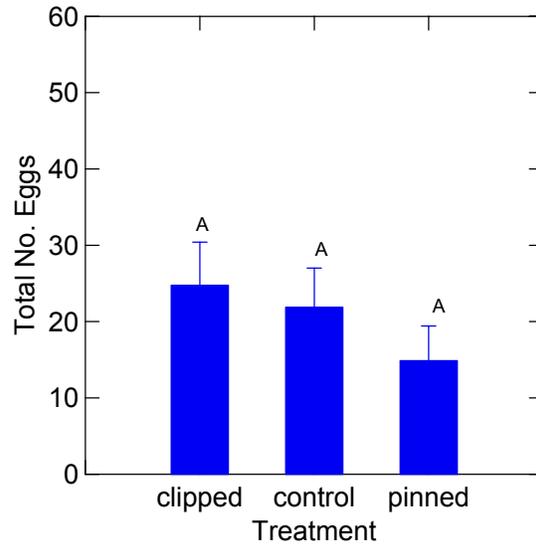


Table 6. Analysis of variance, *Asphondylia borrichiae* gall abundance. Data were log (x+1) transformed to meet assumption of normality. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	3.178	2	1.589	1.581	0.229
Error	21.104	21	1.005		

Figure 5. *Asphondylia borrichiae* gall abundance on *B. frutescens*. Means represent averages of 7 monthly counts of 100 stems per plot, i.e. 700 stems per plot. Bars represent standard error.

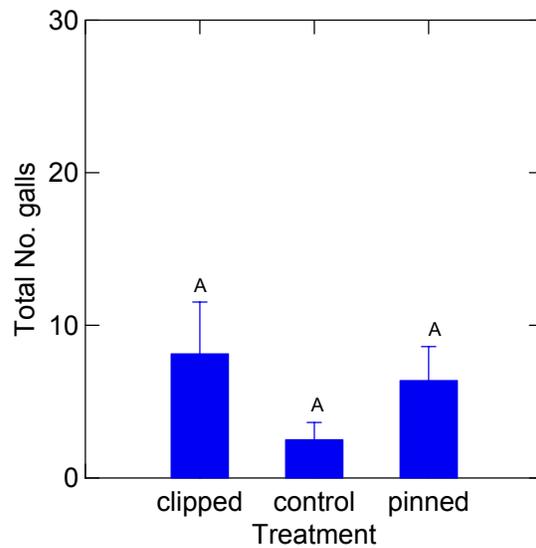


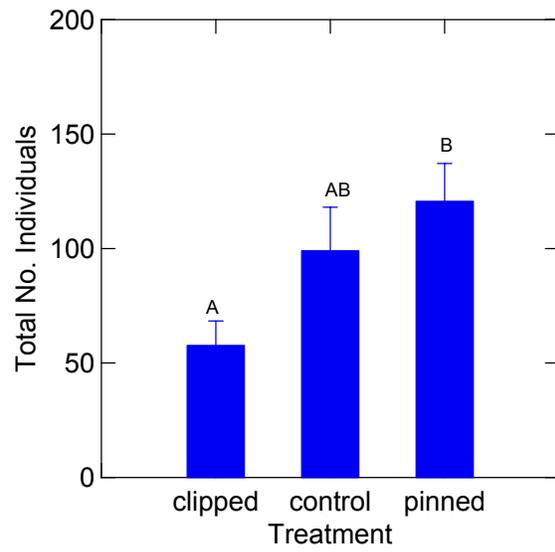
Table 7. Analysis of variance, *Cyarda acutissima* abundance. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	16521.333	2	8260.667	5.496	0.012
Error	31564.625	21	1503.077		

Table 8. Bonferroni matrix of pair wise comparison probabilities, *Cyarda acutissima*.

Treatments	clipped	pinned	control
clipped	1.000		
pinned	0.011*	1.000	
control	0.119	0.907	1.000

Figure 6. *Cyarda acutissima* abundance on *B. frutescens*. Bars represent standard error.



