This is to certify that the

thesis entitled

THE IMPACTS OF GYPSY MOTH (LEPIDOPTERA: LYMANTRIIDAE) ON NATIVE ARTHROPOD ABUNDANCE, SPECIES RICHNESS, AND DIVERSITY IN TWO HARDWOOD ECOSYSTEMS IN NORTHERN LOWER MICHIGAN

presented by

TIMOTHY THERON WORK

has been accepted towards fulfillment
of the requirements for

MASTERS OF SCIENCE degree in ENTOMOLOGY

Major professor

Date 2-AUGUST-1996

O-7639

MSU is an Affirmative Action/Equal Opportunity Institution

[redacted]

THE IMPACTS OF GYPSY MOTH (LEPIDOPTERA: LYMANTRIIDAE) ON NATIVE ARTHROPOD ABUNDANCE, SPECIES RICHNESS, AND DIVERSITY IN TWO HARDWOOD ECOSYSTEMS IN NORTHERN LOWER MICHIGAN

by

Timothy Theron Work

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Entomology

1996

ABSTRACT

THE IMPACTS OF GYPSY MOTH (LEPIDOPTERA: LYMANTRIIDAE) ON NATIVE ARTHROPOD ABUNDANCE, SPECIES RICHNESS, AND DIVERSITY IN TWO HARDWOOD ECOSYSTEMS IN NORTHERN LOWER MICHIGAN

by

Timothy Theron Work

Insects play a critical role in many forest processes. However, little is known about the extent or importance of insect diversity within forests. Ecosystems dominated by red oak and northern hardwoods were surveyed between 1993 and 1995 to obtain baseline data on insect diversity and determine whether gypsy moth (*Lymantria dispar*), an exotic forest defoliator, impacted native arthropods. A method for quantifying effects of defoliation using canopy transmittance was also tested in both ecosystems and stands that experienced differing levels of defoliation. Estimating leaf area index through canopy transmittance was useful in quantifying effects of severe defoliation. Northern hardwood and red oak ecosystems differed in species composition, diversity and abundance of carabid beetles and lepidoptera but not in overall community structure of arthropods. Gypsy moth defoliation negatively impacted abundance of the carabid, *C. limbatus*, and species richness and diversity of lepidoptera, particularly overstory and oak-feeding Noctuidae.

To Julie, Mom, Dad and Katie

ACKNOWLEDGMENTS

I thank my advisor, Deborah G. McCullough, for her seemingly never-ending enthusiasm and dedication as a teacher, a scientist, and most of all a friend. Deb's guidance and motivation inspired me to endeavor for excellence and creativity in my research and in my non-academic life. I would also like to thank Bill Mattson, Carl Ramm and Mark Scriber for their advice and consultation pertaining to this project.

This project could not have been completed without the help of others. I am grateful to Brian Kopper for his assistance sorting, identifying, and preparing the daunting number of insect specimens collected during this project. I also thank Brian for his effort and company during the back-breaking, mosquito-bitten days packing entirely too much equipment all over the Manistee National Forest. I am also grateful to Liz Weber, Katie Albers, and Kevin Elwood for their assistance throughout the summer. I also thank Tom Ellis for his help in thermal fogging after Kevin's 'accident.' I thank John Wilterding, Robert Kriegel, Mogens Nielson, and Fred Stehr for their hard work identifying the multitude of Lepidoptera specimens collected. I thank Dennis Gilliland for his helpful comments and insight into the statistical analysis of this project.

I greatly appreciate the support and comments of my fellow graduate colleagues; Brian Bishop, Lyle Buss, Sean Clark, Beth Dankert, and Cathy Papp. I also appreciate the opportunities and distractions provided by my fellow students in Entomology and Ecology/Evolutionary Biology.

This research was funded by the McIntire-Stennis Cooperative Forestry Research Grant program. Additional funding was provided through the Professor Hutson Student

Research Award from the Department of Entomology and student support funds from the Ecology and Evolutionary Biology program at Michigan State University.

TABLE OF CONTENTS

CHAPTER 3

CHAPTER 4

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

APPENDIX C

APPENDIX D

APPENDIX E

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

LIST OF SYMBOLS, ABBREVIATIONS, AND NOMENCLATURE

Btk	*Bacillus thuringiensis* var. *kurstaki*
cm	centimeter
DBH	diameter breast height
ECS	ecological classification system
ELTP	ecological land type phase
h	hours
ha	hectare
LAI	leaf area index
LTA	landtype association
m	meter
N	nitrogen
NPV	Nucleopolyhedrous virus
PAR	photosynthetically active radiation
SE	standard error
spp	species
TI	total light interception
UV	ultraviolet

INTRODUCTION

In terms of species richness, insects are by far the most abundant group on Earth. The number of described species of insect have been estimated at over 750,000, distantly followed by multicellular plants (248,428) and non-insect arthropods (123,161) (Wilson 1985). The total number of described and undescribed insect species present on Earth has been estimated at 30 million (Erwin 1982). Much of the diversity of insects is concentrated in forests (Erwin 1982).

In light of the tremendous abundance of species, it is not surprising that insects play a critical role in forest ecosystem processes. Insects can be sensitive to changes in ecosystems and can be used to evaluate effects of disturbances such as forest management and land conversion (Kremen et al. 1993). Insects are intertwined in food webs where endemic populations of herbivorous insects are regulated by higher trophic consumers such as predatory and parasitoid insects (Hairston et al. 1960; Lawton 1986; Price 1987). Decomposition of woody material and detritus is facilitated by microarthropods and bark and wood boring insects (Schowalter 1991). Outbreaks of herbivorous insects have been shown to reduce tree growth and increase tree mortality (Kulman (1971), alter the relative composition of stands (Attiwill 1994; Schowalter 1981; Schowalter 1985), increase productivity (Mattson and Addy 1975), and increase nutrient cycling (Risley and Crossely 1993) through defoliation. Outbreaks of defoliating insects have been shown to decrease diversity and abundance of other insects in West Virginia (Sample et al. 1993) presumably by reducing the amount of foliage available for food, shelter, and oviposition sites.

Insect outbreaks represent a disturbance that can directly alter ecosystem processes, but may also indirectly alter ecosystem processes by altering diversity. Diversity has been shown to have a direct effect on ecosystem processes such as resistance to disturbance and primary productivity (Tilman 1994; Tilman 1996; Tilman and Downing 1994). Insect outbreaks represent a disturbance of both intermediate spatial and temporal scales (Risser 1995). Examination of diversity during disturbances of intermediate scales is appropriate because interactions between diversity and ecosystem processes are greatest (Risser 1995). Invasion of exotic organisms, particularly animals, also provides an opportunity to examine ecosystem processes because invaders alter the trophic structure of the native community (Vitousek 1990).

The gypsy moth (*Lymantria dispar* L.), an exotic forest insect, was responsible for defoliating over 10 million ha of forest between 1985 and 1994 in the northeastern United States (Butalla 1996). Gypsy moth will feed on over 400 North American woody plant species including economically valuable species such as *Quercus* and *Populus* spp. (Mauffette et al. 1983). Preferred tree species such as *Quercus* experienced 30% mortality after an average of 37% defoliation over 10 years in New England (Baker 1941). Trees that have been stressed by defoliation can be killed by invasion of secondary mortality agents like two-lined chestnut borer (*Agrilus bilineatus* Weber) and fungal pathogens like *Armillaria* root diseases (Wargo 1977).

In addition to altering the relative composition of forests, gypsy moth defoliation can change nutrient and hydrological patterns. While nitrogen in frass deposited by gypsy moth is immobilized by soil microbes, insect bodies and leaf fragments may be a source of nitrogen loss through leaching (Lovett and Ruesink 1995). Defoliation can also reduce transpiration and increase soil moisture, resulting in increased denitrification (Lovett and Ruesink 1995). Gypsy moth increased water yield and fecal coliform and streptococci concentrations in heavily defoliated watersheds in Pennsylvania during 1984 and 1985 (Corbett and Lynch 1987).

The effects of gypsy moth on native forest insects are relatively unknown, especially in the north central region of the United States. Low levels of defoliation decreased abundance of native lepidoptera in West Virginia, but specific data was not reported and the lack of high levels of defoliation makes interpretation of the effects of gypsy moth difficult (Sample et al. 1993). Heavy defoliation was associated with reduced numbers of predatory insects, but neither defoliation or number of insects collected were quantified in West Virginia (Muzika 1994).

With the current emphasis on ecosystem management, practical and quantitative information about diversity of an area is needed before proper management strategies can be applied (Anonymous 1991). Studies evaluating diversity at regional scales are needed before political, economic, and biological concerns can be integrated into effective guidelines and policy for management of public forests (Probst and Crow 1991; Wilcove 1989).

The purpose of this research was two-fold. The first objective was to obtain baseline information on the abundance, diversity and community structure of native arthropods from two forest types that varied in productivity, tree species composition, and susceptibility to the gypsy moth. The second objective was to quantify the effects of defoliation by gypsy moth on native insect abundance, diversity and community structure within a susceptible forest ecosystem.

Diversity of organisms can be defined at many scales, varying from the level of genetic diversity of a population to the diversity of many species from many trophic levels across a landscape (Probst and Crow 1991; Risser 1995). In this study, I have chosen to evaluate native insect diversity at the species and community level in northern hardwood and red oak stands in northern lower Michigan. I have presented this study as separate chapters to reflect relevant ecological processes that may occur during an outbreak. In chapter 1, I have tested the utility of a portable light sensor to quantify defoliation in terms of leaf area index (LAI) during an outbreak of gypsy moth. Chapter 2 examined the effect of gypsy moth on carabid beetles, a group of predators representative of higher trophic level consumers as well as a group useful as indicators of ecosystem change. The impact of defoliation and resource depletion on native lepidoptera, a group likely to be in competition with gypsy moth, was analyzed in chapter 3. The overall effect of gypsy moth on the community structure of insect guilds at multiple trophic levels was evaluated in chapter 4.

Chapter 1

QUANTIFYING GYPSY MOTH (LEPIDOPTERA:LYMANTRIIDAE) DEFOLIATION IN TWO HARDWOOD ECOSYSTEMS USING A PORTABLE PAR SENSOR

Introduction

Severe defoliation by forest pest insects can have great economic and ecological impacts on commercial and public forests. Defoliation caused by insects can result in growth loss, tree mortality (Gross 1992; Kulman 1971), increased risk of mortality from secondary pests and pathogens (Leonard 1974; Mallett and Volney 1990; Wargo 1977; Wargo and Montgomery 1983) on a variety of tree species. By decreasing the amount of canopy cover, defoliation can alter the abiotic and biotic characteristics of a stand. Increased light interception on the forest floor can increase temperature and reduce available water through evaporation (Klein and Perkins 1988; Perkins et al. 1987; Spurr and Barnes 1980). Plant species normally absent or repressed in an undefoliated stand may be able to invade and compete with the shade tolerant flora (Klein and Perkins 1988).

Gypsy moth (*Lymantria dispar* L.) is a major forest defoliator in the northeastern United States. This exotic pest feeds on over 400 North American woody plants including economically valuable species such as *Quercus* spp. and *Populus* spp. (Mauffette et al. 1983) and was responsible for over 10.4 million ha of defoliation in the United States between 1985 and 1994 (Butalla 1996).

Obtaining efficient, accurate, and consistent assessments of gypsy moth defoliation can be problematic. Methods of estimating defoliation such as visual observation can be inaccurate, subjective and biased due to inter-observer variation in ability and experience (Cooper et al. 1987; Talerico 1981). Although extensive training and repetitive testing of observers can increase precision and accuracy of defoliation estimates (Millers and Lachance 1988), such resources may be unavailable or observer accuracy may vary among cover types. Use of canopy photography with a fish eye lens (Liebhold et al. 1988) and point intercept sampling using a sighting tube (Cooper et al. 1987) have been proposed as alternatives to visual estimates, but have not been widely used.

A consistent and accurate method for quantifying defoliation is needed to provide a standardized measure in stands that experience partial defoliation. Such a method should be accurate, repeatable, provide consistent results, and be applicable to a variety of spatial scales and canopy species.

A portable light meter called a ceptometer (Decagon Devices, Pullman WA.) has been used to estimate leaf area index (LAI) (Pierce and Running 1988). The ceptometer measures photosynthetically active radiation (PAR). It is sensitive to phenological and seasonal changes in LAI (Vose and Swank 1990) and has been recommended for evaluating primary productivity (Pierce and Running 1988). In this study, we examined the ability of the ceptometer to quantify defoliation in oak-dominated sites and the relative ability of the ceptometer to detect limited or patchy defoliation in northern hardwood stands.

Methods

Study Area

This research was conducted in eight stands in the Manistee National Forest in northern lower Michigan. Manistee National Forest has been described using an ecological classification system (ECS) (Cleland et al. 1993). The ECS is a hierarchical classification that groups ecosystem components at spatial scales ranging from the landscape to the stand level. Ecological landtype phases (ELTPs) are classified on the basis of soils, landscape position, and natural vegetation. ELTPs are subsets of larger spatial scale units such as ecological landtypes (ELTs) and landtype associations (LTA). Because stands within the same ELTP will have similar overstory and understory vegetation, soil hydrology, soil types, nitrogen cycling, productivity and geological history, use of the ECS allows ecosystems to be replicated in experimental designs with a high level of confidence that experimental plots are similar.

We randomly chose four sites classified as ELTP 20 and four sites classified as ELTP 45 from maps provided by the Manistee National Forest. All sites were between approximately 12 to 16 ha in area. ELTP 20 was characterized by an overstory dominated by northern red oak and white oak (*Quercus alba* L.) and a non-diverse ground flora (Cleland et al. 1993). Soils on ELTP 20 were typically sandy, xeric soils with low productivity (Host et al. 1987; Host et al. 1988). ELTP 45 had an overstory dominated by northern hardwood species such as sugar maple (*Acer saccharum* Marsh) and American basswood (*Tilia americana* L.) (Cleland et al. 1993). This ELTP was notable for its rich herbaceous understory, well drained mesic soils, and high productivity (Host et al. 1987; Host et al. 1988; Zak et al. 1989; Zak and Pregitzer 1990; Zak et al. 1986).

Two oak-dominated sites (ELTP 20) were located near the town of Branch (44^{o} 00' N, 86^{o} 00' W) and two other sites were located near the village of Freesoil (44^{o} 08' N, 86^{o} 09' W). Although northern red oak and white oak dominated the overstory, big toothed aspen (*Populus grandidentata* Michx.) and red maple (*Acer rubrum* L.) together comprised up to 30% of the canopy in each of the four stands. Overstory trees were approximately 20 m tall. A sparse understory of red maple saplings and witch hazel, *Hamamelis virginiana* L., of diameter breast height (DBH) less than 3 cm was also present.

Two northern hardwood sites (ELTP 45) were located near the town of Mesick (44° 22' N, 86° 44' W) and two similar sites were located near the village of Harrietta (44° 19' N, 86° 44' W). Northern hardwood species including sugar maple and American basswood dominated the overstory. Overstory trees were approximately 30 m tall, and sites had a rich understory of 1 m tall sugar maples with a DBH of less than 3 cm.

Estimation of gypsy moth populations

The size of gypsy moth populations was estimated using mean egg mass counts from four to five 0.01 ha plots within each site (Kolodny-Hirsch 1986). Percentage of current-year egg masses was determined by inspecting all egg masses between ground level and 2 m high. Ratio of current-year egg masses to total egg masses was determined and multiplied by the total number of egg masses counted in the plot.

Estimation of Defoliation

Defoliation was visually assessed within each site by the same observer to eliminate potential inter-observer variance. Visual estimates were expressed as five classes of 0-20%, 21-40%, 41-60%, 61-80%, and 81-100% defoliation.

Photosynthetically active radiation (PAR) (400-700 nm) was measured under the canopy in each site using a "Sunfleck Ceptometer" (Model SF-80), a light sensor manufactured by Decagon Devices, Inc. The ceptometer had eighty individual sensors along a 1 meter wand. Mean light measurements were stored in an attached memory storage unit. PAR below the canopy was compared to PAR measurements taken in adjacent open areas and used to determine total light interception values (TI). TI is defined as the light interception by trunks, boles, branches and leaves. TI was calculated using a derivation of the Beer-Lambert law which incorporates correction factors for time of day, date, and diffusion of light (Decagon Devices 1987). TI was expressed as the relation:

$$\mathrm{TI} = -\ln\left(\frac{\text{PAR under canopy}}{\text{PAR above canopy}}\right) * \text{Constant}$$

The interception value of non-leaf portions of trees (i.e.. the trunks, boles and branches) was subtracted from the TI to get the LAI for foliage alone. To obtain interception values of non-leaf portions, PAR readings were taken in the northern hardwood stands on 6 April 1995 and in the red oak stands on 26 April 1995, after all snow had melted but before budbreak.

PAR samples were taken at 45° angles until a complete 360° was sampled for a total of 8 measurements. Readings were taken by holding the ceptometer level, parallel to the ground, at approximately 1 M above the forest floor. When understory saplings were present, readings were taken by holding the ceptometer level, parallel to the ground, above the shrub foliage. Readings were then averaged and stored in the ceptometer memory. This was repeated 10 times at 10 m intervals along a transect radiating from the center of the site. Four transects, running north, south, east and west, were sampled in this manner. This resulted in a total of 2560 individual measurements, stored as 320 average values, collected in each stand on a single sampling period.

During 1994, visual estimates of defoliation and PAR were measured in northern hardwood sites on 21 June, 28 July, and 16 August and in the red oak sites on 13-14 June, 12 July, and 9 August. During 1995, visual estimates of defoliation and PAR were measured in the northern hardwood sites on 24 May, 15 June, 19 July, and 21-22 August and in the red oak sites on 17 May, 13 June, 11 July, and 16 August. Sample dates roughly corresponded to significant points in gypsy moth and stand phenology. PAR was measured during the typical time of *Bacillus thuringensis* Berliner var. *kurstaki* application for gypsy moth suppression in northern lower Michigan (May), peak fourth instar development (June), peak defoliation (July), and following stand refoliation (August). All sampling was conducted between 1000 and 1400 h. This was done to minimize artifactual sampling of trees outside the site because of the small angle of the sun relative to the plot at early and late hours of the day. PAR was measured on either uniformly sunny days or overcast days, but not on partly sunny days due to the difficulty in obtaining consistent PAR measurements within and outside the stand (Decagon Devices 1987).

Statistical Analysis

Differences in mean density of egg masses between the red oak and northern hardwood ecosystems for 1994 and 1995 were analyzed separately by year using the Mann-Whitney U-test (Conover 1971) because values were non-normally distributed and heteroscedastic. LAI values collected from red oak sites in 1995, and northern hardwood sites in both years, were normalized using the Box-Cox transformation (Sokal and Rohlf 1995). Differences in LAI between sites were analyzed separately within ecosystems and year using a one-way ANOVA with repeated measures to account for monthly variation. Differences in LAI between non-defoliated red oak stands and northern hardwood stands were analyzed within each year using the Mann-Whitney U-test (Conover 1971). All monthly observations were used in the nonparametric ecosystem comparison, resulting in 6 observations from red oak sites and 12 observations from northern hardwood sites. All statistical tests were conducted using $\alpha = 0.05$.

Results

Mean gypsy moth egg mass densities were significantly higher in red oak ecosystems than in northern hardwood ecosystems in both 1994 ($\chi^2 = 4.39$, df=1, p<

0.04) and 1995 (χ^2= 10.33, df=1, p<0.001) (Figure 1.1). In the red oak ecosystem in 1994, Branch sites had more egg masses/ha than Freesoil, but this difference was not statistically significant (χ^2= 1.13, df=1, p<0.29) (Figure 1.1). In 1995 however, egg mass densities were significantly higher at Freesoil sites than at Branch sites (χ^2= 12.66, df=1, p<0.004) (Figure 1.1). Differences between the northern hardwood sites were not significant in 1994 (χ^2= 0.28, df=1, p<0.60) but were significant in 1995 (χ^2= 5.62, df=1, p<0.02) (Figure 1.1). During 1995, differences in mean egg mass density between northern hardwood sites was small (250.3 egg masses/ha) compared to differences observed in red oak sites (11,540.4 egg masses/ha).

Visual estimates indicated generally higher amounts of defoliation in the red oak sites than in the northern hardwood sites (Table 1.1). Spatial distribution of defoliation within sites varied between ecosystems. Red oak sites were dominated by many preferred host plant species of the gypsy moth and most trees were defoliated during outbreaks. Within the red oak ecosystem, Freesoil sites experienced more defoliation than Branch sites in both years (Table 1.1). In the northern hardwood sites where preferred species were scattered, defoliation was only observed on American basswood. This created a patchy distribution of defoliation within these sites.

Mean LAI for June, July, and August were significantly greater in northern hardwood ecosystems than in undefoliated red oak sites in both 1994 (χ^2= 11.37, df=1, p<0.0007) and 1995 (χ^2= 4.25, df=1, p<0.04) (Figure 1.2). Mean LAI determined monthly for undefoliated red oak sites during June, July and August ranged from 2.18 to 6.71 in 1994 and 4.51 to 4.85 in 1995 (Figure 1.3). Mean LAI determined monthly for northern hardwood sites during June, July and August ranged from 10.17 to 12.89 in 1994 and from 4.13 to 11.89 in 1995 (Figure 1.4).

Comparisons of LAI between red oak sites showed LAI initially increased in both sites as leaves expanded. In July, LAI was reduced in defoliated sites when defoliation was severe (Figure 1.3). In 1994, a significant defoliation by month interaction was observed (F=10.31, p<0.03) (Table 1.2). During June 1994 when early instar larvae were feeding, the difference in LAI between sites was small. However, Freesoil sites had significantly less LAI than Branch sites in July and August when defoliation peaked (Figure 1.3). In 1995, the effects of defoliation were not statistically significant (F=3.77, p<0.19). However, when the month of June was excluded from the analysis, Freesoil sites had lower LAI than did Branch sites (F=16.40, p<0.055) (Table 1.2) although the difference was marginally insignificant. No difference in LAI occurred in June 1995 when early stage gypsy moth larvae were beginning to feed. In July 1995 during peak defoliation, LAI in the undefoliated Branch sites was almost 3 times higher than in Freesoil sites, where gypsy moth population were high (Figure 1.3). Defoliated red oak sites had not refoliated by 15 August in 1994 or 1995.

Within the northern hardwood ecosystem, a significant site by month interaction was observed in 1994 (F=35.67, p<0.003) (Table 1.3 and Figure 1.4), but differences between northern hardwood sites were relatively smaller compared to differences observed in the red oak sites (Figure 1.3 and 1.4). Only monthly variation was significant in 1995 (F=164.16, p<0.0001).

Discussion

Ecosystem Differences

Our results indicating that red oak ecosystems have canopies with lower LAI than northern hardwoods ecosystems are consistent with the relative differences in productivity and LAI reported previously in the literature (Bolstad and Gower 1990; Burton et al. 1991; Waring 1983). However, the magnitude of differences we observed was comparatively large. While estimates for red oak sites were similar to previous studies (Bolstad and

Gower 1990), our estimates of maximum LAI (12.88 in 1994 and approximately 12.00 in 1995) in the northern hardwood sites greatly exceeded those of Burton et al. (1991) who estimated a maximum LAI of 8.3 using PAR transmittance.

Plausible explanations for the larger estimates we obtained could include differences in sensitivity of the ceptometer under sunny and cloudy conditions. Under cloudy conditions, PAR is diffuse and "above canopy" readings are dependent on the size of the clearing where the reading was taken (Huston and Isebrands 1995). Furthermore, the ceptometer was shown to overestimate LAI under low light conditions in stands with high LAI such as *Picea abies* (Bolstad and Gower 1990). This could account for some of the variability in PAR readings we observed in northern hardwood sites.

The high variability of monthly readings in northern hardwood stands during 1995 makes seasonal variation in LAI difficult to interpret. Low LAI in the month of May was attributed to new leaves not yet fully expanded. The decrease in LAI in July, the usual time of peak defoliation by gypsy moth in northern lower Michigan, may be attributed to defoliation or leaf drop not detected visually. This suggests the ceptometer could be useful in detecting low level defoliation or defoliation at a small spatial scale within the stand.

However, this hypothesis should be interpreted cautiously. If defoliation caused the decrease in LAI, we would expect to see LAI maintained at approximately 4.5 unless the defoliated trees fully refoliated by August. Trees rarely refoliate unless they experience heavy defoliation. We would also expect to see differences in LAI between the northern hardwood sites related to the relative density of gypsy moth populations. Instead, we saw a decline in LAI in July followed by an increase in LAI in August in both sites, regardless of the density of gypsy moth. It is also possible that the variable pattern of monthly LAI was attributable to defoliation caused by other leaf feeders and pathogens that we did not observe.

In a previous study, when methods of LAI estimation based on PAR transmittance were compared to allometric and litterfall methods, PAR methods yielded results more consistent with litterfall than allometric methods (Burton et al. 1991). Our results were more consistent with the allometric results obtained by Burton et al. (1991). However, while Burton et al (1991) used the Beer-Lambert law directly with extinction coefficients calculated from litterfall data, we used the derivation of the Beer-Lambert law described previously. This difference in calculation may have accounted for our relatively high LAI estimates for northern hardwood sites.

Effects of Gypsy Moth

Within the red oak sites, gypsy moth defoliation reduced cumulative LAI (sum of all monthly values of LAI) by 39% in 1994 and 42% in 1995 at Freesoil when compared to Branch. This corresponds with the increasing amount of defoliation obtained from visual estimates between 1994 and 1995. However, the ceptometer detected the effects of defoliation only during peak defoliation in July and August, not while early larvae were feeding in June. This suggests that the ceptometer was most useful in quantifying defoliation at a broad spatial scale, when defoliation was moderate to severe.

Our results are consistent with other studies that have used PAR transmittance methods to examine the effects of gypsy moth defoliation. Liebhold et al. (1988) observed a significant decrease in LAI between June and peak defoliation in late July using inverted canopy photography to estimate LAI.

While the ceptometer appears to be limited in its sensitivity to spatial scale and defoliation intensity, it still may be a useful tool for quantifying the effects of defoliation. In addition to eliminating biases inherent in visual estimation, the ceptometer expresses defoliation as a reduction in LAI, which is readily comparable to physiological processes within defoliated trees. Using relationships between defoliation and growth loss in oak species previously reported in the literature (Baker 1941; Kulman 1971; Minott and Guild 1925) it may be possible to estimate growth loss using LAI reduction. Plant defensive responses to defoliation such as delayed induced resistance could be evaluated in terms of damage thresholds expressed as reduced LAI.

The ability to predict growth loss due to forest defoliators could be useful to land managers not only for economic assessment of a pest outbreak but also in decision models for pest management. Growth loss incurred from defoliation could be quantified and losses readily compared with costs of pesticide application or biological control to determine an appropriate management strategy.

Table 1.1. Visual estimates of peak defoliation from two locations in red oak ecosystems and two locations in northern hardwood ecosystems.

	1994	1995
Red Oak		
Branch	< 20%	< 20%
Freesoil	40-60%	80-100%
Northern Hardwood		
Harrietta	< 20%	< 20%
Mesick	< 20%	< 20%

Table 1.2. Split-plot ANOVA table for leaf area index (LAI) with two levels of defoliation (severe or none) over two or three months in red oak sites during 1994 and 1995.

	1994				1995[1]			
	df	Mean Square	*F*-value	*p* value	df	Mean Square	*F*-value	*p* value
Defoliation	1	9.19	1.293	0.3733	1	3116.84	16.404	0.0559
Error a	2	7.10			2	190.00		
Month	2	13.34	59.273	0.0011	1	0.23	0.001	0.9762
Defoliation x Month	2	2.32	10.305	0.0264	1	36.95	0.179	0.7133
Error b	4	0.23			2	206.30		

[1] Values transformed using the Box-Cox transformation.

Table 1.3. Split-plot ANOVA table for leaf area index (LAI) analyzing between site differences (Harrietta and Mesick) over three months in northern hardwood sites during 1994 and 1995.

	1994[1]				1995[1]			
	df	Mean Square	*F*-value	*p* value	df	Mean Square	*F*-value	*p* value
Site	1	4.04E5	52.797	0.0184	1	695.17	0.630	0.5106
Error a	2	7659.09			2	1103.84		
Month	2	3.45E5	58.993	0.0011	2	1.73E5	164.158	0.0001
Site x Month	2	2.08E5	35.667	0.0028	2	4965.23	4.709	0.0889
Error b	4	5841.94			4	1054.50		

[1] Values transformed using the Box-Cox transformation.

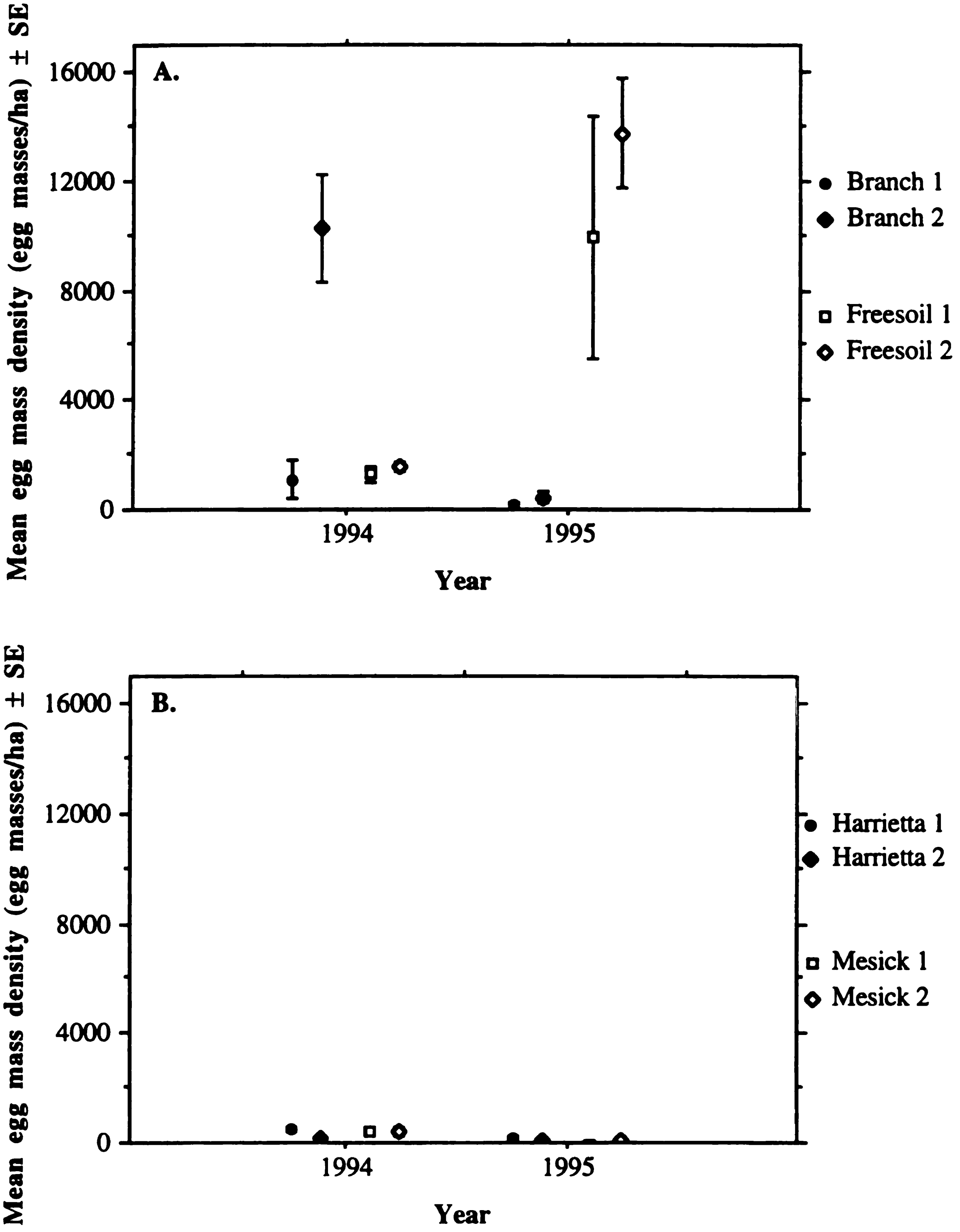


Figure 1.1. Mean density (±SE) of gypsy moth egg masses from four sites in A) red oak ecosystems (ELTP 20) and four sites in B) northern hardwood ecosystems (ELTP 45). Means were calculated from five 0.1 ha fixed-radius plots.

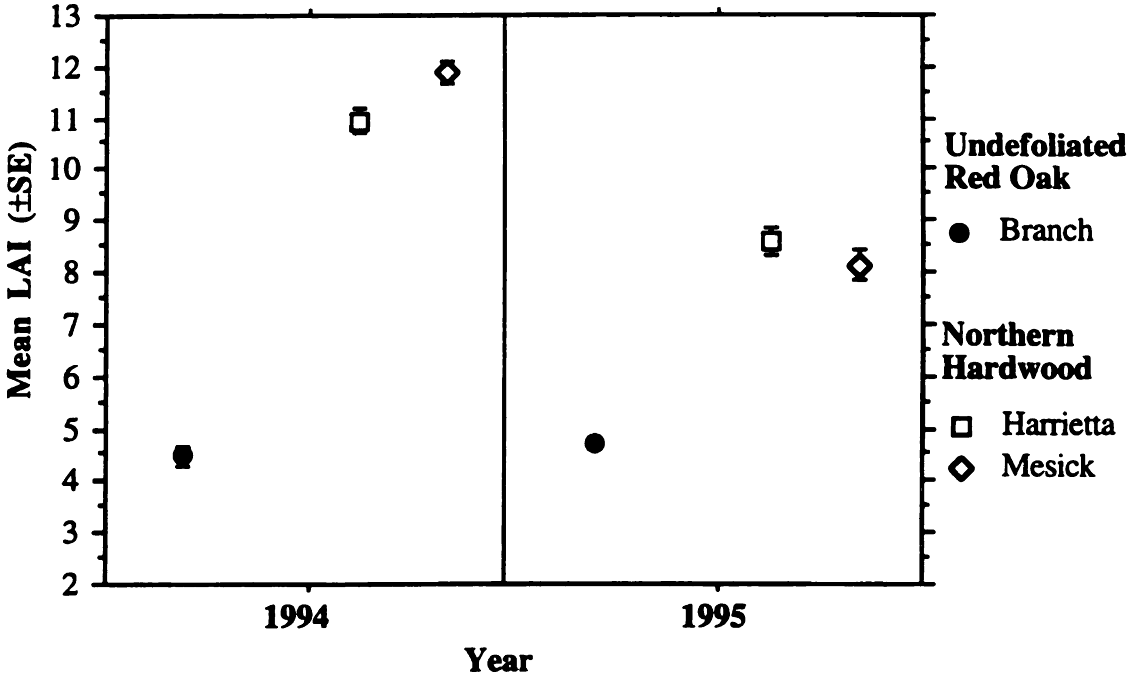


Figure 1.2. Mean LAI (±SE) from June, July, and August for undefoliated red oak sites (Branch) and northern hardwood sites (Harrietta and Mesick) during 1994 and 1995. Means were calculated from n=2 for each site. Error bars were small and may be obscured by data points.

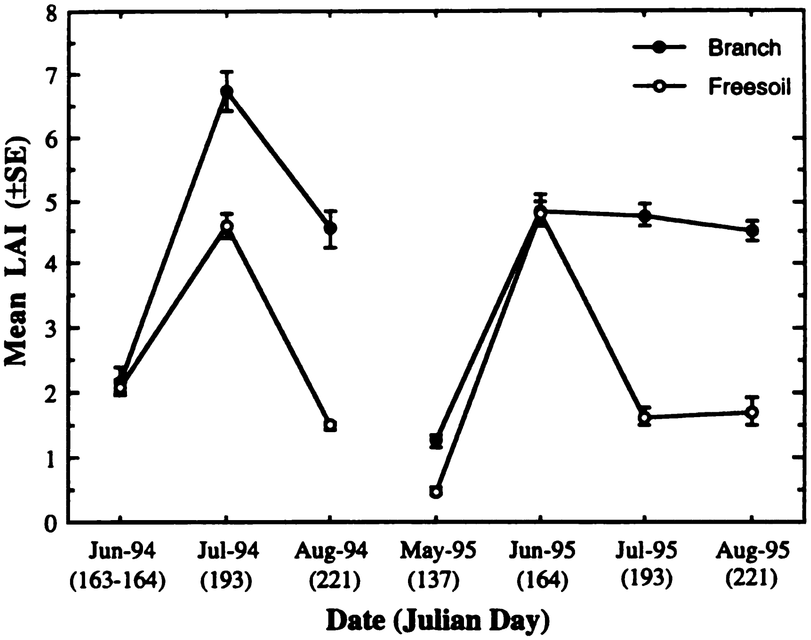


Figure 1.3. Comparison of mean LAI (±SE) from defoliated (Freesoil) and undefoliated (Branch) sites in red oak ecosystems during 1994 and 1995. Means were calculated each month from two sites located near Branch and two sites located near Freesoil.

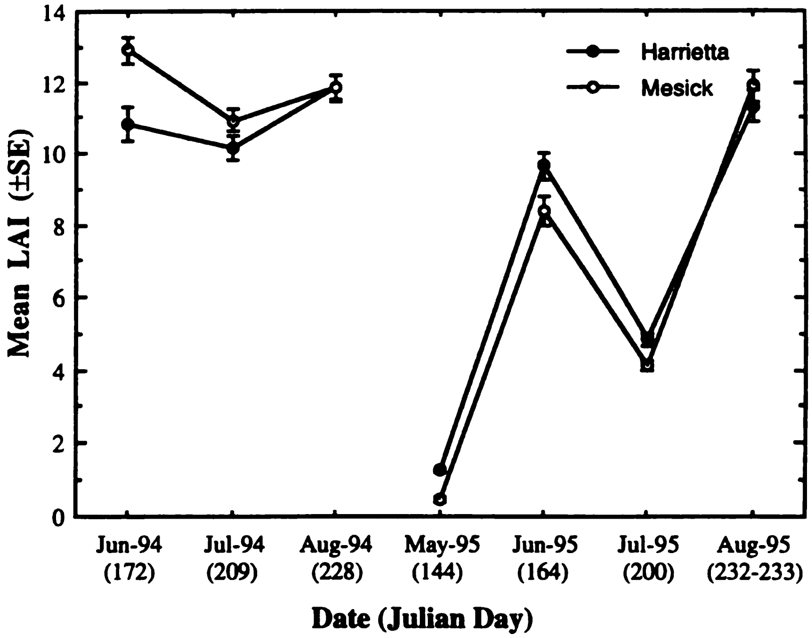


Figure 1.4. Comparison of mean LAI (±SE) from two northern hardwood sites during 1994 and 1995. Means were calculated each month from two sites located near Harrietta and two sites located near Mesick.

Chapter 2

THE IMPACT OF GYPSY MOTH (LEPIDOPTERA: LYMANTRIIDAE) OUTBREAKS ON CARABID BEETLE (COLEOPTERA: CARABIDAE) DIVERSITY IN TWO HARDWOOD ECOSYSTEMS IN NORTHERN LOWER MICHIGAN

Introduction

Sensitive suites of species are useful as indicators of ecosystem health in conservation planning and land management (Kremen et al. 1993). Useful indicator species are defined as well-known taxa that are easily measured, sensitive to environmental change, widely distributed, and able to provide an assessment of ecosystem properties over a wide range of stress (Kremen et al. 1993; Noss 1990). Ground beetles (Coleoptera: Carabidae) satisfy these criteria in that they are sensitive to habitat fragmentation, well-known taxonomically, and vary locally across regional landscapes (Niemela et al. 1988; Niemela et al. 1990; Niemela et al. 1993). Carabids have been used as indicators of ecosystem health across a broad spectrum of disturbance regimes, including impacts of grassland management techniques in agricultural systems (Erye et al. 1989) and clear-cutting in forested ecosystems (Lenski 1982; Niemela et al. 1993).

Generally, carabids are considered opportunistic predators which further emphasizes their importance in ecosystem monitoring. They have been employed as biological control agents in efforts to regulate pest insect outbreaks such as spruce budworm (*Choristoneura fumiferana* Clem.) and gypsy moth (*Lymantria dispar* L.) (Kelly and Regniere 1985). Gut analysis of native carabids in Pennsylvania indicated that 31 of 35 species collected had ingested gypsy moth during an outbreak (Cameron and Reeves 1990). The exotic carabid *Calosoma sychophanta* L., was widely released in the northeastern United States in programs to establish biological control of gypsy moth (Weseloh 1990).

