Impacts of Alternative Timber Harvest Practices on Leaf-Chewing Herbivores of Oak

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Abstract: *Studies of the effects of logging on Lepidoptera rarely address landscape-level effects or effects on larval, leaf-feeding stages. We examined the impacts of uneven-aged and even-aged logging on the abundance, richness, and community structure of leaf-chewing insects of white (*Quercus alba *L.) and black (*Q. velutina *L.) oak trees remaining in unharvested areas by sampling 3 years before and 7 years after harvest. After harvest, white oaks in uneven-aged sites had 32% fewer species of leaf-chewing insects than control sites. This reduction in species richness may have resulted from changes in microclimate (reducing plant quality and/or changing leaf phenology) that affected a much larger total area of each site than did even-aged cuts. For black oak after harvest, species richness in uneven- and even-aged sites increased relative to levels before harvest. Harvesting did not alter total insect density or community structure in the unlogged habitat for either oak species with one exception: insect density on black oak increased in the oldest forest block. Community structure of herbivores of black and white oaks in clearcut gaps differed from that of oaks in intact areas of even-aged sites. Furthermore, both richness and total insect density of black oaks were reduced in clearcut gaps. We suggest that low-level harvests alter herbivore species richness at the landscape level. Treatment effects were subtle because we sampled untreated areas of logged landscapes, only one harvest had occurred, and large temporal and spatial variation in abundance and richness existed. Although the effects of logging were greater in uneven-aged sites, the effects of even-aged management are likely to increase as harvesting continues.*

Key Words: larval Lepidoptera, Missouri, *Quercus*, selective logging, species richness

Impactos de Prácticas Alternativas del Corte de Madera sobre Herbívoros de las Hojas de Roble

Resumen: *Los estudios de los efectos de la tala sobre Lepidoptera raramente abordan los efectos a nivel de paisaje o los efectos sobre etapas larvarias folívoras. Examinamos los impactos de la corta en edad de aprovechamiento impar y par sobre la abundancia, riqueza y estructura de la comunidad de insectos folívoros de árboles de roble blanco (*Quercus alba *L.) y negro (*Quercus velutina *L.) en áreas no taladas que fueron muestreadas 3 años antes y 7 años después de la cosecha. Después de la cosecha, los robles blancos en sitios con edad de aprovechamiento impar tenían 32% menos especies de insectos folívoros que en los sitios control. Esta reducción en riqueza de especies pudo haber resultado de cambios en el microclima (reducción en la calidad de la planta y/o cambio en la fenología de las hojas) que afectaron a una superficie total mucho más grande en cada sitio que en los sitios con edad de aprovechamiento par. Para el roble negro, después de la cosecha, la riqueza de especies en sitios con edad de aprovechamiento impar y par incrementó en relación con los niveles previos a la cosecha. La cosecha no alteró la densidad total de insectos ni la estructura de la comunidad en el hábitat no talado para ninguna especie de roble con solo una excepción la densidad de insectos en roble negro incrementó en el bloque de bosque más viejo. La estructura de la comunidad de*

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herbívoros de roble negro y blanco en claros talados difirió de la de robles en áreas intactas de sitios con edad de aprovechamiento par. Más aun, tanto la riqueza como la densidad total de insectos en robles negros fueron bajas en claros talados. Sugerimos que niveles de cosecha bajos alteran la riqueza de especies de herbívoros al nivel de paisaje. Los efectos de los tratamientos fueron sutiles porque muestreamos áreas no tratadas en paisajes talados, sólo hubo una cosecha y había amplia variación temporal y espacial en la abundancia y riqueza. Aunque los efectos de la tala fueron mayores en sitios con edad impar, es probable que los efectos de la gestión de sitios con edad par incrementen a medida que las cosechas continúen.