Predators

Stem spider abundances on *B frutescens* were not significantly different among treatments (Table 9 and Figure 7). Mean number of stem spiders was 4.33 ± 0.47 SE per 20 stems. The survey of ground-dwelling spiders, however, showed a significant difference among treatments ($P=0.003$, Table 10). Mean number of ground dwelling spiders was 4.75 ± 0.76 SE. Abundances were higher in control and pinned plots, which did not differ from one another, and lowest in clipped plots, which differed from the pinned plots ($P<0.003$, Table 11 and Figure 8).

Table 12 shows that egg parasitism in *P. quadripustulatus* did not differ significantly among treatments ($P=0.139$). Parasitism was apparently high in clipped plots relative to control, a trend also previously observed for *Pissonotus*, but high variances may have masked the significance of the treatment effect (Figure 9).

Mean percent gall parasitism was $8.68 \% \pm 1.96$ SE. Gall parasitism did not differ among treatments ($P=0.429$, Table 13, Figure 10).

Pearson correlations (Table 14) revealed significant positive relationships between *A. borrichiae* gall abundance and salinity ($r = 0.490$), nitrogen ($r = 0.717$) and gall parasitism ($r= 0.467$). *C. acutissima* was positively correlated with ground spider abundance ($r = 0.614$).

Table 9. Analysis of variance, stem spider abundance on *B. frutescens*. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	6.583	2	3.292	0.602	0.557
Error	114.750	21	5.464		

Figure 7. Spider abundance on *B. frutescens* stems, n = 140. Bars represent standard errors.

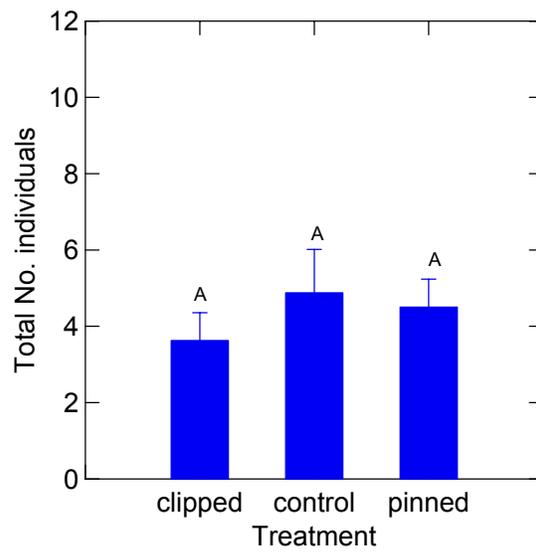


Table 10. Analysis of variance, ground spider abundance. Data were square root (x +1) transformed to meet assumption of normality. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	5.218	2	2.609	7.717	0.003
Error	7.101	21	0.338		

Table 11. Bonferroni matrix of pair wise comparison probabilities, ground spider abundance.

Treatments	clipped	pinned	control
clipped	1.000		
pinned	0.029	1.000	
control	0.003*	1.000	1.000

Figure 8. Ground spider abundance. Bars represent standard error.

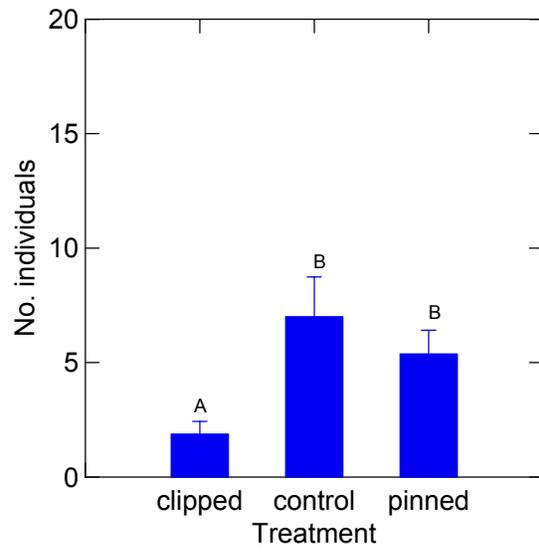


Table 12. Analysis of variance, percent egg parasitism of *Pissonotus quadripustulatus*. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	1053.535	2	526.768	2.174	0.139
Error	5089.015	21	242.334		

Figure 9. Percent egg parasitism of *Pissonotus quadripustulatus* by *Anagrus armatus*. Bars represent standard error.