While inventory and observational studies of ground beetles in the Great Lakes region are available (Jeffords and Case 1987; Leibherr and Mahar 1979; Purrington et al. 1989), little quantitative work has addressed changes of native carabid assemblages during a gypsy moth outbreak. Severe defoliation can alter light penetration through the canopy (see chapter 1) and other microclimatic factors. Decreased canopy cover can result in elevated temperatures (Klein and Perkins 1988; Perkins et al. 1987) and decreased humidity in the understory (Perkins et al. 1987). Gypsy moth invasion may also alter biological interactions by acting as an increased pool of prey resource for predatory carabids and displacing other lepidopteran prey species (see chapter 3).

The purpose of this study was to determine whether large gypsy moth populations and the resulting severe defoliation altered the abundance and species composition of native carabids in two ecosystems, one dominated by preferred host plants and the other dominated by non-preferred host plants of the gypsy moth. Specifically, we tested the null hypothesis that carabid abundance and species composition were not effected by gypsy moth defoliation against the alternate hypothesis that carabid abundance and species composition were effected by gypsy moth defoliation.

Methods

Study Area

This research was conducted in eight sites in the Manistee National Forest in northern lower Michigan. Manistee National Forest has been described using an ecological classification system (ECS) (Cleland et al. 1993). The ECS is a hierarchical classification that groups ecosystem components at spatial scales varying from the landscape to the stand level. Ecological landtype phases (ELTPs) are classified on the basis of soils, landscape position and natural vegetation. ELTPs are subsets of larger spatial scale units such as ecological landtypes (ELTs) and landtype associations (LTA). Because sites within the same ELTP have similar overstory and understory vegetation, soil hydrology, soil type, nitrogen cycling, productivity and geological history, use of the ECS allows ecosystems to be replicated in experimental designs with a high level of confidence that experimental plots are similar.

We randomly chose four sites classified as ELTP 20 and four sites classified as ELTP 45 from maps provided by the Manistee National Forest. All sites ranged from approximately 12 to 16 ha in area. ELTP 20 was characterized by an overstory dominated by northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) and a non-diverse ground flora (Cleland et al. 1993). Soils on ELTP 20 were typically sandy, xeric soils with low productivity (Host et al. 1987; Host et al. 1988). ELTP 45 had an overstory dominated by northern hardwood species including sugar maple (*Acer saccharum* Marsh) and American basswood (*Tilia americana* L.) (Cleland et al. 1993). This ELTP was notable for its rich herbaceous understory, well drained mesic soils, and high productivity (Host et al. 1987; Host et al. 1988).

Tree species typical of ELTP 20 and 45 also differed in susceptibility to gypsy moth defoliation (Houston and Valentine 1985; Mauffette et al. 1983; Twery 1990). Oak species, which dominated ELTP 20, are highly preferred by gypsy moth and oak stands often experience severe defoliation during outbreaks (Houston and Valentine 1985; Mauffette et al. 1983; Twery 1990). Northern hardwood stands, such as the ELTP 45, are less susceptible to gypsy moth defoliation because the dominant canopy species, sugar maple, is only moderately preferred by gypsy moth (Houston and Valentine 1985;

Mauffette et al. 1983; Twery 1990). However, highly preferred species such as American basswood (Mauffette et al. 1983; Twery 1990) were present within this ELTP.

In the red oak ecosystem (ELTP 20), two sites were located at 44° 00' N, 86° 00' W near the town of Branch and two sites were located at 44° 08' N, 86° 09' W near the village of Freesoil. In the northern hardwood ecosystem (ELTP 45), two sites were located at 44° 22' N, 86° 44' W near the town of Mesick and two sites were located at 44° 19' N, 86° 44' W near the village of Harrietta.

Before 1993, none of our study sites had ever experienced any observable gypsy moth defoliation (F. Sapio, MI DNR, Forest Health Management, 1993 *pers comm.*, S. Katovich, USDA For. Serv. NA. S&PF, Forest Health Management, 1992, *pers comm.*). We surveyed these sites in 1992 and found no visible defoliation. Density of gypsy moth egg masses, visual estimates of defoliation, and leaf area index were measured in all stands as part of a related study (see chapter 1). Red oak sites experienced more defoliation (Table 2.1) and had higher densities of gypsy moth egg (Figure 2.1) masses than the northern hardwood sites from 1993 to 1995. Red oak sites had overall lower leaf area index (LAI) than northern hardwood sites, and showed a particular reduction in LAI in areas with large gypsy moth populations in 1994 and 1995 (see chapter 1) (Table 2.1). Within red oak sites, gypsy moth populations fluctuated anually: outbreak populations at Branch in 1993 were followed by a population 'crash' due to NPV infection in 1994. Populations at Freesoil increased in 1994 and reached outbreak levels in 1995 (Figure 2.1).

Beetle Collection

Carabids were collected in 1993, 1994 and 1995. Beetles were collected four times each summer. Collection times roughly corresponded to significant points in gypsy moth management or biology. For example, typical application time of the microbial insecticide *Bacillus thuringensis* Berliner var. *kustaki* (Btk) for gypsy moth suppression in northern lower Michigan occur in mid-May, fourth instar gypsy moth in mid-June, peak defoliation in mid-July, and following stand refoliation in mid-August. During 1993, carabids were collected on 12-13 May, 16 June, 13 July, and 10 August from red oak sites and on 21 May, 22 June, 20 July, and 18 August from northern hardwood sites. In 1994, carabids were collected on 10 May, 13-14 June, 11-13 July, and 9 August from red oak sites and on 18 May , 20 June, 19-20 July, 15-16 August from northern hardwood sites. In 1995, collection dates were 15-16 May, 13-14 June, 10 July, 14-15 August at red oak sites and 22-23 May, 19 June, 18-19 July, and 21-22 August at northern hardwood sites.

Carabids were collected using unbaited pitfall traps and ultraviolet (UV) light traps suspended in the forest canopy. Pitfall traps consisted of plastic containers 11.5 cm in diameter filled with soapy water. Each trap was covered by a four-legged 'roof' to minimize capture of non-ground arthropods and to protect the contents from predation by birds. Ten pifall traps were placed at 10 m intervals along a random transect through each stand. Traps were open for 24 hours each sampling date.

Ultraviolet traps consisted of a 22 watt UV bulb connected to a photosensor and powered by a 6 volt battery. A collection funnel and bucket containing insecticidal pest strips (Vapona TM) were attached below the bulb. The trap was raised into the canopy approximately 1 to 2 M above the lower edge of the canopy in the center of each stand. UV traps were activated for approximately 8 hours during each sampling date. Use of a low wattage bulb and a rain cover over the bulb restricted potential long-distance attraction of nocturnal insects, resulting in a localized sample of insect populations (Bowden 1982).

These trapping methods were used in combination to sample species present all above-ground strata and to represent the total ecosystem fauna as completely as possible given available resources. We recognize trapping biases inherent to these methods, such as the differential trapping ability of UV traps for carabids capable of flight and the confounding of abundance and activity measures involved in pitfall trapping (Leibherr and Mahar 1979). These biases could not be eliminated, but were minimized through use of a consistent, standardized sampling period for each trap type in each site (Coddington et al. 1991).

Beetles collected from the UV traps were packed in plastic containers lined with tissue paper. Beetles collected from pitfall traps were transferred to plastic jars containing 90% ethanol. All insects were stored in a freezer until they could be identified. Voucher specimens were prepared and identified by T. Work at the Center for Biological Diversity at Michigan State University.

Statistical Analysis

Monthly trap catch was pooled for statistical analysis because the relatively short duration of trapping was not adequate to calculate meaningful indices of diversity or to evaluate seasonal changes in carabid species. Numbers of beetles, numbers of species, alpha log series index, Brillouns's and Simpson's indices were evaluated at each site (Magurran 1988). The alpha log series index was used because it provided an estimate of diversity based on species richness. Simpson's index was used because it estimates diversity based on species dominance. Because UV trapping does not sample independently, Brilloun's index, an index that is used when randomness of a sample is in question, was also calculated (Magurran 1988; Southwood 1994). A combination of diversity indicies, species richness and beetle abundance were evaluated because each particular measure was subject to biases related to sample size and distribution of insects (Magurran 1988). We believe that a consistent pattern of diversity that is reflected by multiple measurements is a more reliable estimate than an estimate of diversity based on a single index (Magurran 1988).

Effects of gypsy moth and severe defoliation were examined only in the red oak ecosystem because of the consistently large gypsy moth populations. Site differences within the northern hardwood ecosystem were analyzed to provide baseline data on species composition as well as provide an estimation of natural variation through time in sites without large populations of gypsy moth. Within each ecosystem, differences between sites and among year variation were evaluated using a one-way ANOVA with repeated measures (also known as a split-plot ANOVA). Measurements that were not normally distributed were transformed using the Box-Cox transformation (Sokal and Rohlf 1995). Analyses were conducted using the software package JMP (SAS Institute Inc.).

Similarity of carabid fauna between ecosystems (beta diversity) were examined using Soresnon's quantitative index of similarity (also known as Bray-Curtis index) (Ludwig and Reynolds 1988; Magurran 1988). Multiple dendograms were generated using Bray-Curtis distance measures and four different linkage methods (Ludwig and Reynolds 1988). Clusters were generated using these alternative linkage methods: beta-flexible method ($\beta = -0.25$ and -0.50) (Milligan 1989); average linkage (group average/unweighted pair group); and centroid linkage (Ludwig and Reynolds 1988). Cluster analysis was performed using BASIC software developed by Ludwig and Reynolds (1988). Because varying the value of β between -0.25 and -0.5 resulted in percent similarity values greater than 1, values expressed on dendograms have been scaled by dividing all similarity values by 1.2 and 1.5, respectively.

Results

Ecosystem Differences in Diversity

A total of 47 carabid species were collected in the red oak sites and 38 in the northern hardwood sites. Of the 17 most abundant species, 11 were consistently caught in UV traps, while the remaining 6 were consistently caught in pitfall traps (Table 2.2). Uncommon species (total catch less than 20 individuals) are listed in Table 2.3.

Dendograms generated using the centroid linkage method were not meaningful because of the presence of reversals and therefore were not presented. Consistent patterns were observed in dendograms generated by beta-flexible and group average linkage methods within each year except in 1994. In 1993, three clusters were apparent within all dendograms (Figures 2.2, 2.3, and 2.4). Red oak sites that experienced no defoliation during 1993 (Freesoil 1 and 2) formed a single cluster, as did three northern hardwood sites (Harrietta 1, Harrietta 2, and Mesick 1). Defoliated red oak sites (Branch 1 and 2) clustered with one northern hardwood site (Mesick 2). In 1994, beta-flexible methods formed two distinct clusters one containing three of the red oak sites and one northern hardwood site and the other containing three northern hardwood sites and one red oak site (Figure 2.2 and 2.3). The group average method showed no appreciable pattern in clustering in 1994 (Figure 2.4). In 1995, both beta-flexible methods generated two clusters; one containing all red oak sites, the other containing all northern hardwood sites (Figure 2.3). The group average method generated four separate clusters in 1995 (Figure 2.4). The four distinct clusters were formed by defoliated oak sites (Freesoil 1 and 2), undefoliated oak sites (Branch 1 and 2), three northern hardwood sites (Harrietta 2, Mesick 1, and Mesick 2), and by one northern hardwood site (Harrietta 1). Results of the cluster analyses for 1993 and 1994 were ambiguous in terms ecosystem differences. However, in 1995, results of cluster analysis indicate that the carabid fauna of the red oak sites were more similar to one another than they were to northern hardwood sites.

Red oak sites had greater species richness and total abundance than northern hardwood sites in every year. Twenty-one species were unique to the red oak ecosystem. Nine of these species are known to have particular habitat requirements with respect to moisture and light availability (Lindroth 1969). *Amara convexa* Lec. and *Carabus serratus* Say are restricted to xeric habitats. *Pterostichus mutus* (Say) and *P. melanarius* (Ill.) are commonly found in well-lighted, open forests (Lindroth 1969). *Chlaenius tricolor tricolor* Dej. and *Pterostichus chaleitis* Say are commonly collected in well-lighted flood plain forests (Lindroth 1969). *Dyschirius politis* (Dej.), *Agonum harrisi* Lec., and *Bembidion americanum* Dej. are known hygrophiles and are commonly found near pond edges (Lindroth 1969). The remaining 14 species unique to the red oak stands were eurytropic (Lindroth 1969).

Twelve species were unique to the northern hardwood sites, nine of which were hygrophagous (Lindroth 1969). No strictly xerophilous species were collected from northern hardwood stands. Snail predators, including *Dicaleus teter* Bon., *Scaphinotes bilobus* (Say), and *Spheroderus stenostanus lecontei* Dej. (Lindroth 1969) were found only in this ecosystem.

Impacts of Defoliation on Carabid Species Richness, Abundance, and Diversity

Because gypsy moth populations and the amount of defoliation varied between Branch and Freesoil sites over time, defoliation by year interactions better described the effects of gypsy moth than main effects alone. Defoliation by year interactions were significant in the alpha log series index ($F=6.98$ $p<0.05$) (Table 2.4 and Figure 2.5) and only marginally insignificant in species richness ($F=6.29$ $p<0.06$) (Table 2.4 and Figure 2.6). In 1993, no differences in carabid species richness or alpha log series index were observed (Figure 2.5 and 2.6). However in 1994, richness and diversity declined in Branch sites one year following defoliation at Branch sites. Likewise, in 1995, richness and diversity increased in Freesoil sites one year following defoliation at Freesoil sites (Figures 2.5 and 2.6). No significant differences between Branch and Freesoil sites were observed in terms of beetle abundance, Simpson's or Brilloun's indices (Table 2.4 and 2.5). Among year variation was only significant in the Brilloun index ($F=21.17$ $p<0.01$) (Table 2.4). Brilloun's index increased each year in the red oak sites and ranged from a mean value (±SE) of 0.58 (±0.04) in 1993 to 1.6 (±0.10) in 1995.

In 1993 and 1995 when differences in defoliation and size of gypsy moth populations were greatest, similarity of carabid fauna differed between Branch and Freesoil sites (Figures 2.2, 2.3, and 2.4). Differences in carbid fauna between Branch and Freesoil were reflected in the number of species and genera collected. Like the number of species, the number of genera increased one year following defoliation at Freesoil in 1995. Mean number of genera were greater at Freesoil sites (12.5 ±1.5) than at Branch sites (7.5±0.5) in 1995.

Within the northern hardwood ecosystem, no significant site by year interactions were observed in any measurement (Table 2.6). Differences between northern hardwood sites were less variable in terms of alpha log series index (Figure 2.7) and species richness (Figure 2.8) than red oak sites (Figure 2.5 and 2.6). Among year variation was observed in species richness ($F=15.08$ $p< 0.01$), beetle abundance ($F=9.19$ $p<0.03$), and Brilloun's index ($F=68.47$ $p<0.001$) (Table 2.5 and Table 2.7)

Response of Carabid Species to Gypsy Moth

While species such as *Bembidion partreule* Dej., *B. vericolor* (Lec.), *Stenopholus comma* (F.), and *Synuchus impunctata* (Say) were abundant in one particular year, their populations appeared to be highly variable and showed no trend with gypsy moth populations. However, *Carabus limbatus* Say consistently accounted for at least 10% of the catch each year in red oak sites.

The relative difference in total abundance of *C. limbatus* between Branch and Freesoil suggests that *C. limbatus* was negatively effected by gypsy moth one year following defoliation (Figure 2.9). In 1993, the difference in total catch of *C. limbatus* between Branch and Freesoil was only 6 beetles. However, in 1994 after severe defoliation had occurred at Branch the previous year, Branch sites had 17 fewer *C.*

limbatus than did Freesoil sites. In 1995, following defoliation at Freesoil sites during the previous year, Freesoil had 25 less *C. limbatus* than did Branch sites.

In northern hardwood sites where gypsy moth populations were low, the relative differences in total abundance of *C. limbatus* did not change over three years (Figure 2.9). Mesick sites always had roughly twice as many *C. limbatus* than did Harrietta sites.

Discussion

Ecosystem Differences

Differences in carabid species composition between northern hardwood and red oak sites were likely a result of differences in plant diversity and microclimate between ecosystems. Leibherr and Mahar (1979) concluded that increased plant diversity creates heterogeneity of microhabitat and more opportunities for habitat specialists to find suitable conditions for oviposition. Microclimatic components such as temperature and humidity are directly related to light penetration through the canopy. The amount of light penetration through the canopy of each ecosystem differed considerably (see chapter 1). Humidity and light preference are important factors in determining habitat preference of a forest dwelling carabids (Allen 1976). Likewise, the amount of canopy closure has also been attributed to the amount of free moisture available in the litter (Leibherr and Mahar 1979) Northern hardwood sites had a denser canopy and more leaf area index (LAI) than red oak sites (see chapter 1).

While not directly tested in our study, these results may suggest an association between the diverse understory flora of the northern hardwood sites and the amount of hygrophilous carabid species present. Furthermore, the dense canopy of the northern hardwood sites may have provided a cooler, moister microclimate capable of supporting a relatively large proportion (75%) of hygrophilic species and specialist species that rely on snails, a moisture-dependent prey animal. Red oak sites had lower LAI and smaller relative proportion (15%) of hygrophilous species. Species that preferred well-lighted xeric conditions were present only in red oak stands and comprised 15% of the species unique to the ecosystem. It is likely that a combination of the effects of understory floral diversity and canopy density explain the patterns in carabid species composition that we observed.

Effects of Gypsy Moth and Natural Variation

Because all red oak sites experienced severe defoliation by gypsy moth over the three years in which this experiment was conducted, comparisons of undisturbed red oak and undisturbed northern hardwood sites cannot be made, nor does an optimal control treatment exist for the effects of defoliation in the red oak sites. However, lack of differences between Mesick and Harrietta in species richness and alpha log series provided an estimate of the amount of natural variation in richness and diversity of beetles over time. When red oak and northern hardwood sites are compared in terms of species richness and alpha log series index, red oak sites varied more than northern hardwood sites. While not optimal, we believe that the consistent patterns within the northern hardwood sites provided a useful comparison to assess effects of defoliation on native carabid richness and diversity.

Implications of Gypsy Moth and Defoliation

Disturbance events have been thought to disrupt processes of competitive exclusion and result in an increase in species diversity (Connell 1978; Lenski 1982). Gypsy moth populations and high defoliation may have represented a major disturbance in the red oak sites and could presumably have both positive and negative effects on native carabid species. The presence of high populations of gypsy moth may act as an increased prey source for some carabids, while defoliation may alter microhabitat and decrease availability of other prey items through interspecific competition with other Lepidoptera and foliage feeders (see chapter 3).

The increase in species richness and diversity that we observed one year following severe defoliation could be attributed to exploitation of gypsy moth through predation or scavenging by carabids. Univoltine carabid species that used gypsy moth as a food resource would presumably be more fecund and show increased abundances in the next generation during the following year. However, responses of individual carabid species to large gypsy moth populations, and presumably increased prey abundance, were inconclusive in our study because of the high variability and small numbers of individuals collected between years. We did not collect caterpillar-specialist species such as those in the genus *Calosoma* in great enough numbers to make conclusions about the effects of increased prey abundance. However, because carabid food preference in the field is largely unexplored and because carabids are opportunistic feeders, we do not believe the hypothesis that carabids may be exploiting gypsy moth through predation and scavenging can be dismissed.

Significant defoliation by year interactions were not observed in either Brilloun or Simpson's index. Simspon's index has been characterized as less discriminating than the alpha log series index because of its dependence on abundance of common species (Magurran 1988). Similarly, the Brilloun index has been characterized as moderately indiscriminant and dependent on sample size (Magurran 1988). The variability in the abundance of carabids collected may have accounted for the lack of differences observed using these indices.

While not directly tested in this study, two hypotheses explaining the increase in carabid diversity in terms of relaxed competition for food resources during a gypsy moth outbreak exist (Connell 1978; Lenski 1982). One hypothesis suggests that carabid species diversity increased because more gypsy moth were available for consumption. This would result in relaxed competition among species with similar feeding habits, such as members of the same genus (Lenski 1982) and increased diversity of these similar feeding-carabids. Our second hypothesis is that carabids may be exploiting gypsy moth through scavenging. Scavenging for gypsy moth is a strategy available to all carabids regardless of body size and predation ability because of the decreased cost of subduing prey. If carabids are scavenging gypsy moth cadavers, a greater number of potential competitors from different genera will be able to utilize the influx of gypsy moth as a food resource, and between-genera diversity should increase.

We observed both an increase in the number of species and genera one year following a severe defoliation event. This suggests that carabids may be exploiting gypsy moth as food resource either through predation and or scavenging. This conclusion should be interpreted conservatively because of the lack of available knowledge of carabid feeding habits in the field and the small sample size. Moreover, information on the acceptability of gyspy moth cadavers infected with NPV by carabid species is unavailable.

Effects of defoliation were complicated by the confounding effects of decreasing canopy closure and the increase of potential prey items, e.g. gypsy moth larvae and pupae. Reduction of LAI by gypsy moth defoliation could augment the trapping ability of the canopy UV traps by increasing the visual range at which UV light is detected. This could result in higher estimates of richness, abundance, and diversity in defoliated stands relative to undefoliated stands during the same year of a defoliation event. However, this would not be consistent with the increased species diversity we observed one year after a defoliation event.

The responsive nature of the species and the ease with which large numbers of individual beetles were collected suggests *C. limbatus* may be an appropriate candidate for an indicator species (Kremen et al. 1993) that could be used to monitor environmental change in red oak sites. Defoliated stands had a lower LAI and presumably less available moisture than undefoliated stands (see chapter 1). *C.limbatus*, a moist forest dweller, was less abundant during severe defoliation but recovered to pre-defoliation levels the next year. Disturbances that altered forest canopy caused similar responses in *C. limbatus* in a previous study. For example, *C. limbatus* was intolerant of clearcut conditions in Appalachian forests (Lenski 1982). The high sensitivity and rapid response to disturbance exhibited by *C. limbatus* is similar to the environmental sensitivity of ground beetles described in previous studies (Desender and Turin 1989; Dijk 1986; Holliday 1991; Niemela et al. 1988; Niemela et al. 1990; Turin and denBoer 1988).

Table 2.1. Visual estimation of peak defoliation and estimation of mean LAI (±SE) using photosynthetically active radiation transmittance of sites in red oak and northern hardwood ecosystems.

Peak Visual Estimation of Defoliation

	1993	1994	1995
Red Oak			
Branch	80-100%	< 20%	< 20%
Freesoil	< 20%	40-60%	80-100%
Northern Hardwood			
Harrietta	< 20%	< 20%	< 20%
Mesick	20-40%	< 20%	< 20%

Estimated Leaf Area Index[1]

	1994	1995
Red Oak		
Branch	4.48 ± 0.221	4.71 ± 0.115
Freesoil	2.73 ± 0.076	2.72 ± 0.151
Northern Hardwood		
Harrietta	10.9 ± 0.226	8.61 ± 0.229
Mesick	11.9 ± 0.189	8.14 ± 0.222

[1] Means and standard errors were calculated from two sites (n=2)

Table 2.2. Abundant carabid species collected using suspended UV traps and pitfall traps in sites dominated by red oak (RO) and northern hardwood (NH) species over three years[1]

	1993		1994		1995		
Species	**RO**	**NH**	**RO**	**NH**	**RO**	**NH**	**Total**
UV Collected Species							
Stenopholus comma (F.)	88	3	227	9	3	151	481
Stenopholus ochropezus (Say)	7	0	159	0	27	4	197
Bembidion versicolor (Lec.)	1	0	17	5	161	6	190
Stenopholus lineola (F.)	81	2	0	0	1	24	108
Bembidion partreule Dej.	1	0	19	7	61	2	90
Cymindis platicollis (Say)	0	0	7	20	4	40	71
Agonum placidum (Say)	6	0	6	2	3	28	45
Trichotichnus dichrous (Dej.)	0	0	24	5	3	12	44
Clivina fossor (Linne)	1	0	36	0	6	0	43
Harpalus faunus Say	0	0	13	9	9	4	35
Cymindes limbatus (Dej.)	3	1	7	11	3	4	29
Pitfall Collected Species							
Carabus limbatus Say	36	4	73	34	123	75	345
Synuchus impunctatus (Say)	65	30	22	72	0	45	234
Pterostichus pensylvanicus Lec.	0	5	26	66	11	17	125
Pterostichus sp A	0	0	25	64	0	0	89
Myas cyanescens Dej.	1	15	0	23	0	11	50
Pterostichus corvinus (Dej.)	10	6	1	3	1	2	23
Total	300	66	662	330	416	425	

[1] Species were termed abundant if more than 20 individuals were collected over three years.

Table 2.3. Uncommon carabid species collected in UV and pitfall traps from red oak (RO) and northern hardwood (NH) ecosystems over three years[1]

Species	1993		1994		1995		Total
	RO	NH	RO	NH	RO	NH	
<u>UV Collected Species</u>							
Agonum decorum (Say)	0	0	0	0	0	1	1
Agonum galvestonicum (Csy.)	0	0	0	0	0	1	1
Agonum harrisi Lec.	1	0	0	0	0	0	1
Agonum sordens Kby.	0	0	2	0	1	0	3
Amara convexa Lec.	2	0	0	0	5	0	7
Anadaptus discoides Dej.	0	0	5	0	0	0	5
Bembidion americanum Dej.	0	0	1	0	0	0	1
Brachinus cordicollis Dej.	0	0	0	0	0	1	1
Chlaenius tricolor tricolor Dej.	1	0	2	0	7	0	10
Clivina dentipes Dej.	0	0	1	0	0	0	1
Dyschirius erythrocerus Lec.	0	0	0	0	1	3	4
Dyschirius politis (Dej.)	0	0	0	0	3	0	3
Harpalus lewisi Lec.	0	0	0	5	0	9	14
Harpalus pensylvanicus (DeG.)	0	0	2	1	5	0	8
Harpalus rufipes (DeG.)	0	0	0	1	0	0	1
Lebia atriventalis Say	1	0	0	0	1	4	6
Lebia ornata Say	0	0	1	0	0	0	1
Lebia tricolor Say	0	0	2	0	0	1	3
Lebia viridis Dej.	0	0	4	0	1	1	6
Pterostichus chalcites Say	0	0	2	0	1	0	3
Stenopholus conjunctus (Say)	0	0	12	0	1	5	18
Tachys sp A	0	0	0	0	8	0	8
Tachys sp B	0	0	0	0	3	0	3
Tachys sp C	0	0	0	0	1	0	1
Trechus discus F.	0	0	0	0	2	0	2

Table 2.3. (cont'd)

Pitfall Collected Species							
Calosoma frigidum Kby.	1	0	12	0	2	1	16
Calosoma scrutator (F.)	0	0	1	0	0	0	1
Calathus gregarius (Say)	0	2	0	0	0	0	2
Carabus serratus Say	0	0	2	0	1	0	3
Carabus sylvosus Say	0	0	0	0	0	1	1
Cymindis americana Dej.	0	0	0	1	0	0	1
Cymindis cribicollis Dej.	0	5	0	2	1	0	8
Cymindis pilosa Say	0	4	1	0	0	0	5
Dicaelus teter Bon.	0	2	0	3	0	0	5
Myas coracanus (Say)	2	0	4	0	0	0	6
Pterostichus adstrictus Eschz.	12	7	0	0	0	0	19
Pterostichus adoxus (Say)	0	5	0	0	0	0	5
Pterostichus melanarius (Ill.)	0	0	1	0	2	0	3
Pterostichus mutus (Say)	1	0	11	0	0	0	12
Pterostichus sp	3	0	0	0	0	0	3
Scaphinotus bilobus (Say)	0	2	0	2	0	1	5
Sphaeroderus stenostanus lecontei Dej.	0	1	0	3	0	4	8

---

[1] Species were termed uncommon if less than 20 individuals were collected over three years.

Table 2.4. Statistical significance of treatment effects from split-plot ANOVA of five measures of carabid diversity in four red oak sites.

Source of Variation	df	Species Richness[1]	Abundance	Alpha Log Series	Brilloun's Index[1]	Simpson's Index
		F value of significant treatment effects				
Gypsy Moth	1	0.629	3.414	0.008	0.002	0.002
Year	2	3.806	0.607	2.410	21.169	0.558
Gypsy Moth x Year	2	6.287	1.623	6.981	1.504	0.457
		Probability of significant treatment effects				
Gypsy Moth	1	0.5110	0.2059	0.9539	0.9702	0.9676
Year	2	0.1186	0.5887	0.2057	0.0075	0.6113
Gypsy Moth x Year	2	0.0582	0.3048	0.0496	0.3257	0.6626
				Mean square		
Error a	2	0.0006	0.2030	0.9700	0.1450	0.0040
Error b	4	0.0004	0.6440	1.1160	0.0630	0.0130

[1] Values transformed using the Box-Cox transformation

Table 2.5. Means (±SE) of five measurements of diversity pooled over three years from red oak and northern hardwood sites (n=2).

Variable	Branch	Freesoil	Harrietta	Mesick
Species Richness	12.3 (2.50)	14.2 (2.32)	12.8 (2.21)	10.8 (1.25)
Abundance	129.0 (75.75)	123.3 (14.88)	70.8 (28.92)	29.3 (11.96)
Alpha Log Series	4.14 (0.57)	4.19 (0.76)	4.4 (0.40)	4.2 (0.46)
Brilloun's Index	1.0 (0.17)	1.0 (0.24)	1.0 (0.22)	1.0 (0.19)
Simpson's Index	4.1 (0.72)	4.1 (0.72)	5.5 (0.70)	6.1 (0.93)

Table 2.6. Statistical significance of treatment effects from split-plot ANOVA of five measures of carabid diversity in four northern hardwood sites.

Source of Variation	df	Species Richness	Abundance	Alpha Log Series	Brilloun's Index	Simpson's Index
				F value of significant treatment effects		
Site	1	1.756	1.122	0.288	0.243	0.074
Year	2	15.077	9.188	1.294	68.467	0.091
Site x Year	2	3.692	1.235	2.405	0.928	0.039
				Probability of significant treatment effects		
Site	1	0.3162	0.4006	0.6454	0.6711	0.8115
Year	2	0.0137	0.0320	0.3687	0.0008	0.9147
Site x Year	2	0.1234	0.3823	0.2061	0.4665	0.9625
				Mean square		
Error a	2	6.833	2912.833	0.095	0.037	13.301
Error b	4	4.333	948.333	0.924	0.017	3.250

Table 2.7. Means (±SE) of species richness, beetle abundance, and the Brilloun index from four northern hardwood sites that varied significantly over three years.

Variable	1993	1994	1995
Species Richness	7.5 (0.65)	12.5 (1.85)	15.5 (1.55)
Beetle Abundance	23.5 (2.53)	87.0 (20.89)	114.5 (28.74)
Brilloun Index	0.6 (0.04)	0.8 (0.03)	1.6 (0.9)

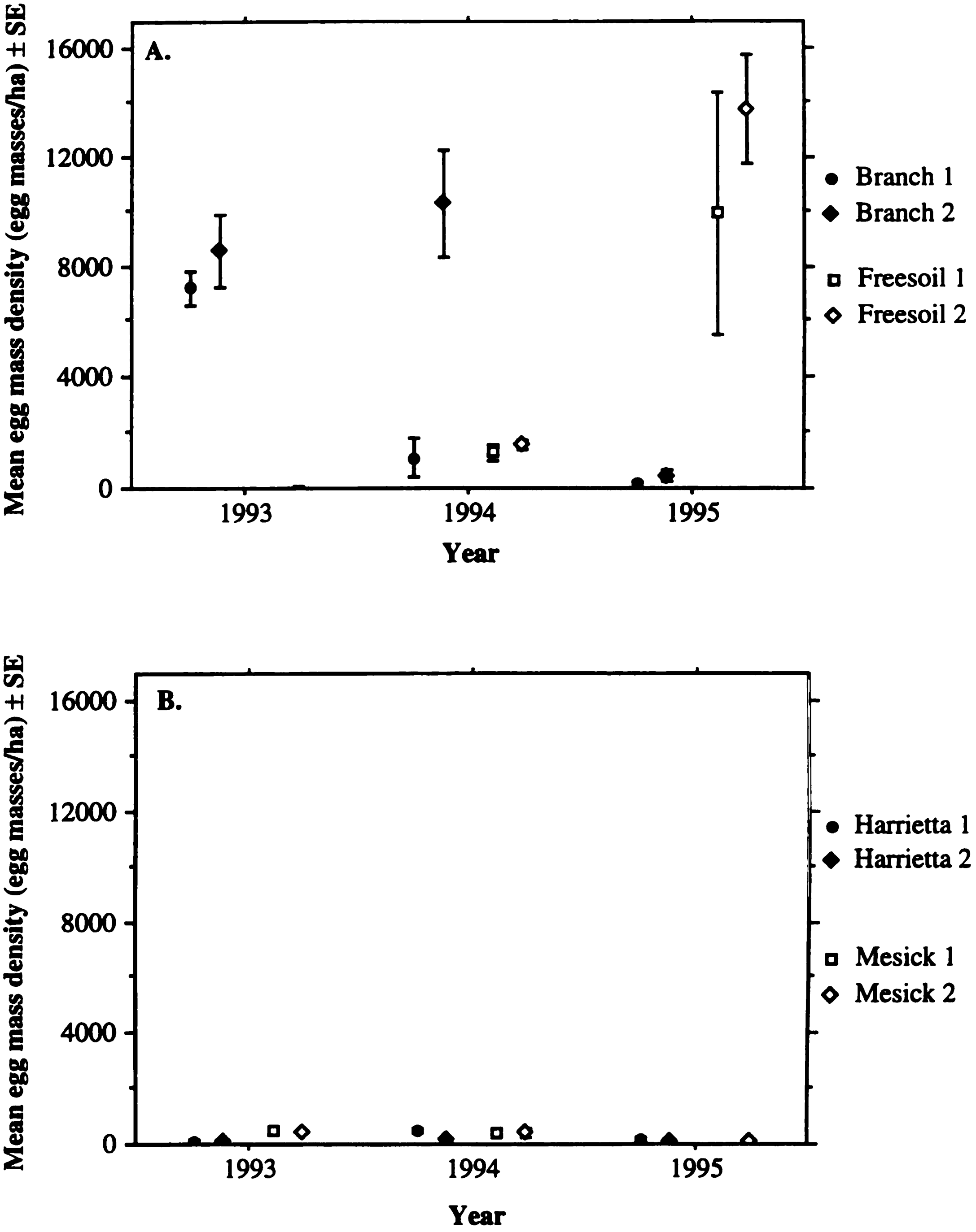


Figure 2.1. Mean density (±SE) of gypsy moth egg masses from four sites in A) red oak ecosystems (ELTP 20) and four sites in B) northern hardwood ecosystems (ELTP 45). Means were calculated from five 0.1 ha fixed-radius plots

Figure 2.2. Hierarchical clusters created using beta-flexible linkage (β=-0.25) and Sorenson's quantitative index of similarity for total carbids collected from eight sites during A) 1993, B) 1994 and C) 1995.

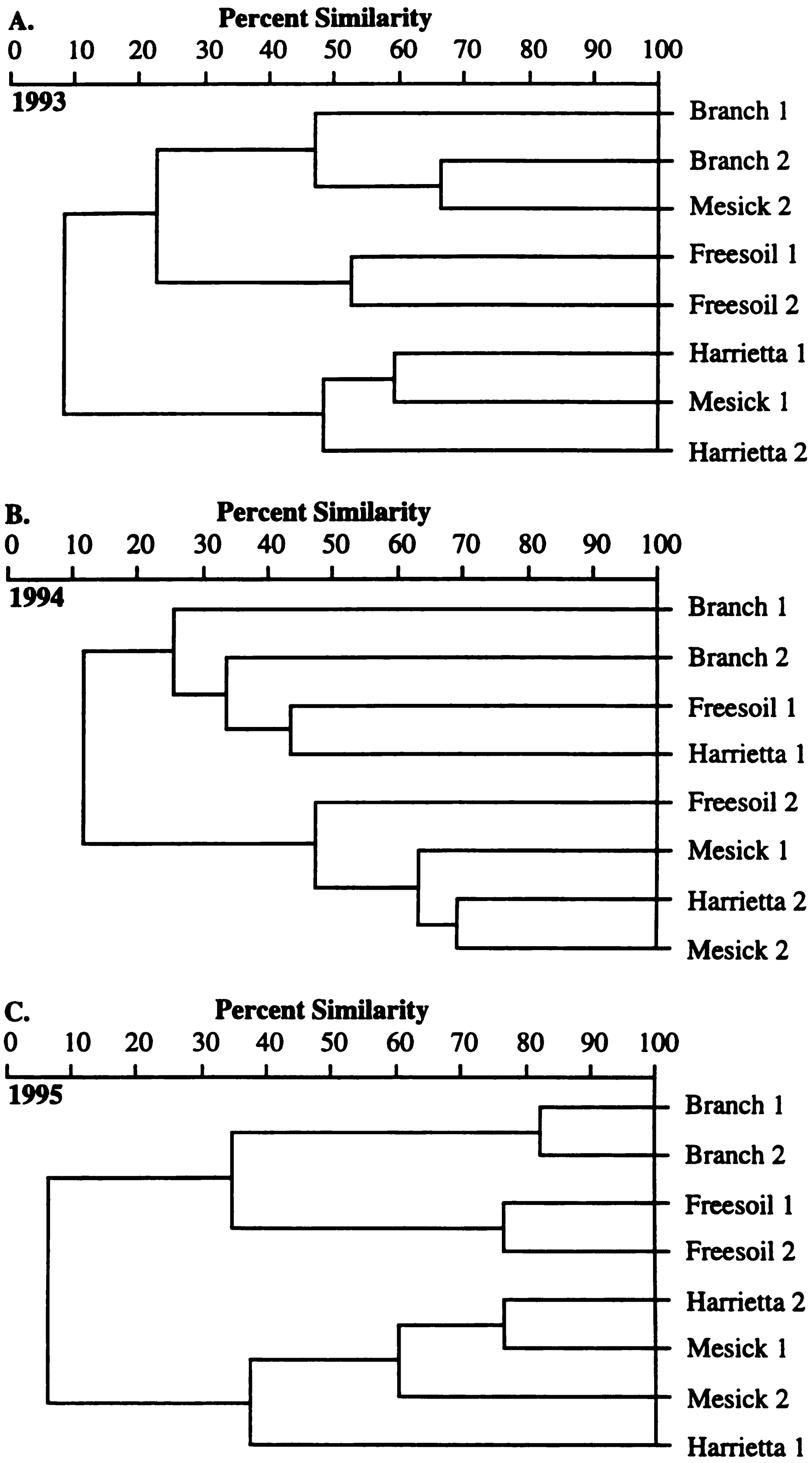

A.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1993
Branch 1
Branch 2
Mesick 2
Freesoil 1
Freesoil 2
Harrietta 1
Mesick 1
Harrietta 2
B.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1994
Branch 1
Branch 2
Freesoil 1
Harrietta 1
Freesoil 2
Mesick 1
Harrietta 2
Mesick 2
C.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1995
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 2
Mesick 1
Mesick 2
Harrietta 1

Figure 2.3. Hierarchical clusters created using beta-flexible linkage (β=-0.50) and Sorenson's quantitative index of similarity for total carbids collected from eight sites during A) 1993, B) 1994 and C) 1995.