Palabras Clave: Lepidoptera larvario, Missouri, *Quercus*, riqueza de especies, tala selectiva

Introduction

By the early 1900s many forests in the United States had been extensively logged (Thomas 1956). Regenerating forests, although they may differ vastly from their original species composition (Guyette & Dey 1997), face similar exploitation pressures today (Haynes 2003). To make informed decisions regarding timber sustainability, forest managers currently focus on the impacts of logging on biodiversity and ecosystem function (Brookshire et al. 1997). The impacts of timber removal on the diversity of Lepidoptera are variable: species richness in logged forests can increase (Willott et al. 2000), decrease (Hill et al. 1995), or remain stable (Willott 1999) relative to richness in intact forests. These contrasting results may be explained in part by variation in habitat requirements, distribution patterns, or dispersal abilities of different species (Murphy 1989; Cooke & Roland 2000); differences among logging treatment replicates in current habitat heterogeneity and historical site factors (Cleary 2003; Hamer et al. 2003); the scale and degree of disturbance or time elapsed since harvest (Greiser Johns 1997); and the degree to which communities are adapted to disturbance (Lewis 2001).

Although studies of Lepidoptera usually focus on fruit and flower-feeding butterflies (DeVries et al. 1997), the impacts of logging on larval Lepidoptera, and leaf-feeding herbivores in general, may be equally important because of their role in ecosystem function (Schowalter et al. 1986), effect on plant productivity (Mattson & Addy 1975; Coffelt et al. 1993), and role as food for higher trophic levels (Holmes et al. 1979; Marshall & Cooper 2004). Nonetheless, research on the effects of logging on larval Lepidoptera and other leaf-chewing herbivores is sparse (Roland 1993; Martel & Mauffette 1997). The few published studies have been restricted to a single species (Roland 1993; Radeloff et al. 2000) or a limited time period (Schowalter 1995; Progar et al. 1999). It is unclear whether results obtained for communities of adult Lepidoptera (e.g., Summerville & Crist 2002) can be predicted by logging effects on larvae and vice versa. Differences between life stages in feeding habitat, microclimate requirements, mobility, and trophic interactions suggest that larval Lepidoptera may show widely different responses to timber extraction.

Timber harvest can affect leaf-chewing stages of insects through multiple direct and indirect mechanisms. Logging may alter microclimate as a result of increased canopy openness, creating inhospitable temperatures for larval development (Casey 1993). Changes in temperature or light levels may indirectly alter densities of herbivorous insects by changing foliage quality of remaining or regenerating plants (Dudt & Shure 1994; Forkner & Marquis 2004). Additionally, timber extraction may reduce host plant density by direct removal of specific tree species or subsequent changes in plant species composition. Reduced host plant density may decrease population sizes of herbivorous insects if resources are limiting (Ohgushi 1992) or increase densities if host plant quality increases as a result of reduced competition (Barbosa & Wagner 1989; Carr et. al. 1998; Teder & Tammaru 2002). Logging also may alter abundances or richness of leaf-chewing herbivores indirectly by altering the density, richness, or foraging behavior of their predators.

One would expect most animal communities to differ between logged (i.e., disturbed) and undisturbed sites. An additional important question is whether a landscape maintains its diversity under a given harvesting regime. Even-aged cutting of small areas of forest may be more desirable than removing an equal amount of timber by uneven-aged management or thinning if the latter disturbs a greater area of forest. The degree to which logging practices affect herbivorous insect populations at the landscape scale depends on the amount of timber removed, the size of cuts, the severity of edge effects, and how the effects of localized disturbance propagate through the habitat matrix. Only long-term, replicated, landscape-level, multispecies investigations will elucidate the relative value of alternative management practices (Sparrow et al. 1994; Gram et al. 2001).

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a large-scale, long-term, replicated before-after/control-impact experiment designed to determine the effects of even-aged and uneven-aged management on multiple forest flora and fauna. Our objective within MOFEP was to examine the effects of these two management treatments on the richness and density of leaf-chewing insects feeding on the two dominate tree species of MOFEP forests, black oak (*Quercus velutina* L.) and white oak (*Q. alba* L.). We censused herbivores in intact forest stands of replicate sites undergoing even- and uneven-aged management and in control sites (no-harvest management) for 3 years before and 7 years after timber extraction. Because uneven-aged management not only disturbs a greater amount of forest to harvest an equal amount of timber but also generates forest stands with less dense overstories, we predicted that it would cause a greater short-term reduction in herbivore species richness and density in the remaining forest matrix. We expected, however, that both logging treatments would show changes in herbivore richness, density, and community structure relative to unlogged sites.

