PATTERNS OF BEETLE (COLEOPTERA) DIVERSITY IN CROWNS OF REPRESENTATIVE TREE SPECIES IN AN OLD-GROWTH TEMPERATE DECIDUOUS FOREST

JON C. GERING* AND THOMAS O. CRIST

Department of Zoology, Miami University, Oxford, OH 45056 USA.
E-mail: geringjc@muohio.edu

ABSTRACT. Patterns of spatial variation, temporal change, and host-tree differences of beetle communities in crowns of representative tree species were examined in an old-growth temperate deciduous forest in Hueston Woods State Park, Preble County, southwestern Ohio in 1998. The three study plots were separated spatially. Each had two 1-ha subplots containing one individual of four tree species: American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), and white oak (*Quercus alba*). We obtained samples of the insect communities from one subplot per day using insecticide fogging, for a total of six sampling days in early summer (18 June–6 July 1998) and late summer (21 August–5 September 1998). A total of 1459 beetles representing 272 morphospecies and > 40 families were captured. Two-way mixed ANOVA models identified significant interaction effects (plot × tree species) on mean beetle richness and abundance in the early summer, but only tree species effects were identified in late summer. Although spatial variation may be a key diversity determinant in the early season, attributes of tree species, such as constitutive defenses, may be more important in late summer. Species richness, which exhibited a marked decline from early summer (194 morphospecies) to late summer (119 morphospecies), was coupled with only a 10% similarity between beetle assemblages during these periods. Abundance and composition changes between samples suggest that species-specific patterns of emergence and voltinism may be instrumental in structuring arboreal beetle communities in temperate tree crowns. This study highlights the need for detailed studies on recolonization and spatial dependence of arboreal insect communities in temperate forest ecosystems.

Key words: Beetles, Coleoptera, old growth, canopy, fogging, insecticide

INTRODUCTION

Several ecological patterns that characterize canopy insect communities have emerged from insecticide fogging studies conducted in Central and South America, England, and South Africa during the past three decades.

First, insect species richness is not distributed equally among tree species. Davies et al. (1997), for example, recorded 168 beetle species on *Brownea grandiflora* (Caesalpiniaceae) and 253 beetle species on *Cassia grandis* (Caesalpiniaceae), corresponding to a faunal similarity of < 10%. Host-tree differences evident in other studies (e.g., Southwood 1960, Kitching et al. 1997, Wagner 1997) were a key aspect in estimates of global insect diversity made by Erwin (1982).

Second, canopy insect communities vary spatially according to landscape position. In Amazonian forest fragments, the diversity of canopy insects was attributable to the effects of forest edge rather than forest area (Malcolm 1997). Similarly Ozanne et al. (1997) documented decreased abundance in most arthropod taxa along an edge-to-interior gradient in British conifer plantations.

Third, canopy insect communities exhibit pronounced temporal variability. Sampling from a single tree species in Panama, Erwin and Scott (1980) documented a loss of > 50% in beetle species richness from the minor wet season (July) to the dry season (March–April). In Sulawesi, Stork and Brendell (1990) noted that insect abundance varied considerably throughout the year, but that species composition of the insect community remained essentially the same.

Although each of these patterns has been documented several times, they may not be representative of all tree-crown insect communities in all locations. Large collections of canopy arthropods (those from fogging, smoking, and gassing) exist from only about 500 individual trees and < 100 tree species or 0.002% of the tree species in the world (Erwin 1997). The majority of these collections are from tropical or subtropical sites. Few large-scale chemical knockdown studies have been conducted in temperate forests; yet eastern deciduous forests of North America and tropical forests are threatened by the same forces—urban and agricultural development. Primeval forests covered 98.8% (25 million acres) of Ohio in 1800, but by 1940 only 14.1% (3.7 million acres) of the state was woodland (Noble & Korsok 1975). By 1975, < 6% of northwest-

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* Corresponding author.

ern Ohio remained woodland (Laub et al. 1979). Mature deciduous forests (i.e., old growth > 150 years) now occur only in isolated patches in some state parks and preserves.