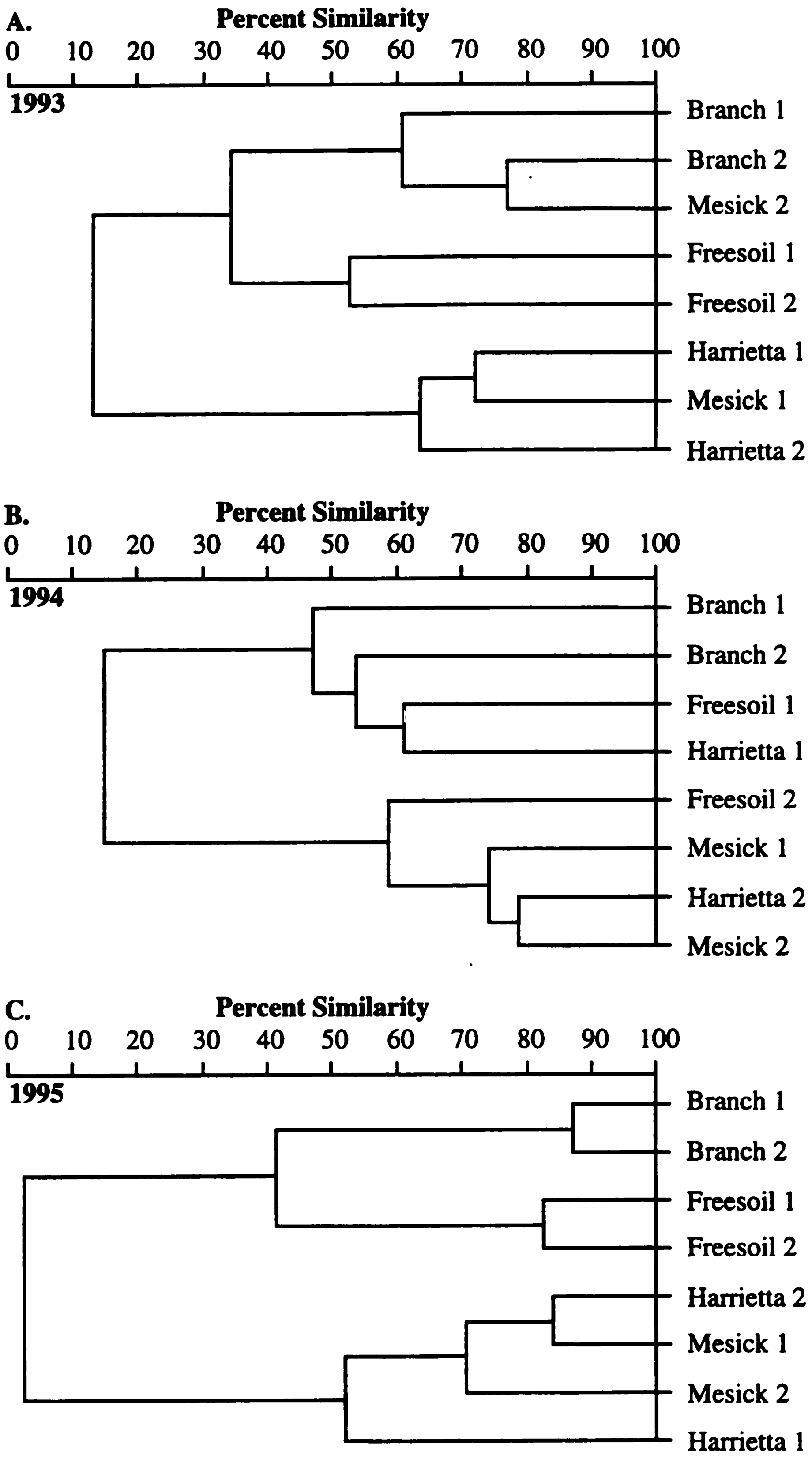
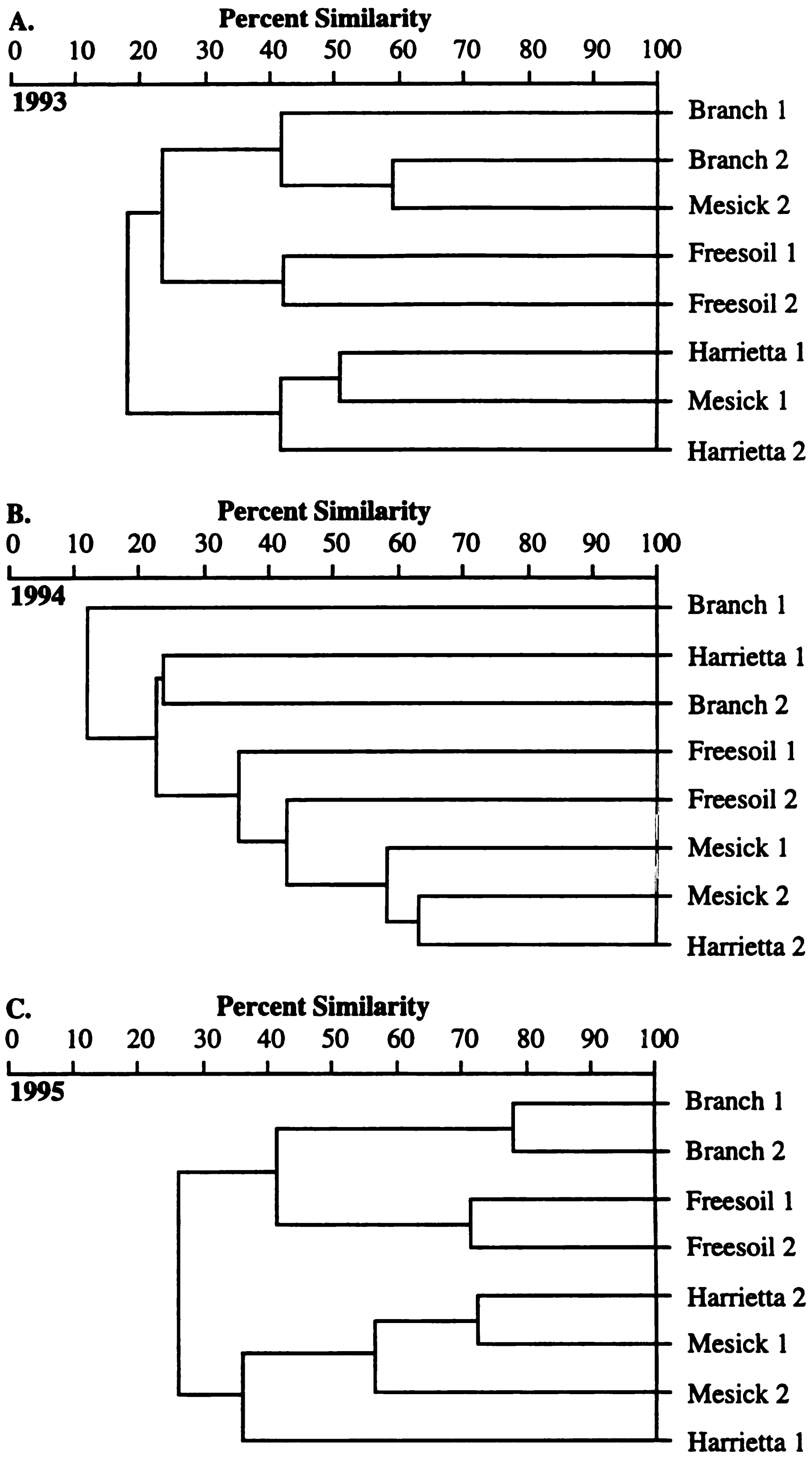

A.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1993
Branch 1
Branch 2
Mesick 2
Freesoil 1
Freesoil 2
Harrietta 1
Mesick 1
Harrietta 2
B.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1994
Branch 1
Branch 2
Freesoil 1
Harrietta 1
Freesoil 2
Mesick 1
Harrietta 2
Mesick 2
C.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1995
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 2
Mesick 1
Mesick 2
Harrietta 1

Figure 2.4. Hierarchical clusters created using average linkage (β=-0.25) and Sorenson's quantitative index of similarity for total carbids collected from eight sites during A) 1993, B) 1994 and C) 1995.


A.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1993
Branch 1
Branch 2
Mesick 2
Freesoil 1
Freesoil 2
Harrietta 1
Mesick 1
Harrietta 2
B.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1994
Branch 1
Harrietta 1
Branch 2
Freesoil 1
Freesoil 2
Mesick 1
Mesick 2
Harrietta 2
C.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1995
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 2
Mesick 1
Mesick 2
Harrietta 1

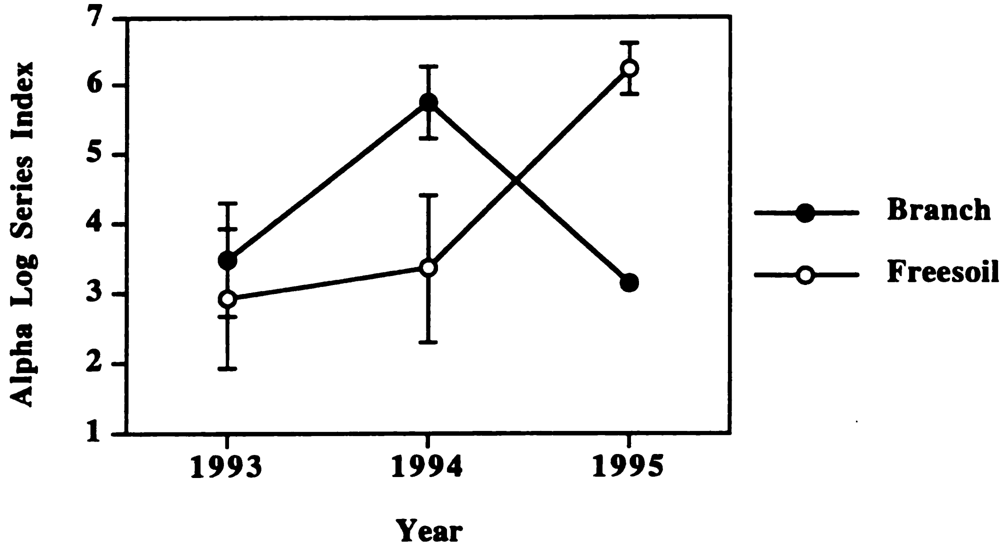


Figure 2.5. Means (±SE) of the alpha log series index from red oak sites that experienced differential amounts of defoliation over three years. Means were calculated from n=2. Standard errors were small during some years and may be obscured by size of data points.

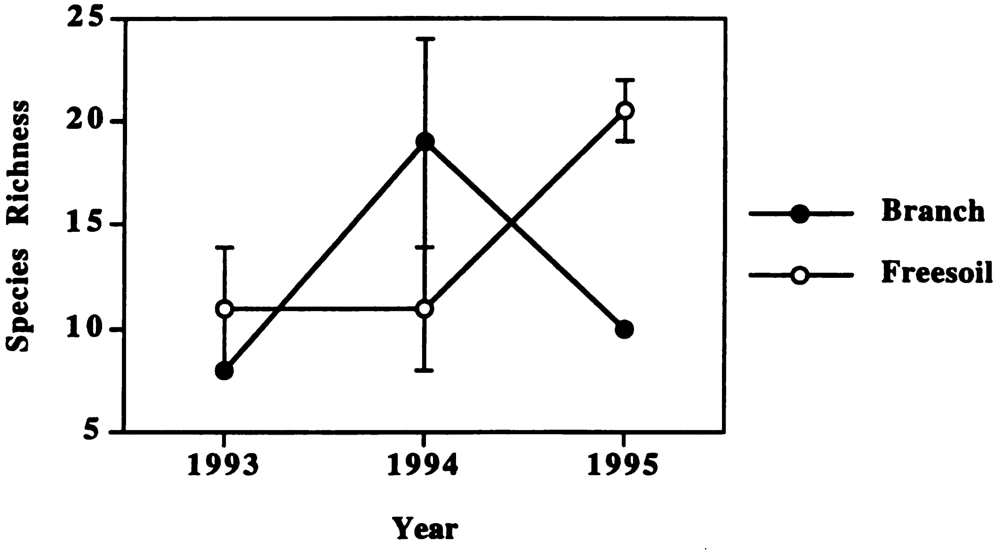


Figure 2.6. Means (±SE) of species richness from red oak sites that experienced differential amounts of defoliation over three years. Means were calculated from n=2. Standard errors were small during some years and may be obscured by size of data points.

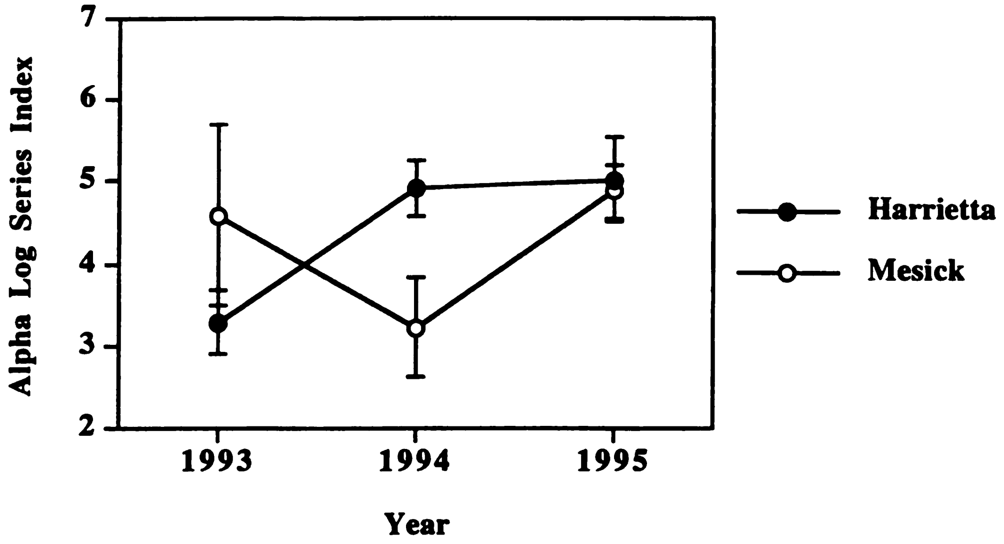


Figure 2.7. Means (±SE) of the alpha log series index from Harrietta and Mesick sites in the northern hardwood ecosystem. Means were calculated from n=2.

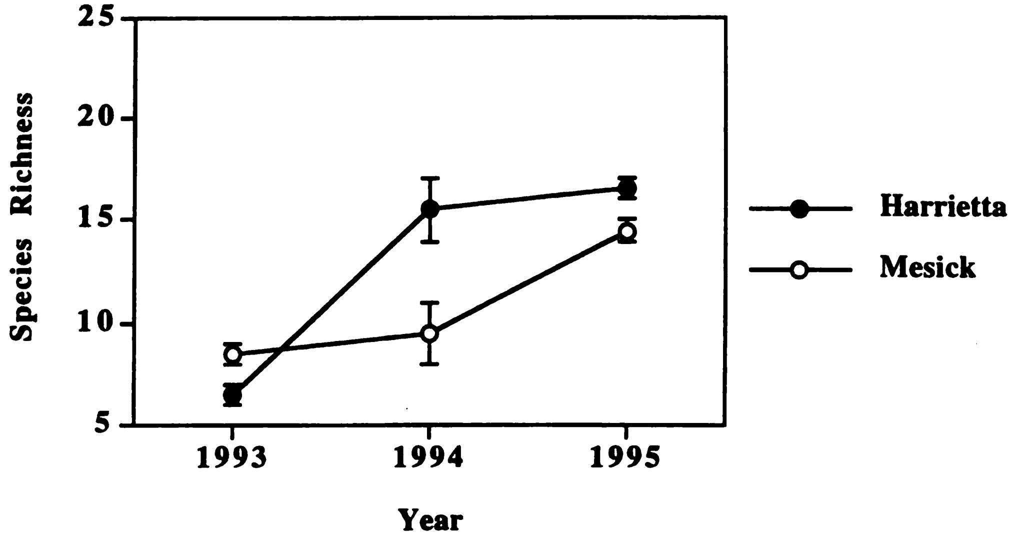


Figure 2.8. Means (±SE) of species richness from Harrietta and Mesick sites in the northern hardwood ecosystem. Means were calculated from n=2.

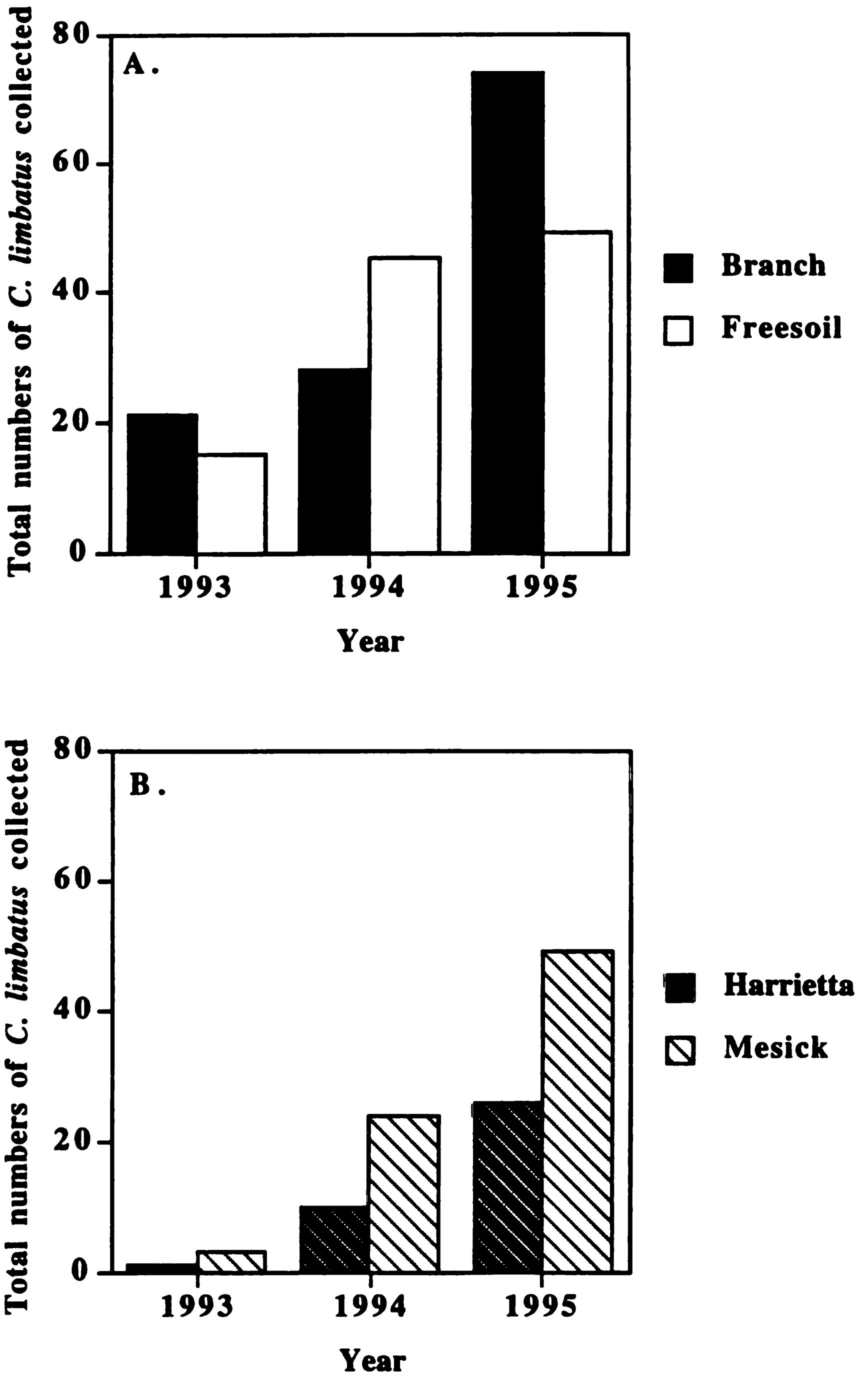


Figure 2.9. Total number of *C. limbatus* collected from A) Branch and Freesoil sites and B) Harrietta and Mesick sites.

Chapter 3

THE IMPACT OF GYPSY MOTH (LEPIDOPTERA: LYMANTRIIDAE) OUTBREAKS ON NATIVE LEPIDOPTERA IN TWO NORTHERN HARDWOOD ECOSYSTEMS IN NORTHERN LOWER MICHIGAN

Introduction

Herbivorous insects play an important role in forest ecosystems. During outbreaks, herbivores insects can remove up to 100% of available foliage causing reduced tree growth and tree mortalilty (Kulman 1971). Forest defoliators can alter plant community structure, nutrient cycling, and regulate primary productivity (Mattson and Addy 1975; Swank et al. 1981). Foliage allelochemicals can be affected by insect feeding, subsequently affecting other plant feeders (Schultz and Baldwin 1982).

In the northeastern United States, the gypsy moth, *Lymantria dispar* L., is a major forest insect that defoliated over 10 million ha of forest between 1985 and 1994 (Butalla 1996). This exotic pest feeds on over 400 North American woody plant species including economically valuable species such as *Quercus* and *Populus* spp. (Mauffette et al. 1983). Trees that have been stressed by defoliation can be killed by invasion of secondary mortality agents like two-lined chestnut borer (*Agrilus bilineatus* Weber) and fungal pathogens like *Armillaria* root diseases (Wargo 1977).

Gypsy moth can alter species composition of a stand by reducing the relative abundance of oaks or other preferred species. Repeated defoliation from 1911 to 1931 by gypsy moth not only increased the mortality rates of oaks five years following defoliation, but also decreased the relative proportion of oaks within defoliated stands in New England (Campbell and Sloan 1977). Likewise, relative proportion of oaks declined by 10% in forests defoliated by gypsy moth in Pennsylvania between 1971 and 1979 (Gansner et al. 1983).

In addition to altering the relative composition of forests, gypsy moth defoliation can change nutrient and hydrological patterns. While nitrogen accrued via deposition of gypsy moth frass is immobilized by soil microbes, insect bodies and leaf fragments may be a source of nitrogen loss (Lovett and Ruesink 1995). Defoliation can also reduce transpiration and increase soil moisture resulting in increased denitrification (Lovett and Ruesink 1995). Severe defoliation increased water yield and concentration of fecal coliform and streptococci occurred in watersheds in the northeastern United States (Corbett and Lynch 1987).

However, effects of gypsy moth on native forest insects are relatively unknown, especially in the north central region of the United States. One study in West Virginia showed low levels of defoliation decreased abundance of native lepidoptera species, but species-specific data was not reported and severe defoliation did not occur in the area of study (Sample et al. 1993). In another West Virginia study, gypsy moth defoliation was associated with reduced numbers of predatory insects, but few quantitative data were reported (Muzika 1994).

The first objective of this research was to obtain baseline information on the abundance, species richness, and diversity of the native lepidopteran fauna from two forest ecosystems that varied in productivity, tree species composition, and susceptibility to the gypsy moth. The second objective was to determine whether gypsy moth invasion affected native lepidopteran abundance, species richness and diversity within the susceptible forest ecosystem. We hypothesized that gypsy moth would reduce the abundance and diversity of native lepidoptera, particularly those that feed on oak.

Methods

Study Area

This research was conducted in eight sites in the Manistee National Forest in northern lower Michigan. Manistee National Forest has been described using an ecological classfication system (ECS) (Cleland et al. 1993). The ECS is a hierarchical classification that groups ecosystem components at spatial scales varying from the landscape to the stand level. Ecological landtype phases (ELTPs) are classified on the basis of soils, landscape position and natural vegetation. ELTPs are subsets of larger spatial scale units such as ecological landtypes (ELTs) and landtype associations (LTA). Because stands within the same ELTP have similar overstory and understory vegetation, soil hydrology, soil type, nitrogen cycling, productivity and geological history, use of the ECS allows ecosystems to be replicated in experimental designs with a high level of confidence that experimental plots are similar.

We randomly chose four sites classified as ELTP 20 and four sites classified as ELTP 45 from maps provided by the Manistee National Forest. All sites ranged from 12 to 16 ha in area. ELTP 20 was characterized by an overstory dominated by northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) and a non-diverse ground flora (Cleland et al. 1993). Soils on ELTP 20 were typically sandy, xeric soils with low productivity (Host et al. 1987; Host et al. 1988). ELTP 45 had an overstory dominated by northern hardwood species particularly sugar maple (*Acer saccharum* Marsh) and, to a lesser extent, other overstory species including American basswood (*Tilia americana* L.), white ash (*Fraxinus americana* L.), red maple (*Acer rubra* L.) and red oak (Cleland et al. 1993). This ELTP was notable for its rich herbaceous understory, well-drained mesic soils, and high productivity (Host et al. 1987; Host et al. 1988; Zak et al. 1989; Zak and Pregitzer 1990; Zak et al. 1986).

Dominant tree species within ELTP 20 and 45 also differed in susceptibility to gypsy moth defoliation. Oak species, which dominated ELTP 20, are highly preferred by gypsy moth and oak stands often experience severe defoliation during outbreaks (Mauffette et al. 1983; Twery 1990). Northern hardwood stands, such as ELTP 45, are less susceptible to gypsy moth defoliation because the dominant canopy species, sugar maple, is only moderately preferred by gypsy moth (Mauffette et al. 1983; Twery 1990).

In the red oak ecosystem (ELTP 20), two sites were located at 44° 00' N, 86° 00' W near the town of Branch and two sites were located at 44° 08' N, 86° 09' W near the village of Freesoil. In the northern hardwood ecosystem (ELTP 45), two sites were located at 44° 22' N, 86° 44' W near the town of Mesick and two sites were located at 44° 19' N, 86° 44' W near the village of Harrietta.

Gypsy moth were first discovered in the eastern central region of Michigan's lower peninsula in 1954, but defoliation due was not apparent until 1979 (Gage et al. 1990). Populations slowly radiated westward reaching central Michigan by 1977 (Dreistadt 1983); significant defoliation did not occur in this area until 1987 (Gage et al. 1990). Before 1993, none of our study sites had ever experienced any observable gypsy moth defoliation (F. Sapio, MI DNR, Forest Health Management, 1993 *pers comm.*, S. Katovich, USDA For. Serv. NA. S&PF, Forest Health Management, 1992, *pers comm.*). We surveyed these sites in 1992 and found no visible defoliation or evidence of previous infestation.

Number of gypsy moth egg masses/ha, visual estimates of defoliation, and leaf area index were measured in all stands as part of a related study (see chapter 1). Red oak sites experienced more defoliation (Table 3.1) and had higher gypsy moth egg mass densities (Figure 3.1) than the northern hardwood sites from 1993 to 1995. Red oak sites had lower leaf area index (LAI) than northern hardwood sites, and leaf area was significantly reduced by large gypsy moth populations in 1994 and 1995 (see chapter 1) (Table 3.1). Gypsy moth populations in red oak sites fluctuated annually. Outbreak populations at Branch sites in 1993 were followed by a population 'crash' due to NPV infection in 1994 (Table 3.1). Populations at Freesoil sites increased in 1994 and reached outbreak levels in 1995 (see chapter 1) (Figure 3.1).

Collection of Lepidoptera

Lepidoptera were collected during 1993, 1994 and 1995. Lepidoptera were collected four times a summer. Collection times roughly corresponded to significant points in gypsy moth management or biology. For example, typical application time of the microbial insecticide *Bacillus thuringensis* Berliner var. *kurstaki* for gypsy moth suppression in northern lower Michigan occur in mid-May, fourth instar gypsy moth in mid-June), peak defoliation in mid-July, and stand refoliation in mid-August. During 1993, lepidoptera were collected on 12-13 May, 15-17 June, 13-15 July, and 10-12 August from red oak sites and on 21-22 May, 22-23 June, 20-22 July, and 18-20 August from northern hardwood sites. In 1994, lepidoptera were collected on 10-12 May, 15-16 June, 11-13 July, and 9-10 August from red oak sites and on 18-20 May , 20-21 June, 19-20 July, 15-17 August from northern hardwood sites. In 1995, collection dates were 15-17 May, 12-14 June, 10-11 July, 15-16 August at red oak sites and 22-24 May, 19-20 June, 17-19 July, and 21-22 August at northern hardwood sites. Lepidoptera were collected from the canopy and shrub strata using a variety of sampling methods in an effort to adequately represent the total lepidopteran diversity within each site.

Canopy strata- In 1993, canopies were sampled using a pole pruner with a 9 m extendible handle, modified sweep nets with a 10 m extendible handle, and suspendable

UV traps. In 1994 and 1995, pole pruners and extended sweep nets were replaced with a suspendable thermal fogger to facilitate collection of diurnal canopy and immature lepidoptera.

Ultraviolet traps consisted of a 22 watt UV bulb connected to a photosensor and powered by a 6 volt motorcycle battery. UV traps were operated approximately 8 hours each sampling period. A collection funnel and bucket loaded with insecticidal pest strips (Vapona ^{TM}) were attached below the bulb. Use of a low wattage bulb and a rain cover over the bulb restricted potential long-distance attraction of nocturnal insects, presumably resulting in a localized sample reflecting endemic insect populations (Bowden 1982). The trap was raised into the canopy approximately 1 to 2 m above the lower edge of the canopy foliage in the center of each site.

Pole pruners were used to clip a 1 m length branch tip from the lower canopy six times along a random transect through each stand at 20 m intervals. Samples were collected from the lower canopy of the nearest tree to each 20 m interval. Samples were clipped over a large plastic tarp spread on the ground. Branch cuttings were collected off the tarp and quickly placed in plastic bags until they could be examined for lepidoptera. Extended sweep net samples were collected from lower canopy foliage six times along a random transect through each stand at 20 m intervals. Four sweeps with a 50 cm diameter net were made from lower canopy foliage at each interval.

A thermal fogger (Dyna-fog^{TM}) (Erwin 1983) modified with a radio-controlled switch was raised into the canopy five times along a randomly selected transect through the stand at 20 m intervals. The fogger was suspended by ropes and pulleys placed over large tree limbs with an arrow-line. A 25 m^2 diameter column of the canopy was then fogged with 1% pyrethroid (Pyrocide Fogging Concentrate 7338^{TM}, McLaughlin Gormley King Company) applied for 15 seconds at a rate of 0.377 L/minute. Pyrethroid was selected for its quick "knock-down ability" and minimal persistence. The fogged foliage was thoroughly shaken using additional suspended ropes. Insects were collected in 25 1 m^2

funnels arranged in a grid below the fogger. All fogging was done between 0400 and 0800 h when winds were calm.

Shrub strata- Lepidoptera were also collected using malaise traps and sweep nets. One malaise trap with an insecticidal pest strip was set up in the center of each stand. Malaise traps were left open for 24 hours. Sweep samples were collected using a 38 cm diameter net. Sixteen sweeps (4 at each cardinal direction) were made six times along a random transect through the stand at 20 m intervals.

We assumed that the location where insects were captured was typical of the location they occupy within the site. For example, lepidoptera collected from UV traps were considered overstory dwellers while lepidoptera collected in malaise traps were considered understory dwellers. All lepidoptera were placed into plastic containers lined with tissue paper to minimize damage of specimens between collection and identification. Voucher specimens were prepared from each site and sample period. Lepidoptera were identified to species or morpho-species by J. Wilterding, R. Kriegel, and M. Neilson at the Center for Insect Diversity at Michigan State University.

Statistical Analysis

Number of insects, number of species, and Brilloun and Simpson's indices of diversity were determined for each site (Magurran 1988). Brilloun's diversity index was selected for use because the majority of insects were collected with UV traps, a non-random sampling technique (Magurran 1988). Furthermore, Brilloun's index provided an estimate of diversity based on species richness (Magurran 1988). Simpson's index was chosen because it provided an estimate of diversity based on species dominance (Magurran 1988). The combination of diversity indices, species richness and abundance was used to evaluate differences among sites because each particular measure was subject to biases related to sample size and distribution of insects (Magurran 1988). We believe that a consistent pattern of diversity that is reflected by multiple indices is a more reliable indicator than any single index (Magurran 1988).

Diversity indices, species richness and insect abundance were calculated from yearly totals of all lepidoptera collected. Within each ecosystem, all measurements were evaluated for normality and homoscedascity. Site differences in variables that approached normailty were analyzed using a one-way ANOVA with repeated measures (also known as a split -plot ANOVA) (Sokal and Rohlf 1995). Site differences in variables with non-normal distributions were analyzed using the nonparametric Kruskal-Wallis test (Conover 1971). An alpha value of 0.05 was used for both parametric and nonparametric tests.

Similarity of lepidoptera fauna among all sites was examined using cluster analysis of the Sorenson's quantitative index of similarity (also known as the Bray-Curtis index) (Ludwig and Reynolds 1988; Magurran 1988). Dendograms were generated using the Bray-Curtis distance measures and four different linkage methods: the beta-flexible method with β= -0.25 and -0.5 (Milligan 1989); the average linkage grouping method; and centroid linkage method (Ludwig and Reynolds 1988).

While species and morpho-species identifications were available for all lepidoptera, life history data, including host plant preference and patterns of voltinism, were most available for lepidoptera in the family Noctuidae. For this reason, additional analysis of the noctuids was conducted by examining the early (May and June) and late season (July and August) catches. Extensive sampling of Noctuidae was prohibited by limited resources, and thus many species were represented by small numbers of insects. Because of this relative paucity of insects, diversity indices and formal inferential statistical analysis were inappropriate. We have presented our data as totals numbers of insects collected, with the caveat that while differences may illustrate effects of gypsy moth, conclusions should be interpreted cautiously.

Results

Over the course of this study 12,116 lepidoptera were collected from 38 families. A total of 35 families were collected from the red oak sites and 30 families were collected from the northern hardwood sites. While three trapping methods were used, over 90% of lepidoptera collected each year were collected in the UV traps. Of the families collected, 21 families accounted for 99% of the total lepidoptera collected within each year. Abundance of tortricids, noctuids, gelechiids, geometrids, and pyralids was consistently high in both ecosystems over all three years (Table 3.2 and 3.3). Of the 38 families collected, 17 rarely caught families accounted for less than 1% of the total lepidoptera collected within each year (Table 3.4 and 3.5). Species richness in both ecosystems was dominated by four families; the Noctuidae, Torticidae, Geometridae, and Pyralidae (Table 3.6 and 3.7). Species caught within these families and their total abundance within each ecosystem are listed as Appendix A through Appendix D. Species collected from families other than Noctuidae, Tortricidae, Geometridae, or Pyralidae are listed in Appendix E. Abundance of individual species was not great enough to determine whether gypsy moth directly affected particular species.

Within the red oak ecosystem, defoliation by month interactions significantly affected total abundance and total species richness in 1993 (Table 3.8 and 3.9) and total species richness again in 1994 (Table 3.8 and 3.10 and Figure 3.2). Marginally significant defoliation by month interactions were observed in Brilloun's index in 1993 (Table 3.8 and 3.9) and in total species richness in 1995 (Table 3.8 and Table 3.11).

Within the northern hardwood ecosystem, total abundance, species richness and Simpson's index in 1993 significantly differed among months (Table 3.12). Marginally significant monthly differences were apparent in total species richness in 1994 (Table 3.13). Differences in species richness between Mesick and Harrietta were not significant in any year (Table 3.8 and 3.12-3.14 and Figure 3.3). During 1993, total species richness increased throughout the summer (Figure 3.3). In 1994 and 1995, species richness was generally greatest in the months of June and July (Figure 3.3).

Hierarchical cluster analysis was used to compare species composition of the two ecosystems. Dendograms created using the beta flexible method with β= -0.25, revealed two distinct clusters, one containing all the red oak sites, and the other containing all the northern hardwood sites in 1993 and 1995 (Figure 3.4). In 1994, both Branch sites formed a single cluster while Freesoil sites and the northern hardwood sites comprised the remaining cluster (Figure 3.4).

Dendograms created using the beta flexible method with β= -0.5 (Figure 3.5), gave similar results to the clustering using β= -0.25. However, the dendogram created for 1994 data using β= -0.5 could have been interpreted as two clusters or three clusters with equal confidence. Northern hardwood sites formed one cluster, while Branch sites and Freesoil sites could have been interpreted as one or two clusters.

When the group average/unweighted pair-grouping method was used, Branch sites consistently clustered separately from Freesoil sites and the northern hardwood sites in 1993 and 1994 (Figure 3.6). In 1995, red oak sites clustered separately from northern hardwood sites (Figure 3.6). The centroid/median method produced dendograms that were fraught with reversals and had little biological meaning; these were not considered further.

Effects of Gypsy Moth on Lepidoptera Collected During the Early Season

Adult lepidoptera collected in the early season months of May and June were presumably larvae the previous year. Consistent patterns of decreased species richness and abundance in early season adult lepidoptera were observed in red oak sites one year following severe defoliation. In the red oak ecosystem, species richness of all adult lepidoptera was marginally lower in June 1994 at sites that experienced almost 100% defoliation the previous year (Branch) (Figure 3.2). Likewise, in 1995, total species richness was lower in the early season months of May and June in Freesoil sites that experienced 40-60% defoliation the previous year (Figure 3.2).

Total species richness of early season Noctuidae was lower in Branch sites than in Freesoil sites one year following heavy defoliation at Branch in 1993. Similarly, the year after heavy defoliation at Freesoil sites in 1994, species richness of early season noctuids was lower in Freesoil sites than in Branch sites (Figure 3.7). Total abundance of noctuids during May and June was lower at Branch sites than at Freesoil sites during 1994 (Figure 3.8). Likewise, abundance of noctuids collected during May and June was lower at Freesoil sites than at Branch sites during 1995 (Figure 3.8). Abundance of overstory (Figure 3.9) and understory noctuids (Figure 3.10) showed similar patterns to total abundance of noctuids. Abundance of oak-feeding noctuids collected in the early season months of May and June (Figure 3.11) also suggested negative interactions with gypsy moth one year after severe defoliation in 1993.

However, the difference in abundance of oak-feeding noctuids between Branch and Freesoil sites is small in 1995, one year following severe defoliation at Freesoil. Few oak-feeding noctuids were collected in 1995 relative to the numbers collected in 1993 and 1994. This may indicate that if early season oak feeders in Branch sites were affected in 1993, they did not recover to pre-defoliation levels even two years after a defoliation event.

Within the northern hardwood ecosystem, the magnitude of differences between sites in species richness, total noctuid abundance, and over and understory abundance were generally smaller than differences among red oak sites and were not related to gypsy moth defoliation (Figure 3.7-3.10). However species richness was significantly greater in Harrietta than in Mesick sites in 1995 (Figure 3.8).

Effects of Gypsy Moth on Lepidoptera Collected from the Late Season

Most adult lepidoptera collected from late season months of July and August were presumably larvae earlier during the same year. Species richness and abundance of adult lepidoptera collected from the late season months of July and August declined in oak-dominated sites that experienced gypsy moth defoliation in 1993 and 1994 during the same year as the defoliation occurred. In the red oak ecosystem, species richness of all lepidoptera was lower in defoliated sites (Branch) during the late season months of July and August of 1993 than in non-defoliated (Freesoil) sites (Figure 3.2). Similarly, in 1994, defoliated sites (Freesoil) had lower species richness during July than did non-defoliated sites (Branch) (Figure 3.2). Species richness of late season noctuids was lower in Branch than in Freesoil in 1993 (Figure 3.7). In 1994, total species richness of noctuids was lower in Freesoil than in Branch (Figure 3.7). Similar patterns were observed for the total abundance of noctuids (Figure 3.8).

In 1995, however, species richness, abundance of total lepidoptera and total Noctuidae collected from late season months was greater at Freesoil than at Branch, even though Freesoil experienced nearly 100% defoliation (Figure 3.2, 3.7 and 3.8). Understory Noctuidae were also more abundant in Freesoil than in Branch in 1995 (Figure 3.10).

Overstory and oak-feeding Noctuidae also appeared to be more abundant in Freesoil than in Branch during July and August in 1995. However, one species, *Hyperstrotia pervetrens*, comprised 23% (35 individuals) of the total noctuid catch. This species had not been caught during our study in any site previous to July and August 1995, and is at the northwestern edge of its distribution in Michigan (J. Wilterding, MSU, *pers comm.*). If *H. pervetrens* is excluded from the analysis, the difference in overstory noctuids between Branch and Freesoil becomes much smaller. Likewise, when *H. pervetrens* was excluded from analysis, Branch and Freesoil had the same amount of oak-feeding lepidoptera in the months of July and August in 1995 (Figure 3.12). The decline in Noctuidae in Freesoil in 1995 suggests oak-feeding Noctuidae may be negatively affected during the same year as a defoliation event.

In the northern hardwood ecosystem, differences in species richness, total noctuid abundance, and over and understory abundance between sites were again smaller than differences in the red oak ecosystem (Figure 3.7-3.10). However, Mesick did have greater numbers of overstory noctuids in 1993 than did Harrietta (Figure 3.9).

Discussion

Differences in Lepidopteran Fauna Between Ecosystems

It was surprising that red oak sites had more species diversity and generally greater abundance of lepidoptera than did northern hardwood sites. The high productivity typical of northern hardwood sites (Zak et al. 1989) suggests that insects would not be as nutritionally limited as insects within the less productive red oak sites (Mattson 1980; Mattson and Scriber 1987; Scriber and Slansky 1981). Likewise, greater diversity of overstory and understory flora within the northern hardwood sites also suggests greater diversity of herbivores than would be expected in the non-diverse flora of the red oak sites.

One explanation for the higher species richness in red oak sites may be related to the differences in light penetration and microclimate between each ecosystem. Red oak sites typically had more light reaching the forest floor and were presumably warmer than northern hardwood sites. This warmer microclimate may have promoted insect development and activity and may account for the greater diversity and abundance collected from red oak sites.

Another potential explanation for the greater diversity and abundance at red oak sites may be related to the current successional stage of each ecosystem. In plant communities, species richness rapidly increases in early successional stages through immigration and colonization (Huston 1994). As succession continues, species richness begins to decrease due to competition for resources (Huston 1994). In late successional types, diversity is relatively low and the community is dominated by fewer species than in intermediate successional stages (Huston 1994).