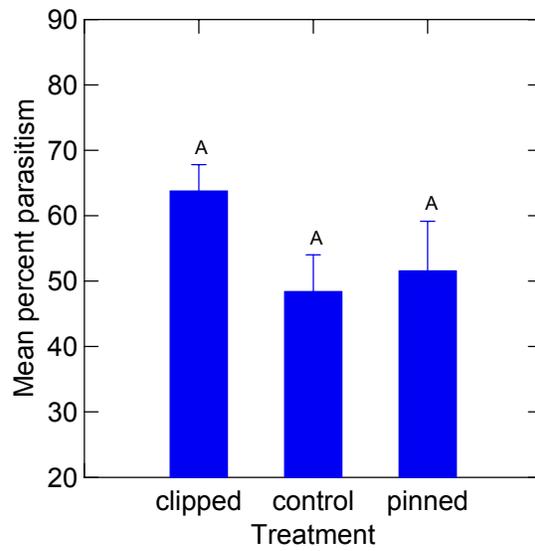


Table 13. Analysis of variance, proportion of *Asphondylia borrichiae* galls parasitised by hymenopterans. $\alpha=0.05$

Source	Sum of squares	df	Mean square	F ratio	P
Treatment	131.513	2	65.757	0.892	0.429
Error	1179.732	16	73.733		

Figure 10. Proportion of *Asphondylia borrichiae* galls parasitised by hymenopterans. Bars represent standard error.

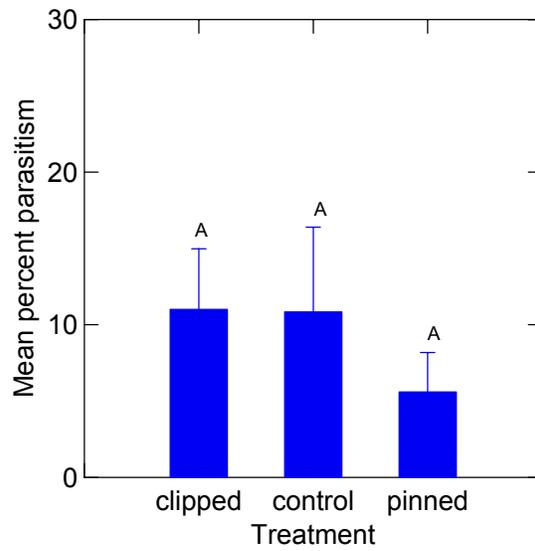


Table 14. Pearson Correlation values (r) among variables. Significance tested with Student's t test.

	Salinity	Leaf Nitrogen	Ground Spiders	Parasitism
<i>P. quadripustulatus</i>	-0.145	0.004	0.402	-0.401
<i>A. borrichiae</i>	0.490*	0.717*	-	0.467*
<i>C. acutissima</i>	-0.129	-0.275	0.614*	-

Discussion

Plant communities are the foundation for establishment of most communities. Components of the plant community such as plant richness, abundance, and structure have direct and indirect impacts on both the herbivore community and natural enemies. Herbivore-natural enemy interactions can be effected by the mere presence of non-host plant species in a community, i.e. by changing chemical cues or creating physical structures that affect herbivore and natural enemy behavior and movement, or by the presence of other herbivore species associated with the non-host plants, an example of which would be the secondary herbivore serving as an alternative host to predators (Price et al., 1980). The structural complexity of diverse habitats can affect an herbivore's ability to seek refuge from predators while plant diversity *per se* can affect the quality of herbivore prey, both of which have significant affects on herbivore diversity (Siemann 1998). Plant structural complexity also affects predators by providing habitat that may or may not be favorable in terms of climatic conditions, providing shelter, and by altering their movement patterns and search efficiency. For example, web-building spiders are dependent upon vegetation architecture (Greenstone 1984) and ground cover is important to supporting rich spider assemblages because of moderate temperature and high humidity requirements for development and as shelter for hide-and-wait predatory spiders (Riechert and Bishop 1990, Dobel et al. 1990). Parasitoid search efficiency is highly influenced by plant structural complexity (Andow and Prokrym 1990, Coll and Bottrell 1996). The extent to which herbivores respond to plant diversity and

habitat structure is often highly individualized, given its lifestyle, host plant preferences, method of dispersal and relationships to its primary predators.