Methods

Missouri Ozark Forest Ecosystem Project

The MOFEP sites are located in southeastern Missouri and encompass nearly 18,000 ha (91°01′–91°13′W, 37°00′–37°12′N). This area is primarily upland oak-hickory and oak-pine communities, and is 84% forested (Brookshire & Hauser 1993; Xu et al. 1997). White oak, black oak, and scarlet oak (*Q. coccinea* Muenchh) dominate the canopy. White and black oak, dogwood (*Cornus florida* L.), and sassafras (*Sassafras albidum* Ness) constitute the majority of woody understory species.

The experimental design was a randomized complete block, including nine sites (three sites within each of three blocks), ranging from 266 to 527 ha. Sites were chosen and blocked based on geographic proximity, forest age, vegetation, and soil composition (Brookshire et al. 1997; Sheriff & He 1997). Entire sites within blocks were randomly assigned to even-aged, uneven-aged, or no-harvest cutting regimes. Sites were subdivided into stands, averaging 4 ha, of similar ecological land types defined by slope, aspect, vegetation composition, and soil type. To conduct timber sales, stands to be clearcut in even-aged management sites were chosen such that the size class distribution of remaining forest contained 10% seedlings, 20% small trees (6–14 cm dbh), 30% poletimber (14–29 cm dbh), and 40% saw timber (>29 cm dbh). To accomplish this distribution, some stands were clearcut and others treated with intermediate cutting (Roach & Gingrich 1968). Stands to be thinned in uneven-aged management sites were chosen such that the distribution of the target size class approximated the size-class distribution in even-aged management sites (Brookshire et al. 1997). These trees were removed in small group cuts, individually, or girdled and left standing. Ten percent of each logged site was designated as old growth and not available for harvest. No-harvest management sites are not manipulated, except that wildfires and large-scale insect outbreaks, should they occur, are suppressed. These sites serve as experimental controls (Sheriff & He 1997). The first MOFEP harvests were in 1996, and future harvests will be at 15-year intervals. Before MOFEP, no harvesting had taken place since 1950, and most overstory trees were 50 to 90 years old.

Herbivore Censuses

We surveyed at ground level (<2.5 m) a mixture of sapling and low-hanging branches of subcanopy and canopy trees on ecological land types 17 and 18 (south- and west-facing and north- and east-facing slope aspects, respectively). Analyses of data for understory trees of five size classes (<1 m, 1–2 m, 2–4 m, 4 m to canopy, canopy) indicated that species richness and insect density did not differ between saplings and understory branches of subcanopy or canopy trees (R.E.F., unpublished data). Preliminary analysis showed that five trees per oak species and three stands per site adequately identified leaf-chewing herbivore densities and richness (Marquis & Le Corff 1997).

In 1993 three stands of each slope-aspect category were randomly chosen in each site with the caveat that, in even-aged sites, potential stands were restricted to those to be harvested in the second round of cutting (in 2011) to ensure that our stands were not clearcut in 1996. In uneven-aged sites, chosen stands may have had individual trees removed or girdled, but sampling locations were not within group cuttings. For black oak, it was not always possible to locate appropriately sized trees in all stands, so the number of stands ranged from one to three per slope-aspect per site. In all, we censused 43 understory stands (3 to 6 per site in 3 sites in each of 3 treatments) for black oak and 54 (6 per site in 3 sites in each of 3 treatments) for white oak. We chose five trees of each species haphazardly from those available within a stand based on a minimum leaf number criterion of 600 leaves per white oak individual and 200 leaves per black oak individual. When only trees with fewer leaves were available, more trees were chosen, such that we initially censused approximately 3000 and 1000 leaves per stand, respectively.