Likewise, species richness and diversity of insects also increase during early stages of succession because of the increased spatial heterogeneity and architectural diversity of the plant community (Brown 1984). Later in succession when plant diversity decreases, insect communities no longer increase in diversity although species turnover does still occur (Brown 1984).

The highly productive northern hardwood sites represent late successional seres. Predicted compositional changes for the northern hardwood sites included replacement of the already minor component of basswood by more sugar maple or beech (Host et al. 1987). This decrease in plant species diversity may help explain the relatively low species richness of lepidoptera we observed. The insect community, like the plant community may have been reflecting competitive exclusion typical of late stage succession as decreased species richness and diversity.

Red oak sites may be representative of a more intermediate successional sere than northern hardwood sites. Future compositional changes to red maple or northern hardwood species are predicted for red oak sites (Host et al. 1987). The relatively greater species richness of insects we observed in red oak sites may have been related to this earlier successional stage of the plant community.

Our findings have interesting implications for ecosystem management and forest health. Information about diversity at regional scales is needed before political, economic, and biological concerns can be integrated into effective guidelines and policy for management of public forests (Probst and Crow 1991; Wilcove 1989). It should also be realized that diversity within an ecosystem is likely to change over time through succession. The northern hardwood sites we studied are under consideration for designation as sites to be set aside to become old-growth forest (R. Ingram, Huron-Manistee National Forest Silviculturalist, pers. comm.). While these sites represent a unique habitat type in terms of plant diversity and productivity, they had lower lepidopteran diversity than less productive red oak sites. This illustrates that ecosystems that are initially managed to promote diversity may eventually become less diverse over time.

Effects of Gypsy Moth on Native Lepidoptera Diversity

The lepidopteran fauna collected from red oak sites was different than the fauna collected at northern hardwood sites. This baseline information has implications for the pool of species potentially affected by gypsy moth. Species common to the northern hardwood ecosystem are less likely to interact with gypsy moth because sugar maple, the dominant species, is not a preferred host of gypsy moth. Lepidopteran species common in the red oak ecosystem were more likely to interact with gypsy moth because the dominant species, red oak, is a preferred host of gypsy moth.

Because all red oak sites experienced severe defoliation by gypsy moth over the three years in which this experiment was conducted, comparisons of undisturbed red oak and undisturbed northern hardwood sites cannot be made, nor does an optimal control treatment exist for the effects of defoliation in the red oak sites. However, the lack of differences between Mesick and Harrietta in species richness of all lepidoptera, Noctuid abundance, and the overall similarity of lepidopteran fauna provide an estimate of the amount of natural variation in abundance and diversity of lepidoptera over time. When red oak and northern hardwood sites were compared in terms of total species richness, red oak sites had significantly more variation between sites than did northern hardwood sites.

When the abundance of noctuids was compared, red oak sites varied more than did northern hardwood sites. While not optimal, we believe that the consistent patterns within the northern hardwood sites provided a realistic and adequate control treatment to assess whether defoliation affected lepidoptera richness and abundance.

While specific mechanisms responsible for the patterns in species richness and abundance we observed were not directly tested in our experiment, we have posed potential explanations for the negative effects of gypsy moth on native lepidoptera, particularly the Noctuidae. Consistent patterns of decreased species richness and abundance in early season lepidoptera one year following a defoliation event may be attributed to a lag effect apparent in univoltine and second generation multivoltine lepidoptera. This suggests that univoltine and second generation multivoltine lepidoptera were negatively affected by gypsy moth in immature lifestages and consequently reflected this interaction as decreased numbers of adult insects the following year. It is possible that other non-noctuid lepidoptera that consume oak foliage, such as tortricid leafrollers, could also face resource depletion during a defoliation event. However, without specific life history data on each species collected and without greater sample size of each species, interpretation of species compositional changes are difficult.

Species richness and abundance of lepidoptera collected from the late season months of July and August, during peak gypsy moth defoliation, declined in sites that experienced gypsy moth defoliation in 1993 and 1994. This decline occurred during the same year as the defoliation. This decline was also reflected in the abundance of noctuids. The decrease in adult lepidoptera during these periods of intense defoliation may reflect unsuitable microhabitat conditions created by gypsy moth. Microclimatic factors and structural features of the site are potentially more important than food resources to adult lepidoptera collected during the late season. During a defoliation event, an open canopy increases temperature and decreases the relative humidity within the site (Klein and Perkins 1988; Perkins et al. 1987; Spurr and Barnes 1980). Furthermore, defoliation depletes potential ovipositional sites and can result in egg or larval mortality caused by poor oviposition site selection (Dethier 1959).

However, the species richness and abundance of lepidoptera and Noctuidae was higher in the severely defoliated Freesoil sites than in undefoliated Branch sites in 1995 during July and August. This increase in diversity is not easily explained. Our method of trapping could be biased during a defoliation event. The UV trap would be more visible when foliage was removed than in undefoliated sites. This seems an unlikely explanation, however, because similar conditions existed in Branch in 1993 and Freesoil in 1994 and there was a consistent decrease in abundance and richness in these defoliated sites.

Another explanation may be found upon further examination of the understory noctuids. By defoliating overstory trees, herbivorous insects can increase the growth of understory flora through increased light penetration and/or increased nitrogen, phosphorus, and potassium availability in the form of insect frass, corpses, and unused food (Mattson and Addy 1975). Freesoil experienced heavy defoliation and an opened canopy two consecutive years, while Branch only experienced one year of open canopy. The two years of open canopy at Freesoil could have promoted availability and/or quality of understory herbaceous plants and increased the abundance and diversity of understory feeders. More understory noctuids were collected from Freesoil sites than Branch sites. The relative difference of understory noctuids between Branch and Freesoil in 1995 is greater than the difference between the abundance of overstory feeders in these same sites, particularly after *H. pervetrens* is excluded from analysis. The increase in understory noctuids may be a response to increased understory plant resource availability or quality and may explain the increase in noctuid abundance in Freesoil during late season 1995.

Effects of Gypsy Moth on Oak-Feeders

Decreased abundance of oak-feeding noctuids collected from the early season months of May and June may be evidence of negative interactions with gypsy moth one year after severe defoliation in 1993. However, the difference between Branch and Freesoil sites was small in 1995, one year following defoliation at Freesoil. Abundance of oak-feeding noctuids collected during early season months at Branch increased from 1994 to 1995. This may be evidence of a gradual recovery of the oak-feeders. This conclusion should be interpreted cautiously because any lag effect present at Freesoil during 1995 will be confounded with the defoliation that also occurred during that same year. The potential effect of gypsy moth on oak-feeding noctuids present during early season months warrants further study to determine the rate of recovery of native noctuid populations.

Late season oak-feeders may have been negatively affected by gypsy moth during the same year as a defoliation event, but again this conclusion should be interpreted cautiously. Abundance of oak-feeders was lower in sites that experienced defoliation in 1993 and 1994, but no effects of gypsy moth were apparent in Freesoil sites during 1995, even after the removal of *H. pervetrens* from the analysis.

Interspecific competition for oak foliage with gypsy moth may have been responsible for the observed decline in adult oak-feeding Noctuidae during May and June at Branch in 1994 and Freesoil in 1995. Defoliation removed between 40 and 100% of foliage otherwise available to oak-feeding noctuids. Any immature oak-feeder that was present between the end of June and July was presumably in direct competition with gypsy moth for oak foliage. Gypsy moth has been shown to negatively impact native lepidoptera even when defoliation was light (Sample et al. 1993).

While competition is disfavored by some investigators as the ecological principle governing community organization of herbivorous insects (Lawton and Strong 1981), insect outbreaks may be an exception to this viewpoint (Denno et al. 1995). Leafhoppers were occasionally out-competed for sycamore foliage by lacebugs and other leafhopper species when large competitor populations exhausted food reserves of leafhoppers (McClure 1974; Ross 1957). In rangeland ecosystems where grasshoppers can consume large proportions of available plant resources, eight species overlapped significantly in food items consumed (Hansen and Ueckert 1970). In forested ecosystems, pine needle scale (*Chionaspis pinifoliae* (Fitch)) outcompeted black pineleaf scale (*Nuculaspis californica* (Coleman)) on ponderosa pine growing along roadways when parasites were eliminated by increased dust concentrations (Edmunds 1973). Likewise, four species of pine-defoliating moths experienced interspecific competition for food during outbreaks on rare occasions (Varley 1949). Monarch butterflies (*Danaus plexippus* (L.)) eliminated the milkweed bug (*Oncopeltus* spp.) from the island of Barbados by depleting the shared food plant *Asclepias curassavica*. (Blakley and Dingle 1978).

The apparently minor and short-term effects of gypsy moth on native lepidopteran abundance and diversity may be related to the spatial scale of gypsy moth outbreaks. Spatial scale can affect the recolonization of a disturbed area (Huston 1994). Aerial surveys in northwestern lower Michigan by the Michigan DNR indicated that between 1993 to 1995, severe defoliation occurred in areas less than 115 contiguous ha in size. Approximately 80% of the severe gypsy moth defoliation that occurred during this period was concentrated in areas of no larger than 120 ha (Sapio 1996). Similarly, approximately 80% of moderate defoliation was concentrated in areas no larger than 130 ha (Sapio 1996). Larger outbreaks that exceeded 480 contiguous ha accounted for only 4% of heavy defoliation and 3% of moderate defoliation (Sapio 1996). In our study sites, severe defoliation did not exceed 65 ha and lasted no more than 2 years before populations collapsed due to NPV infection. Lepidoptera may have been temporarily displaced to surrounding unaffected forest, but were presumably able to recolonize disturbed areas because of the relatively small area and short duration of severe defoliation.

Management Implications

Our conclusions have implications for forest pest management, including the use of the microbial insecticide *Bacillus thuringiensis kurstaki.* (Btk). While the oak-feeding guild may be negatively impacted by gypsy moth, other lepidoptera collected from the early season appeared to recover within two years after a defoliation event. Similarly, non-oak feeders such as understory Noctuidae may even be positively affected by gypsy moth. In contrast, field studies indicated Btk persisted for up to 30 d following application and negatively affected survival of two *Papilio* spp. and *Callosamia promethea* (Drury) (Johnson et al. 1995). Application of Btk to control gypsy moth populations reduced native lepidoptera species richness and abundance for up to two years after application (Miller 1990; Sample et al. 1993). While one feeding guild in particular (the oak-feeders) was negatively affected by gypsy moth, comparatively more species may be at risk from application of Btk than are likely to be at risk from gypsy moth.

Table 3.1. Visual estimation of peak defoliation and estimation of mean LAI (±SE) using photosynthetically active radiation transmittance of sites in red oak and northern hardwood ecosystems.

Peak Visual Estimation of Defoliation

	1993	1994	1995
Red Oak			
Branch	80-100%	< 20%	< 20%
Freesoil	< 20%	40-60%	80-100%
Northern Hardwood			
Harrietta	< 20%	< 20%	< 20%
Mesick	20-40%	< 20%	< 20%

Estimated Leaf Area Index[1]

	1994	1995
Red Oak		
Branch	4.48 ± 0.221	4.71 ± 0.115
Freesoil	2.73 ± 0.076	2.72 ± 0.151
Northern Hardwood		
Harrietta	10.9 ± 0.226	8.61 ± 0.229
Mesick	11.9 ± 0.189	8.14 ± 0.222

[1] Means and standard errors were calculated from two sites (n=2)

Table 3.2. Total number of insects/family that comprised greater than 1% of the total number of lepidoptera collected from two sites near Branch and two sites near Freesoil within red oak ecosystems.

	1993		1994		1995	
Family	**Branch**	**Freesoil**	**Branch**	**Freesoil**	**Branch**	**Freesoil**
Tortricidae	104	419	328	224	487	599
Noctuidae	133	379	127	273	176	204
Lyonetiidae	1	-	2	-	56	33
Gelechiidae	29	52	171	67	127	116
Geometridae	145	76	40	48	24	46
Pyralidae	8	56	55	55	24	83
Blastobasidae	13	11	47	18	34	28
Oecophoridae	4	5	2	83	3	14
Arctiidae	-	19	9	-	23	24
Lasiocampidae	5	4	4	-	1	9
Lymantriidae	46	17	-	-	1	-
Argyresthiidae	-	1	1	-	1	14
Notodontidae	6	10	12	15	1	-
Nepticulidae	-	-	-	2	24	44
Tineidae	12	24	1	3	-	5
Coleophoridae	-	-	3	-	7	21
Gracillariidae	-	7	12	1	7	4
Hydroptilidae	-	-	33	3	-	-
Limacodidae	-	1	1	1	2	1
Eriocraniidae	1	-	16	7	1	-
Cochylidae	1	-	-	-	-	-

Table 3.3. Total number of insects/family that comprised greater than 1% of the total number of lepidoptera collected from two sites near Harrietta and two sites near Mesick within northern hardwood ecosystems.

	1993		1994		1995	
Family	**Harrietta**	**Mesick**	**Harrietta**	**Mesick**	**Harrietta**	**Mesick**
Tortricidae	451	996	305	260	960	725
Noctuidae	59	92	78	76	137	143
Lyonetiidae	-	1	-	-	584	226
Gelechiidae	20	47	35	59	49	44
Geometridae	41	31	50	71	51	83
Pyralidae	25	41	43	30	27	60
Blastobasidae	5	11	12	2	77	80
Oecophoridae	-	3	2	12	10	6
Arctiidae	13	14	6	3	5	11
Lasiocampidae	7	2	14	19	26	17
Lymantriidae	18	11	-	-	-	-
Argyresthiidae	2	3	20	6	22	21
Notodontidae	28	8	5	5	-	-
Nepticulidae	-	2	1	-	4	4
Tineidae	3	2	2	14	2	-
Coleophoridae	-	1	1	-	14	11
Gracillariidae	-	4	1	1	9	10
Hydroptilidae	-	-	-	-	-	-
Limacodidae	2	1	8	2	2	10
Eriocraniidae	-	-	4	1	-	-
Cochylidae	2	6	12	2	-	-

Table 3.4. Total number of insects/family that comprised less than 1% of the total number of lepidoptera collected each year from two sites near Branch and two sites near Freesoil within red oak ecosystems.

	1993		1994		1995	
Family	**Branch**	**Freesoil**	**Branch**	**Freesoil**	**Branch**	**Freesoil**
Sphingidae	1	-	-	6	1	-
Cosmopterigidae	-	3	-	-	-	8
Satyridae	-	-	4	2	1	2
Hesperiidae	-	-	-	-	2	3
Olenthreutinae	-	-	-	1	-	-
Plutellidae	-	-	-	-	2	1
Yponomeutidae	-	-	-	-	-	1
Glyphipterigidae	-	-	-	-	1	1
Pieridae	-	1	-	-	-	-
Psychidae	3	-	-	-	-	-
Sesiidae	-	-	-	3	-	-
Agonexenidae	-	-	-	-	-	1
Cossidae	1	-	-	-	-	-
Thyatiridae	1	-	-	-	-	-
Zygaenidae	-	1	-	-	-	-

Table 3.5. Total number of insects/family that comprised less than 1% of the total number of lepidoptera collected each year from two sites near Harrietta and two sites near Mesick within northern hardwood ecosystem.

	1993		1994		1995	
	Harrietta	Mesick	Harrietta	Mesick	Harrietta	Mesick
Sphingidae	2	1	1	-	1	3
Cosmopterigidae	-	-	-	-	-	1
Satyridae	1	-	-	-	-	1
Olenthreutinae	-	-	1	3	-	-
Plutellidae	-	-	-	-	2	-
Yponomeutidae	-	-	2	-	1	-
Glyphipterigidae	-	-	-	-	-	1
Pieridae	2	-	-	-	-	-
Agonoxenidae	-	1	-	-	-	-
Decophoridae	-	-	-	-	-	1
Drepanidae	-	-	-	-	1	-

Table 3.6. Total number of species within each lepidopteran family collected over three years from two sites near Branch and two sites near Freesoil within a red oak ecosystem.

	1993		1994		1995	
Family	**Branch**	**Freesoil**	**Branch**	**Freesoil**	**Branch**	**Freesoil**
Noctuidae	40	62	55	49	37	68
Tortricidae	15	44	39	17	57	61
Geometridae	12	23	18	23	15	22
Pyralidae	6	25	21	10	17	29
Gelechiidae	8	8	8	9	22	19
Blastobasidae	5	4	5	3	12	12
Lyonetiidae	1	-	1	-	21	16
Arctiidae	-	6	5	-	7	11
Notodontidae	5	3	6	7	2	-
Oecophoridae	1	6	2	2	3	6
Coleophoridae	-	-	2	-	6	5
Gracillariidae	-	3	1	1	4	4
Tineidae	2	6	1	2	-	3
Nepticulidae	-	-	-	2	4	6
Argyresthiidae	-	1	1	-	1	3
Lasiocampidae	2	1	2	-	1	2
Limacodidae	-	1	1	1	2	1
Lymantriidae	5	6	-	-	1	-
Sphingidae	1	-	-	3	1	-
Eriocraniidae	1	-	3	3	1	-
Cochylidae	1	-	-	-	-	-
Satyridae	-	-	2	2	1	1
Cosmopterigidae	-	-	-	-	-	5
Hesperiidae	-	-	-	-	2	3
Pieridae	-	1	-	-	1	1
Olenthreutinae	-	-	-	1	-	-
Hydroptilidae	-	-	2	1	-	-
Yponomeutidae	-	-	-	-	-	1

Table 3.6 (cont'd.)

Psychidae	2	-	-	-	-	-
Agonexenidae	-	-	-	-	-	1
Cossidae	1	-	-	-	-	-
Glyphipterigidae	-	-	-	-	1	-
Sesiidae	-	-	-	1	-	-
Thyatiridae	1	-	-	-	-	-
Zygaenidae	-	1	-	-	-	-

Table 3.7. Total number of species within each lepidopteran family collected over three years from two site near Harrietta and two sites near Mesick within northern hardwood ecosystems.

	1993		1994		1995	
Family	**Harrietta**	**Mesick**	**Harrietta**	**Mesick**	**Harrietta**	**Mesick**
Noctuidae	32	46	42	33	68	83
Tortricidae	30	43	29	31	57	82
Geometridae	15	18	20	15	25	31
Pyralidae	12	15	16	18	16	18
Gelechiidae	5	7	6	7	11	17
Blastobasidae	3	4	5	2	19	22
Lyonetiidae	-	1	-	-	18	20
Arctiidae	3	7	3	2	5	5
Notodontidae	5	5	3	4	-	2
Oecophoridae	-	3	2	1	6	3
Coleophoridae	-	1	1	-	5	9
Gracillariidae	-	2	1	1	4	5
Tineidae	2	1	2	3	2	-
Nepticulidae	-	2	1	-	4	4
Argyresthiidae	1	1	3	1	4	5
Lasiocampidae	2	1	2	2	2	2
Limacodidae	2	1	4	2	2	2
Lymantriidae	2	3	-	-	-	-
Sphingidae	2	1	1	-	1	3
Eriocraniidae	-	-	3	1	-	-
Cochylidae	2	2	2	1	-	-
Satyridae	1	-	-	-	-	1
Cosmopterigidae	-	-	-	-	-	1
Pieridae	1	-	-	-	1	-
Olenthreutinae	-	-	1	2	-	-
Glyphipterigidae	-	-	-	-	-	1
Yponomeutidae	-	-	1	-	1	-
Agonoxenidae	-	1	-	-	-	-
Decophoridae	-	-	-	-	-	1

Table 3.7 (cont'd.)

Drepanidae	-	-	-	-	1	-

Table 3.8 Means (±SE) of total abundance, species richness, Brilloun's index, and Simpson's index for Lepidoptera collected from red oak and northern hardwood ecosystems over three years (means calculated from data pooled over four months).

	Branch	Freesoil	Harrietta	Mesick
	Mean (±SE)	Mean (±SE)	Mean (±SE)	Mean (±SE)
Abundance				
1993	64.25 (25.181)	137.00 (34.927)	85.25 (29.364)	161.50 (55.885)
1994	108.50 (50.188)	101.50 (45.797)	74.25 (22.162)	69.25 (21.641)
1995	321.38 (113.304)	206.38 (50.314)	206.88 (55.170)	129.88 (44.372)
Species Richness				
1993	13.63 (2.235)	25.25 (5.793)	15.13 (4.514)	20.88 (5.709)
1994	21.88 (4.980)	17.13 (5.386)	18.50 (2.860)	15.75 (3.447)
1995	46.88 (4.845)	40.38 (6.533)	35.75 (7.158)	31.13 (3.925)
Brilloun's Index				
1993	0.70 (0.067)	0.87 (0.125)	0.58 (0.147)	0.61 (0.138)
1994	0.86 (0.111)	11.31 (7.214)	0.84 (0.061)	0.74 (0.087)
1995	1.03 (0.052)	1.02 (0.062)	0.95 (0.068)	1.02 (0.026)
Simpson's Index				
1993	5.93 (1.369)	9.35 (2.578)	5.60 (2.537)	3.77 (1.120)
1994	12.33 (3.413)	10.08 (1.926)	9.47 (1.979)	8.04 (2.378)
1995	8.21 (1.687)	8.85 (1.254)	7.23 (1.236)	13.69 (2.654)

Table 3.9. Statistical significance of treatment effects from split-plot ANOVA of five measures of Lepidoptera diversity in four red oak sites in 1993.

Source of Variation	df	Species Richness[1]	Abundance[1]	Brilloun's Index	Simpson's Index
		F value of significant treatment effects			
Gypsy Moth	1	42.596	11.090	5.080	6.606
Month	3	1.790	3.225	1.214	0.873
Gypsy Moth x Month	3	8.862	6.823	4.512	0.288
		Probability of significant treatment effects			
Gypsy Moth	1	0.0227	0.0796	0.1529	0.1239
Month	3	0.2491	0.1035	0.3827	0.5054
Gypsy Moth x Month	3	0.0127	0.0232	0.0555	0.8326
		Mean square			
Error a	2	0.122	4.514	0.025	7.080
Error b	6	0.778	7.581	0.047	48.822

[1] Values transformed using the Box-Cox transformation

Table 3.10. Statistical significance of treatment effects from split-plot ANOVA of five measures of Lepidoptera diversity in four red oak sites in 1994.

Source of Variation	df	Species Richness[1]	Abundance[1]	Brilloun's Index[2]	Simpson's Index[1]
		F value of significant treatment effects			
Gypsy Moth	1	8.721	3.106	χ^2=0.71	0.637
Month	3	16.926	7.979	χ^2=9.26	5.635
Gypsy Moth x Month	3	5.209	3.020	-	1.910
		Probability of significant treatment effects			
Gypsy Moth	1	0.0981	0.2201	0.4008	0.5085
Month	3	0.0025	0.0162	0.0260	0.0352
Gypsy Moth x Month	3	0.0415	0.1157	-	0.2291
		Mean square			
Error a	2	0.015	0.012	-	0.015
Error b	6	0.020	0.128	-	0.033

[1] Values transformed using the Box-Cox transformation
[2] Values tested using the Kruskal-Wallis test

Table 3.11. Statistical significance of treatment effects from split-plot ANOVA of five measures of Lepidoptera diversity in four red oak sites in 1995.

Source of Variation	df	Species Richness	Abundance[1]	Brilloun's Index[2]	Simpson's Index[1]
		F value of significant treatment effects			
Gypsy Moth	1	11.965	4.460	χ^2=0.01	0.216
Month	3	1.486	0.523	χ^2=4.37	0.876
Gypsy Moth x Month	3	4.184	1.503	-	0.460
		Probability of significant treatment effects			
Gypsy Moth	1	0.0744	0.1691	0.9162	0.6880
Month	3	0.3105	0.6820	0.2242	0.5042
Gypsy Moth x Month	3	0.0644	0.3064	-	0.7206
		Mean square			
Error a	2	14.125	0.027	-	7.683
Error b	6	159.792	0.146	-	23.189

[1] Values transformed using the Box-Cox transformation

[2] Values tested using the Kruskal-Wallis test

Table 3.12. Statistical significance of treatment effects from split-plot ANOVA of five measures of Lepidoptera diversity in four northern hardwood sites in 1993.

Source of Variation	df	Species Richness	Abundance[1]	Brilloun's Index[2]	Simpson's Index
		F value of significant treatment effects			
Site	1	1.164	1.675	χ^2=0.04	0.650
Month	3	9.969	6.650	χ^2=14.20	76.661
Site x Month	3	0.658	0.450	-	0.806
		Probability of significant treatment effects			
Site	1	0.3935	0.3249	0.8832	0.5407
Month	3	0.0095	0.0230	0.0026	0.0001
Site x Month	3	0.6069	0.7268	-	0.5348
		Mean square			
Error a	2	113.625	22.732	-	0.007
Error b	6	72.292	20.748	-	0.003

[1] Values transformed using the Box-Cox transformation

[2] Values tested using the Kruskal-Wallis test

Table 3.13. Statistical significance of treatment effects from split-plot ANOVA of five measures of Lepidoptera diversity in four northern hardwood sites in 1994.

Source of Variation	df	Species Richness	Abundance[1]	Brilloun's Index	Simpson's Index[1]
		F value of significant treatment effects			
Site	1	6.050	0.327	10.589	0.082
Month	3	4.370	3.116	3.095	0.156
Site x Month	3	0.700	0.373	0.431	1.233
		Probability of significant treatment effects			
Site	1	0.1331	0.6249	0.0829	0.8011
Month	3	0.0592	0.1097	0.1110	0.9224
Site x Month	3	0.5855	0.7762	0.7388	0.3770
		Mean square			
Error a	2	5.000	4.856	0.004	0.026
Error b	6	52.500	4.019	0.038	0.012

[1] Values transformed using the Box-Cox transformation

Table 3.14. Statistical significance of treatment effects from split-plot ANOVA of five measures of Lepidoptera diversity in four northern hardwood sites in 1995.

Source of Variation	df	Species Richness[1]	Abundance[2]	Brilloun's Index	Simpson's Index[1]
		F value of significant treatment effects			
Site	1	0.114	χ^2=2.50	0.451	3.638
Month	3	0.928	χ^2=3.26	2.388	3.034
Site x Month	3	0.318	-	2.016	1.584
		Probability of significant treatment effects			
Site	1	0.7678	0.1141	0.5710	0.1967
Month	3	0.4827	0.3530	0.1676	0.1147
Site x Month	3	0.8123	-	0.2133	0.2887
		Mean square			
Error a	2	2.585	-	0.047	0.009
Error b	6	1.986	-	0.011	0.003

[1] Values transformed using the Box-Cox transformation
[2] Values tested using the Kruskal-Wallis test

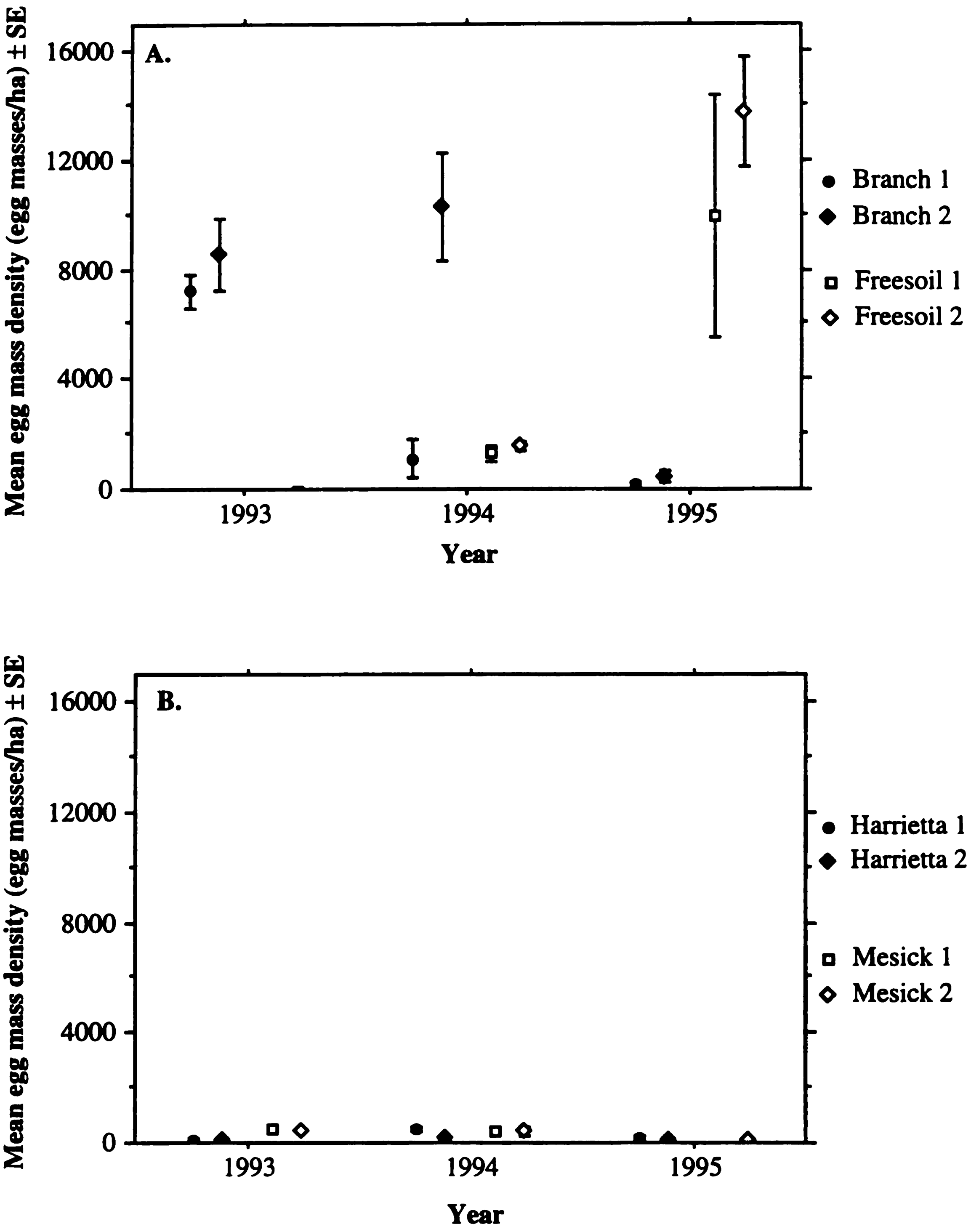


Figure 3.1. Mean density (±SE) of gypsy moth egg masses from four sites in A) red oak ecosystems (ELTP 20) and four sites in B) northern hardwood ecosystems (ELTP 45). Means were calculated from five 0.1 ha fixed-radius plots

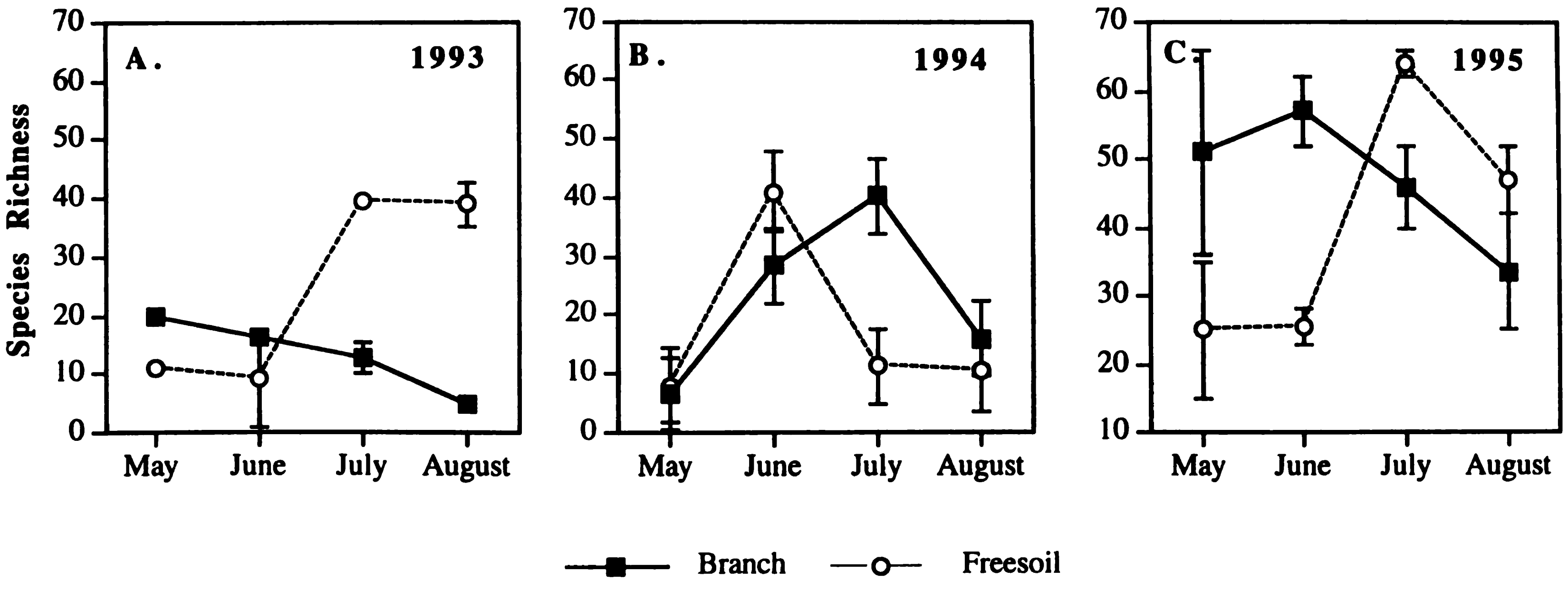


Figure 3.2. Means for species richness in A) 1993, B) 1994, and C) 1995. Data from 1993 and 1994 were backtransformed and error bars depict 95% confidence intervals. Error bars depict standard errors for 1995 data. Means were calculated from n=2 in each month.

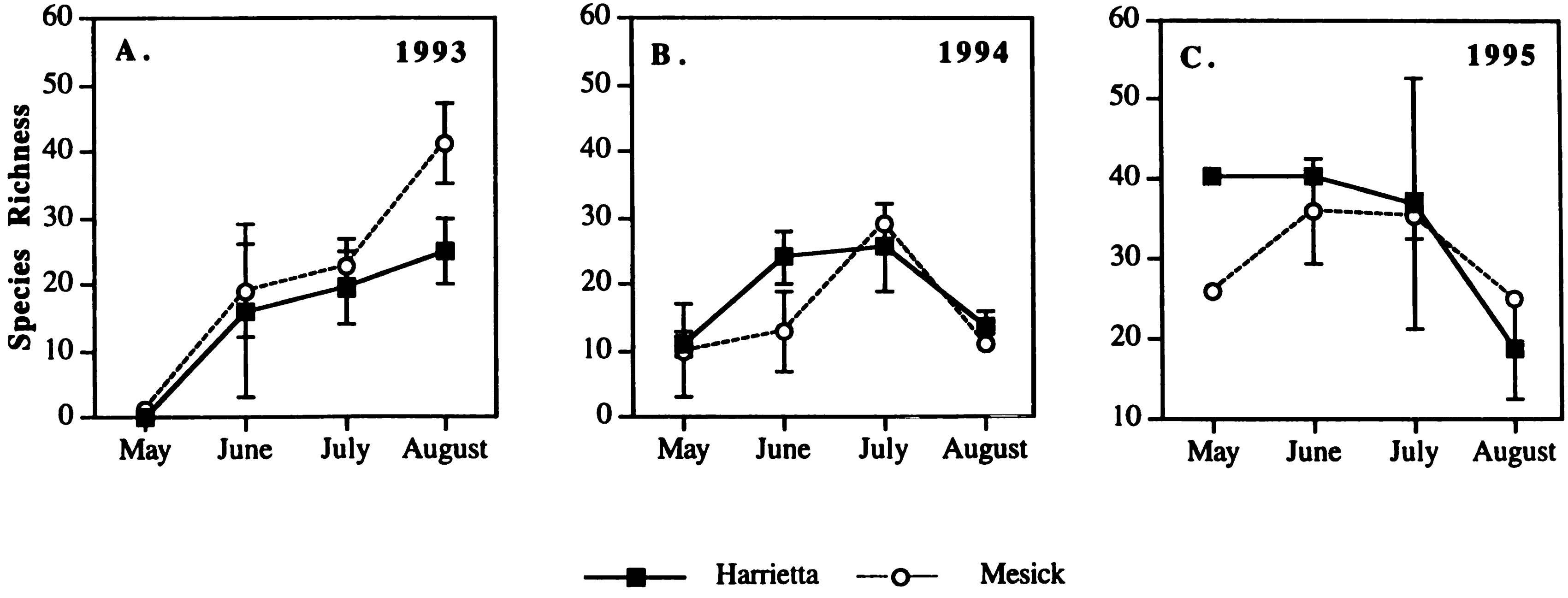


Figure 3.3. Means for species richness in A) 1993, B) 1994, and C) 1995. Error bars depict standard errors for 1993 and 1994 data. Data from 1995 were backtransformed and error bars depict 95% confidence intervals. Means were calculated from n=2 in each month.

Figure 3.4. Hierarchical clusters created using beta-flexible linkage (β= -0.25) method and Sorenson's quantitative index of similarity for total lepidoptera collected from eight sites during A) 1993, B) 1994 and C) 1995.