Plant diversity and habitat structure were separated in this experiment to observe the effects each had on a host plant, its common herbivores and predator abundances. The simple habitats (clipped plots) were significantly higher in salinity and percent leaf nitrogen. This may have been the result of increased evaporation and reduced plant competition for available nitrogen. Both the structurally reduced habitats (pinned plots) and unmanipulated diverse habitats had similarly low salinity and leaf nitrogen means showing that community diversity can directly alter the abiotic environment of the herbivores, especially plant quality. Lack of significant treatment effects for the monophagous herbivores, the sap sucker *P. quadripustulatus* and the gall fly *A. borrichiae*, suggests that either (1) the number of replicates was too low to detect a difference, (2) herbivore densities were too low to obtain reliable results, or (3) the changes in abiotic and biotic factors that resulted from the experimental treatments were insufficient to cause changes in herbivore abundances. The number of replicates used in this experiment was twice the number (eight compared to four) previously used in studies conducted on both of the monophagous herbivores at this same study site (Moon and Stiling 2000, --2001a, --2001b). The abundances of galls were lower than previously reported (1-5 galls per 200 *B. frutescens* stems Moon and Stiling 2001a compared with 0-10 galls per 700 stems in the current study). It is likely that gall density was too low to obtain a reliable result. *P. quadripustulatus* abundances were comparable to those found in previous studies yet were unaffected by the differences in plant diversity and habitat structure between the simple and diverse habitats. Parasitism estimates for the

monophagous herbivores were also insignificant for treatment effects. Parasitism rates on *P. quadripustulatus* were comparable to those found in previous studies yet parasitoid efficiency was not significantly affected by the presence of non-host plant in a plot. In the case of gall parasitism it is likely that parasitism rates were too low to detect a significant difference (<9% of all galls were parasitised and gall abundance was unusually low as reported above).

Stem spider abundances were unaffected by plant diversity or habitat structure. Ground spider abundances were significantly higher in the diverse habitats. Ground dwelling hide-and-wait spiders are very sensitive to ground cover for shelter and for the environmental conditions that ground cover supplies for juveniles (Riechert and Bishop 1990, Robinson 1981).

The Enemies Hypothesis predicts that diverse habitats have higher predator abundances. This was the case for ground-dwelling spiders. Parasitism rates in the diverse habitats, however, were not higher. Review of experiments testing the Enemies Hypothesis generally find that predators are more abundant in diverse habitats but connecting the abundances of predators to herbivore mortality is less often measured (Russell 1989, Sheehan 1986). In this study parasitism rates were reported but no differences between habitat types were found.

Unlike the monophagous herbivores, the polyphagous *Cyrtus acutissima* showed significant response to habitat structure and plant diversity. *Cyrtus acutissima* was much more abundant in the polyculture plots, particularly the structurally reduced pinned plots. *C. acutissima* has been recorded as a highly polyphagous herbivore and has been seen feeding on all of the plants in the diverse habitat at the study site. If *B. frutescens* is a

preferred host for *C. acutissima*, densities of the planthopper should have been equally abundant in both the structurally reduced polyculture and the simple monoculture as physical obstruction to host finding is eliminated in both of the habitat types. This was not the case. Densities were lowest in the simple monoculture. *C. acutissima* may feed preferentially on one host, perhaps *B. frutescens*, but utilize another host for reproduction. It also follows that if the effects of natural enemies are important, herbivore densities should be significantly lower where the abundance of natural enemies is higher. This was also not the case. Both ground spider abundances and planthopper abundances were highest in the diverse habitats. The spiders and the planthoppers seem to both be responding positively to some aspect(s) of the diverse habitats.