The purpose of this study was to document patterns of host-tree differences, spatial variation, and temporal change among beetle communities in crowns of representative tree species in an old-growth temperate deciduous forest.

MATERIALS AND METHODS

Study Site

This study was conducted in Hueston Woods State Park in Preble County, southwestern Ohio in 1998. The park consists of a reservoir (Acton Lake), recreational areas, and 1042 ha of natural areas, of which 316 ha is mature deciduous forest. The present-day stands of old-growth forest were purchased in 1797 (Runkle et al. 1982). Selective logging and grazing have occurred sparingly since that time, resulting in fairly undisturbed old-growth stands. As remnants of old-growth forest, these areas have received much attention from botanists (e.g., Braun 1938, Vankat et al. 1975). The mosaic of other vegetative types in the park (FIGURE 1) is a result of old-field succession, conifer plantings, and intensive agriculture uses (Ray & Vankat 1982).

The three study plots, identified as northernmost, middle, and southernmost, were located in a 1-km^2 section of old-growth forest. Dominant species were American beech (*Fagus grandifolia* Marshall) and sugar maple (*Acer saccharum* Ehrh.) and to a lesser extent red oak (*Quercus rubra*), white oak (*Quercus alba* L.), and ashes (*Fraxinus* spp.). The topography throughout the park is characterized by ridges separated by shallow (10–15 m) sloping drainages that terminate in the reservoir. The study plots, separated by drainages, each had a pair of sampling subplots ~1 ha in size with one individual of four tree species: American beech, sugar maple, red oak, and white oak. We selected this suite of tree species because they are representative of old-growth beech-maple forest; and they are canopy rather than emergent or subcanopy species, a requirement for the fogging procedure. They also provided a preliminary assessment of faunal overlap between two tree families: Fagaceae (beech and oaks) and Aceraceae (maple), between two genera within a family (*Quercus* and *Fagus*), and between two species within a genus (*Q. rubra* and *Q. alba*).

Insect Sampling

Samples of insect communities were collected from one subplot per day (four trees, one of each species) for a total of six days in both early summer (18 June–6 July 1998) and late summer (21 August–5 September 1998). Subplots were separated by > 50 m to avoid overlap in fogging events from insecticide drift. We sampled the same 24 trees in early and late summer, for a total of 24 trees and 48 fogging events. The faunal recovery time for fogged trees, which is highly variable, has only been assessed by comparing insect communities from re-foggings with insect communities from initial foggings. Floren and Linsenmair (1997) found decreased ant abundance and different species composition in trees re-fogged after seven months, suggesting that several months is inadequate for full recolonization to occur. In contrast, Stork and Hammond (1997) recorded similar abundance levels in re-fogging samples separated by three months, implying that full recolonization had occurred. The experimental design of our study did not allow full discrimination of seasonal and fogging effects to explain temporal patterns in beetle richness and abundance. Consistent with previous studies, we drew inferences about the magnitude of these effects based upon our data on species abundance and composition.

At dawn on windless mornings, the canopy of each tree was inundated for three minutes with 0.5 L of a 0.5% pyrethrin-based insecticide (Pyrenone 50, AgrEvo Products) emitted from a radio-controlled Curtis Dyna-Fogger. The fogger, suspended from the canopy, was rotated through a circular arc as the insecticide was applied to ensure dispersal throughout the tree crown. During the following two hours, insects fell into a ground-based array of eight 0.5-m^2 collecting trays mounted on 1-m steel poles. Four trays were located 1 m from the trunk in each cardinal direction; the four remaining trays were located (along the same cardinal bearings) halfway between the trunk and perimeter of the tree crown, so that insects from neighboring tree crowns were unlikely to be collected. The sampling protocol was based on previous studies (Adis et al. 1984, Stork 1987, Davies et al. 1997) and on the detailed evaluation of drop time, insecticide concentration, and recovery time provided by Stork and Hammond (1997). Fogging was selected as the sampling technique, because it is relatively unselective and independent of arthropod activity and because it results in comparable samples (cf. Basset et al. 1997 with Stork & Hammond 1997).