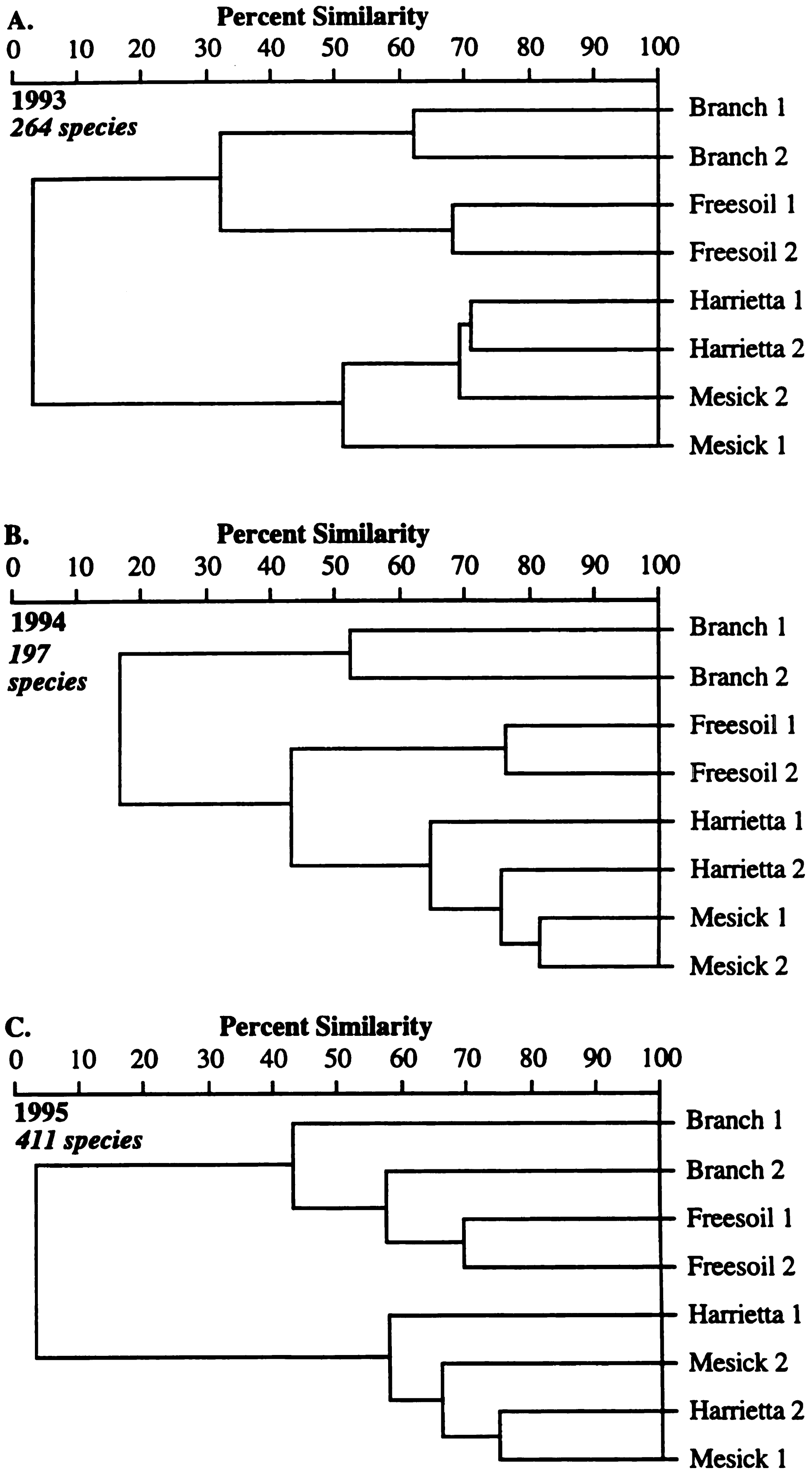
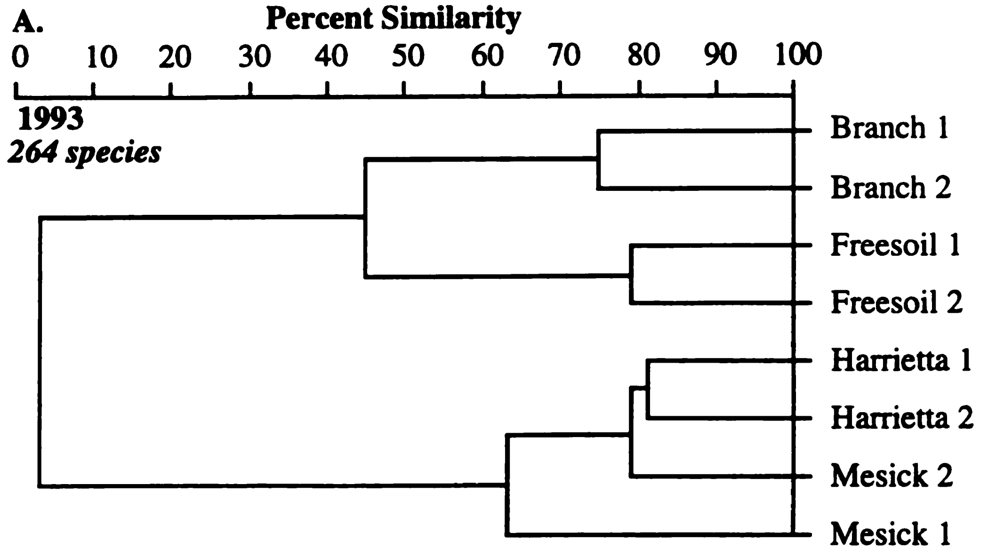
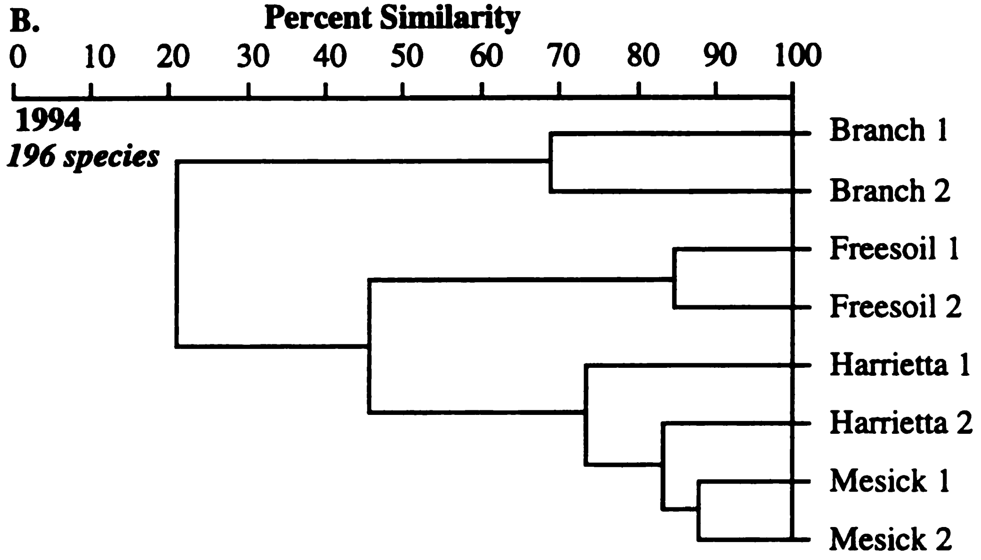

A.
Percent Similarity
0
10
20
30
40
50
60
70
80
90
100
1993
264 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Harrietta 2
Mesick 2
Mesick 1
B.
Percent Similarity
0
10
20
30
40
50
60
70
80
90
100
1994
197 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Harrietta 2
Mesick 1
Mesick 2
C.
Percent Similarity
0
10
20
30
40
50
60
70
80
90
100
1995
411 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Mesick 2
Harrietta 2
Mesick 1

Figure 3.5. Hierarchical clusters created using beta-flexible linkage (β= -0.50) method and Sorenson's quantitative index of similarity for total lepidoptera collected from eight sites during A) 1993, B) 1994 and C) 1995.


A.
Percent Similarity
0
10
20
30
40
50
60
70
80
90
100
1993
264 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Harrietta 2
Mesick 2
Mesick 1


B.
Percent Similarity
0
10
20
30
40
50
60
70
80
90
100
1994
196 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Harrietta 2
Mesick 1
Mesick 2

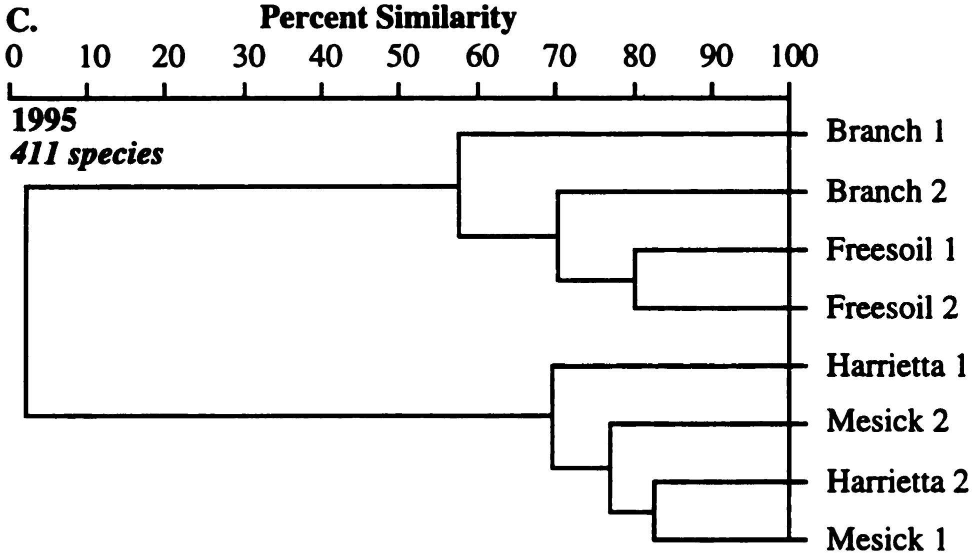
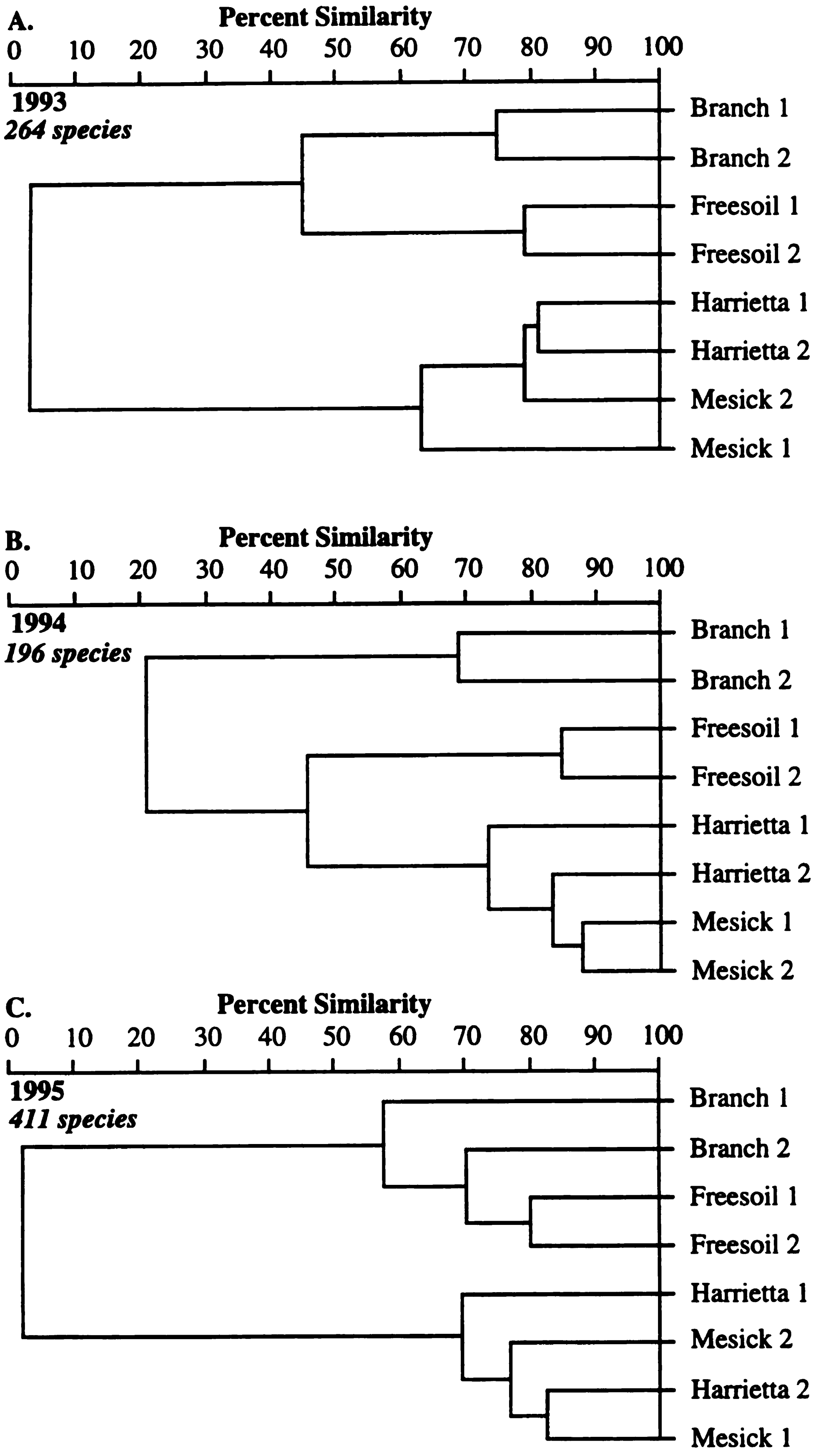

C.
Percent Similarity
0
10
20
30
40
50
60
70
80
90
100
1995
411 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Mesick 2
Harrietta 2
Mesick 1

Figure 3.5. Hierarchical clusters created using average linkage and Sorenson's quantitative index of similarity for total lepidoptera collected from eight sites during A) 1993, B) 1994 and C) 1995.


A.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1993
264 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Harrietta 2
Mesick 2
Mesick 1
B.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1994
196 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Harrietta 2
Mesick 1
Mesick 2
C.
Percent Similarity
0 10 20 30 40 50 60 70 80 90 100
1995
411 species
Branch 1
Branch 2
Freesoil 1
Freesoil 2
Harrietta 1
Mesick 2
Harrietta 2
Mesick 1

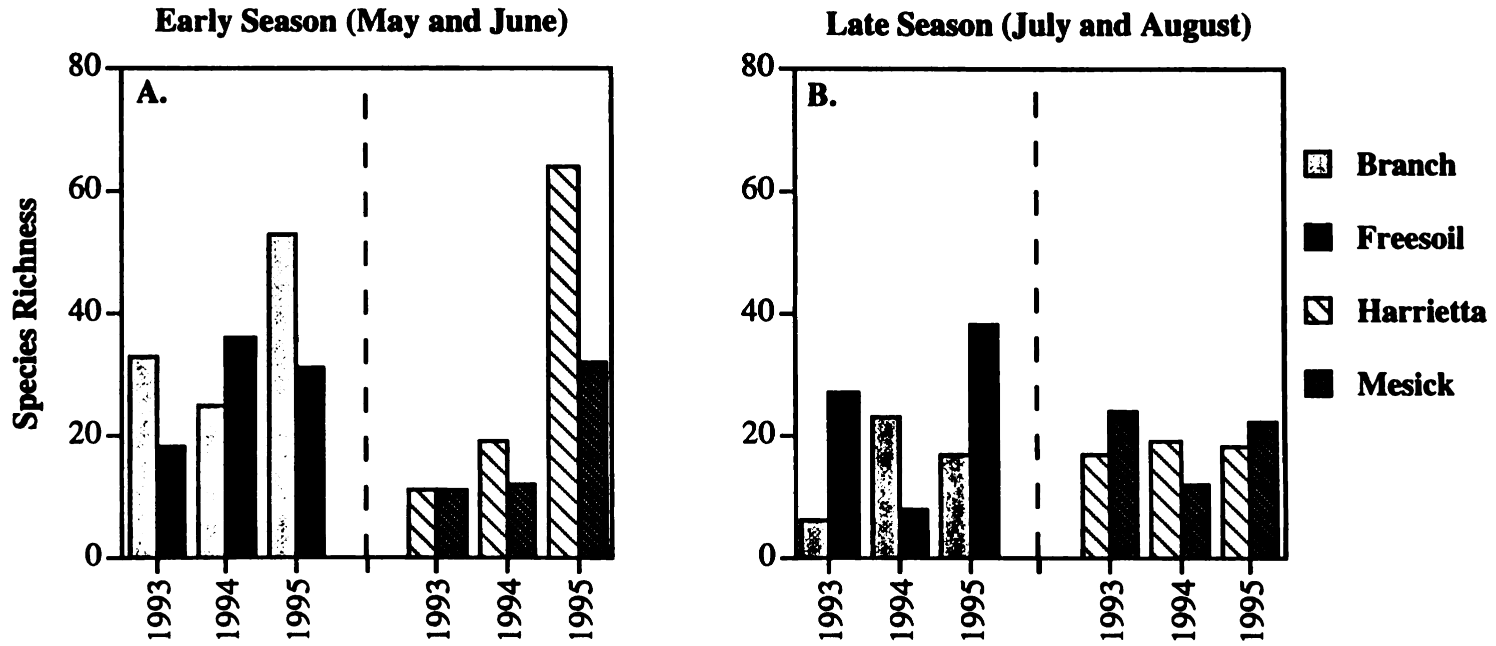


Figure 3.7. Species richness of noctuids collected during A) early season months of May and June and B) late season months of July and August from red oak sites (Branch and Freesoil) and northern hardwood sites (Harrietta and Mesick) over three years.

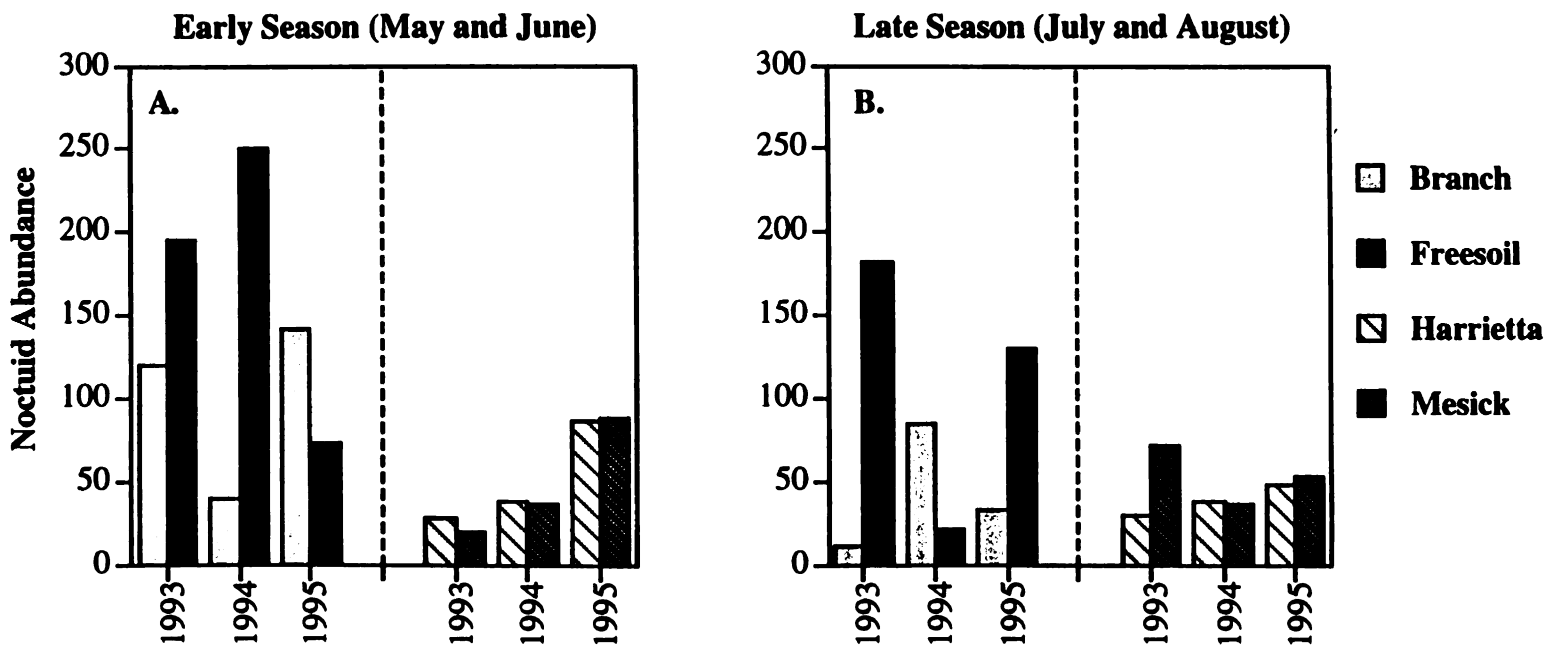


Figure 3.8. Total abundance of noctuids collected during A) early season months of May and June and B) late season months of July and August from red oak sites (Branch and Freesoil) and northern hardwood sites (Harrietta and Mesick) over three years.

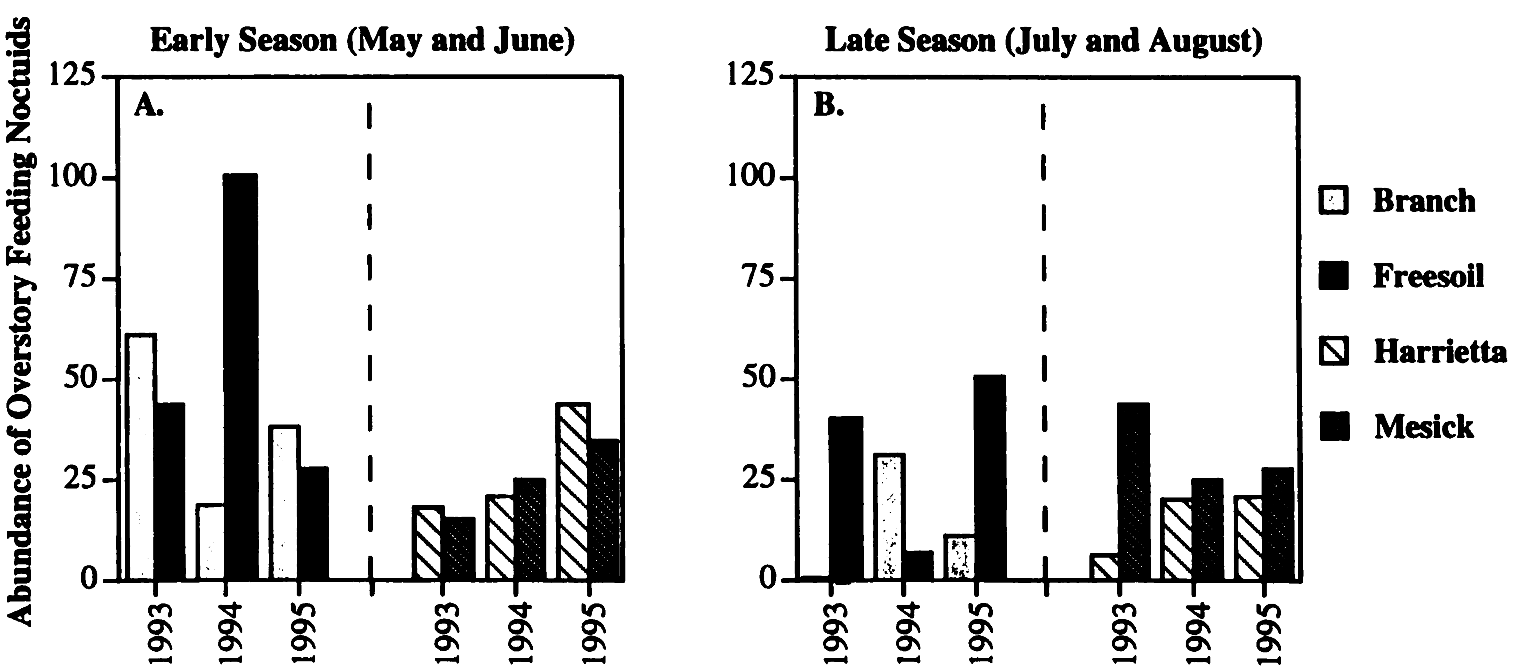


Figure 3.9. Abundance of overstory noctuids collected during A) early season months of May and June and B) late season months of July and August from red oak sites (Branch and Freesoil) and northern hardwood sites (Harrietta and Mesick) over three years.

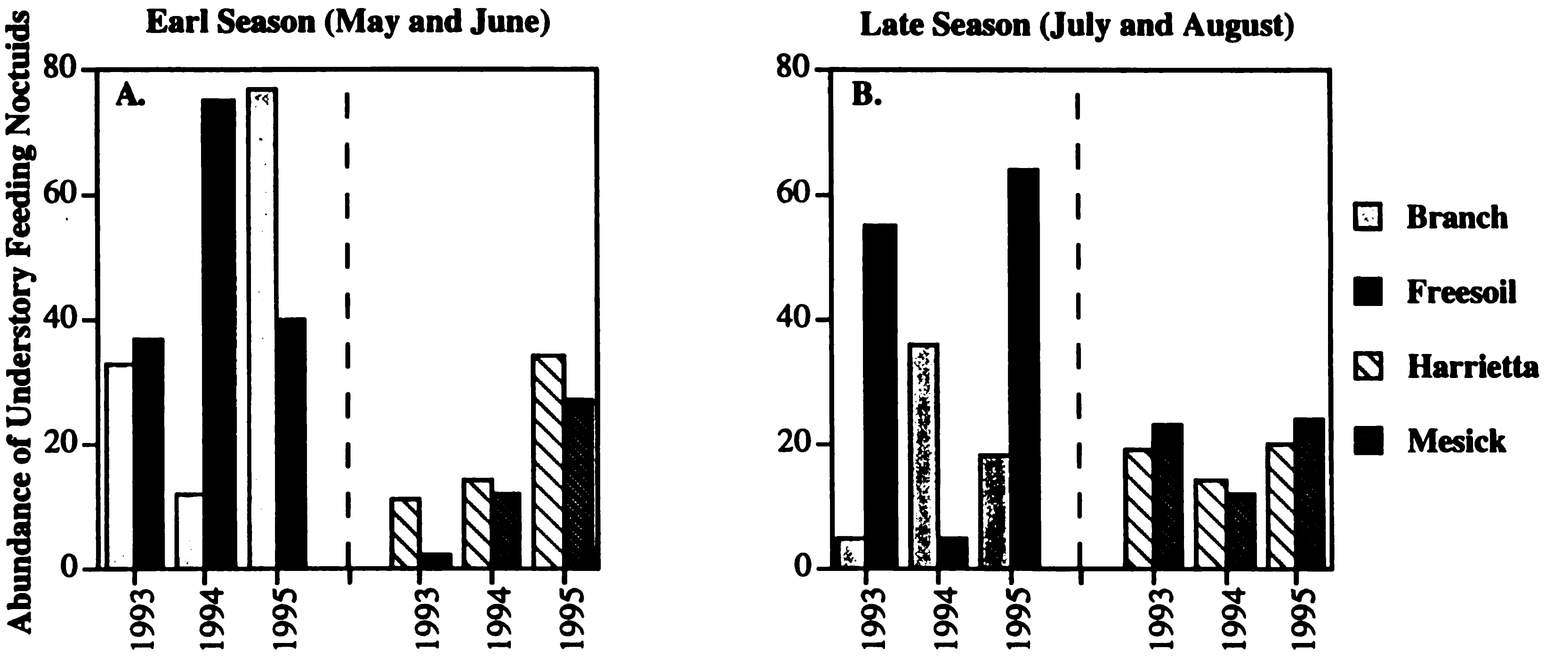


Figure 3.10. Abundance of understory noctuids collected during A) early season months of May and June and B) late season months of July and August from red oak sites (Branch and Freesoil) and northern hardwood sites (Harrietta and Mesick) over three years.

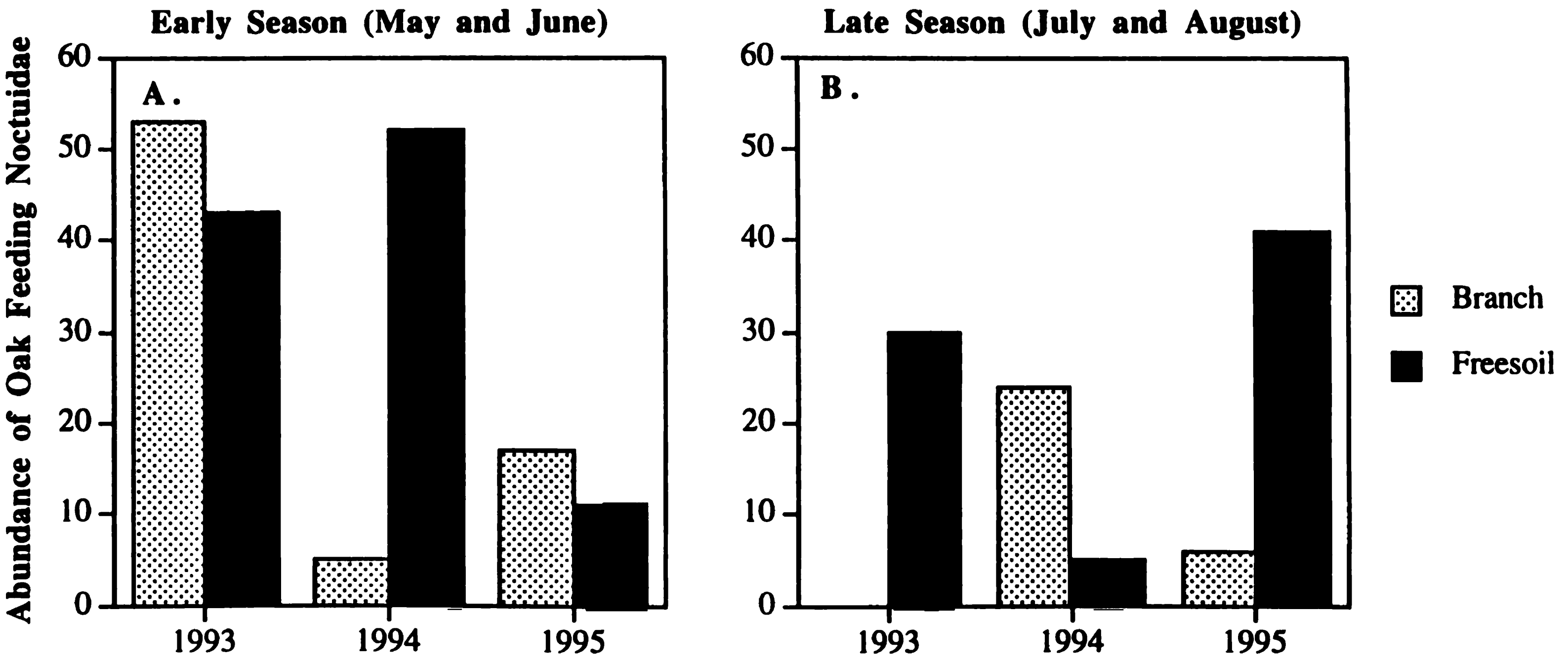


Figure 3.11. Abundance of oak-feeding noctuidae collected over three years during A) early season months of May and June and B) late season months of July and August from defoliated and undefoliated red oak sites. Branch sites were heavily defoliated in 1993, while Freesoil sites were moderately defoliated in 1994 and heavily defoliated in 1995.

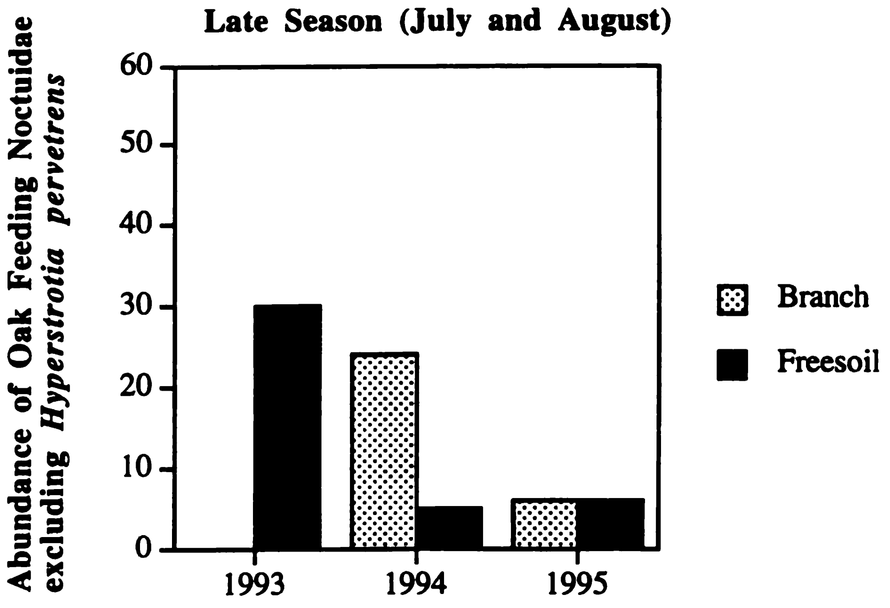


Figure 3.12. Abundance of oak-feeding Noctuidae excluding *Hypostrotia pervetrens* collected over three years during late season months of July and August from defoliated and undefoliated red oak sites. Branch sites were heavily defoliated in 1993, while Freesoil sites were moderately defoliated in 1994 and heavily defoliated in 1995.

Chapter 4

THE IMPACT OF GYPSY MOTH (LEPIDOPTERA:LYMANTIIDAE) OUTBREAKS ON THE COMMUNITY STRUCTURE OF ARTHROPODS IN TWO NORTHERN HARDWOOD ECOSYSTEMS IN NORTHERN LOWER MICHIGAN

Introduction

Since the term 'guild' was defined by (Root 1967; Root 1973) to mean 'a group of species that exploit the same class of environmental resources in a similar way,' the concept has been used in many ecological studies to describe arthropod community structure (see Hawkins and MacMahon (1989) for a review). The guild concept is typically applied in systems where inter-trophic interactions or species diversity are too complex to be explained using a species by species comparison.

Guilds have been used to compare the arthropod community structure in forest canopies over large spatial and temporal scales. Community structure of arthropods was found to be surprisingly consistent in tropical and temperate forests regardless of taxonomic relatedness of canopy trees (Moran and Southwood 1982; Stork 1987). Regenerating forests in western Oregon were shown to have relatively more sap-sucking arthropods than did old growth forests (Schowalter 1989).

Guilds have also been used to examine the response of forest arthropod communities to natural and anthropogenic disturbances. Hurricanes decreased the amount of folivores, predators, and detritivores but increased the amount of sap-feeders in disturbed areas in a tropical rain forest in Puerto Rico (Schowalter 1994). Similarly, forest management practices such as clearcutting (Schowalter et al. 1981) and partial harvesting (Schowalter 1995) also decreased the amounts of defoliators, predators, and detritivores but increased the relative amounts of sap-feeders in disturbed areas.

In the northeastern United States, gypsy moth, *Lymantria dispar* L., is a major forest pest responsible for defoliating over 10 million ha of forest between 1985 and 1994 (Butalla 1996). By 1994, gypsy moth infestation had extended as far west as Michigan and as far south as Virginia (Anonymous 1995). This exotic pest feeds on over 400 North American woody plant species including economically valuable species such as *Quercus* and *Populus* spp. (Mauffette et al. 1983). Defoliation can make trees susceptible to mortality agents like two-lined chestnut borer (*Agrilus bilineatus* Weber) and fungal pathogens like *Armillaria* root diseases (Wargo 1977).

Gypsy moth can alter species composition of a stand by reducing the relative abundance of oak species. Preferred tree species such as *Quercus* experienced 30% mortality after an average of 37% defoliation over 10 years in New England (Baker 1941) Repeated defoliation from 1911 to 1931 by gypsy moth not only increased the mortality rates of preferred host plant species such as oaks in stands with a greater diversity of non-preferred host plant species five years following defoliation, but also decreased the relative proportion of oaks within defoliated stands in New England (Campbell and Sloan 1977). Likewise, relative proportion of oaks decreased in forests defoliated by gypsy moth in Pennsylvania between 1971 and 1979 (Gansner et al. 1983).

In addition to altering the relative composition of forests, gypsy moth defoliation can change nutrient cycling and hydrological patterns. While nitrogen (N) in gypsy moth frass is immobilized by soil microbes, insect bodies and leaf fragments may be a source of nitrogen that is lost through leaching (Lovett and Ruesink 1995). Defoliation can also reduce transpiration and increase soil moisture resulting in increased denitrification (Lovett and Ruesink 1995). Severe gypsy moth defoliation has been demonstrated to increase water yield and fecal colliform concentrations in watersheds in the northeastern United States (Corbett and Lynch 1987).

Gypsy moth populations and subsequent defoliation may further disturb forest stands by decreasing canopy cover and altering the microclimate of the stand, increasing competition within the folivorous feeding guilds, and disrupting inter-trophic interactions by altering the abundance of prey items available to higher trophic consumers (see chapters 1, 2 and 3). However, little quantitative information is available on the overall effects of gypsy moth on the native arthropod community structure.

In this study, our objectives were to examine the effects of gypsy moth populations and defoliation on community structure of native arthropods in Michigan forest stands experiencing the first invasion of gypsy moth. Our goals were to evaluate differences in community structure of native arthropods between ecosystems that have high productivity and available N, but low susceptibility to gypsy moth defoliation (northern hardwood) and ecosystems that have moderate productivity but are very susceptible to defoliation (red oak).

Methods

Study Area

This research was conducted in eight sites in the Manistee National Forest in northern lower Michigan. Manistee National Forest has been described using an ecological classification system (ECS) (Cleland et al. 1993). The ECS is a hierarchical classification that groups ecosystem components at spatial scales varying from the landscape to the stand level. Ecological landtype phases (ELTPs) are classified on the basis of soils, landscape position and natural vegetation. ELTPs are subsets of larger spatial scale units such as ecological landtypes (ELTs) and landtype associations (LTA). Because stands within the same ELTP have similar overstory and understory vegetation, soil hydrology, soil type, nitrogen cycling, productivity and geological history, use of the ECS allows ecosystems to be replicated in experimental designs with a high level of confidence that experimental plots are similar.

We randomly chose four sites classified as ELTP 20 and four sites classified as ELTP 45 from maps provided by the Manistee National Forest. All sites ranged from approximately 12 to 16 ha in area. ELTP 20 was characterized by an overstory dominated by northern red oak (*Quercus rubra* L.) with a minor component of white oak (*Quercus alba* L.) and a non-diverse ground flora (Cleland et al. 1993). Soils on ELTP 20 were typically sandy, xeric soils with low productivity (Host et al. 1987; Host et al. 1988). ELTP 45 had an overstory dominated by northern hardwood species including sugar maple (*Acer saccharum* Marsh) with a minor component of American basswood (*Tilia americana* L.) (Cleland et al. 1993). This ELTP was notable for its rich herbaceous understory, well drained mesic soils, and high productivity (Host et al. 1987; Host et al. 1988; Zak et al. 1989; Zak and Pregitzer 1990; Zak et al. 1986).

Dominant tree species within ELTP 20 and 45 also differed in susceptibility to gypsy moth defoliation. Oak species, which dominated ELTP 20, are highly preferred by gypsy moth and oak stands often experience severe defoliation during outbreaks (Mauffette et al. 1983; Twery 1990). Northern hardwood stands, such as ELTP 45, are less susceptible to defoliation because the dominant canopy species, sugar maple, is only moderately preferred by gypsy moth (Mauffette et al. 1983; Twery 1990).

In the red oak ecosystem (ELTP 20), two sites were located at 44° 00' N, 86° 00' W near the town of Branch and two sites were located at 44° 08' N, 86° 09' W near the village of Freesoil. In the northern hardwood ecosystem (ELTP 45), two sites were located at 44° 22' N, 86° 44' W near the town of Mesick and two sites were located at 44° 19' N, 86° 44' W near the village of Harrietta.

Before 1993, none of our study sites had ever experienced any observable gypsy moth defoliation (F. Sapio, MI DNR, Forest Health Management, 1993 *pers comm.*, S. Katovich, USDA For. Serv. NA. S&PF, Forest Health Management, 1992, *pers comm.*). We surveyed these sites in 1992 and found no visible defoliation. Number of gypsy moth egg masses/ha, visual estimates of defoliation, and leaf area index were measured in all stands as part of a related study (see chapter 1). Red oak sites experienced more defoliation (Table 4.1) and had higher gypsy moth egg mass densities (Figure 4.1) than the northern hardwood sites from 1993 to 1995. Red oak sites had overall lower leaf area index than northern hardwood sites, and mid-summer leaf area index was reduced in areas with large gypsy moth populations in 1994 and 1995 (see chapter 1) (Table 4.1). Within red oak sites, gypsy moth populations fluctuated annually: outbreak populations at Branch in 1993 were followed by a population 'crash' due to larval infection by Nucleopolyhedrous virus (NPV) in 1994. Populations at Freesoil increased in 1994 and reached outbreak levels in 1995 (see chapter 1) (Figure 4.1).

Collection of Arthropods

Arthropods were collected during 1993, 1994 and 1995 growing seasons. Arthropods were collected four times a summer. Collection times roughly corresponded to significant points in gypsy moth management or biology. For example, typical application time of the microbial insecticide *Bacillus thuringensis* Berliner var. *kurstaki* (Btk) occurs in mid-May, fourth instar gypsy moth in mid-June, peak defoliation in mid-July, and stand refoliation in mid-August. During 1993, arthropods were collected on 12-13 May, 15-17 June, 13-15 July, and 10-12 August from red oak sites and on 21-22 May, 22-23 June, 20-22 July, and 18-20 August from northern hardwood sites. In 1994, arthropods were collected on 10-12 May, 15-16 June, 11-13 July, and 9-10 August from red oak sites and on 18-20 May , 20-21 June, 19-20 July, 15-17 August from northern hardwood sites. In

1995, collection dates were 15-17 May, 12-14 June, 10-11 July, 15-16 August at red oak sites and 22-24 May, 19-20 June, 17-19 July, and 21-22 August at northern hardwood sites. Arthropods were collected from the canopy, shrub and ground strata using a variety of sampling methods in an effort to adequately represent the total insect diversity within each site.

Canopy strata- In 1993, canopies were sampled using a pole pruner with a 9 m extendible handle, modified sweep nets with a 10 m extendible handle, and suspendable UV traps. In 1994 and 1995, pole pruners and extended sweep nets were replaced with a suspendable thermal fogger to facilitate collection of diurnally active canopy arthropods.

Pole pruners were used to clip one branch tip, 1 m in length, from the lower canopy of six trees along a random transect at 20 m intervals through each stand. Branch cuttings were then placed in plastic bags until they could be examined for arthropods. Extended sweep net samples were collected along a random transect from six trees at 20 m intervals. Four sweeps were made with a 50 cm diameter net at each interval.

Ultraviolet traps consisted of a 22 watt UV bulb connected to a photosensor and powered by a 6 volt motorcycle battery. UV traps were operated approximately 8 hours each sampling period. A collection funnel and bucket containing insecticidal pest strips (Vapona ^{TM}) were attached below the bulb. Traps were raised into the canopy in the center of each stand. Use of a low wattage bulb and a rain cover over the bulb restricted potential long-distance attraction of nocturnal arthropods, resulting in a localized sample reflective of endemic arthropod populations (Bowden 1982). The trap was raised into the canopy approximately 1 to 2 m above the lower edge of the canopy foliage in the center of each site.