Root's Resource Concentration Hypothesis would have predicted that the monophagous herbivores exhibit greater abundance in monoculture because of the importance of host plant concentration. In this experiment, host plant concentration (density) was held constant among all of the plots. However, the apparent concentration of host plants differed between the control plots and the pinned/clipped plots. Plots that consisted of only upright host plant stems may have been experienced by the herbivores as having a higher host plant concentration than the control plots consisting of the host plant and a complex mix of other vegetation even though the actual host plant stem density was the same among treatments. If this is the case and Root's resource concentration hypothesis can be applied, *Pissonotus quadripustulatus* and *Asphondylia borrichiae* did not respond to the monoculture as would have been predicted. The polyphagous herbivore, however, was significantly more abundant in the diverse habitats perhaps because host plant concentration was highest in these plots. Generalist predator

abundances (ground spiders) were also highest in the diverse plots, which holds support for the Enemies Hypothesis prediction that diverse communities have greater numbers of predators.

In the field, the behavior of many herbivore species agree with the predictions made by Root's theories. As suggested in a review by Andow (1991), monophagous species were less abundant in polyculture in 60.8% of the studies reviewed while polyphagous species were less abundant in polyculture in only 47.1% of the studies reviewed. This latter result suggests that food resources may be more important than natural enemies are for polyphagous species. This study supports the result that food resources may be more important than natural enemies for the polyphagous herbivore studied, as it was more abundant in the diverse habitats where generalist predator abundances were highest. The monophagous herbivores seemed to show no response to the habitat manipulations. Some herbivore species have been reported to have unique and unpredicted responses to plant diversity that resulted from specific ecological interactions within a habitat (Letourneau 1986, Letourneau 1995). For example, Hacker and Bertness (1995) studied salt marsh aphids and found that they were more abundant on lower quality, short form *Iva frutescens* in mixed stands than on healthy tall form *I. frutescens* in pure stands despite the insects' improved growth on the tall form plants. Such a result was due to significantly higher predation rates by ladybird beetles in monoculture, an example of a complex interaction between a host plant and predators. Demographic measures on the bean beetle *Epilachna varivestis* have revealed that resource concentration in monoculture was more influential than mortality from natural enemies in producing lower beetle populations in diverse vegetation through

impediments to adult colonization (Andow 1990). The striped cucumber beetle, *Acalymma vittata*, was more abundant in monoculture than polyculture due directly to plant diversity, not host plant or total plant density, via longer tenure time in monocultures (Bach 1980). In grassland experiments, only specialist herbivore abundances, particularly of leafhoppers, were negatively affected by plant diversity while other herbivore groups showed no numerical response to diversity, the mechanisms for which also involved impediments to herbivore movement among less mobile insects (Koricheva et al. 2000).

Understanding the many effects of plant diversity on plant-herbivore-natural enemy interactions is an ambitious goal. At the very least, plant diversity must be divided into separate effects, i.e. structural complexity of diverse habitats and plant species richness, to determine cumulative influences in a community. The factors that determine herbivore abundance in monoculture may not be the same in polyculture nor may they be the same for all insects at the same trophic level. This study gives an example of two monophagous herbivores and one polyphagous exhibiting very different responses to monoculture. Identifying and manipulating the key factors important to specific species and/or organisms at a particular trophic level are critical to understanding the mechanisms by which tri-trophic relationships differ between simple and complex habitats.

Appendix A.

t Test for normality.

Values obtained from SYSTAT:

- Skewness (g_1)
- Standard error of skewness (Sg_1)
- Kurtosis (g_2)
- Standard error of kurtosis (Sg_2)

T test: $H_0: \gamma_1 = 0$, $H_1: \gamma_1 \neq 0$

Skewness $t = (g_1 - \gamma_1) / Sg_1$

$H_0: \gamma_2 = 0$, $H_1: \gamma_2 \neq 0$

Kurtosis $t = (g_2 - \gamma_2) / Sg_2$

Appendix B.

Burr Foster Q test for homogeneity of variance.

$$q = \frac{\sum_{i=1}^n S_i^4}{n (\sum_{i=1}^n S_i^2)^2}$$

where S = treatment variance

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