Insect Processing

All beetle specimens were sorted and identified to families and Recognizable Taxonomic
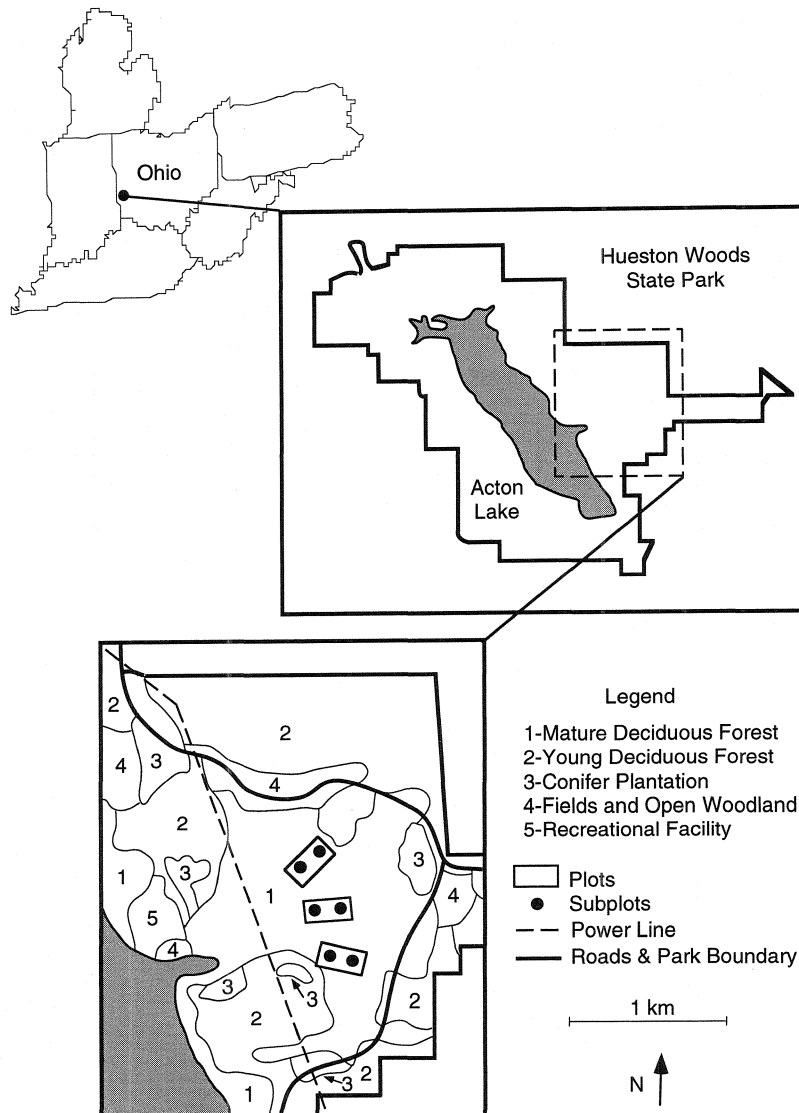
FIGURE 1. Vegetative associations and study plots within Hueston Woods State Park in Preble County, southwestern Ohio, USA (adapted from Ray & Vankat 1982).

Units (RTUs) or morphospecies (Oliver & Beattie 1993). Researchers working on canopy arthropod communities frequently adopt the morphospecies approach, because collections are large and taxonomic expertise is often unavailable (Erwin 1997). In addition, species grouped by coarse morphological features closely correspond to expert taxonomic identification (Longino & Colwell 1997), although this may vary among taxa with morphologically similar species.