A thermal fogger (Dyna-fog^{TM}) (Erwin 1983) modified with a radio-controlled switch was raised into the canopy at five points (20 m intervals) along a 100 m transect through the stand. The fogger was suspended by ropes and pulleys placed over large tree limbs with an arrow-line. A 25 m^2 diameter column of the canopy was then fogged with 1% pyrethroid (Pyrocide Fogging Concentrate 7338™, McLaughlin Gormley King Company) applied for 15 seconds at a rate of 0.377 L/minute. Pyrethroid was selected for its quick "knock-down ability" and low persistence. The fogged foliage was thoroughly shaken using additional suspended ropes. Arthropods were collected in 25 1 m^2 funnels arranged in a grid below the fogger. All fogging was done between 0400 and 0800 h when winds were calm.

Shrub strata- Arthropods were collected from shrub and understory vegetation less than 3 m tall using sweep nets. Sweep samples were collected using a 38 cm diameter net. Sixteen sweeps (4 from each cardinal direction) were made six times along a random transect through the stand at 20 m intervals. In addition to sweep netting, one malaise trap with an insecticidal pest strip was set up in the center of each stand. Malaise traps were left open for 24 hours primarily to collect diurnal flying insects and Hymenopteran parasitoids.

Ground strata- Ground-dwelling arthropods were sampled using 10 unbaited pitfall traps located along a randomly selected transect through the stand at 10 m intervals. Pitfall traps contained soapy water and were covered with four legged 'roofs' to minimize capture of non-ground dwelling arthropods and prevent predation by birds. Traps were left open for 24 hours. Arthropods collected in pitfall traps were placed in plastic containers with 70% ethanol as a preservative.

Arthropod Identification and Guild Assignments

All samples were placed in portable coolers in the field and transferred to freezers upon arrival at the laboratory. Arthropods were identified to family by T. Work and parataxonmists at Michigan State University.

Guilds were assigned using systematic literature and corroboration from previous studies, (LaVigne et al. 1990; Moran and Southwood 1982; Stork 1987). A hierarchical approach was employed when assigning insect families to guilds. If the guild classification of a family was consistent in the three guild studies cited above, that classification was also used in our study. If a guild classification was suggested by only one or two of the studies or conflicts in guild assignment developed, references to natural history from systematic literature were used to determine guild assignment (Arnett et al. 1980; Borror et al. 1989; Erwin 1983; Goulet and Huber 1993).

Collembola were collected only sporadically and in disproportionately large numbers relative to other families. Our results were expressed as number of arthropods and guilds represented the relative proportions of arthropods collected. Collembola were excluded from analyses to prevent them from overestimating the relative importance of other groups.

Because our sampling units were large spatial areas (forest stands), we assumed most of the arthropods spent both their immature and adult life within the stand. For this reason, members of Moran and Southwood's (1982) and Stork's (1987) tourist guild were reassigned to other guilds. Guild assignments used by LaVigne et al. (1990) for immature insects were used. Guilds were assigned according to immature life-stages because members of higher trophic level guilds such as parasitoids and some predators most likely impacted other insect groups only in the juvenile stage. Likewise, plant tissue-feeders such as folivorous lepidoptera most likely affect ecosystem processes during immature stages and experience more effects from direct competition with gypsy moth as immatures.

Guilds included in this study were ants, parasitoids, predators, plant sap-feeders, plant tissue-feeders and saprophages (Table 4.2). These guilds were included because they comprised a major proportion of the total arthropods collected each year. Arthropods from guilds that fed on algae, fungus, animal tissue, pollen and nectar were rarely collected and were not included in our analyses.

Statistical Analysis

Numbers of insects and numbers of families within each guild were recorded at each sampling period for three years (12 sample periods total). Numbers of insects and families were expressed as relative proportions of collected totals. Within the red oak ecosystem, guild data were analyzed using a split-plot ANOVA (e.g. a one-way ANOVA with repeated measures) to test for differences between sites with high and low defoliation, and monthly variation (Sokal and Rohlf 1995). Differences in arthropod guilds between Mesick and Harrietta sites and monthly variation within the northern hardwood ecosystem were similarly analyzed using a split-plot ANOVA. Data from all months were analyzed collectively to determine if effects of defoliation and variation among years were significant using a split-plot ANOVA within each ecosystem. Differences between ecosystems were analyzed using yearly totals with a one-way ANOVA with repeated measures. Variables that did not meet the assumptions of normality or heteroscedasticity were transformed using the arcsine transformation (Sokal and Rohlf 1995). Variables that could not be normalized or homoscedastic through transformation were tested separately for differences between sites and differences in time using the nonparametric Wilcoxin t-test (Conover 1971). All analyses were conducted using the software package JMP (SAS Institute Inc. 1995) and with $\alpha = 0.05$.

Results

A total of 49,973 arthropods from 207 families were collected and assigned to six guilds (Table 4.3 and 4.4). Number of total arthropods collected declined from 1993 to 1994 presumably because of adverse weather conditions during collection dates. Collection dates in 1994 were generally cooler and wetter when compared to either 1993 and 1995.

Abundance of Arthropods within Guilds

Within the red oak ecosystem, the relative number of individuals within each guild did not differ significantly between high and low levels of defoliation except in the ant guild during 1993 (Table 4.5-4.8). Ants comprised a greater proportion of total insects captured in Freesoil (6.2%) than in Branch (2.7%) in 1993 (Table 4.6). Monthly variation within guilds was significant for ants in 1995, sap-feeders in 1994 and 1995, and saprophages in 1993 and 1995 (Table 4.6-4.9). When data from all months were analyzed, only the saprophage guild was significantly affected by defoliation (Table 4.10). Saprophages comprised a greater proportion of total insects collected at Branch (28%) than Freesoil (17%) (Table 4.10). Variation among years was significant only for the sap-feeder guild (Table 4.10).

Within the northern hardwood ecosystem, the relative proportion of arthropods did not differ between Harrietta and Mesick sites, except for the saprophage guild during 1994 (Table 4.11-4.14). Saprophages comprised a larger proportion of total insects captured in Mesick (36%) than in Harrietta (22%) during 1994 (Table 4.13). Monthly variation within guilds was significant for ants in 1995 and sap feeders in 1994 and 1995 (Table 4.13-4.15). When total annual collection data were examined, saprophages were significantly affected by the interaction between site and year (Table 4.16). Relatively more saprophages were collected from Harrietta (32%) than Mesick (22%) in 1993. However, Mesick had more saprophages than Harrietta in 1994 (40% and 24% respectively) and again in 1995 (36% and 20% respectively). Among year variation was significant in the parasitoid guild (Table 4.16).

When differences between ecosystems were examined, only predators and tissue-feeders significantly differed in relative proportions between red oak sites and northern hardwood sites (Table 4.17 and Figure 4.2). Predators comprised a significantly greater proportion of arthropods at red oak sites (18%) than at northern hardwood sites (12%)

(Table 4.17). A significant interaction between ecosystem and year was apparent for the tissue-feeder guild (Table 4.17). Tissue-feeders increased in red oak sites from 35% to 41% between 1993 and 1994 respectively, but decreased to 35% by 1995. In the northern hardwood sites, tissue-feeders decreased from 50% in 1993 to 28% in 1994, then increased to 41% in 1995. The drop in relative proportion of tissue-feeders during 1994 in the northern hardwood sites reflected a large catch of saprophagous insects, particularly Sciarid flies.

Diversity of Families within Guilds

Within the red oak sites, the relative number of families within each guild did not differ between high and low levels of defoliation for any guild (Table 4.18-4.20). Monthly variation was significant for ants in 1995, the parasitoids in 1993, and sap-feeders in 1993 and 1994 (Table 4.18-4.19 and 4.21). When all data were examined, there were significant differences between the relative number of families of predators and tissue-feeders between Branch and Freesoil sites (Table 4.22). Greater relative proportions of predator families were observed in Freesoil (26%) than in Branch (23%). However, there were greater proportions of tissue-feeders in Branch (37%) than in Freesoil (34%) (Table 4.22). No significant interactions between defoliation and year were observed for any guild (Table 4.22). Furthermore within the red oak ecosystems, there was no significant variation among year within any guild (Table 4.22).

Within the northern hardwood sites, no differences in the relative number of families within each guild were observed between Mesick and Harrietta, except for the saprophage guild in 1994 (Table 4.23-4.25). In 1994, Mesick sites had more families in the saprophage guild than did Harrietta sites (30% and 24% respectively) (Table 4.24). Monthly variation in the number of families within each guild was much higher in the northern hardwood sites than in the red oak sites. Ants, sap-feeders, and saprophages all varied significantly among month in 1994 and 1995 (Table 4.26). Predators varied significantly among months in 1993 and tissue-feeders varied among months in 1995 (Table 4.26). When total annual catch was examined all samples were pooled, no differences between sites were observed, and variation among year was only significant for the parasitoid and saprophage guild (Table 4.27).

The relative number of families within each guild did not vary significantly between ecosystems except for the saprophage guild (Table 4.28 and Figure 4.3). More saprophagous families were observed within northern hardwood sites (21%) than in red oak sites (19%).

Discussion

Justification for Guild Assignments

While guilds are commonly used in entomological studies, concerns have been raised about how the term 'guild' is defined and used in community ecology. The original definition of guild was "...a group of species that exploit the same class of environmental resources in a similar way." (Root 1967; Root 1973). Many investigators have emphasized the 'same class of environmental resources' e.g. resource utilization rather than 'in a similar way' e.g. resource acquisition (Simberloff and Dayan 1991). This was seen as problematic when the role of competition, which is implied by Root's definition of guild, was further examined (Simberloff and Dayan 1991). Individuals that exploit the same resource may not be directly in competition if they are separated from accessing resources in time or by morphological differences that promote different methods of exploitation (Simberloff and Dayan 1991).

However, when feeding methods and specific food preference are unknown, or if species are omnivorous, both of which are true in the case of many arthropods, defining the phrase 'in a similar way' (resource acquisition) becomes much more difficult. Hawkins and MacMahon (1989) dismiss the matter of resource acquisition with the reasoning that the consequences to the ecosystem and the community are the same, regardless of how a resource is used.

Likewise, guild assignments are only as accurate as are the taxonomic identifications (Stork 1987). Arthropod families such as Pentatomidae and Miridae include both both predatory and sap-feeding species. In this study we classified both these families as sap-feeders, recognizing that some predatory species may be potentially incorrectly assigned to the sap-feeding guild. However, the effects of erroneous guild assignments of these families may be negligible because pentatomids and mirids accounted for less than 1% and 4% respectively, of the total arthropods collected in every year.

Obviously, the term 'guild' is somewhat elusive and open to interpretation depending on the objectives of the investigator. We have defined our guilds with more emphasis on resource utilization than resource acquisition. We justified our interpretation of guilds because of the paucity of information on the specific feeding habits of most forest arthropods and because our objectives were to examine the effects of a disturbance rather than to specifically determine mechanisms by which communities are formed or maintained.

Another concern regarding the use of guilds is whether the guilds chosen by the investigator truly reflect the community structure (Simberloff and Dayan 1991; Stork 1987). While we could not directly demonstrate vertical interactions between higher and lower trophic level consumers, we assumed that higher level consumers such as ants, predators, and parasitoids, interacted with lower level guilds such as tissue-feeders, sap-feeders, and saprophages. Similar classifications from previous studies in other temperate forests have shown a high degree of association between predacious and herbivorous arthropods (Schowalter 1995).

Effects of Gypsy Moth on Community Structure

Because gypsy moth populations and the amount of defoliation observed varied among years in the red oak ecosystem, effects of gypsy moth on arthropod communities are relevant only when defoliation by year interactions are significant. Defoliation by year interactions did not significantly affect either relative abundance of arthropods or relative number of families within in any guild. The consistent proportionality of guilds over time within the red oak ecosystem indicate that gypsy moth did not significantly alter the community structure of arthropods in these sites although individual species could have been affected.

Previous studies have found gypsy moth populations can affect specific groups such as oak-feeding lepidoptera (see chapter 3 and Sample et al. 1993), lepidoptera families including notodontids and lasiocampids (Sample et al. 1993), and some ground-dwelling arthropods (Muzika 1994). All of these studies demonstrated an effect of gypsy moth, but none evaluated the effects of gypsy moth at the community level.

The apparent lack of effect of gypsy moth defoliation on the community structure of native arthropods may result from the nature of gypsy moth as a disturbance. Intensity and area of disturbance both play an important role in determining the effects of disturbance (Huston 1994). The gypsy moth defoliation we observed, while intense when compared to background levels of defoliation, is relatively benign when compared to disturbances such as hurricanes or catastrophic fires. Defoliation removes foliage from particular host plants temporarily during the months of June and July, but trees usually refoliate by August. While defoliation can lead to mortality of host trees (Kulman 1971) or altered host plant quality through delayed induced resistance (Schultz and Baldwin 1982), the removal of foliage physically alters forest stands for a relatively short amount of time. Spatial scale of disturbance can also affect the recolonization of a disturbed area (Huston 1994). Between 1993 and 1995 in the four counties where our surveys were conducted, severe defoliation did not typically exceed 120 contiguous ha (Sapio 1996). During these years, approximately 80% of the severe gypsy moth defoliation that occurred was concentrated in areas no larger than 120 ha (Sapio 1996). Similarly, approximately 80% of moderate defoliation occurred in areas no larger than 130 ha in size (Sapio 1996). Larger outbreaks of greater than 480 ha accounted for only 4% of the total area of heavy defoliation and 3% of moderate defoliation (Sapio 1996).

Intensity and area of disturbance caused by gypsy moth defoliation may provide explanations for the effects of gypsy moth seen in previous studies and the lack of effect we observed. In our study sites, outbreaks did not exceed 65 ha and lasted no more than 2 years before they collapsed due to larval infection by NPV. While outbreak areas encompassed entire stands, defoliation did not extend over the entire range of surrounding forest stands. We believe that the removal of oak foliage during gypsy moth outbreaks may be detrimental to those organisms that rely specifically on oak for food or as habitat, but these organisms may be capable of recolonizing disturbed areas from surrounding undisturbed forest. Within red oak sites (ELTP 20), many organisms will rely on oak foliage to some extent as habitat. These organisms are probably less affected by defoliation than those that require oak foliage for nutrition. The relatively short time in which habitat is altered through defoliation may be insufficient to affect community structure as a whole. Gypsy moth presumably has greater impacts on individual species which rely only on oak. Guilds such as tissue-feeders presumably utilize multiple species of host plants, and thus may be less affected by the removal of oak foliage.

Higher trophic level guilds were not affected by gypsy moth in this study. Relative abundance of higher trophic guilds would be expected to decrease only if there was a decrease in the abundance of available prey items such as tissue and sap-feeders.

However, we observed no effect of defoliation on plant-feeding guilds. We would not expect the relative abundance of higher trophic guilds to increase during defoliation, unless generalist predators and parasitoids began to exploit gypsy moth as a resource. While some native species do exploit gypsy moth as a resource (Cameron and Reeves 1990), overall increased abundance of the guild may be unlikely because native predators and parasitoids have not coevolved with the gypsy moth.

Management Implications

The apparent resistance of the arthropod community to gypsy moth invasion has implications for current management strategies employed for controlling gypsy moth. Management of gypsy moth using Btk has been shown to reduce the abundance and diversity of non-target lepidoptera (Johnson et al. 1995; Miller 1990; Sample et al. 1993). Application of Btk may not only decrease the abundance of native lepidoptera, but may alter the balance of the trophic community. A decrease in the amount of tissue-feeders would presumably increase the relative proportion of other guilds and could potentially concentrate mortality from higher trophic consumers. The abundance of parasitoids decreased following application of microbial insecticides to gypsy moth in a laboratory setting presumably due to premature death of hosts and reduced abundance of available hosts (Vinson 1990). Arthropod orders associated with the soil such as Acarina, Nemotoda, Collembolla, and Hymenoptera may be adversely affected by residual build-up of Btk in the soil (Addison 1993).

Ecosystem Differences in Community Structure

Community structure of the red oak and northern hardwood forests were similar and significantly differed only in the predator and tissue-feeder guild. Difference in the relative number of predatory arthropods was small (6%) and the biological relevance of this difference should be interpreted cautiously. However, northern hardwood sites had overall greater abundance of tissue-feeders than red oak sites after the effects of large catches of saprophages like Sciarids were removed.

Greater tissue-feeder abundance within northern hardwood sites may reflect the high productivity and plant species diversity typical of this ecosystem. Northern hardwood ecosystems represented in this study by ELTP 45 have higher rates of net N mineralization and nitrification than oak ecosystems such as ELTP 20 (Zak and Pregitzer 1990). These rates translate into more available nitrogen available to be utilized by trees (Binkley 1986). Herbivorous insects in nitrogen poor environments generally have slower growth rates (Mattson 1980) and lower survivorship (Strong et al. 1984) than herbivores in nitrogen rich environments. Furthermore, northern hardwood ecosystem had richer diversity and abundance of understory herbaceous plants than did the red oak ecosystem (Cleland et al. 1993). Herbivores that feed on forbs generally have greater growth rates than those that feed on older foliage from woody plants (Mattson and Scriber 1987; Scriber and Slansky 1981). Presumably, greater abundance and diversity of understory plants supplied tissue-feeders with an exploitable source of nitrogen which was not available in the red oak system.

Temporal Variation in Guilds

Numbers of insects and numbers of families in the predator and tissue-feeder guilds remained relatively constant through time. Within both ecosystems, however, we observed variation within and among years in the numbers of insects and the number of families in the ant, parasitoid, sap feeder, and saprophage guilds. This variation was statistically significant, although differences were small and their biological relevance is questionable.

Seasonal and phenological changes over time may have accounted for much of the within year variation, but temporal variation may have been partly attributable to our use of multiple types of insect collection methods. Particular collection methods may have been differentially affected by environmental factors such as weather. For instance, malaise traps captured a large proportion of parasitoids such as parasitic Hymenoptera, while sweep nets tended to catch larger proportions of sap feeders such as aphids. However, malaise traps may be less effective during high winds (Southwood 1994) because of decreased Hymenopteran flight activity, whereas sweep netting is less affected by wind. This particular example would result in over-representation of sap feeders on a particular sampling date, and would contribute to the variation we have observed.

Guilds and Constancy

Moran and Southwood (1982) defined the term 'proportional constancy' when they observed that the number of arthropod species within predator and phytophage guilds from arboreal communities was relatively constant in communities dominated by broad- and narrow-leaved trees. Proportional constancy was stressed by Moran and Southwood as an interesting phenomenon that had been previously observed by Simberloff and Wilson (1969) during arthropod recolonization of six islands where all arthropods had been previously killed with insecticide. Since then, proportionality of arthropod guilds has also been demonstrated in tropical forests (Stork 1987). While we cannot define mechanisms by which communities are formed or maintained with our observations, we observed similar 'proportional constancy' within all guilds except saprophages between ecosystems with different levels of productivity and over a period of three years. Our observations provide additional evidence that the phenomenon of proportional constancy exists not only in communities with different evolutionary origins (Moran and Southwood 1982; Stork

1987), but also over time in communities with different nitrogen availability, a resource critically important to insect development and survival.

High Variability of Saprophages

We cannot explain the high variability observed in the saprophage guild. Saprophages varied between levels of defoliation in the red oak ecosystem, between sites within the northern hardwood ecosystem, and between ecosystems. These differences appeared to be independent of the effects of defoliation because the amount of saprophages was always higher in Branch sites than in Freesoil sites. Saprophages were mostly represented by Diptera. Our sampling regime may have been spatially too small to adequately and consistently represent the Diptera, but other factors such as differential attraction to traps due to environmental heterogeneity may have played a role. Also, heterogeneity may have been caused by stochastic mortality patterns of animals, which would be an attractive resource to many saprophagous Diptera, within each site.

Table 4.1. Visual estimation of peak defoliation and estimation of mean LAI (±SE) using photosynthetically active radiation transmittance of sites in red oak and northern hardwood ecosystems.

Peak Visual Estimation of Defoliation

	1993	1994	1995
Red Oak			
Branch	80-100%	< 20%	< 20%
Freesoil	< 20%	40-60%	80-100%
Northern Hardwood			
Harrietta	< 20%	< 20%	< 20%
Mesick	20-40%	< 20%	< 20%

Estimated Leaf Area Index[1]

	1994	1995
Red Oak		
Branch	4.48 ± 0.221	4.71 ± 0.115
Freesoil	2.73 ± 0.076	2.72 ± 0.151
Northern Hardwood		
Harrietta	10.9 ± 0.226	8.61 ± 0.229
Mesick	11.9 ± 0.189	8.14 ± 0.222

[1] Means and standard errors were calculated from two sites (n=2)

Table 4.2. Arthropod families assigned to six guilds based on feeding habits and corroboration with previous classifications.

Ants

Hymenoptera

Formicidae

Parasitoids

Hymenoptera

Aphelinidae
Aulacidae
Bethylidae
Braconidae
Ceraphronidae
Chalcididae
Chalcidoidea
Chrysididae
Diapriidae
Dryinidae
Elasmidae
Encyrtidae
Eucoilidae
Eulophidae
Eupelmidae
Figitidae
Ichneumonidae
Mutillidae
Mymaridae
Ormyiidae
Perilampidae
Platygasteridae
Pteromalidae
Scleonidae
Scoliidae
Torymidae
Trichogrammatidae

Diptera

Acroceridae
Pipunculidae
Ptychopteridae
Sarcophagidae
Tachinidae

Predators

Coleoptera

Carabidae
Cincindelidae
Cleridae
Coccinellidae
Colydiidae
Cucujidae
Derodontidae
Dytiscidae
Histeridae
Hydrophilidae
Lampyridae
Lycidae
Meloidae
Psephalidae
Pyrochroidae
Staphylinidae

Diptera

Asilidae
Athericidae
Bombyliidae
Chamaemyiidae
Dolichopodidae
Empididae
Rhagionidae
Syrphidae
Tabanidae
Xylophagidae

Table 4.2 (cont'd)

Hymenoptera	*Hemiptera*	*Neuroptera*	*Other Predators*
Mymeleontidae	Anthocoridae	Chrysopidae	Aranae
Pompilidae	Corixidae	Corydalidae	Chilopoda
Sphecidae	Gerridae	Hemerobiidae	
Vespidae	Nabidae	Mantispidae	
	Reduviidae		
	Saldidae		

Plant Sap Feeders

Hemiptera	*Homoptera*		*Thysanoptera*
Coreidae	Aphididae	Derbidae	Phlaeothripidae
Lygaeidae	Cercopidae	Membracidae	
Miridae	Cicadellidae	Psyllidae	
Pentatomidae	Cicadidae		

Plant Tissue Feeders

Coleoptera		*Diptera*	*Hymenoptera*
Anobiidae	Curculionidae	Agromyzidae	Cephidae
Anthicidae	Elateridae	Anthomyiidae	Cimbicidae
Anthribidae	Eucnemidae	Argomyzidae	Cynipidae
Apionidae	Haliplidae	Bibionidae	Diprionidae
Bostrichidae	Mordellidae	Cecidomyiidae	Symphyta
Brentidae	Ostomatidae	Chironomidae	Tenthredinidae
Buprestidae	Phalacridae	Chloropidae	Xiphyrididae
Byrrhidae	Scolytidae	Tephritidae	Xyelidae
Cerambycidae	Trogossitidae		
Chrysomelidae			
Curculionidae			

Table 4.2 (cont'd)

Lepidoptera	*Orthoptera*	*Phasmida*	*Acari*
All Lepidoptera	Acrididae	Phasmatidae	Tetranyctidae
	Tetrigidae		
	Tettigoniidae		

Saprophages

Coleoptera	*Diptera*		
Alleculidae	Anisopodidae	Heleomyzidae	Phoridae
Elmidae	Calliphoridae	Lauxaniidae	Scatopsidae
Endomychidae	Carnidae	Lonchopteridae	Sciaridae
Erotylidae	Clusiidae	Milichiidae	Sepsidae
Helodidae	Culicidae	Muscidae	Simulidae
Heteroceridae	Curtonotidae	Mycetophilidae	Sphaeroceridae
Nitidulidae	Dixidae	Neottiophilidae	Stratiomyidae
Oedemeridae	Drosophilidae	Odiniidae	
Ptinidae	Dryomyzidae	Otitidae	
Tenebrionidae			

Blattaria	*Hemiptera*	*Mecoptera*	*Other Saprophages*
Blattelidae	Largidae	Panorpidae	Diplopoda
Blattidae			Rhinotermitidae

Table 4.3. Total number of arthropods collected within red oak (R.O.) and northern hardwood (N.H.) sites over 1993, 1994, 1995 and overall.

	1993		1994		1995		Total
	R.O.	N.H.	R.O.	N.H.	R.O.	N.H.	
Ants	258	72	121	44	506	182	1183
Parasitoids	315	449	219	218	672	418	2291
Predators	939	493	1032	907	3071	2076	8518
Sap Feeders	377	381	194	205	1398	1041	3596
Tissue Feeders	2011	3363	2350	1786	4948	6407	20865
Saprophages	1667	1838	979	2044	2565	4427	13520
	5567	**6596**	**4895**	**5204**	**13160**	**14551**	**49973**

Table 4.4. The total number of arthropod families collected within red oak (R.O.) and northern hardwood (N.H.) during 1993, 1994, 1995 and overall.

	1993			1994			1995			TOTAL
	R.O.	N.H.	Shared Families	R.O.	N.H.	Shared Families	R.O.	N.H.	Shared Families	
Ants	1	1	1	1	1	1	1	1	1	1
Parasitoid	19	18	15	18	15	13	22	15	14	31
Predator	32	30	25	36	28	25	35	33	25	54
Sap Feeders	8	8	6	7	8	6	11	10	10	12
Tissue Feeders	48	41	30	52	41	37	66	50	46	67
Saprophages	22	22	18	25	27	24	31	35	27	42
	130	**120**		**139**	**120**		**166**	**144**		**207**

Table 4.5. Mean values (±SE) of the relative proportional abundance of six feeding guilds collected from two sites near Branch and two sites near Freesoil between 1993 and 1995.

	1993		1994		1995	
Guild	**Branch**	**Freesoil**	**Branch**	**Freesoil**	**Branch**	**Freesoil**
Ants	2.73 (0.47)	6.21 (0.85)	2.78 (0.82)	3.53 (1.19)	3.53 (0.73)	3.26 (0.44)
Parasitoids	6.74 (1.27)	4.33 (0.79)	4.44 (1.24)	4.74 (0.92)	4.51 (0.80)	5.53 (1.02)
Predators	12.90 (3.30)	17.46 (4.27)	20.52 (3.47)	17.37 (3.99)	22.67 (3.75)	20.82 (2.56)
Sap Feeders	9.41 (3.06)	7.08 (2.85)	3.25 (0.88)	2.24 (0.66)	9.27 (2.33)	9.68 (1.71)
Tissue Feeders	27.15 (7.66)	37.78 (6.26)	38.00 (3.89)	35.22 (7.48)	33.23 (2.80)	39.81 (4.59)
Saprophages	37.35 (8.39)	19.70 (4.58)	19.13 (2.71)	18.24 (4.31)	24.63 (5.44)	15.34 (2.12)

Table 4.6. Statistical significance of treatment effects from split-plot ANOVA of the relative abundance of insects within six feeding guilds in four red oak sites in 1993.

Source of Variation	df	Ants[1]	Parasitoids[1]	Predators[1]	Tissue Feeders	Sap Feeders[2]	Saprophages
F value of significant treatment effects							
Gyspy Moth	1	28.162	2.115	1.068	8.550	$\chi^2=1.10$	8.965
Month	3	0.722	0.626	1.938	2.105	$\chi^2=11.05$	7.753
Gypsy Moth x Month	3	0.329	2.836	2.406	6.007	-	1.907
Probability of significant treatment effects							
Gyspy Moth	1	0.0337	0.2831	0.4100	0.0998	0.2936	0.0958
Month	3	0.5744	0.6242	0.2248	0.2010	0.0115	0.0173
Gypsy Moth x Month	3	0.8053	0.1283	0.1658	0.0307	-	0.2296
Mean square							
Error a	2	0.0012	0.0056	0.016	52.729	-	138.963
Error b	6	0.0036	0.0032	0.013	177.293	-	138.346

[1] Values transformed using arcsine $(y)^{0.5}$

[2] Values tested using the Kruskal-Wallis test

Table 4.7. Statistical significance of treatment effects from split-plot ANOVA of the relative abundance of insects within six feeding guilds in four red oak sites in 1994.

Source of Variation	df	Ants	Parasitoids[1]	Predators	Tissue Feeders	Sap Feeders	Sapro-phages
			F value of significant treatment effects				
Gyspy Moth	1	0.334	0.053	5.135	0.140	0.801	0.022
Month	3	1.495	0.399	0.834	1.088	11.881	0.824
Gypsy Moth x Month	3	0.309	2.022	1.111	0.422	1.868	0.169
			Probability of significant treatment effects				
Gyspy Moth	1	0.6215	0.8390	0.1517	0.7444	0.4653	0.8956
Month	3	0.3083	0.7591	0.5225	0.4231	0.0062	0.5268
Gypsy Moth x Month	3	0.8189	0.2124	0.4153	0.7439	0.2359	0.9134
				Mean square			
Error a	2	6.643	0.0054	7.738	221.634	5.109	142.378
Error b	6	9.058	0.0048	131.048	335.578	1.224	130.114

[1] Values transformed using arcsine $(y)^{0.5}$

Table 4.8. Statistical significance of treatment effects from split-plot ANOVA of the relative abundance of insects within six feeding guilds in four red oak sites in 1995.

Source of Variation	df	Ants	Parasitoids	Predators	Tissue Feeders	Sap Feeders	Sapro-phages[1]
			F value of significant treatment effects				
Gyspy Moth	1	0.042	0.448	0.119	7.355	0.034	2.375
Month	3	7.274	3.682	1.011	3.885	4.639	5.775
Gypsy Moth x Month	3	0.590	0.287	0.201	2.217	0.515	0.958
			Probability of significant treatment effects				
Gyspy Moth	1	0.8567	0.5720	0.7629	0.1133	0.8708	0.2632
Month	3	0.0201	0.0818	0.4506	0.0740	0.0526	0.0334
Gypsy Moth x Month	3	0.6437	0.8336	0.8922	0.1868	0.6868	0.4709
				Mean square			
Error a	2	0.0007	0.0009	0.012	0.002	0.002	0.0001
Error b	6	0.0001	0.0004	0.009	0.006	0.002	0.0001

[1] Values transformed using arcsine $(y)^{0.5}$

Table 4.9. Mean values (±SE) of the relative abundance of arthropods in guilds that varied significantly among month in red oak sites (n=4).

Guild	May	June	July	August	F ratio	P value
Ants 1995	3.5 (0.5)	2.3 (0.9)	2.6 (0.8)	5.1 (0.4)	7.27	0.020
Sap Feeders 1994	0.0 (0.0)	3.3 (1.1)	4.4 (0.7)	3.2 (0.6)	11.88	0.006
Sap Feeders 1995	3.8 (2.7)	7.2 (2.2)	13.9 (1.0)	13.0 (1.7)	4.64	0.053
Saprophages 1993	4.9 (0.7)	30.4 (6.3)	41.4 (8.8)	37.3 (12.0)	7.75	0.017
Saprophages 1995	23.7 (7.8)	30.5 (6.7)	11.9 (1.1)	13.9 (2.3)	11.20	0.020

Table 4.10. Statistical significance of treatment effects from split-plot ANOVA of the relative number of insects within six feeding guilds in four red oak sites over three years.

Source of Variation	df	Ants	Parasitoids	Predators	Tissue-Feeders	Sap-Feeders	Sapro-phages
			F value of significant treatment effects				
Gyspy Moth	1	2.272	0.621	0.510	3.968	3.613	60.832
Year	2	6.817	1.341	0.836	3.134	8.977	3.901
Gypsy Moth x Year	2	5.376	2.030	0.090	3.650	1.507	0.761
			Probability of significant treatment effects				
Gyspy Moth	1	0.2707	0.5132	0.5494	0.1846	0.1977	0.0160
Year	2	0.0515	0.3584	0.4972	0.1518	0.0332	0.1149
Gypsy Moth x Year	2	0.0735	0.2463	0.9161	0.1253	0.3252	0.5245
				Mean square			
Error a	2	1.65E-4	2.88E-5	1.27E-3	2.90E-3	1.68E-4	6.31E-4
Error b	4	8.14E-4	3.89E-5	4.39E-3	1.73E-3	5.22E-4	5.04E-3

Table 4.11. Mean values (±SE) of the relative proportional abundance of six feeding guilds collected from two sites near Harrietta and two sites near Mesick between 1993 and 1995.

	1993		1994		1995	
Guild	**Harrietta**	**Mesick**	**Harrietta**	**Mesick**	**Harrietta**	**Mesick**
Ants	0.55 (0.21)	1.41 (0.35)	0.64 (0.23)	0.71 (0.46)	0.88 (0.33)	0.98 (0.44)
Parasitoids	6.87 (1.59)	5.82 (1.58)	5.05 (0.94)	3.46 (0.56)	2.38 (0.43)	3.29 (0.35)
Predators	7.30 (1.32)	9.72 (2.93)	20.68 (3.15)	15.23 (3.00)	18.97 (3.61)	15.78 (1.92)
Sap Feeders	10.01 (4.71)	7.84 (2.40)	3.18 (1.06)	2.54 (0.98)	4.82 (1.48)	4.38 (1.19)
Tissue Feeders	35.14 (6.09)	45.32 (8.40)	33.68 (3.78)	28.75 (6.14)	43.95 (3.75)	39.56 (3.69)
Saprophages	26.89 (5.79)	23.44 (3.25)	22.14 (1.64)	36.45 (5.81)	25.03 (3.90)	32.97 (3.07)

Table 4.12. Statistical significance of treatment effects from split-plot ANOVA of the relative abundance of insects within six feeding guilds in four northern hardwood sites in 1993.

Source of Variation	df	Ants[1]	Parasitoids[2]	Predators[2]	Tissue Feeders	Sap Feeders[1]	Saprophages
				F value of significant treatment effects			
Site	1	$\chi^2=3.43$	0.514	5.182	1.439	$\chi^2=0.01$	2.553
Month	3	$\chi^2=2.01$	1.743	1.647	1.132	$\chi^2=12.20$	3.009
Site x Month	3	-	1.189	0.025	0.058	-	3.942
				Probability of significant treatment effects			
Site	1	0.0641	0.5447	0.1506	0.3532	0.9164	0.2512
Month	3	0.5705	0.2575	0.2757	0.4048	0.0067	0.1163
Site x Month	3	-	0.3902	0.9939	0.9801	-	0.0721
				Mean square			
Error a	2	-	0.0035	0.0007	287.921	-	18.645
Error b	6	-	0.0066	0.0140	570.325	-	90.687

[1] Values tested using the Kruskal-Wallis test

[2] Values transformed using arcsine $(y)^{0.5}$

Table 4.13. Statistical significance of treatment effects from split-plot ANOVA of the relative abundance of insects within six feeding guilds in four northern hardwood sites in 1994.

Source of Variation	df	Ants[1]	Parasitoids[2]	Predators	Tissue Feeders	Sap Feeders[2]	Saprophages[1]
			F value of significant treatment effects				
Site	1	$\chi^2=0.29$	1.939	1.083	0.966	0.110	$\chi^2=7.46$
Month	3	$\chi^2=7.49$	1.497	1.566	1.321	14.566	$\chi^2=2.51$
Site x Month	3	-	1.643	0.035	0.351	3.412	-
			Probability of significant treatment effects				
Site	1	0.5895	0.2984	0.4072	0.4293	0.7721	0.0063
Month	3	0.0577	0.3078	0.2926	0.3518	0.0037	0.4726
Site x Month	3	-	0.2765	0.9905	0.7907	0.0937	-
			Mean square				
Error a	2	-	0.0030	109.688	100.445	0.0038	-
Error b	6	-	0.0019	77.935	246.214	0.0021	-

[1] Values tested using the Kruskal-Wallis test

[2] Values transformed using arcsine $(y)^{0.5}$

Table 4.14. Statistical significance of treatment effects from split-plot ANOVA of the relative abundance of insects within six feeding guilds in four northern hardwood sites in 1995.

Source of Variation	df	Ants[1]	Parasitoids	Predators	Tissue Feeders	Sap Feeders	Saprophages
				F value of significant treatment effects			
Site	1	0.059	3.434	0.318	0.361	1.652	4.997
Month	3	29.565	1.026	1.444	1.052	86.119	3.703
Site x Month	3	0.919	0.182	1.044	0.761	3.341	3.774
				Probability of significant treatment effects			
Site	1	0.8310	0.2050	0.6299	0.6090	0.3275	0.1549
Month	3	0.0005	0.4450	0.3203	0.4358	<0.0001	0.0809
Site x Month	3	0.4862	0.9048	0.4386	0.5558	0.0973	0.0781
				Mean square			
Error a	2	1.97E-5	0.00009	0.0130	0.0210	4.96E-5	0.0050
Error b	6	4.52E-6	0.00016	0.0051	0.0098	7.31E-5	0.0045

[1] Values transformed using arcsine $(y)^{0.5}$

Table 4.15. Mean values (±SE) of the relative abundance of arthropods in guilds that varied significantly by month in northern hardwood sites (n=4).

Guild	May	June	July	August	F ratio	P value
Ants 1995	0.0 (0.0)	2.0 (0.5)	0.7 (0.1)	1.1 (0.3)	29.35	0.001
Sap Feeders 1994	0.2 (0.2)	5.3 (1.3)	2.0 (0.1)	3.8 (1.8)	14.57	0.004
Sap Feeders 1995	0.5 (0.2)	10.0 (0.7)	3.4 (0.3)	4.5 (0.6)	86.12	0.000

Table 4.16. Statistical significance of treatment effects from split-plot ANOVA of the relative number of insects within six feeding guilds in four northern hardwood sites over three years.

Source of Variation	df	Ants	Parasitoids	Predators	Tissue-Feeders	Sap-Feeders	Saprophages
			F value of significant treatment effects				
Site	1	1.034	0.022	0.948	1.902	0.011	11.513
Year	2	1.209	10.200	3.029	5.413	5.925	2.658
Site x Year	2	0.822	0.846	0.593	0.903	0.555	22.629
			Probability of significant treatment effects				
Site	1	0.4163	0.8949	0.4330	0.3018	0.9268	0.0770
Year	2	0.3885	0.0269	0.1582	0.0728	0.0637	0.1844
Site x Year	2	0.5022	0.4938	0.5947	0.4747	0.6125	0.0066
				Mean square			
Error a	2	3.23E-5	3.05E-5	1.64E-3	1.57E-3	2.49E-4	1.41E-3
Error b	4	3.02E-6	8.74E-6	2.52E-3	8.61E-3	2.00E-4	1.03E-3

Table 4.17. Statistical significance of treatment effects of ecosystem and year from split-plot ANOVA of the relative number of insects within six feeding guilds.

Source of Variation	df	Ants	Parasitoids	Predators	Tissue-Feeders	Sap-Feeders	Sapro-phages
				F value of significant treatment effects			
Ecosystem	1	23.639	3.246	16.108	1.187	5.350	2.848
Year	2	3.545	4.683	3.629	1.981	13.254	0.802
Ecosystem x Year	2	1.631	1.224	0.689	6.992	1.790	2.615
				Probability of significant treatment effects			
Ecosystem	1	0.0028	0.1165	0.0070	0.3178	0.0600	0.1425
Year	2	0.0617	0.0338	0.0585	0.1805	0.0009	0.4710
Ecosystem x Year	2	0.2363	0.3313	0.5207	0.0097	0.2088	0.1142
				Mean square			
Error a	6	1.30E-4	7.00E-5	1.34E-3	3.91E-3	2.40E-4	9.79E-3
Error b	12	1.20E-4	1.72E-4	2.63E-3	5.80E-3	3.91E-4	6.56E-3

Table 4.18. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within six feeding guilds in four red oak sites in 1993.

Source of Variation	df	Ants	Parasitoids	Predators	Tissue Feeders	Sap Feeders	Sapro-phages
			F value of significant treatment effects				
Gyspy Moth	1	1.249	5.973	0.176	0.110	0.142	0.952
Month	3	0.330	6.038	0.353	0.989	4.917	0.138
Gypsy Moth x Month	3	1.135	1.598	0.525	1.302	1.852	2.724
			Probability of significant treatment effects				
Gyspy Moth	1	0.3800	0.1345	0.7157	0.7715	0.7424	0.4321
Month	3	0.8045	0.0304	0.7889	0.4588	0.0468	0.9336
Gypsy Moth x Month	3	0.4075	0.2858	0.6809	0.3572	0.2385	0.1369
				Mean square			
Error a	2	1.80E-4	9.90E-4	0.0036	0.0088	3.42E-4	0.0065
Error b	6	7.01E-5	0.0019	0.0087	0.0016	9.01E-4	0.0038

Table 4.19. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within six feeding guilds in four red oak sites in 1994.