We censused the same trees within stands within and across years. During the first census of each year (in May), study trees (or branches) that had died were replaced with acceptable nearby neighbors to maintain comparable sample sizes. Pretreatment sampling commenced in May 1993, and post-treatment sampling began in May 1997. During timber extraction in 1996, many understory trees were damaged; therefore leaf counts were slightly reduced after treatment. We counted the total number of leaves censused on each tree in June of each year to control for sampling effort. Leaf counts over the 10 years averaged 879 ± 56 leaves/stand for black oak and 2470 ± 85 leaves/stand for white oak (approximately 8.5 and 14.5 m^2 leaf area/stand, respectively).

We censused herbivores four times each year, early May, mid-June, mid-July, and late August, to account for seasonal changes in oak herbivore abundance and composition (Marquis & Le Corff 1997). During each census we searched tops and bottoms of all leaves of marked saplings or branches and recorded the number of individuals of each species of leaf-chewing herbivore encountered. These in situ identifications were based on larval morphology and natural history and were made possible through the work of Marquis et al. (2006). All insects were left undisturbed on the plant unless they could not be identified. These unknowns were collected, photographed, and observed through development until their identity was confirmed or they were classified as a species new to our inventory. In our analysis, we included only species observed to feed on white or black oak (confirmed through field observations or laboratory rearings).

In 2002, at which time regrowth within clearcuts in even-aged sites was sufficient to produce adequate leaf material for censusing, we haphazardly selected six stands that had been clearcut in 1996 (one stand of each slope aspect within each of the three clearcut sites) to assess abundance and richness of oak herbivores. Sapling selection and insect censusing protocols were the same as described above for stands in the remaining forested matrix. Over the 100-year duration of MOFEP, these comparisons will allow determination of whether and when clearcut gaps return to original species composition. We predicted that insect communities in these gaps would be the most highly affected of all areas sampled because of the dramatically different microclimates and plant densities.

To determine species richness and total insect density, we summed the number of species or individuals encountered and the total number of leaves censused across all trees within a stand separately for white and black oak. The number of species or individuals encountered per stand was expressed as per square meter leaf area by dividing the total number of individuals or species encountered by the number of leaves sampled per stand and by the mean leaf size for the relevant oak species (0.00587 and 0.00967 m^2 for white and black oak, respectively, Le Corff & Marquis 1999).

Data Analysis

We assessed differences in species richness (number of species per square meter leaf area) and total insect density (number of individuals per square meter leaf area) per stand among timber-harvest treatments with repeated measures analysis of variance (rmANOVA) in SAS (1999), with timber-harvest treatment and block as between-subject effects and years and censuses as within-subject effects. Slope aspect was a split-plot factor. Block was a random factor, and F tests for treatment and block effects were calculated using the treatment × block interaction as the error term. Before and after treatment analyses were conducted separately, as were analyses for white and black oak. Because we were testing for an effect of harvesting on populations sampled from unlogged portions of treated landscapes, we accepted p values ≤ 0.1. The F approximations for within-subject effects were based on Pillai's trace test statistic. The ANOVA tables are available online (see Supplementary Material section at end of article).

Analyzing these data at the site level, based on means of stands within sites, did not appreciably change the outcome of our analyses. Furthermore, these analyses did not produce multivariate test results for within-subject effects because of limited degrees of freedom. Therefore we present the results of tests with stands as the unit of replication. Because analyzing data as a before-after/control-impact design (Smith 2002) provided similar results to rmANOVA, we present only the latter. For analyses of clearcut versus intact stands within even-aged sites, in which cut stands were paired spatially with uncut stands of the same slope aspect, treatment was considered nested within slope aspect. Total insect density was log $(x + 1)$ transformed to meet assumptions of normality.