Data Analysis

Three response variables were recorded for the beetle communities in each tree: richness (no. RTUs), abundance (no. individuals), and composition (RTUs). Constructing a two-way mixed ANOVA model, we tested for spatial (plot) variation and host-tree effects on mean richness and abundance, using tree species as a fixed effect and plot as a random effect. To conduct hypothesis tests, we measured the fixed ef-

fect of tree species, using the tree-by-plot interaction error. The random effect of plot was tested against the model error term. The two hypothesis tests differ in their interpretations: inferences for fixed effects are directed at the particular suite of subjects (the four tree species), whereas inferences for random effects are directed at the entire population (all possible plots); see Neter et al. (1990) and Littell et al. (1991). Because the two inferences are identical in their assumptions about the underlying distributions, we log-transformed the abundance values prior to analysis. Separate analyses were conducted for richness and abundance in each season, for a total of four tests. Significant ANOVA results were followed by Tukey post-hoc tests to determine differences among tree species (Neter et al. 1990). ANOVA and Tukey tests were conducted using PC-SAS for Windows (SAS Institute 1996) and SYSTAT (1992), respectively.

To examine the similarity of beetle communities between seasons and among tree species, we used agglomerative cluster analysis with Bray-Curtis percent similarity (Bray & Curtis 1957). The Bray-Curtis index compares samples based on the shared species abundance of each sample divided by the total of all species abundances for the two samples (Ludwig & Reynolds 1988). Effectively used for a range of ecological studies (Beals 1984), the index is affected little by the presence of rare species (Krebs 1999), which were abundant in our samples. The replicate samples (N = 6) for each tree species were combined to arrive at a composite community for that tree species. The cluster analysis was performed using the average linkage method in SYSTAT (1992).

Species accumulation curves were conducted to assess the adequacy of sample size, and jackknife estimates of species richness were made. Species accumulation curves, which relate sampling effort to the cumulative number of species, frequently have been used as a diagnostic tool for sampling effectiveness in studies of canopy arthropod communities (e.g., Harada & Adis 1997, Longino & Colwell 1997, Wagner 1997). The accumulation curves for this study were constructed using PC-ORD, which subsamples the entire sample 500 times to determine the number of species as a function of subsample size (MjM Software 1995). Jackknife estimates are nonparametric resampling procedures designed to produce unbiased estimates of species richness when subsampling from a restricted area (Palmer 1990). These estimates also were made using PC-ORD.
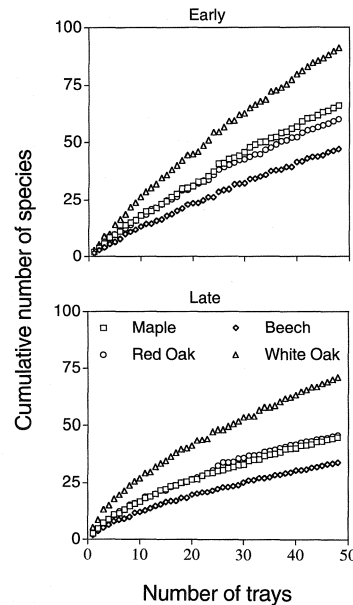

FIGURE 2. Species accumulation curves for four tree species sampled by insecticide fogging during early and late summer 1998 in Hueston Woods State Park. Eight collecting trays were used to sample from each of the six replicates of each tree species, for a total of 48 trays for each tree species in each season.

RESULTS

A total of 1459 beetles were captured, representing 272 RTUs and > 40 families. More than 65% of individuals (960+) were collected during late summer, but more species were collected in early summer (194) than in late (119). Only 55 RTUs were represented by more than two individuals; less than a fifth (48) of the species were doublets and > 60% (169) were singletons. Curculionidae (snout beetles) and Chrysomelidae (leaf beetles) were the most speciose and abundant families (APPENDIX).

Accumulation curves did not reach an asymptote for any tree species in any season, but a clear and consistent relationship was found among trajectories of the curves in both seasons: the white oak curve had the steepest slope, and the beech curve had the shallowest (FIGURE 2). Sampling provided a more thorough representation of beetle communities in the late rather than the early season.