Source of Variation	df	Ants[1]	Parasitoids	Predators[1]	Tissue Feeders	Sap Feeders	Sapro-phages
			F value of significant treatment effects				
Gyspy Moth	1	χ^2=1.73	0.689	χ^2=0.33	12.492	1.025	2.77E-4
Month	3	χ^2=6.56	0.084	χ^2=4.09	0.715	18.054	1.912
Gypsy Moth x Month	3	-	1.165	-	0.783	0.688	0.389
			Probability of significant treatment effects				
Gyspy Moth	1	0.1889	0.4938	0.5632	0.0716	0.4179	0.9882
Month	3	0.0873	0.9661	0.2522	0.5778	0.0021	0.2288
Gypsy Moth x Month	3	-	0.3979	-	0.5453	0.5917	0.7654
				Mean square			
Error a	2	-	0.0033	-	6.54E-5	0.0016	0.0022
Error b	6	-	0.0025	-	0.0033	0.0004	0.0025

[1] Values tested using the Kruskal-Wallis test

Table 4.20. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within six feeding guilds in four red oak sites in 1995.

Source of Variation	df	Ants[1]	Parasitoids	Predators	Tissue Feeders	Sap Feeders	Saprophages
F value of significant treatment effects							
Gyspy Moth	1	χ^2=0.54	1.829	0.347	0.666	0.474	0.551
Month	3	χ^2=10.86	1.712	1.596	1.702	1.117	0.402
Gypsy Moth x Month	3	-	0.156	2.223	0.617	0.301	0.765
Probability of significant treatment effects							
Gyspy Moth	1	0.4616	0.3088	0.6157	0.5003	0.5624	0.5352
Month	3	0.0125	0.2632	0.2861	0.2650	0.4135	0.7570
Gypsy Moth x Month	3	-	0.9217	0.1862	0.6290	0.8242	0.5536
Mean square							
Error a	2	-	3.00E-5	7.39E-4	0.0014	1.76E-4	0.0016
Error b	6	-	0.0016	7.21E-4	0.0015	5.69E-4	0.0013

[1] Values tested using the Kruskal-Wallis test

Table 4.21. Mean values (±SE) of the relative number of families of arthropods in guilds that varied significantly among month in red oak sites (n=4).

Guild	May	June	July	August	F ratio	P value
Ants 1995[1]	2.6 (0.1)	2.0 (0.2)	1.5 (0.0)	1.5 (0.0)	$\chi^2=10.87$	0.013
Parasitoids 1993	8.2 (3.3)	12.4 (2.2)	20.2 (1.7)	17.8 (2.4)	6.03	0.030
Sap Feeders 1993	5.0 (1.7)	13.0 (2.2)	8.7 (1.0)	7.5 (0.6)	4.92	0.047
Sap Feeders 1994	0.0 (0.0)	8.2 (1.2)	7.0 (1.1)	8.6 (1.9)	18.05	0.002

[1] Monthly variation was tested with the Kruskal-Wallace test.

Table 4.22. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within five feeding guilds in four red oak sites over three years.

Source of Variation	df	Parasitoids	Predators	Tissue-Feeders	Sap-Feeders	Saprophages
				F value of significant treatment effects		
Gyspy Moth	1	1.039	68.177	229.407	0.357	0.112
Year	2	2.860	2.735	1.104	2.283	0.723
Gypsy Moth x Year	2	1.761	2.213	1.203	1.931	2.070
				Probability of significant treatment effects		
Gyspy Moth	1	0.4152	0.0144	0.0043	0.6110	0.7700
Year	2	0.1694	0.1784	0.4153	0.2180	0.5393
Gypsy Moth x Year	2	0.2827	0.2253	0.3899	0.2589	0.2415
				Mean square		
Error a	2	2.6411	0.5253	0.1323	2.6584	0.7544
Error b	4	2.0585	6.4668	4.4117	1.0097	7.5342

Table 4.23. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within six feeding guilds in four northern hardwood sites in 1993.

Source of Variation	df	Ants[1]	Parasitoids[1]	Predators[1]	Tissue Feeders	Sap Feeders	Saprophages[1]
				F value of significant treatment effects			
Site	1	χ^2=1.26	χ^2=0.71	χ^2=1.33	0.159	0.455	χ^2=0.72
Month	3	χ^2=2.20	χ^2=6.64	χ^2=9.09	4.096	0.125	χ^2=1.04
Site x Month	3	-	-	-	1.244	0.135	-
				Probability of significant treatment effects			
Site	1	0.2623	0.4005	0.5135	0.7284	0.5696	0.3962
Month	3	0.5329	0.0842	0.0281	0.0670	0.9418	0.7907
Site x Month	3	-	-	-	0.3736	0.9356	-
				Mean square			
Error a	2	-	-	-	0.0018	7.74E-4	-
Error b	6	-	-	-	0.0025	0.0020	-

[1] Values tested using the Kruskal-Wallis test

Table 4.24. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within six feeding guilds in four northern hardwood sites in 1994.

Source of Variation	df	Ants[1]	Parasitoids[1]	Predators	Tissue Feeders	Sap Feeders	Saprophages
				F value of significant treatment effects			
Site	1	$\chi^2=0.06$	$\chi^2=1.28$	1.085	1.524	0.030	63.244
Month	3	$\chi^2=20.75$	$\chi^2=5.02$	0.444	2.964	5.635	6.159
Site x Month	3	-	1.165	2.226	1.215	1.622	2.340
				Probability of significant treatment effects			
Site	1	0.8035	0.2578	0.4070	0.3424	0.8787	0.0154
Month	3	0.0001	0.1702	0.7305	0.1193	0.0352	0.0291
Site x Month	3	-	0.3979	0.1858	0.3823	0.2808	0.1728
				Mean square			
Error a	2	-	0.0033	0.0028	5.90E-4	9.31E-4	1.90E-4
Error b	6	-	0.0025	0.0026	8.13E-4	6.87E-4	3.04E-4

[1] Values tested using the Kruskal-Wallis test

Table 4.25. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within six feeding guilds in four northern hardwood sites in 1995.

Source of Variation	df	Ants[1]	Parasitoids	Predators	Tissue Feeders	Sap Feeders	Saprophages
			F value of significant treatment effects				
Site	1	χ^2=0.10	1.315	0.193	0.728	5.083	3.138
Month	3	χ^2=14.37	0.872	2.329	12.202	7.248	8.526
Site x Month	3	-	0.799	3.420	2.354	0.890	0.229
			Probability of significant treatment effects				
Site	1	0.7506	0.3701	0.7033	0.4834	0.1529	0.2185
Month	3	0.0024	0.5058	0.1740	0.0058	0.0202	0.0139
Site x Month	3	-	0.5381	0.0934	0.1713	0.4984	0.8253
			Mean square				
Error a	2	-	0.0016	0.0029	8.53E-4	7.30E-4	4.00E-4
Error b	6	-	9.01E-4	7.02E-4	3.25E-4	8.82E-4	8.02E-4

[1] Values tested using the Kruskal-Wallis test

Table 4.26. Means values (±SE) of the relative number of families of arthropods from guilds that varied significantly among month from four northern hardwood sites.

Guild	May	June	July	August	F ratio	P value
Ants 1994[1]	0.0 (0.0)	2.0 (0.2)	1.6 (0.5)	2.3 (0.8)	χ^2=20.75	0.000
Ants 1995[1]	0.0 (0.0)	1.4 (0.1)	2.5 (0.1)	3.0 (0.8)	χ^2=14.37	0.002
Predators 1993[1]	44.4 (2.2)	24.6 (0.8)	22.1 (1.8)	23.8 (1.9)	χ^2=6.64	0.028
Sap Feeders 1994	1.7 (1.7)	5.0 (0.7)	7.4 (1.3)	8.7 (1.6)	5.63	0.035
Sap Feeders 1995	3.8 (1.5)	8.1 (1.2)	10.1 (1.0)	13.4 (1.6)	7.25	0.020
Tissue Feeders 1995	21.2 (1.6)	18.7 (1.0)	15.7 (0.5)	14.1 (1.2)	12.20	0.058
Saprophages 1994	37.1 (5.5)	21.1 (2.4)	25.0 (0.4)	27.1 (2.8)	6.16	0.029
Saprophages 1995	35.7 (1.6)	27.2 (0.4)	29.6 (1.2)	26.7 (1.5)	8.53	0.014

[1] Monthly variation was tested with the Kruskal-Wallace test.

Table 4.27. Statistical significance of treatment effects from split-plot ANOVA of the relative number of families within five feeding guilds in four northern hardwood sites over three years.

Source of Variation	df	Parasitoids	Predators	Tissue-Feeders	Sap-Feeders	Saprophages
		F value of significant treatment effects				
Site	1	χ^2= 1.59	1.412	χ^2= 0.33	1.923	0.000
Year	2	χ^2= 7.54	0.108	χ^2= 3.08	1.965	15.689
Site x Year	2	-	0.015	-	0.183	0.6718
		Probability of significant treatment effects				
Site	1	0.2069	0.3567	0.5632	0.2993	0.9952
Year	2	0.0231	0.9001	0.2142	0.2544	0.0128
Site x Year	2	-	0.9854	-	0.8396	0.5604
		Mean square				
Error a	2	-	0.1980	-	1.2265	6.6931
Error b	4	-	9.7993	-	2.8246	1.6386

Table 4.28. Statistical significance of treatment effects of ecosystem and year from split-plot ANOVA of the relative number of families within five feeding guilds.

Source of Variation	df	Parasitoids	Predators	Tissue-Feeders	Sap-Feeders	Saprophages
		F value of significant treatment effects				
Ecosystem	1	3.514	0.010	0.156	0.740	13.009
Year	2	6.663	1.316	1.522	4.282	4.066
Ecosystem x Year	2	2.657	1.077	0.300	0.370	1.269
		Probability of significant treatment effects				
Ecosystem	1	0.1100	0.9257	0.7065	0.4228	0.0113
Year	2	0.0115	0.3042	0.2575	0.0395	0.0448
Ecosystem x Year	2	0.1109	0.3713	0.7465	0.6987	0.3162
		Mean square				
Error a	6	4.2087	6.2561	8.6454	1.8736	2.4897
Error b	12	2.7176	7.8309	6.6115	0.1689	5.8398

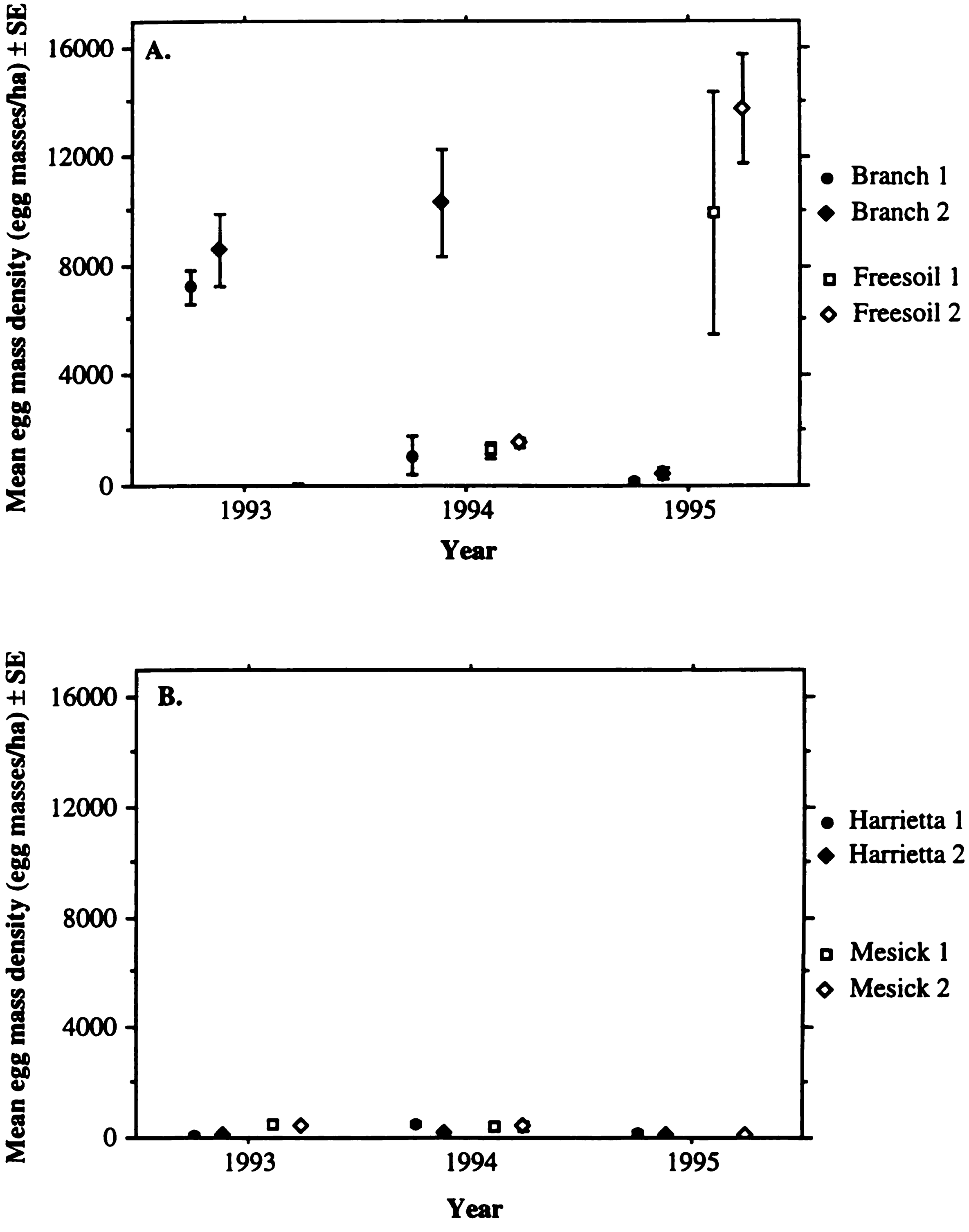


Figure 4.1. Mean density (±SE) of gypsy moth egg masses from four sites in A) red oak ecosystems (ELTP 20) and four sites in B) northern hardwood ecosystems (ELTP 45). Means were calculated from five 0.1 ha fixed-radius plots

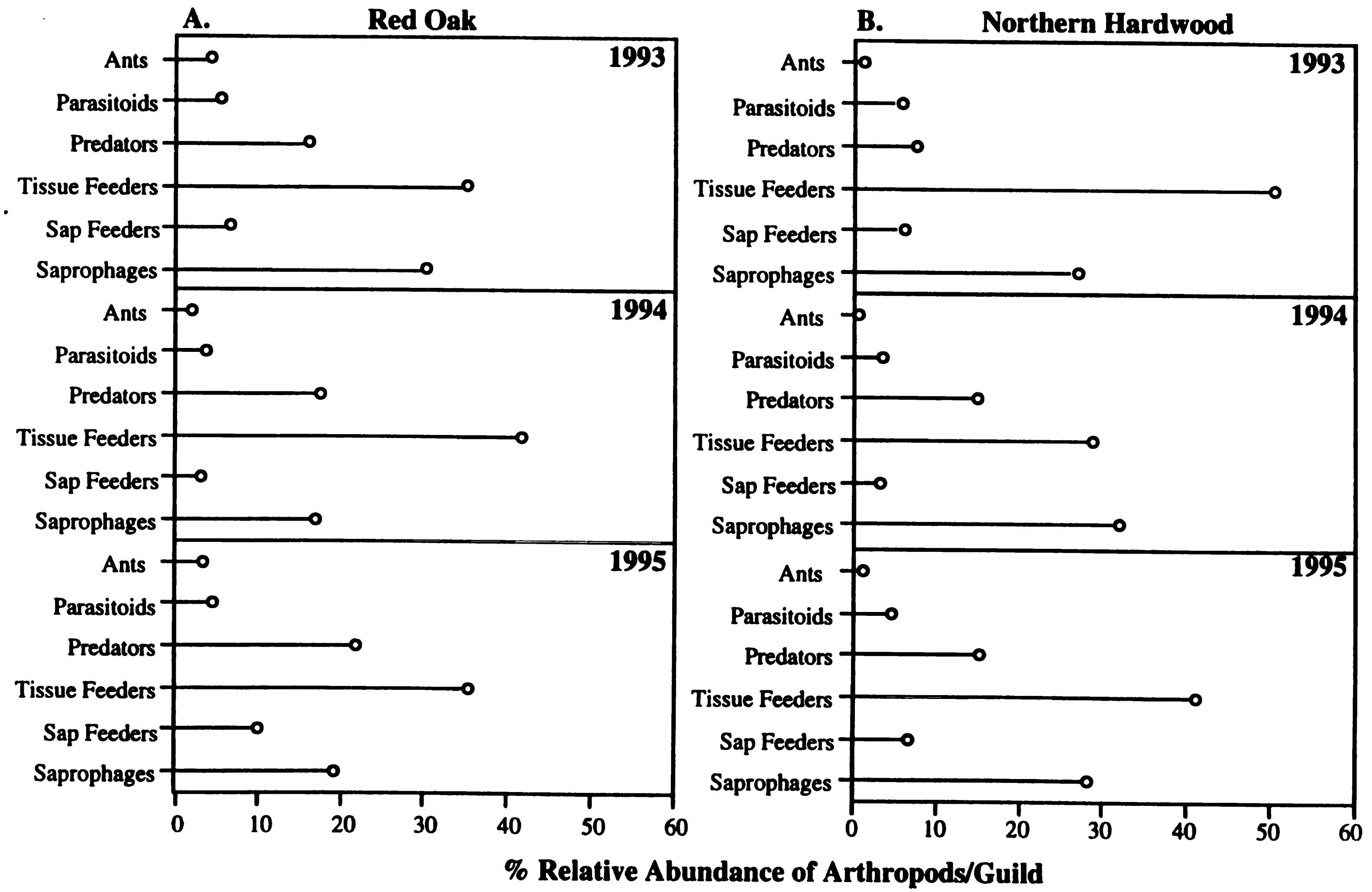


Figure 4.2. Relative number of arthropods within six feeding guilds collected from four red oak and four northern hardwood sites from 1993 to 1995.

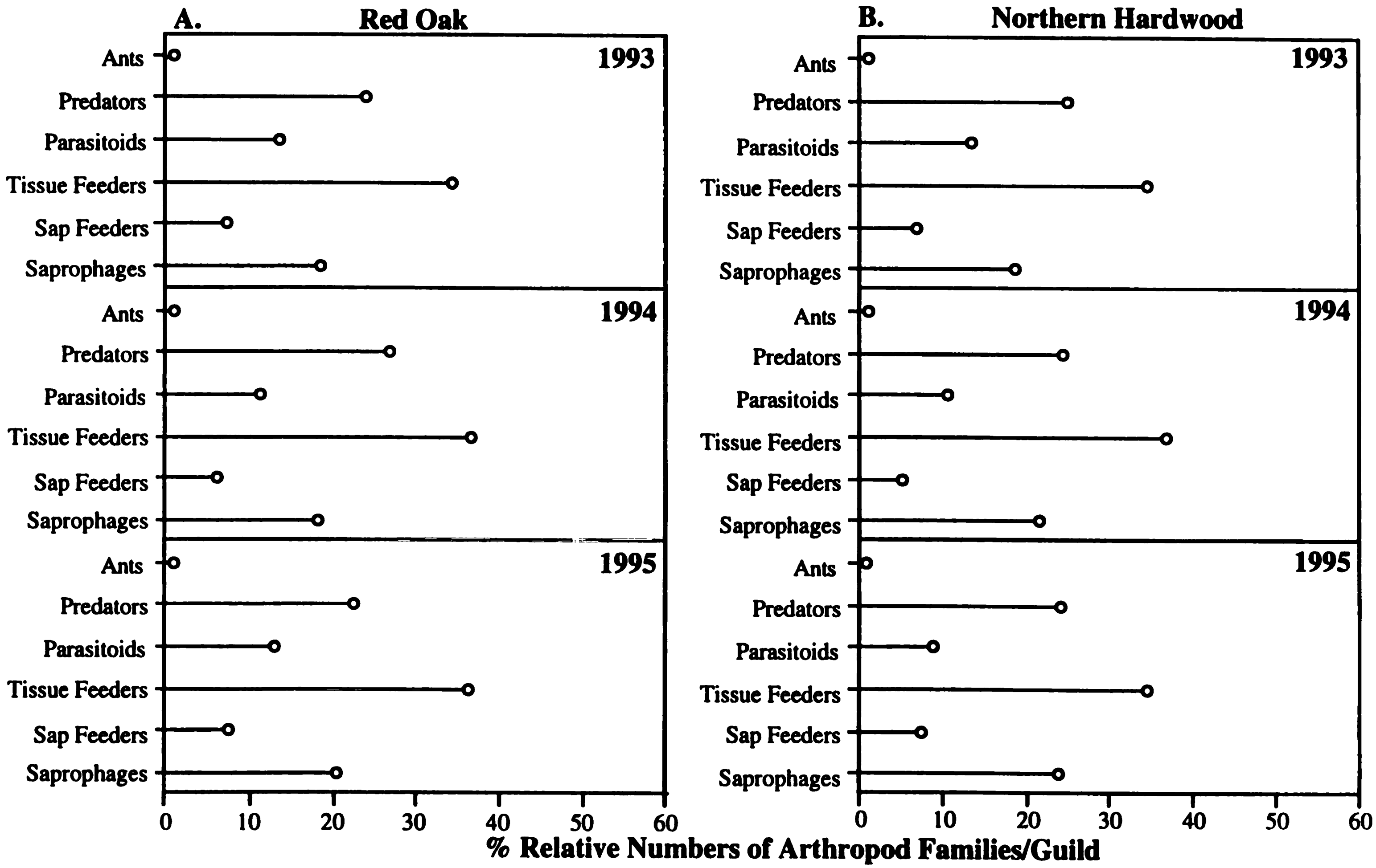


Figure 4.3. Relative proportions of arthropod families within six feeding guilds collected from four red oak and four northern hardwood sites from 1993 to 1995.

APPENDICES

APPENDIX A

Appendix A

Table A1. Total number of Noctuid species collected from four red oak sites and four northern hardwood sites over three years.

	Red Oak			Northern Hardwood		
	1993	1994	1995	1993	1994	1995
Abagrotis alternata (Grt.)	-	1	1	1	1	2
Achatia distincta Hbn.	19	1	3	-	1	4
Achatia spp.	1	-	-	-	-	-
Acronicta dactylina Grt.	-	-	-	1	-	-
Acronicta haesitata (Grt.)	-	4	1	-	2	-
Acronicta hamamelis Gn.	-	2	-	-	1	-
Acronicta hasta Gn.	-	1	-	-	-	2
Acronicta impleta Wlk.	-	-	1	-	-	-
Acronicta inclara Sm.	1	1	3	-	-	1
Acronicta increta Morr.	3	3	-	-	1	1
Acronicta modica Wlk.	-	-	2	-	-	1
Acronicta morula G. & R.	-	1	-	-	-	1
Acronicta ovata Grt.	12	2	3	-	-	-
Acronicta tritona (Hbn.)	-	1	-	-	-	-
Agriopodes fallax (H. -S.)	1	1	-	-	1	-
Agriopodes teratophora (H. -S.)	-	1	-	-	1	-
Agrotis ipsilon (Hufn.)	1	-	-	-	-	1
Amphipoea americana (Speyer)	-	-	1	-	-	-
Amphipoea velata (Wlk.)	-	-	1	-	-	-
Amphipyra tragopoginis (Cl.)	-	-	-	1	-	-
Anagrapha falcifera (Kby.)	1	-	-	-	-	-
Anaplectoides prasina (D. & S.)	-	2	-	-	1	1
Anathix ralla (G. & R.)	-	-	-	1	-	-
Autographa precationis (Gn.)	-	-	-	-	-	-
Baileya australis (Grt.)	-	-	-	1	-	-
Baileya ophthalmica (Gn.)	-	1	-	2	1	1
Bleptina caradirinalis Gn.	-	-	2	1	-	1
Bomolocha baltimoralis (Gn.)	-	1	2	-	-	1
Bomolocha deceptalis (Wlk.)	-	-	-	-	1	1
Bomolocha madefactalis (Gn.)	-	-	-	-	-	1
Callopistria cordata (Ljungh)	1	3	4	1	2	3
Callopistria mollissima (Gn.)	-	-	-	-	1	-
Catocala amica (Hbn.)	-	-	2	-	-	-

Table A1. (cont'd)

Catocala antinympha (Hbn.)	-	-	1	-	-	-
Catocala ilia (Cram.)	-	-	1	-	-	-
Catocala unijuga Wlk.	-	-	-	-	-	1
Cerastis tenebrifera (Wlk.)	-	-	-	-	-	4
Charadra deridens (Gn.)	-	-	-	-	-	1
Chrysanympha formosa (Grt.)	1	-	-	-	-	-
Chytonix palliatricula (Gn.)	2	3	2	6	2	3
Cissusa spadix (Cram.)	8	2	3	-	3	2
Copivaleria grotei (Morr.)	-	-	-	-	-	1
Cosmia calami (Harv.)	11	3	-	-	2	-
Crocigrapha normani (Grt.)	9	-	1	1	-	4
Crymodes devastator (Brace)	-	-	-	-	-	-
Cryphia pallida (B. & L.)	-	1	-	-	1	-
Egira alternans (Wlk.)	1	-	1	-	-	-
Egira dolosa Grt.	43	3	-	-	3	2
Elaphria festivoides (Gn.)	8	4	3	17	4	4
Elaphria georgii (Moore & Rawson)	9	1	1	-	1	-
Elaphria veriscolor (Grt.)	-	-	-	-	1	-
Enargia decolor (Wlk.)	1	-	-	-	-	-
Eueretagrotis attenta (Grt.)	-	-	1	-	-	-
Euplexia benesimilis McD.	-	-	1	-	1	-
Eupsilia morrisoni (Grt.)	-	-	-	-	-	-
Eupsilia tristigmata (Grt.)	-	1	-	-	1	-
Eutolype rolandi Grt.	24	-	-	-	-	-
Euxoa declarata (Wlk.)	-	-	1	-	-	-
Euxoa messoria (Harr.)	-	-	-	1	-	-
Euxoa perpolita (Morr.)	-	-	-	1	-	-
Euxoa redimicula (Morr.)	-	-	-	1	-	-
Euxoa tessellata (Harr.)	-	3	-	-	2	3
Feltia geniculata G. & R.	2	-	-	1	1	1
Feltia jaculifera (Gn.)	-	-	-	1	1	1
Galgula partita Gn.	-	1	-	-	1	-
Graphiphora haruspica (Grt.)	-	-	-	-	1	-
Hadeninae spp.	-	-	-	2	-	-
Homohadena infixa (Wlk.)	-	-	-	-	-	1
Homorthodes furfurata (Grt.)	6	-	-	35	2	-
Hypenodes caducus (Dyar)	1	-	-	-	-	-
Hypenodes fractilinea (Sm.)	72	1	3	2	2	2
Hypenodes sombrus Fgn.	-	-	-	-	1	-
Hypenodes spp.	13	3	1	1	3	-
Hyperstrotia pervertens (B. & McD.)	-	1	3	-	1	-

Table A1. (cont'd.)

Hyperstrotia villificans (B. & McD.)	-	1	-	-	1	-
Hyppa xylinoides (Gn.)	-	-	-	-	1	-
Idia aemula Hbn.	2	-	1	7	1	4
Idia americalis (Gn.)	8	2	-	-	2	-
Idia diminuendis (B. & McD.)	10	1	-	-	1	-
Idia julia (B. & McD.)	21	2	1	-	-	-
Idia lubricalis (Gey.)	1	-	-	-	-	-
Idia new species	-	-	-	-	1	-
Idia rotundalis (Wlk.)	20	-	3	1	-	-
Ipimorpha pleonectusa Grt.	-	-	1	1	-	1
Lacanobia lilacina (Harr.)	-	-	-	-	-	1
Lacinipolia implicata McD.	-	-	1	-	-	1
Lacinipolia lorea (Gn.)	-	-	-	-	-	1
Lacinipolia lustralis (Grt.)	-	-	1	-	-	-
Lacinipolia meditata (Grt.)	-	-	-	1	-	2
Lacinipolia olivacea (Morr.)	-	1	-	6	1	-
Lacinipolia renigera (Steph.)	-	-	-	2	-	-
Lacinipolia vicina (Grt.)	-	-	-	-	-	1
Leucania commoides Gn.	-	-	-	-	1	-
Leucania pseudargyria Gn.	-	1	1	-	1	1
Leuconycta dipteroides (Gn.)	-	1	-	-	-	1
Lithacodia albidula (Gn.)	1	1	1	1	-	1
Lithacodia carneola (Gn.)	-	1	1	3	2	2
Lithacodia concinnimacula (Gn.)	-	-	-	1	-	2
Lithacodia muscosula (Gn.)	-	-	1	-	-	3
Lithacodia synochitis (G. & R.)	-	-	2	-	-	4
Lithophane hemina Grt.	-	-	-	-	1	-
Lithophane innominata (Sm.)	-	-	-	-	-	-
Lithophane patefacta (Wlk.)	2	-	-	-	-	-
Lithophane petulca Grt.	1	-	-	-	-	1
Lithophane semiusta Grt.	-	-	-	-	-	4
Lithophane spp.	2	-	-	-	-	-
Marathyssa inficita (Wlk.)	-	-	-	-	-	1
Meganola minuscula (Zell)	15	3	3	-	2	1
Melanchra adjuncta (Gn.)	-	-	-	1	-	-
Melipotus spp.	1	-	-	-	-	-
Morrisonia confusa (Hbn.)	-	-	-	-	1	-
Morrisonia evicta (Grt.)	-	-	-	-	1	2
Nedra ramosula (Gn.)	-	1	1	-	-	2
Nephelodes minians Gn.	-	-	-	1	-	-
Nigetia formosalis Wlk.	-	1	2	-	-	-

Table A1. (cont'd.)

Noctuidae 1	-	-	-	-	-	1
Noctuidae 2	-	-	-	-	-	1
Noctuidae 3	-	-	1	-	-	-
Noctuinae spp.	1	-	-	-	-	-
Nolinae spp.	1	-	-	-	-	-
Ochropleura plecta (L.)	1	-	1	-	-	-
Oligia exhausta (Sm.)	-	-	-	-	1	-
Orthodes crenulata (Butler)	-	-	-	3	-	-
Orthodes cynica Gn.	-	2	2	4	2	4
Orthodes spp.	-	2	-	-	1	-
Orthosia hibisci (Gn.)	-	-	2	-	-	3
Orthosia revicta (Morr.)	-	-	-	-	-	1
Orthosia rubescens (Wlk.)	-	1	-	-	2	-
Palthis angulalis (Hbn.)	4	-	-	-	-	-
Peridroma saucia (Hbn.)	-	1	-	-	1	-
Phlogophora iris Gn.	-	-	1	1	-	-
Phlogophora perculosa Gn.	-	-	-	4	-	1
Phoberia atomaris Hbn.	16	1	1	-	-	-
Plathypena scabra (F.)	-	-	1	-	-	-
Polia delecta B. & McD.	-	-	-	-	-	-
Polia detracta (Wlk.)	1	-	1	4	-	-
Polia latex (Gn.)	-	-	-	3	-	-
Polia nimbosa (Gn.)	-	-	1	-	-	-
Protorthodes oviduca (Gn.)	1	7	1	-	3	1
Proxenus miranda (Grt.)	-	-	1	-	-	-
Psaphida resumens Wlk.	1	-	2	-	-	-
Pseudorthodes vecors (Gn.)	-	-	-	-	-	4
Pyreferra ceromatica (Grt.)	1	-	-	-	-	-
Raphia frater Grt.	3	4	2	1	2	-
Rhynchagrotis adulta (Gn.)	-	-	-	2	-	-
Rhynchagrotis anchoceloides (Gn.)	-	1	-	1	2	-
Rhynchagrotis cupida (Grt.)	-	-	-	1	-	3
Rivulinae spp.	5	-	-	-	-	-
Schinia arcigera (Gn.)	-	-	1	-	-	-
Spaelotis clandestina (Harr.)	-	-	-	-	-	2
Spodoptera frugiperda (J. E. Smith)	-	-	1	-	-	-
Sunira bicolorago (Gn.)	-	-	1	1	-	4
Synedoida grandirena (Haw.)	1	2	-	-	-	1
Tarachidia erastrioides (Gn.)	-	-	-	1	-	-
Ulolonche culea (Gn.)	22	4	3	-	2	2
Ulolonche modesta (Morr.)	1	-	-	-	1	2

Table A1. (cont'd.)

Xestia adela Franc.	-	-	-	2	-	-
Xestia dolosa Franc.	-	1	-	-	-	4
Xestia normaniana (Grt.)	1	-	-	12	-	3
Xestia smithii (Snell)	-	-	-	1	-	-
Xestia tenuicula (Morr.)	-	-	-	1	-	-
Xestia spp.	-	-	-	1	-	-
Zale duplicata (Bethune)	-	-	1	-	-	-
Zale helata (Sm.)	-	-	1	-	-	-
Zale lunifera (Hbn.)	-	-	-	-	-	1
Zale minerea (Gn.)	-	-	1	-	1	3
Zale submediana Strand	-	-	-	-	-	2
Zale undularis (Drury)	1	-	-	-	-	-
Zale unilineata (Grt.)	1	1	-	-	-	1
Zanclognatha jacchusalis (Wlk.)	2	-	-	-	2	1
Zanclognatha laevigata (Grt.)	-	-	-	2	2	4
Zanclognatha ochreipennis (Grt.)	4	-	-	1	-	-
Zanclognatha pedipilalis (Gn.)	-	-	1	-	-	-
Unidentified species	107	1	-	4	-	-

APPENDIX B

Appendix B

Table B1. Total number of Tortricid species collected from four red oak sites and four northern hardwood sites over three years.

	Red Oak			Northern Hardwood		
	1993	1994	1995	1993	1994	1995
Acleris 1	-	-	1	-	-	-
Acleris 2	-	-	1	-	-	-
Acleris forbesana (McD.)	-	-	-	2	-	-
Acleris oxycoccana (Pack.)	-	-	-	3	-	-
Acleris spp.	17	-	-	163	-	-
Ancylis burgessiana (Zell)	1	1	-	-	1	1
Ancylis fuscociliana (Clem.)	-	-	1	-	-	1
Ancylis metamelana (Wlk.)	1	-	-	-	-	-
Ancylis nubeculana (Clem.)	-	1	-	-	-	-
Archips argyrospila (Wlk.)	44	3	4	2	1	3
Archips cerasivorana (Fitch)	-	-	1	1	-	1
Archips fervidana (Clem.)	37	-	-	1	-	-
Archips purpurana (Clem.)	6	-	-	5	-	-
Archips rosana (L.)	69	-	-	4	-	-
Archips semiferana (Wlk.)	-	1	2	-	-	1
Argyrotaenia alisellana (Rob.)	-	-	1	-	-	-
Argyrotaenia mariana (Fern.)	-	-	1	-	-	1
Argyrotaenia quercifoliana (Fitch)	40	2	4	1	-	-
Argyrotaenia spp.	-	-	-	5	-	-
Choristoneura conflictana (Wlk.)	-	-	-	-	-	2
Choristoneura fractivittana (Clem.)	2	2	-	-	-	1
Choristoneura fumiferana (Clem.)	-	-	-	5	-	-
Choristoneura obsoletana (Wlk.)	7	-	-	-	-	-
Choristoneura pinus Free.	-	2	-	-	-	-
Choristoneura rosaceana (Harr.)	22	4	4	313	4	4
Choristoneura spp.	6	-	-	-	-	-
Clepsis melaleucana (Wlk.)	-	1	-	391	3	4
Clepsis persicana (Fitch)	-	-	-	-	-	2
Croesia albicomana (Clem.)	12	-	1	-	-	-
Croesia semipurpurana (Kft.)	-	1	-	-	-	-
Ecdytolopha punctidiscana (Dyar)	-	1	-	-	1	-
Epinota timidella (Clem.)	-	1	-	-	-	-
Eucosma dorsisignatana (Clem.)	-	-	1	-	-	-
Melissopus lariferreanus Wlsm.	1	-	1	2	-	1

Table B1. (cont'd.)

Olethreutes 1	-	-	1	-	-	4
Olethreutes 2	-	-	2	-	-	2
Olethreutes 3	-	-	-	-	-	1
Olethreutes 4	-	-	-	-	-	1
Olethreutes fasciatana (Clem.)	11	-	4	7	-	3
Olethreutes nigrana (Heinr.)	1	-	-	-	-	-
Olethreutes permundana (Clem.)	4	1	-	-	2	-
Olethreutes spp.	100	2	-	34	1	-
Olethreutinae spp.	5	4	29	3	4	45
Olethreutres footiana (Fern.)	1	-	-	-	-	-
Olethruete appendicea (Zell)	1	-	-	-	-	-
Pandemis canadana Kft.	-	-	-	-	-	1
Pandemis limitata (Rob.)	-	-	1	-	-	-
Petrova gemistrigulana (Kft.)	-	-	2	-	-	-
Phaneta raracana (Kft.)	1	-	-	-	-	-
Platynotus idaeusalis (Wlk.)	-	-	2	3	-	-
Proteoteras aesculana (Riley)	-	-	-	-	1	-
Proteoteras moffatiana Fern.	-	-	-	73	-	2
Pseudexentera costomaculana (Clem.)	-	-	1	-	-	-
Pseudosciaphila duplex (Wlsm.)	1	-	-	-	-	2
Pytcholoma peritana (Clem.)	-	4	4	27	3	4
Sparganothis diluticostana (Wlsm.)	-	-	-	-	1	1
Sparganothis directana (Wlk.)	3	-	-	-	-	-
Sparganothis niveana (Wlsm.)	-	-	-	2	-	-
Sparganothis pettitana (Rob.)	14	2	1	343	2	2
Sparganothis reticulatana (Clem.)	1	-	4	3	1	4
Sparganothis sulfureana (Clem.)	-	-	-	2	-	-
Sparganothis tristriata Kft.	-	-	-	3	-	-
Sparganothis xanthoides (Wlk.)	-	1	-	-	1	-
Sparganothis spp.	1	-	-	-	-	-
Spargonothis unifasciana (Clem.)	-	-	1	-	-	-
Syndemis afflictana (Wlk.)	-	1	-	-	-	-
Tortricinae	-	3	21	-	3	15
Unidentified species	114	-	-	51	-	-

APPENDIX C

Appendix C

Table C1. Total number of Geometrid species collected from four red oak sites and four northern hardwood sites over three years.

	Red Oak			Northern Hardwood		
	1993	1994	1995	1993	1994	1995
Anavitrinelia pampinaria (Gn.)	-	-	1	3	-	2
Besma endropiaria (G. & R.)	-	-	-	4	-	-
Besma quercivoraria (Gn.)	1	-	1	1	-	-
Biston betularia (L.)	-	1	-	-	-	1
Cabera variolaria Gn.	1	-	-	1	-	-
Cabera spp.	1	-	-	-	-	-
Campaea perlata (Gn.)	5	-	-	12	-	1
Caripeta divisata Wlk.	-	-	1	-	-	-
Cladara anguilineata (G. & R.)	-	-	-	-	-	-
Cladara atroliturata (Wlk.)	-	-	-	-	-	2
Cladara limitaria (Wlk.)	-	-	-	-	-	1
Cleora projecta (Wlk.)	-	-	1	-	-	-
Ectropis crepuscularia (D. & S.)	1	-	-	-	-	-
Ennominae spp.	1	-	-	-	-	-
Ennomos subsignaria (Hbn.)	-	1	-	5	-	-
Eubaphe mendica (Wlk.)	-	-	-	1	-	-
Euchlaena johnsonaria (Fitch)	-	-	-	-	-	1
Euchlaena tigrinaria (Gn.)	-	-	-	-	1	-
Eugonobapta nivosaria (Gn.)	-	-	-	3	-	-
Eupithecia spp.	3	3	2	3	4	4
Geometridae 1	-	-	2	-	2	1
Geometridae 2	-	2	-	-	2	1
Geometridae 3	-	2	-	-	-	1
Geometridae 4	-	2	1	-	2	-
Geometridae 5	-	1	1	-	1	-
Geometridae 6	-	-	1	-	1	-
Geometridae 7	-	1	-	-	1	-
Geometridae 8	-	1	-	-	1	-
Heliomata cycladata G. & R.	-	1	-	-	1	1
Hydria prunivorata (Fgn.)	-	-	-	-	-	3
Hydria spp.	-	-	-	-	1	-
Hydromena spp.	118	2	3	-	2	-
Itame argillacearia (Pack.)	-	-	1	-	-	-

Table C1. (cont'd.)