We analyzed community structure with nonmetric multidimensional scaling (NMS) (McCune & Grace 2002) in PC-ORD (McCune & Mefford 1999) with the Sørensen distance measure. Because preliminary ordinations indicated that before and after treatment time series differed in community structure, as did communities on white and black oak, we analyzed treatment effects separately by year and by oak species. Densities for each species in each stand were summed across all censuses within a year, except for two Lepidoptera taxa (*Morrisonia confusa* Hübner [Noctuidae] and *Erynnis* spp. [Hesperiidae]) whose larvae require more than 1 month to develop. For these species we used the maximum density in any single census as a conservative estimate. To account for yearly differences in abundance in ordinations involving multiple years of data, we summed densities across stands within a slope aspect class and then relativized by the highest density for any single species in that year. Finally, we weighted species abundances by column (species) totals to weight equally common and infrequent species. Analyses including rare species and singletons did not alter our assessments of treatment effects. For simplicity, however, we conducted multiyear ordinations with only those species for which we encountered ≥ 100 individuals over the course of our study ($n = 99$ species). To determine dimensionality we analyzed 15 runs of real data and 30 runs of randomized data, beginning with four axes and using time as a random number seed. Final instability for all ordinations was ≤ 0.0001. Values for stress and coefficients of determination (R^2) for correlations between ordination distances and distances in original space for each axis are given in the figure legends. Species scores for ordination axes are available from R.E.F. on request.

Results

Effects of Timber Harvest

Over the 10 years we recorded 225,343 individuals and 260 leaf-chewing herbivore species feeding on white and black oak. Eighty-eight percent of the herbivore species we encountered were larval Lepidoptera. Early-season (May) fauna consisted mainly of free-feeding Noctuidae and Tenthredinidae and leaf-rolling species of Gelechiidae and Tortricidae. Leaf-tying Gelechiidae and Oecophoridae and web-building Pyralidae dominated early-and midsummer fauna (June and July). Limacodidae and Notodontidae contributed to late-season (August) peaks in species richness. Other leaf chewers included species of Phasmatidae, Chrysomelidae, Curculionidae, Tettigoniidae, and Acrididae. We encountered only one introduced species: the Asiatic oak weevil (*Cyrtepistomes castaneus* Roelofs) (Coleoptera: Curculionidae). Five species accounted for more than 20% of the total individuals encountered: a free-feeding dagger moth (Noctuidae: *Acronicta increta* Morrison), a leaf miner (Gracillariidae: *Phyllonorycter fitchella* Clemens), a leaf tier (Gelechiidae: *Pseudotelphusa* sp.), a leaf roller (Gelechiidae: *Chionodes adamas* Hodges), and the Asiatic oak weevil.

Both species richness and total herbivore density showed large temporal variation, with highly significant year and census effects before and after the logging treatment. Mean species richness per stand (± 1 SE) was 1.1 ± 0.1 (range: 0.3–3.0) and 1.6 ± 0.1 (range: 0.0–9.5) species/m^2 for white and black oak, respectively, before treatment and 1.2 ± 0.1 (range: 0.5–3.1) and 1.2 ± 0.1 (range: 0.0–7.8) species/m^2 for white and black oak, respectively, after treatment. Mean total insect density per stand (± 1 SE) was 1.9 ± 0.04 (range: 0.5–3.1) and 1.6 ± 0.1 (range: 0.0–6.8) for white and black oak, respectively, before treatment and 1.7 ± 0.1 (range: 0.1–3.8) and 1.3 ± 0.1 (range: 0.0–3.5) for white and black oak, respectively, after treatment. In general, both density and richness were highest in May on black oak, whereas density was highest for white oak during mid- and late-season censuses.

We detected no differences before treatment in species richness of leaf-chewing herbivores on either of the two oak species (white oak: $F_{2,4} = 0.02$, $p = 0.9774$; black oak: $F_{2,4} = 0.98$, $p = 0.4502$, Fig. 1). Species richness on black oak was 26% lower in uneven-aged sites compared with control and even-aged sites before treatment (Fig. 1); this difference, however, was not significant. Species richness was 17% lower and 8% higher on black oak trees within uneven- and even-aged sites, respectively, relative to controls after harvest ($F_{2,4} = 4.80$, $p = 0.0865$, Fig. 1). Duncan's post hoc means separation indicated that black oaks in even-aged sites had higher species richness than those in uneven-aged sites but that neither management scheme differed from control sites.