White oak had the highest species richness, and beech the lowest in both seasons (TABLE 1), as expected from the accumulation curves. A high 78–87% of species richness in the early season was the result of singletons, which caused estimates to add an additional 35–60 species to the observed values. The percentage of

TABLE 1.　Observed species richness, number and percentage of singletons, and first-order jackknife estimates of beetle species richness from four tree species sampled by insecticide fogging during early summer (18 June–6 July) and late summer (20 August–5 September) 1998 in Hueston Woods State Park, Preble County, southwestern Ohio. Each tree species is represented by six replicates in each season.

Tree species	Beetle spp. richness		Singletons				Jackknife estimate	
	Early	Late	Early	Late	Early	Late	Early	Late
	RTUs		RTUs		%		RTUs	
Sugar maple	66	45	54	28	82	62	111	68
American beech	47	34	41	25	87	74	81	55
Red oak	60	46	47	26	78	57	99	68
White oak	95	71	77	49	81	69	159	112

RTUs = Recognizable Taxonomic Units or morphospecies.

singletons in the samples decreased in the late season for all tree species; and the corresponding estimates of species richness were substantially lower than in the early season.

Mean beetle richness exhibited a significant interaction effect during the early season (TABLE 2), because the oaks had their lowest mean richness in the middle plot, whereas maple and beech contained the highest mean richness in the middle plot. During the late season, mean beetle richness was significantly different among tree species (FIGURE 3, TABLE 2), with white oak containing more beetle species than the other trees (P < 0.032 for all post-hoc comparisons with white oak).

Abundance patterns were similar to those for richness. Early season data suggested a main effect of plot as well as an interaction effect between tree species and plot. The main effect of plot was caused by a higher mean beetle abundance in the northernmost plot. The interaction effect also was the result of oaks having their lowest mean abundance in the middle plot, whereas maple and beech reached their highest mean abundance in this plot. During the late season, significant differences in abundance were evident among tree species (FIGURE 3, TABLE 2), with white oak having a higher mean abundance than the other tree species (P < 0.042 for all post-hoc comparisons with white oak).

Dendograms from cluster analysis show different patterns for early and late summer. During early summer, composition of the beetle community on beech was dissimilar to composition of beetle communities on other trees, while compositions of beetle communities on maple and on red oak (two different families) were most similar (FIGURE 4). In contrast, compositions of beetle communities were nearly identical on the two oak species (in the same genus) during late summer. Overall, the beetle communities were more similar in late than early summer.

DISCUSSION

The purpose of this study was to examine patterns of beetle diversity as they related to spatial variation, temporal change, and host-tree effects. Because most information about these patterns comes from research in the tropics or subtropics, studies in temperate forests can add considerable breadth to our understanding of the ecology of arboreal insect communities, especially as they relate to global patterns of species richness. The 272 beetle morphospecies (RTUs) collected from 48 fogging events (24 trees) are far fewer than the ~950 beetle morphospecies recorded in < 20 foggings in both Panama (Erwin and Scott 1980) and Venezuela (Davies et al. 1997). The lower beetle numbers verify that arboreal beetle

TABLE 2.　Two-way mixed ANOVA values for differences in mean richness and abundance of beetles from four tree species and three plots sampled by insecticide fogging.

Source of variation	df	Early summer				Late summer			
		Richness		Abundance		Richness		Abundance	
		MS	F	MS	F	MS	F	MS	F
Tree species	3	116.61	1.5	0.76	0.9	157.44	13.8**	2.22	11.4**
Plot	2	18.04	0.9	0.84	4.2*	10.13	0.3	0.51	1.8
Tree species × plot	6	78.65	3.9*	0.82	4.1*	11.40	0.4	0.19	0.7
Error	12	20.33		0.19		29.25		0.28	