Itame coortaria (Hulst)	-	-	3	-	-	1
Itame evagairia (Hulst)	1	1	-	-	1	-
Itame pustularia (Gn.)	31	2	-	-	1	-
Lobophora montanata Pack.	-	-	-	1	-	-
Lomographa glomeraria (Grt.)	-	1	-	-	2	4
Lomographa semiclarata (Wlk.)	-	-	1	1	-	-
Lomographa vestaliata (Gn.)	-	2	-	2	1	1
Melanolophia canadaria (Gn.)	-	-	-	-	-	2
Metanema inatomaria Gn.	1	-	-	-	-	-
Metarranthis refractaria (Gn.)	1	-	-	-	-	-
Nematocampa limbata (Haw.)	-	-	-	2	-	3
Nepytia canosaria (Wlk.)	1	-	1	-	-	-
Orthonama centrostrigaria (Woll.)	-	-	-	2	-	4
Orthonama obstipata (F.)	-	-	-	-	-	1
Pero hubneraria (Gn.)	-	1	-	-	-	-
Plagodis alcoolaria (Gn.)	-	1	3	6	-	2
Plagodis fervidaria (H. -S.)	3	-	-	-	-	-
Plagodis phlogosaria (Gn.)	-	1	-	-	3	4
Plagodis serinaria H. -S.	1	-	-	3	-	-
Plagodis spp.	1	-	-	1	-	-
Probole alienaria H. -S.	-	-	-	-	-	1
Protitame virginalis (Hulst)	1	-	-	-	-	-
Protoboarmia porcelaria (Gn.)	-	-	1	-	-	2
Scopula inductata (Gn.)	-	-	3	-	-	2
Scopula limboundata (Haw.)	1	-	-	-	-	-
Semiothisa bisignata (Wlk.)	1	-	2	-	-	-
Semiothisa ocellinata (Gn.)	-	-	-	-	-	1
Synchlora aerata (F.)	-	-	1	-	-	-
Tetracis cachexiata Gn.	-	1	2	-	1	3
Tetracis crocallata Gn.	-	-	-	7	1	-
Xanthorhoe ferrugata (Cl.)	-	-	1	-	-	-
Unidentified species	46	4	-	10	4	-

APPENDIX D

Appendix D

Table D1. Total number of Pyralid species collected from four red oak sites and four northern hardwood sites over three years.

	Red Oak			Northern Hardwood		
	1993	1994	1995	1993	1994	1995
Acentria nivea (Olivier)	1	-	-	5	-	-
Acrobasis spp.	-	-	2	-	-	2
Aethiophysa lentiflualis (Zell.)	1	-	-	-	-	-
Aglossa cuprina Zell.	9	-	3	1	-	-
Blephanomastix ranalis (Gn.)	-	4	-	-	2	-
Chrysoteuchia topiaria (Zell.)	2	-	-	-	-	-
Crambinae 1	2	-	-	4	-	-
Crambinae 2	-	1	-	-	2	-
Crambinae 3	-	1	-	-	-	-
Crambinae spp.	-	1	-	-	-	-
Crambus agitatellus Clem.	-	-	3	-	-	3
Crambus albellus Clem.	1	-	1	-	-	2
Crambus spp.	-	-	-	1	-	-
Eulogia ochrifrontella (Zell.)	14	2	1	-	1	1
Fumibotys fumalis (Gn.)	-	-	-	1	-	1
Herculia olinalis (Gn.)	1	1	2	-	2	-
Herpetogramma pertextalis (Led.)	-	1	-	-	1	-
Microcrambus elegans (Clem.)	1	-	-	1	-	-
Munroessa gyralis (Hulst)	-	-	2	-	-	-
Munroessa icciusalis (Wlk.)	1	-	3	1	-	1
Nephopterix vetustella (Dyar)	-	1	-	-	2	3
Nephopterix virgatella (Clem.)	-	-	-	-	-	2
Nephopterix spp.	-	-	-	-	-	-
Nymphalinae spp.	-	1	-	-	1	3
Oneida lunulalis (Hulst)	-	-	1	-	-	-
Ostrinia nubilalis (Hbn.)	-	-	4	-	-	1
Palpita arsaltealis (Wlk.)	-	-	-	-	-	-
Parapoynx maculalis (Clem.)	-	-	2	-	-	-
Petrophilia fulicalis (Clem.)	-	-	-	-	-	1
Phycitinae spp.	11	-	-	2	1	1
Platytes vobisne Dyar	-	-	-	4	-	1
Pyla fusca (Haw.)	-	-	2	-	-	1
Pyralidae 1	-	-	-	1	-	1

Table D1. (cont'd.)

Pyralidae 2	-	-	2	-	-	-
Pyralidae 3	-	-	-	-	-	1
Pyralidae 4	-	-	-	-	-	1
Pyralidae 5	-	-	-	-	-	-
Pyralidae 6	-	-	-	-	-	-
Pyralidae 7	-	-	1	-	-	4
Pyrausta acrionalis (Wlk.)	-	-	-	-	-	-
Pyrausta signatalis (Wlk.)	-	1	-	-	1	-
Pyrausta spp.	-	1	-	-	-	-
Pyraustinae 1	-	-	-	-	-	-
Pyraustinae 2	-	-	1	-	-	-
Salebriaria turpidella (Rag.)	-	-	-	1	-	-
Scoparia basalis Wlk.	-	-	3	-	-	-
Scoparia biplagialis Wlk.	3	-	-	-	-	-
Scoparia spp.	1	-	-	-	-	-
Scoparia/Eudonia spp.	7	1	4	38	-	-
Scoparinae spp.	-	4	-	-	4	-
Sitochroa chortalis (Grt.)	1	-	-	-	-	-
Synclita tinealis Mun.	-	-	2	-	-	-
Thaumatopsis gibsonella Kft.	-	-	1	-	-	-
Udea rubigalis (Gn.)	-	-	-	1	-	-
Urola nivalis (Drury)	1	-	-	-	-	-
Unidentified species	8	2	-	5	3	-

APPENDIX E

Appendix E

Table E1. List of species collected from families other than Noctuidae, Tortricidae, Geometridae, and Pyralidae.

Agonoxenidae *Glyphipteryx linneella* (Bsk.)
Arctiidae *Apantesis parthenice* (W. Kirby)
Arctiidae *Clemensia albata* Pack.
Arctiidae *Crambidia pallida* Pack.
Arctiidae *Cycnia oregonensis* (Stretch)
Arctiidae *Dryocampa rubicunda* (F.)
Arctiidae *Halysidota tesselaria* (J. E. Smith)
Arctiidae *Haploa reversa* (Stretch)
Arctiidae *Holomelina aurantiaca* (Hbn.)
Arctiidae *Hypoprepia fucosa* Hbn.
Arctiidae *Phragmatobia assimilans* Wlk.
Arctiidae *Spilosoma congrua* Wlk.
Arctiidae spp.
Argyresthiidae *Argyresthia oreasella* Clem.
Argyresthiidae spp.
Blastobasidae *Gerdana caritella* Bsk.
Blastobasidae spp.
Cochylidae spp.
Coleophoridae *Batrachedrinae* spp.
Coleophoridae spp.
Cosmopterigidae *Euclemensia bassettella* (Clem.)
Cosmopterigidae spp.
Cossidae *Acossus centerensis* (Lint.)
Decophoridae spp.
Drepanidae *Drepana arcuata* Wlk.
Eriocraniidae *Mnemonica auricyanea* (Wlsm.)
Eriocraniidae spp.
Gelechiidae *Aristotelia* spp.
Gelechiidae *Chionodes* spp.
Gelechiidae *Coleotechnites* spp.
Gelechiidae *Dichomeris ligulella* Hbn.

Table E1. (cont'd.)

Gelechiidae *Dichomeris* spp.
Gelechiidae spp.
Gelechiidae *Trichotaphe setosilla* Clem.
Gelechiidae *Walshia* spp.
Gelechioid spp.
Glyphipterigidae *Abrenthia cuprea* Bsk.
Gracillariidae *Caloptilia* spp.
Gracillariidae spp.
Hesperiidae *Erynnis brizo* (Bdv. & LeConte)
Hesperiidae *Poanes hobomok* (Harr.)
Hydroptilidae spp.
Lasiocampidae *Malacosoma americanum* F.
Lasiocampidae *Malacosoma disstria* Hbn.
Lasiocampidae *Phyllodesma americana* (Harr.)
Lasiocampidae spp.
Limacodidae *Apoda biguttata* (Pack.)
Limacodidae *Lithacodes fasciola* (H. -S.)
Limacodidae spp.
Limacodidae *Tortricidia flexuosa* (Grt.)
Limacodidae *Tortricidia pallida* (H. -S.)
Limacododae *Lithacodes testacea* Pack.
Lymantriidae *Lymantria dispar* (L.)
Lymantriidae *Orygia leucostigma* (J. E. Smith)
Lymantriidae *Orygia*
Lymantriidae spp.
Lyonetiidae *Bucculatrix*
Lyonetiidae spp.
Nepticulidae spp.
Notodontidae *Dasylopha thytiroides* (Wlk.)
Notodontidae *Ellidia caniplaga* (Wlk.)
Notodontidae *Furcula modesta* (Hudson)
Notodontidae *Gluphisia septentrionalis* Wlk.
Notodontidae *Heterocampa guttivita* (Wlk.)
Oecophoridae *Polex coloradella* (Wlsm.)

Table E1 (cont'd.)

Oecophoridae *Psilocorsis spp.*
Oecophoridae *Semiosopis inornata* Wlsm.
Oecophoridae spp.
Olenthreutinae spp.
Pieridae *Phoebis sennae* (L.)
Plutellidae *Plutella xylostella* (L.)
Psychidae spp.
Satyridae *Megisto cymela* (Cram.)
Sesiidae *Syanthedon acerni* (Clem.)
Sphingidae *Ceratomia undulosa* (Wlk.)
Sphingidae *Pachysphinx modesta* (Harr.)
Sphingidae *Paonias excaecatus* (J. E. Smith)
Sphingidae *Paonis myops* (J. E. Smith)
Sphingidae *Sphecodina abbottii* (Swainson)
Thyatiridae *Euthyatira pudens* (Gn.)
Tineidae *Acrolophus* spp.
Tineidae spp.
Tinieoid spp.
Yponomeutidae *Atteva punctella* (Cram.)
Yponomeutidae *Yponomeuta multipunctella* Clem.
Yponomeutidae *Zelleria haimbachi* Bsk.
Zygaenidae spp.

APPENDIX F

APPENDIX F

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1996-6

Title of thesis or dissertation (or other research projects):

THE IMPACTS OF GYPSY MOTH (LEPIDOPTERA:LYMANTRIIDAE) ON NATIVE ARTHROPOD ABUNDANCE, SPECIES RICHNESS, AND DIVERSITY IN TWO HARDWOOD ECOSYSTEMS IN NORTHERN LOWER MICHIGAN

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)
Timothy Theron Work

Date 8/1/96

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original:	Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies:	Included as Appendix 1 in copies of thesis or dissertation. Museum(s) files. Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX F

Voucher Specimen Data

Page 1 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited		Number of:							
			Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Carabus limbatus	16 AUG 1994	15 JUN 1994								
	22 AUG 1995	11 MAY 1994								
	20 MAY 1994	11 MAY 1994								
	20 MAY 1994	11 AUG 1995								
	27 MAY 1993	22 AUG 1995								
	20 JUN 1995	11 MAY 1994								
	13 JUN 1995	22 AUG 1995								
	17 MAY 1995	20 MAY 1994								
	20 MAY 1994	22 AUG 1995								
	20 MAY 1994	20 MAY 1994								
	17 MAY 1995	17 MAY 1995								
	13 JUN 1995									
Calosoma frigidum	15 JUN 1994	15 JUN 1994								
Calosoma sycophanta	13 JUL 1994									
Carabus sylvosus	22 AUG 1995									
Carabus serratus	13 JUN 1995									
Dicaelus teter	21 JUN 1994	21 JUN 1994								
Harpalus lewisi	21 JUN 1994	20 JUN 1995								
	21 JUN 1994									
Agonum sordens	15 AUG 1995									

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 2 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Cymindis platicollis	19 JUL 1994 13 JUN 1995 21 JUN 1994 22 MAY 1995 22 AUG 1995								
Cymindis limbatus	22 JUN 1995 15 AUG 1995 21 JUL 1993 21 JUN 1994 11 AUG 1995								
Cymindis cribicollis	21 JUN 1994								
Cymindis americana	20 JUL 1994								
Cymindis pilosa	12 JUL 1994								
Calathus gregarius	22 JUL 1993 21 JUL 1993								
Sphaeroderus stenostanus lecontei	20 MAY 1994 20 MAY 1994 22 AUG 1995								
Scaphinotes bilobus	20 JUL 1994 16 AUG 1994 22 AUG 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 3 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Pterostichus chaleites	15 AUG 1995 15 JUN 1994								
Pterostichus pennsylvannicus	12 JUL 1994 21 JUN 1994 11 MAY 1994 20 MAY 1994 20 MAY 1994 13 JUL 1994 21 JUN 1994 11 MAY 1994 20 MAY 1994 20 MAY 1994 21 JUL 1993 11 MAY 1994 20 MAY 1994								
Pterostichus melanarius	11 JUL 1995 11 JUL 1995								
Pterostichus lachrymosus	22 AUG 1995								
Pterostichus mutus	13 JUL 1994 15 JUN 1994								
Pterostichus corvinus	11 AUG 1995 10 AUG 1994 22 AUG 1995								
Chlaenius tricolor	15 AUG 1995 12 JUL 1994 11 AUG 1993								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy T. Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 4 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited		Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Synuchus impunctatus	13 JUL 1994 18 AUG 1993	13 JUL 1994 22 JUL 1993								
Anadaptus discoides	15 JUN 1994	15 JUN 1994								
Stenopholus lineolis	23 JUN 1993 10 JUL 1995	15 JUN 1994 12 JUL 1994								
Stenopholus comma	20 JUN 1995	23 JUN 1993								
Trichotichnus dichrous	15 JUN 1994 22 JUN 1995	15 JUN 1994 20 JUN 1995								
Dyschirius politis	15 AUG 1995 10 JUL 1995	10 JUL 1995								
Bembidion versicolor	12 JUL 1994									
Bembidion partreule	21 JUN 1994	15 AUG 1995								
Bembidion americanum	12 JUL 1994	15 AUG 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Aug 2 1996

Date

APPENDIX F

Voucher Specimen Data

Page 5 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Agonum decorum	22 JUN 1995								
Agonum placidum	20 JUN 1995 22 JUN 1995 22 JUN 1995 15 JUN 1994								
Amara convexa	15 AUG 1995 15 AUG 1995								
Lebia atriventris	15 AUG 1995								
Lebia viridis	15 AUG 1995								
Lebia ornata	15 JUN 1994								
Lebia tricolor	14 JUN 1994 22 MAY 1995								
Brachinus cordicollis	22 JUN 1995								
Myas coricanus	15 JUL 1993 13 JUL 1994 13 JUL 1994								
Myas cyanescens	18 JUL 1995 20 JUL 1994 20 JUL 1994 21 JUN 1994 20 JUN 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator **Date** Aug 2 1996

APPENDIX F

Voucher Specimen Data
Page 6 of 11 Pages

		Number of:							
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Clavini dentipes	15 JUN 1994								
Clavini fossor	15 AUG 1995								
Tachys proximus	15 AUG 1995 15 AUG 1995 10 JUL 1995 10 JUL 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 7 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Lithophane petulca	22 MAY 1995								
Lacinopolia implicata	22 AUG 1995								
Baileya ophthalmica	24 MAY 1995								
Crambus agitatellus	20 JUN 1995								
Hypenodes fractulinea	18 JUL 1995								
Gluphisia septentrionalis	18 JUL 1995								
Panthea frater	20 JUN 1995								
Chytonix palliatricula	20 JUN 1995								
Cycnia oregonensis	20 JUN 1995								
Ostrinia nubialis	18 JUL 1995								
Lithacodia albidula	18 JUL 1995								
Sunira bicolorago	22 AUG 1995								
Feltia geniculata	22 AUG 1995								
Orthosia revicta	22 MAY 1995								
Probole alienaria	24 MAY 1995								
Callima argentionetella	11 JUL 1995								
Besma quecivoraria	17 MAY 1995								
Zale duplicata	15 MAY 1995								
Catocala ilia	15 AUG 1995								
Acronicta inclara	11 JUL 1995								
Eulogia ochrifrontella	11 JUL 1995								
Zale mineria	17 MAY 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 8 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Leucania pseudargyria	11 JUL 1995								
Antequerinae bassettella	11 JUL 1995								
Nigetia formosalis	11 JUL 1995 11 JUL 1995								
Eueretagrotis attenta	11 JUL 1995								
Crambidia pallida	15 AUG 1995								
Schinia arcigera	15 AUG 1995								
Caridetadivisata	15 AUG 1995								
Nedra ramulosa	15 AUG 1995								
Thaumatopsis gibsonella	15 AUG 1995								
Apantesis parthenice	15 AUG 1995								
Platydena scabra	15 AUG 1995								
Euplexia benesimilis	15 AUG 1995								
Pyrausta signatalis	15 AUG 1995								
Catocala antinympha	15 AUG 1995								
Paonias excaecatus	18 JUL 1995								
Ceratomia undulosa	18 JUL 1995								
Sparganothis reticulatana	18 JUL 1995								
Sparganothis diluticostana	18 JUL 1995								
Euptychia cymela	20 JUN 1995								
Zale Unilineata	22 MAY 1995								
Tetracis cachexiata	20 JUN 1995								
Ulonche culea	22 MAY 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy T. Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 9 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Hydria prunivorata	20 JUN 1995								
Dichomeris ligulella	18 JUL 1995								
Abagrotis alternata	22 AUG 1995								
Nephopterix virgatella	22 AUG 1995								
Elaphria festivoides	13 JUN 1995								
Sphecodina abbottii	15 MAY 1995								
Erynnis brizo	17 MAY 1995								
Platynota idaeusalis	15 AUG 1995								
Synchlora aerata	15 AUG 1995								
Poanes hobomok	13 JUN 1995								
Idia julia	11 JUL 1995								
Eucosma dorsisignata	11 JUL 1995								
Tortricini albicoma	11 JUL 1995 11 JUL 1995								
Herculia olinalis	11 JUL 1995								
Sparganothis unifasciana	11 JUL 1995								
Phragmatobia assimilans	22 MAY 1995								
Acronicta hasta	18 JUL 1995								
Euxoa tesselata	18 JUL 1995								
Abigrotis alternata	18 JUL 1995								
Platytes vobisne	10 JUL 1995								
Psaphida resumens	15 MAY 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 10 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Tortricidia flexuosa	20 JUN 1995								
Choristoneura rosaceana	11 JUL 1995 20 JUN 1995								
Plagodis alcoolaria	20 JUN 1995								
Plagodis phlogosaria	22 MAY 1995								
Achatia distincta	22 MAY 1995 15 MAY 1995								
Argyresthia oreasella	22 AUG 1995								
Clepsis persicana	22 JUN 1995								
Charadra deridens	20 JUN 1995								
Synedoida grandirena	20 JUN 1995								
Lithacodia carneola	20 JUN 1995								
Heliomata cycladata	20 JUN 1995								
Callopistria cordata	20 JUN 1995 11 JUL 1995								
Argyrotaenia mariana	22 MAY 1995								
Malacomosa disstria	18 JUL 1995 11 JUL 1995								
Xestia dolosa	20 JUN 1995								
Lithacodia synochitis	20 JUN 1995								
Archips argyospirla	11 JUL 1995 18 JUL 1995								
Zanclognatha laevigata	20 JUL 1994								
Hyppa xylenoides	20 MAY 1994								
Cladara atroliturata	22 MAY 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothty Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date Aug 2 1996

APPENDIX F

Voucher Specimen Data

Page 11 of 11 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Clepsis melaleucana	20 JUN 1995								
Paonias myops	20 JUN 1995								
Hypoprepia fucosa	11 JUL 1995 18 JUL 1995								
Sparganothis petitana	18 JUL 1995 11 JUL 1995								
Phlogophora periculosa	22 AUG 1995								
Lomographa glomerula	24 MAY 1995								
Crocigrapha normani	24 MAY 1995								
Eupsilea tristigmata	11 MAY 1994								
Bomolocha baltimoralis	17 MAY 1995								
Phyllodesma americana	15 MAY 1995								
Dryocampa rubicunda	12 JUN 1995								
Pachysphinx modesta	14 JUN 1994								
Ipimorpha pleonectussa	15 AUG 1995								
Atteva punctella	15 AUG 1995								
Meganola minuscula	12 JUN 1995								
Ochropleura plecta	15 AUG 1995								
Peridroma saucia	12 JUL 1994								
Peridroma angulossa	9 AUG 1994								
Cosmia calami	12 JUL 1994								
Pandemis limitana	11 JUL 1995								
Archips semiferana	11 JUL 1995								
Polia nimbosa	11 JUL 1995								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Timothy Theron Work

Date Aug 2 1996

Voucher No. 1996-6

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Aug 2 1996

Curator Date

LIST OF REFERENCES

Addison, J.A. 1993. Persistence and nontarget effects of *Bacillus thuringensis* in soil: a review. *Canadian Journal of Forest Research* 23:2329-2342.

Allen, R.T. 1976. The occurence and importance of ground beetles in agricultural and surrounding habitats. In: *Carabid Beetles: Their Evolution, Natural History, and Classification*. Proceedings. Smithsonian Institution, Washington D. C.

Anonymous. 1991. Task Force Report on Biological Diversity in Forest Ecosystems: Society of American Foresters.

Anonymous. 1995. Gypsy Moth Management in the United States: *a cooperative approach* Final Environmental Impact Statement: USDA, USFS, and APHIS.

Arnett, R.H., N.M. Downie, and H.E. Jaques. 1980. *How to Know the Beetles*. Second ed. Dubuque, IA: Wm. C. Brown Company.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. *Forest Ecology and Management* 63:247-300.

Baker, W.L. 1941. Effect of gypsy moth defoliation on certain forest trees. *Journal of Forestry* 39:1017-1022.

Binkley, D. 1986. *Forest Nutrition Management*. New York: John Wiley and Sons.

Blakley, N.R., and H. Dingle. 1978. Competition: Butterflies eliminate milkweed bugs from a Caribbean island. *Oecologia* 37:133-136.

Bolstad, P.V., and S.T. Gower. 1990. Estimation of leaf area index in fourteen southern Wisconsin forests stands using a portable radiometer. *Tree Physiology* 7:115-124.

Borror, D.J., C.A. Triplehorn, and N.F. Johnson. 1989. *An Introduction to the Study of Insects*. Sixth Edition ed. Fort Worth: Saunders College Publishing.

Bowden, J. 1982. An analysis of factors affecting catches of insects in light-traps. *Bulletin of Entomological Research* 72:535-556.

Brown, V.C. 1984. Secondary succession: insect-plant relationships. *BioScience* 34:710-716

Burton, A.J., K.S. Pregitzer, and D.D. Reed. 1991. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. *Forest Science* 37:1041-1059.

Butalla, H.A. The GMDigest. <http://www.fsl.wvnet.edu/fhp/gm_digest/gmdigest.html> May 22, 1996. (Accessed June 12, 1996).

Cameron, E.A., and R.M. Reeves. 1990. Carabidae (Coleoptera) associated with gypsy moth, *Lymantria dispar* (L.)(Lepidoptera:Lymantriidae), populations subjected to *Bacillus thuringiensis* Berliner treatments in Pennsylvania. *Canadian Entomologist* 122:123-129.

Campbell, R.A., and R.J. Sloan. 1977. Forest stand responses to defoliation by the gypsy moth. *Forest Science Monograph* 19:1-35.

Cleland, D.T., J.B. Hart, G.E. Host, K.S. Pregitzer, and C.W. Ramm. 1993. Ecological classification and inventory system of the Huron-Manistee National Forests. In *USDA Forest Service, Huron-Manistee National Forest*

Coddington, J.A., C.E. Griswold, D.S. Davila, E. Penaranda, and S.F. Larcher. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. pp. 10-48. In *The unity of evolutionary biology: Proceedings from the fourth international congress of systematic and evolutionary biology.*, edited by E. C. Dudley. Portland, Oregon: Dioscorides Press.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.

Conover, W.J. 1971. *Practical Nonparametric Statistics*. New York: John Wiley and Sons, Inc.

Cooper, R.J., K.M. Dodge, and R.C. Whitmore. 1987. Estimating defoliation using stratified point intercept sampling. *Forest Science* 33:157-163.

Corbett, E.S., and J.A. Lynch. 1987. The gypsy moth-does it affect soil and water resources? pp. 39-46. In *Coping with the gypsy moth in the new frontier*, Proceedings. Workshop for Forest Managers. 1987, West Virginia University, Morgantown, WV.

Decagon Devices, I. 1987. Sunfleck PAR Ceptometer Plant Canopy Measurement Operator's Manual. Pullman, Washington USA.

Denno, R.F., M.S. McClure, and J.R. Ott. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* 40: 297-331.

Desender, K., and H. Turin. 1989. Loss of habitats and changes in the composition of the ground and tiger beetle fauna in West European countries since 1950 (Coleoptera: Carabidae, Cincindelidae). *Biological Conservation* 48:277-294.

Dethier, V.G. 1959. Egg-laying habitats of lepidoptera in relation to available food. *Canadian Entomologist* 91:554-561.

Dijk, T.S.V. 1986. Changes in the carabid fauna of a previously agricultural field during the first twelve years of impoverishing treatments. *Netherlands Journal of Zoology* 36:413-437.

Dreistadt, S.H. 1983. An assessment of gypsy moth eradication attempts in Michigan (Lepidoptera: Lymantriidae). *Great Lakes Entomologist* 16:143-148.

Edmunds, G.F. 1973. Ecology of black pineleaf scale (Homoptera:Diaspididae). *Environmental Entomology* 2:765-777.

Erwin, T.L. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* 36:74-75.

Erwin, T.L. 1983. Beetles and other insects of tropical forest canopies at Manuas, Brazil, sampled by insecticidal fogging. 59-76. In *Tropical Rain Forest Ecology and Management*, edited by S. L. Sutton, T. C. Whitmore and A. C. Chadwick: Blackwell, Oxford.

Erye, M.D., M.L. Luff, S.P. Rushton, and C.J. Topping. 1989. Ground beetles and weevils (Carabidae and Curculionoidea) as indicators of grassland management practices. *Journal of Applied Entomology* 107:508-517.

Gage, S.H., T.M. Wirth, and G.A. Simmons. 1990. Predicting regional gypsy moth (Lymantriidae) population trends in an expanding population using pheromone trap catch and spatial ananlysis. *Environmental Entomology* 19:370-377.

Gansner, D.A., O.W. Herrick, P.S. DeBald, and R.E. Acciavatti. 1983. Changes in forest condition associated with gypsy moth. *Journal of Forestry* 81:155-157.

Goulet, H., and J.T. Huber. 1993. Hymenoptera of the world: An identification guide to families. In *Research Branch Argriculture Canada Bulletin 1894/E.*

Gross, H.L. 1992. Impact analysis for a jack pine budworm infestation in Ontario. *Canadian Journal of Forestry* 22:818-831.

Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421-425.

Hansen, R.M., and D.N. Ueckert. 1970. Dietary similarity of some primary consumers. *Ecology* 51:640-648.

Hawkins, C.P., and J.A. MacMahon. 1989. Guilds: the multiple meanings of a concept. *Annual Review of Entomology* 34:423-451.

Holliday, N.J. 1991. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. *Canadian Entomologist* 123:1369-1389.

Host, G.E., K.S. Pregitzer, C.W. Ramm, J.B. Hart, and D.T. Cleland. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern lower Michigan. *Forest Science* 33:445-457.

Host, G.E., K.S. Pregitzer, C.W. Ramm, D.P. Lusch, and D.T. Cleland. 1988. Variation in overstory biomass among glacial landforms and ecological land units in northwestern Lower Michigan. *Canadian Journal of Forest Research* 18:659-668.

Houston, D.R., and H.T. Valentine. 1985. Classifying forest suscetibility to gypsy moth defoliation. *Agriculture Handbook* No. 542. USDA Combined Forest Pest Research and Development Program 19 pp.

Huston, M.A. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. New York: Cambridge University Press.

Huston, M., and J.G. Isebrands. 1995. Monitoring interception of photosynthetically active radiation in forests. *Bulletin of the Ecological Society of America* 76:95-97.

Jeffords, M.R., and L.J. Case. 1987. Effect of prey density on diurnal activity and development in *Calosoma calidum* (Coleoptera: Carabidae): Implications for biological control of the gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae) in the Midwest. *Great Lakes Entomologist* 20:93-97.

Johnson, K.S., J.M. Scriber, J.K. Nitao, and D.R. Smitley. 1995. Toxicity of *Bacillus thuringiensis* var. *kurstaki* to three nontarget Lepidoptera in field studies. *Environmental Entomology* 24:288-297.

Kelly, B., and J. Regniere. 1985. Predation on the pupae of the spruce budworm (Lepidoptera: Tortricidae) on the forest floor. *Canadian Entomologist* 117:33-38.

Klein, R.M., and T.D. Perkins. 1988. Primary and secondary causes and consequences of contempory forest decline. *The Botanical Review* 54:1-43.

Kolodny-Hirsch, D.M. 1986. Evaluation of methods for sampling gypsy moth (Lepidoptera: Lymantriidae) egg mass populations and development of sequential sampling plans. *Environmental Entomology* 15:122-127.

Kulman, H.M. 1971. Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology* 16:289-324.

Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: Their use in conservation planning. *Conservation Biology* 7:796-808.

LaVigne, R.J., J.A. Lockwood, and T. Christiansen. 1990. Insect response to the 1988 fires in Yellowstone National Park: Final Report 1989-1990: University of Wyoming and the National Park Service Research Center. Unpublished Report.

Lawton, J.H. 1986. The effects of parasitoids on phytophagous insect communities. 265-287. In *Insect Parasitoids*, edited by J. Waage and D. Greathead. London: Academic Press.

Lawton, J.H., and D.R. Strong. 1981. Community patterns and competition in folivorous insects. *American Naturalist* 118:317-338.

Leibherr, J., and J. Mahar. 1979. The carabid fauna of the upland oak forest in Michigan: Survey and analysis. *Coleopterists Bulletin* 33:183-197.

Lenski, R.E. 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. *Ecological Entomology* 7:385-390.

Leonard, D.E. 1974. Recent developments in ecology and control of the gypsy moth. *Annual Review of Entomology* 19:197-229.

Liebhold, A.M., J.S. Elkington, D.R. Miller, and Y.S. Wang. 1988. Estimating oak leaf area index and gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), defoliation using canopy photographs. *Environmental Entomology* 17:560-566.

Lindroth, C.H. 1969. The ground-beetles of Canada and Alaska. *Opuscula Entomologica Supplenta* 20, 24, 26, 29, 33, 34, 35:1-1192.

Lovett, G.M., and A.E. Ruesink. 1995. Carbon and nitrogen mineralization from decomposing gypsy moth frass. *Oecologia* 104:133-138.

Ludwig, J.A., and J.F. Reynolds. 1988. *Statistical Ecology: A Primer on Methods and Computing*. New York: John Wiley and Sons.

Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. Princeton: Princeton University Press.

Mallett, K.I., and W.J.A. Volney. 1990. Relationships among jack pine budworm damage, selected tree characteristics, and *Armillaria* root rot in jack pine. *Canadian Journal of Forest Research* 20:1791-1795.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecological Systematics* 11:119-61.

Mattson, W.J., and N.D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190:515-522.

Mattson, W.J., and J.M. Scriber. 1987. Nutrional ecology of insect folivores of woody plants: Nitrogen, water, fiber, and mineral considerations. 105-146. In *Nutrional Ecology of Insects, Mites, and Spiders*, edited by F. Slansky and J. G. Rodriguez. New York: John Wiley and Sons Inc.

Mauffette, Y., M.J. Lechowicz, and L. Jobin. 1983. Host preferences of the gypsy moth, *Lymantria dispar* (L.), in southern Quebec. *Canadian Journal of Forest Research* 13:53-60.

McClure, M.S. 1974. Biology of *Erythroneura lawsoni* (Homoptera: Cicadellidae) and coexistence in the Sycamore leaf-feeding guild. *Environmental Entomology* 3:59-68.

Milligan, G.W. 1989. A study of the beta-flexible clustering method. *Multivariate Behavioral Research* 24:163-176.

Miller, J.C. 1990. Field assessment of the effects of a microbial pest control agent on nontarget Lepidoptera. *American Entomologist* 36:135-139.

Millers, I., and D. Lachance. 1988. North American sugar maple decline project: Appendix 7.3, Quality assurance and quality control plan. In *Eastern Hardwoods Research Cooperative- National Acid Precipitation Assessment Program of U. S. A.* Canada Agriculture Forestry Service and USDA Forest Service. 13 pp.

Minott, C.W., and I.T. Guild. 1925. Some results of the defoliation of trees. *Journal of Economic Entomology* 18:345-348.

Moran, V.C., and T.R.E. Southwood. 1982. The guild composition of arthropod communities in trees. *Journal of Animal Ecology* 51.

Muzika, R.-M. 1994. Defoliation and thinning effects on gypsy moth predators. *Gypsy Moth News* 36:2-3.

Niemela, J., Y. Haila, E. Halme, T. Lahti, T. Pajunen, and P. Punttila. 1988. The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. *Annales Zoologici Fennici* 25:107-119.

Niemela, J., Y. Haila, E. Halme, T. Pajunen, and P. Punttila. 1990. Diversity variation in carabid beetle assemblages in the southern Finnish taiga. *Pedobiologia* 34:1-10.

Niemela, J., D. Langor, and J.R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in Western Canada. *Conservation Biology* 7:551-561.

Noss, R.F. 1990. Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology* 4:355-364.

Perkins, T.D., H.W. Vogelmann, and R.M. Klein. 1987. Changes in light intensity and soil temperature as a result of forest decline on Camels Hump, Vermont. *Canadian Journal of Forestry Research* 17:565-568.

Pierce, L.L., and S.W. Running. 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. *Ecology* 69:1762-1767.

Price, P.W. 1987. The role of natural enemies in insect populations. 578. In *Insect Outbreaks*, edited by P. Barbosa and J. C. Schultz. San Diego: Academic Press.

Probst, J.R., and T.R. Crow. 1991. Integrating biological diversity and resource management: An essential approach to productive, sustainable ecosystems. *Journal of Forestry* 89:12-17.

Purrington, F.F., J.E. Bater, M.G. Paoletti, and B.R. Stinner. 1989. Ground beetles from remnant oak-maple-beech forest and its surroundings in northeastern Ohio (Coleoptera: Carabidae). *Great Lakes Entomologist* 22:105-110.

Risley, L.S., and D.A. Crossley. 1993. Contribution of herbivore-caused greenfall to litterfall nitrogen flux in several southern Appalachian forested watersheds. *American Midland Naturalist* 129:67-74.

Risser, P.G. 1995. Biodiversity and ecosystem function. *Conservation Biology* 9:742-746.

Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* 4.

Root, R.B. 1973. Organization of plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124.

Ross, H.H. 1957. Principles of natural coexistence indicated by leafhopper populations. *Evolution* 11:113-129.

Sample, B.E., L. Butler, C. Zivkovich, and R.C. Whitmore. 1993. Evaluation of *Bacillus thuringiensis* and defoliation effects on native lepidoptera. In *AIPM Preliminary Report.*

Sapio, F. Michigan DNR Forest Management Division, Forest Health Web Page. <http://www.dnr.state.mi.us/www/fmd/pest/forheal.html> May 1, 1996. (Accessed June 13, 1996).

SAS Institute, 1995. JMP Statistics and Graphics Guide Version 3.1. Cary, North Carolina, USA.

Schowalter, T.D. 1981. Insect herbivore relationship to the state of the host plant: Biotic regulation of ecosystem nutrient cycling through ecological succession. *Oikos* 37:126-130.

Schowalter. T.D. 1985. Adaptations of insects to disturbance. 235-252. In *The Ecology of Natural Disturbance and Patch Dynamics*, edited by S.T.A. Pickett and P.S. White. New York: Academic Press.

Schowalter, T.D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. *Canadian Journal of Forestry Research* 19:318-322.

Schowalter, T. D. 1991. Roles of insects and diseases in sustaining forests. Paper read at Siviculture, Forest Genetics and Tree Improvement, Forest Pest Management, and Soils section, SAF National Convention, at San Francisco, CA.

Schowalter, T.D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Biotropica* 26:312-319.

Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78:115-125.

Schowalter, T.D., J.W. Webb, and D.A. Crossley. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* 62:1010-1019.

Schultz, J.C., and I.T. Baldwin. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217:149-151.

Scriber, J.M., and F. Slansky. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* 26:183-211.

Simberloff, D., and T. Dayan. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology* 22:115-43.

Simberloff, D.S., and E.O. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* 50:278-296.

Sokal, R.R., and F.J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research.* Third Edition ed. New York: W. H. Freeman and Company.

Southwood, T.R.E. 1994. *Ecological Methods: With Particular Reference to the Study of Insect Populations*. Second Edition ed. London: Chapman and Hall.

Spurr, S.H., and B.V. Barnes. 1980. *Forest Ecology*. Third ed. New York: John Wiley and Sons.

Stork, N.E. 1987. Guild structure of arthropods from the Bornean rain forest trees. *Ecological Entomology* 12:69-80.

Strong, D.R., J.H. Lawton, and T.R.E. Southwood. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Cambridge: Harvard University Press.

Swank, W.T., J.B. Waide, D.A. Crossely, and R.L. Todd. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia* 51:297-299.

Talerico, R.L. 1981. The gypsy moth: Research toward integrated pest management. In *Forest Service Science and Education Agency Technical Bulletin*.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2-16.

Tilman, D. 1996. Biodiversity: Population versus ecosystem stability. *Ecology* 72:350-363.

Tilman, D., and J.A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367:363-364.

Turin, H., and P.J. denBoer. 1988. Changes in the distribution of carabid beetles in the Netherlands since 1880. II. Isolation of habitats amd long-term trends in the occurence of carabid species with different powers of dispersal (Coleoptera, Carabidae). *Biological Conservation* 44:179-200.

Twery, M.J. 1990. Effects of defoliation by gypsy moth. pp. 27-39. In: *USDA Interagency Gypsy Moth Research Review 1990*, Proceedings. General Technical Report NE-146. USDA Forest Service. 1990, East Windsor, CT.

Varley, G.C. 1949. Population changes in German forest pests. *Journal of Animal Ecology* 18:117-122.

Vinson, S.B. 1990. Potential impact of microbial insecticides on beneficial arthropods in the terrestrial environment. 259. In *Safety of Microbial Insecticides*, edited by M. Laird, L. A. Lacy and E. W. Davidson. Boca Raton: CRC Press Inc.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57:7-13.

Vose, J.M., and W.T. Swank. 1990. Assessing seasonal leaf area dynamics and vertical leaf area distribution in eastern white pine (*Pinus strobus* L.) with a portable light meter. *Tree Physiology* 7:125-134.

Wargo, P.M. 1977. *Armillaria mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees. *Forest Science* 23:485-492.

Wargo, P.M., and M.E. Montgomery. 1983. Colonization by *Armillaria mellea* and *Agrilus bilineatus* of oaks injected with ethanol. *Forest Science* 29:848-857.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Research* 13:327-354.

Weseloh, R.A. 1990. Experimental forest releases of *Calosoma sycophanta* (Coleoptera: Carabidae) against the gypsy moth. *Journal of Economic Entomology* 83:2229-2234.

Wilcove, D.S. 1989. Protecting biodiversity in multiple-use lands: lessons from the US Forest Service. *Trends in Ecology and Evolution* 4:385-388.

Wilson, E.O. 1985. The biological diversity crisis. *BioScience* 35:700-706.

Zak, D.R., K.S. Pregitzer, and G.E. Host. 1986. Landscape variation in nitrogen mineralization and nitrification. *Canadian Journal of Forest Research* 16:1258-1263.

Zak, D.R., G.E. Host, and K.S. Pregitzer. 1989. Regional variability in nitrogen mineralization, nitrifiaction, and overstory biomass in northern Lower Michigan. *Canadian Journal of Forestry Research* 19:1521-1526.

Zak, D.R., and K.S. Pregitzer. 1990. Spatial and temporal variability of nitrogen cycling in northern lower Michigan. *Forest Science* 39:367-380.