The decrease in species richness on white oak after treatment in logged sites compared with controls was marginally significant ($F_{2,4} = 3.74$, $p = 0.12$, Fig. 1). Significant census × treatment × block and year × census × treatment × block interactions for both response variables complicated our interpretation of year × treatment interactions, which would have allowed us to determine whether treatment effects were delayed. A reduced model examining only the years 2000–2003, however, showed an effect of treatment on species richness on white oak: uneven-aged sites had 32% and even-aged sites had 18% fewer species/m^2 leaf area compared with control sites ($F_{2,4} = 5.19$, $p = 0.0775$). May censuses contributed the most to this difference: uneven-aged sites had lower species richness than controls for both the entire after treatment time series ($F_{2,4} = 6.25$, $p = 0.0588$) and for 2000–2003 ($F_{2,4} = 7.85$, $p = 0.0412$) when we analyzed May censuses separately.

Total herbivore density did not differ among sites before treatment (white oak: $F_{2,4} = 0.30$, $p = 0.7583$; black oak: $F_{2,4} = 0.01$, $p = 0.9908$) and was unaffected after treatment for white oak ($F = 0.59$, $p = 0.5980$, Fig. 2). The effect of logging on total herbivore density on black oak differed among blocks (significant treatment × block effect, $F_{4,36} = 2.82$, $p = 0.0456$). In block 1, black oaks in logged sites had 12% fewer herbivores after treatment. The amount of variation, however, was equal to that present before treatment (significant before treatment, treatment × block effect, $F_{4,36} = 3.45$, $p = 0.0217$). In block 2, black oaks in logged sites had 9% fewer herbivores before treatment. Even-aged sites in block 2, however, had 14% more herbivores after treatment, whereas uneven-aged and control sites had equivalent herbivore densities. In block 3, total density did not differ among sites before or after treatment.

Community ordinations run separately by year showed no treatment differences in community structure, although herbivore community structure on both white and black oaks differed significantly among years both before and after treatments (results not shown).

Spatial Variation

Blocks did not differ in species richness or total density on either oak species before treatment (Fig. 3). Black oaks in block 2, however, had 47% more herbivore species than black oaks in blocks 1 and 3 in post-timber-harvest years ($F_{2,4} = 37.52$, $p = 0.0026$, Fig. 3). White oak did not differ in species richness among blocks after treatment ($F_{2,4} = 3.59$, $p = 0.1282$). Community structure differed among blocks (Fig. 4). In general, ordinations separated block 3 from blocks 1 and 2. For black oak, differences among blocks were the result of lower densities in block 3 of some species such as the ruby quaker (Noctuidae: *Orthosia rubescens* Walker), shivering pinion (Noctuidae: *Lithophane querquera* Grote), and a leaf webber