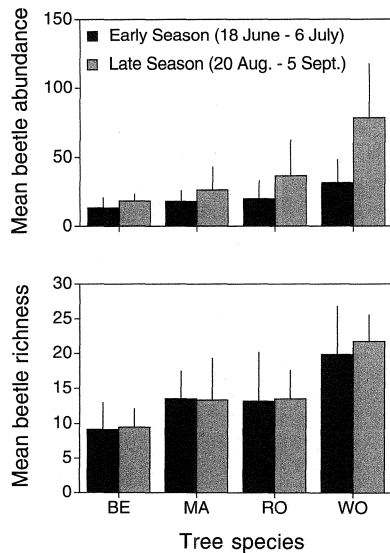* P < 0.05; ** P < 0.01; df, degrees of freedom; MS, mean-square; F, F statistic.

FIGURE 3. Histograms showing mean beetle richness and abundance (SE) of four tree species sampled by insecticide fogging: beech (BE), maple (MA), red oak (RO), and white oak (WO).

FIGURE 4. Dendogram showing percent similarity of beetle assemblages on four tree species sampled by insecticide fogging. Percent similarity is based on agglomerative cluster analysis with the Bray-Curtis index. The replicate trees (N = 6) for each tree species were combined to arrive at a composite community for that tree species.

diversity is lower in temperate than in tropical regions (Erwin 1982). Beetle richness and abundance figures are similar to those found in other temperate forests. For example, Stork and Hammond (1997) fogged 50 oak trees in a mature deciduous forest during a 2-year study in the United Kingdom and found 7596 individuals representing 202 beetle species. The species richness in our study may have been higher because we sampled more tree species, but patterns of species richness at regional and global scales will materialize only as additional studies are conducted at other locations.

Our beetle communities were characterized by a few dominant and many rare species (>78% singletons in the early season), which is typical of species abundance distributions of other ecological communities (Jongman et al. 1995). Basset and Arthington (1992) also recorded high numbers of singletons in fogging samples taken from tree crowns in Australian subtropical rain forest, but Stork and Hammond (1997) reported that < 15% of the beetle species in fogging samples from six oak trees were singletons. The high percentage of singletons in our samples may be the result of the number of trays used to sample each tree. The trees in our study were similar in age (~200 years old) and size (55–110 cm dbh) to those used by Stork and Hammond (60–70 cm dbh), but they used > 20 1-m² trays to sample from each tree, whereas we used eight 0.5-m² trays per tree. For a similar
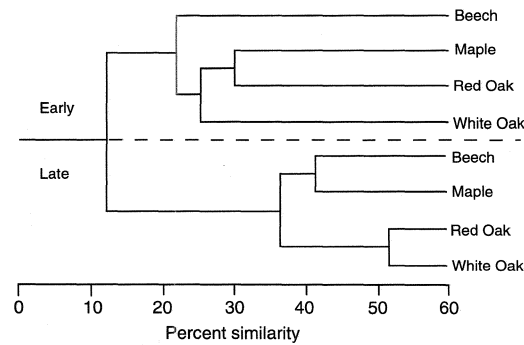
number of fogging events, they recorded five times as many individuals and a much lower percentage of singletons (~15% from morning fogging events). These figures suggest that their trees were adequately sampled and that our sampling effort may not have detected all beetle species present in the crown of each tree species. Our effort was sufficient to distinguish patterns of species accumulation among tree species, however. The beech trees, which we sampled most effectively (FIGURE 2), contained a higher percentage of singletons than the other tree species (TABLE 1), suggesting that high numbers of singletons may represent a meaningful biological pattern.

The pattern of temporal change in beetle richness in our study mirrors findings from other studies. Erwin and Scott (1980), for example, documented a loss of > 50% in beetle species richness from the minor wet season (July) to the dry season (March–April). Seasonal variation in species richness has been explained by minimal air temperatures (Basset 1991) and humidity (Erwin & Scott 1980). Although these factors may be important in temperate forests, we attribute the loss in species richness primarily to schedules of emergence and voltinism. Temperate insects that use seasonally restricted resources are often univoltine, having one generation per year (Gullan & Cranston 1994). Many beetle species typically overwinter as late instar larvae (Borror et al. 1989) and emerge as adults around June. Beetle species with bivoltine life cycles also overwinter as larvae and emerge once in early summer and once in late summer. The higher species richness in early summer could be explained by the overlapping emergence of

univoltine and bivoltine adults. The species-poor community in late summer may have been comprised of adult populations of bivoltine or multivoltine species making a second or third emergence. Our explanation for temporal change is supported by the life history attributes of several species. A univoltine species, the Rose chafer *Macrodactylus subspinosus* (Fab.) (Scarabaeidae: Melolonthinae), was dominant in the early summer samples but not recorded at all in late summer. Flea beetles (Chrysomelidae: Alticinae) are bivoltine, with adult emergence occurring in April and May and again in late summer and early fall. Not surprisingly, species in this subfamily were absent from our early samples but quite plentiful (49 individuals) in our late samples. Life history characteristics thus may be important in understanding temporal variation in canopy insect communities of temperate forests.

Our experimental design did not allow us to distinguish seasonal change from the effects of resampling each tree. The rate of tree recolonization by insects has been evaluated by comparing insect abundance in re-fogging samples with that in initial fogging samples. Re-fogging samples of lower abundance generally are interpreted as evidence that a tree has not recovered fully from the initial fogging (Floren & Linsenmair 1997, Stork & Hammond 1997). We collected > 65% of our total beetle abundance in the late season (i.e., in re-fogging samples) and thus believe that the insect communities in our trees had recovered. Re-fogging samples similar in species composition to initial samples may indicate incomplete recolonization of a fogged tree, especially when the similarity is coupled with low abundance in re-fogging samples. Beetle species composition changed sharply between the initial and re-fogging samples in our study, resulting in low similarity (<15%) between samples. For example, we recorded only 13 individuals of a leaf-eating broad-nosed weevil (Curculionidae: Otiorhynchinae) in early summer but collected 204 individuals of the same species in late summer. An early season dominant, *Macrodactylus subspinosus,* was not recorded at all in the late summer. The increase in abundance and low similarity in species composition between sampling periods suggest meaningful ecological patterns rather than an artifact of re-fogging the same trees; but detailed studies on the dynamics of insect recolonization following canopy fogging are needed in temperate forest ecosystems.

Superimposed on the seasonal decline in species richness and change in species composition were quite different beetle assemblages on trees, especially in the early season when maple and red oak exhibited a maximum similarity of 30%.

Beetle assemblages were more similar among tree species in the late season than in the early season, and one biological explanation may be the change in constitutive defenses of leaves against herbivory (Price 1997). The production of tannins (a secondary metabolite) by oak trees exhibits pronounced seasonal differences: Harinder et al. (1991) found that concentrations of condensed tannins increased with leaf maturity in four oak species. The late season beetle samples may have been comprised of a few abundant beetle species that were able to withstand high tannin concentrations. For example, two of the most abundant late-season beetle species (both Curculionids) feed on leaves as adults. Since the Bray-Curtis index incorporates abundance as well as species identity, the similarity measures likely were driven by these few abundant weevil species. Because the beetle community in a tree crown can change within a period of weeks, estimates of species diversity based on point samples may lead to erroneous conclusions.

Significant plot effects in the early season suggest that richness and abundance of beetle communities have a spatial component. The effects of spatial variation and its relationship to patterns of host-specificity have not been emphasized in the canopy arthropod literature because host-tree effects prevailed in early studies (e.g., Erwin 1982). An exception is Davies et al. (1997), who found that distances > 20 km were sufficient to drive similarity indices of beetle communities on the same tree species below 10%. Our finding that significant plot effects existed for richness and abundance in the early season suggests that this distance could be much lower. Consequently, even the most thorough tree-specific sampling approaches may not capture sufficiently the insect diversity present in a single tree species, because trees separated by < 1 km can have very different levels of richness and abundance. Distance effects had a bearing on many previous studies because they suggest that descriptive community parameters, such as richness and diversity, change over spatial scales and that conclusions drawn from one area or study plot have limited value in explaining broader biogeographic patterns of insect distributions. Hence spatial heterogeneity in richness and abundance should be acknowledged in the design of canopy insect studies by implementing hierarchically structured sampling protocols (Palmer 1995).

CONCLUSIONS

In addition to documenting spatial, temporal, and host-tree patterns of beetle diversity in tem-

perate tree crowns, this study identified the urgent need for studies on recolonization and spatial dependence of arboreal insect communities in temperate forests. Beetle abundance increased between sampling periods, and early and late summer beetle assemblages showed different composition (10% similarity). These findings suggest that insect life cycles may be used to interpret seasonal patterns. Although such temporal patterns are uncharacteristic of re-fogging effects, as documented by other authors, further studies are needed to fully understand the dynamics of insect recolonization in temperate forest canopies. Significant plot effects on beetle abundance in the early season suggest that spatial heterogeneity can be a determinant of insect diversity in temperate forest canopies. Thus researchers need to consider carefully sampling designs to adequately account for spatial variation. Host-tree differences in beetle diversity exhibited a seasonal component, suggesting that leaf chemistry might influence the structuring of arboreal beetle communities. Studies that link host-tree preferences of insects with seasonal changes in leaf chemistry will be valuable to understanding seasonal changes in beetle composition.

ACKNOWLEDGMENTS

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APPPENDIX. Abundance and species richness of 41 beetle families collected from four tree species using insecticide fogging in early summer (18 June–6 July) and late summer (20 August–5 September) of 1998 in Hueston Woods State Park, Preble County, southwestern Ohio.

Family	Common name	Species richness RTUs	Abundance no. ind.
Curculionidae	Snout weevils	32	460
Chrysomelidae	Leaf beetles	31	275
Staphylinidae	Rove beetles	22	53
Anobiidae	Death-watch beetles	19	41
Elateridae	Click beetles	12	20
Scarabaeidae	Scarab beetles	11	36
Tenebrionidae	Darkling beetles	10	30
Coccinellidae	Lady-bird beetles	9	136
Cerambycidae	Long-horned beetles	9	11
Buprestidae	Metallic wood-boring beetles	8	32
Melandryidae	False darkling beetles	8	22
Mordellidae	Tumbling flower beetles	7	11
Cucujidae	Flat dark beetles	7	8
Phalacridae	Shining flower beetles	6	26
Carabidae	Ground beetles	6	25
Euglenidae	Antlike leaf beetles	6	12
Cleridae	Checkered beetles	5	9
Colydiidae	Cylindrical bark beetles	5	8
Corylophidae	Minute fungus beetles	4	68
Cryptophagidae	Silken fungus beetles	4	16
Ciidae	Minute tree-fungus beetles	4	10
Eucnemidae	False click beetles	4	9
Mycetophagidae	Hairy fungus beetles	3	15
Nitidulidae	Sap beetles	3	11
Ptiliidae	Feather-winged beetles	3	7
Lampyridae	Lightningbugs, fireflies	4	6
Latridiidae	Minute brown scavenger beetles	2	32
Anthicidae	Antlike flower beetles	2	23
Cantharidae	Soldier beetles	2	11
Lycidae	Net-winged beetles	2	4
Monotomidae	Root-eating beetles	2	4
Leiodidae	Round fungus beetles	2	3
Anthribidae	Fungus weevils	2	2
Histeridae	Hister beetles	1	4
Bostrichidae	Branch and twig borers	1	2
Attelabidae	Tooth-nosed weevils	1	1
Brentidae	Straight-snouted weevils	1	1
Dermestidae	Skin beetles	1	1
Ptilodactylidae	Ptilodactylid beetles	1	1
Scydmaenidae	Antlike stone beetles	1	1
Unknown		9	12
TOTAL		272	1459