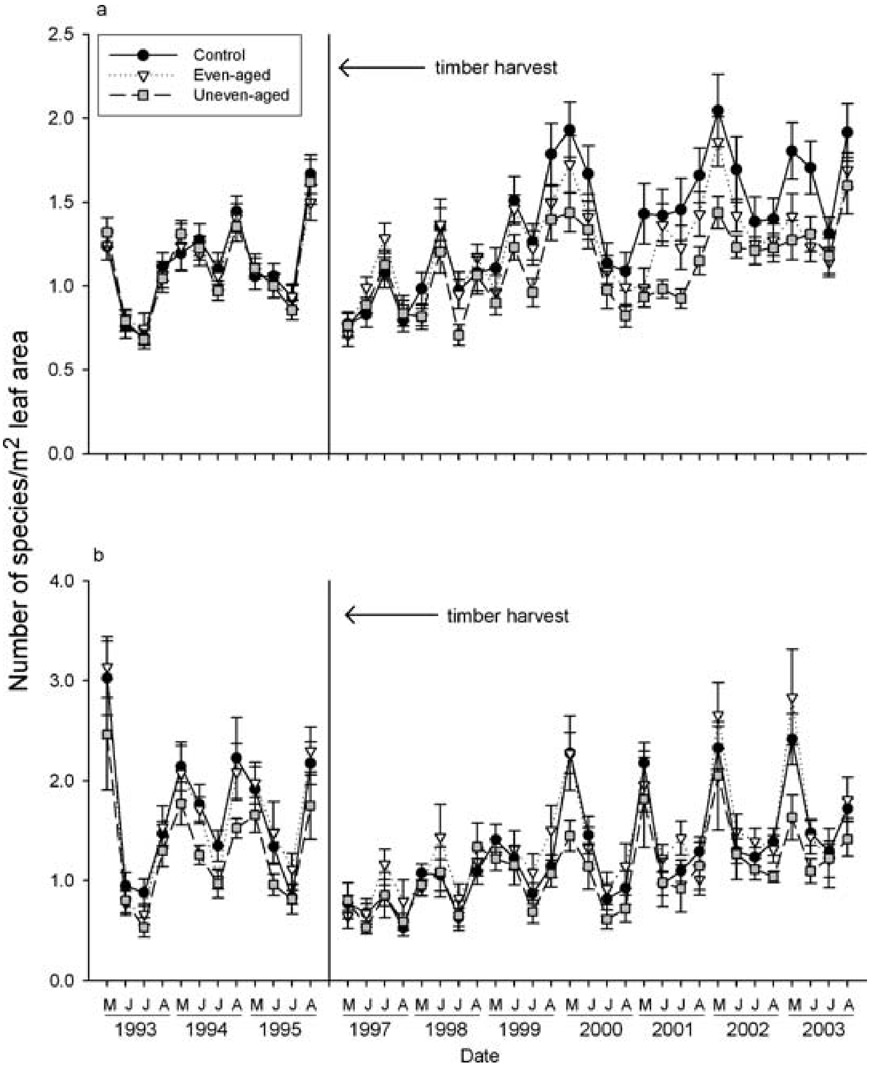

Figure 1. Mean species richness (number of species/m² leaf area ± SE) of leaf-chewing herbivores on (a) white oak and (b) black oak in control and timber-harvest treatments (even-aged and uneven-aged harvest; date is year and month).

(Pyralidae: *Salebriaria engeli* Dyar), and higher densities of other species, including a leaf roller (Gelechiidae: *Chionodes formosella* Murtfeldt), red-fringed emerald (Geometridae: *Nemoria bistriaria* Hübner), and oak besma (Geometridae: *Besma quercivoraria* Guenee). For white oak, block 3 had higher densities of three-lined leaf rollers (Totricidae: *Pandemis limitata* Robinson), *C. formosella,* and *L. querquera* but lower densities of species such as the small phigalia (Geometridae: *Phigalia strigataria* Minot) and a leaf tier (Oecophoridae: *Setiostoma xanthobasis* Zeller).

Before treatment, species richness was 25% and 50% greater on white ($F_{1,36} = 12.61$, $p = 0.0011$) and black oak ($F_{1,26} = 20.60, p < 0.0001$), respectively, growing on north- and east-facing compared with south- and west-facing slopes. This difference persisted after treatment, although the magnitude decreased slightly (15% and 40% on north- and east-facing slopes for white [$F_{1,36} = 4.19, p = 0.0481$] and black oak [$F_{1,26} = 19.81, p < 0.0001$], respectively). Differences were consistent across management regimes for white oak (i.e., no significant treatment × slope-aspect interaction). There was a significant treatment × slope-aspect interaction for black oak after treatment, however, with an amelioration of the slope effect in the control treatment only ($F_{2,26} = 2.83, p = 0.0771$). Total insect density was also 9% and 7% higher on white oaks on north- and east-facing slopes before ($F_{1,36} = 17.34, p = 0.0002$) and after treatment ($F_{1,36} = 6.71, p = 0.0178$), respectively, and 7% higher on the same slope-aspect class for black oak after treatment ($F_{1,26} = 6.20, p = 0.0195$). Community structure did not differ between slope-aspect classes for either oak species.

Gaps versus Intact Stands within Clearcut Sites

Species richness and total density were reduced by 47% and 33%, respectively, on black oak saplings regenerating in even-aged clearcut gaps compared to nearby trees in intact stands (species richness: $F_{2,8} = 10.96, p = 0.0051$; total density: $F_{2,8} = 5.69, p = 0.0290$, Fig. 5). Reductions in total density in clearcuts were greatest during May (census × treatment: $F_{6,14} = 3.08, p = 0.0389$) and reductions

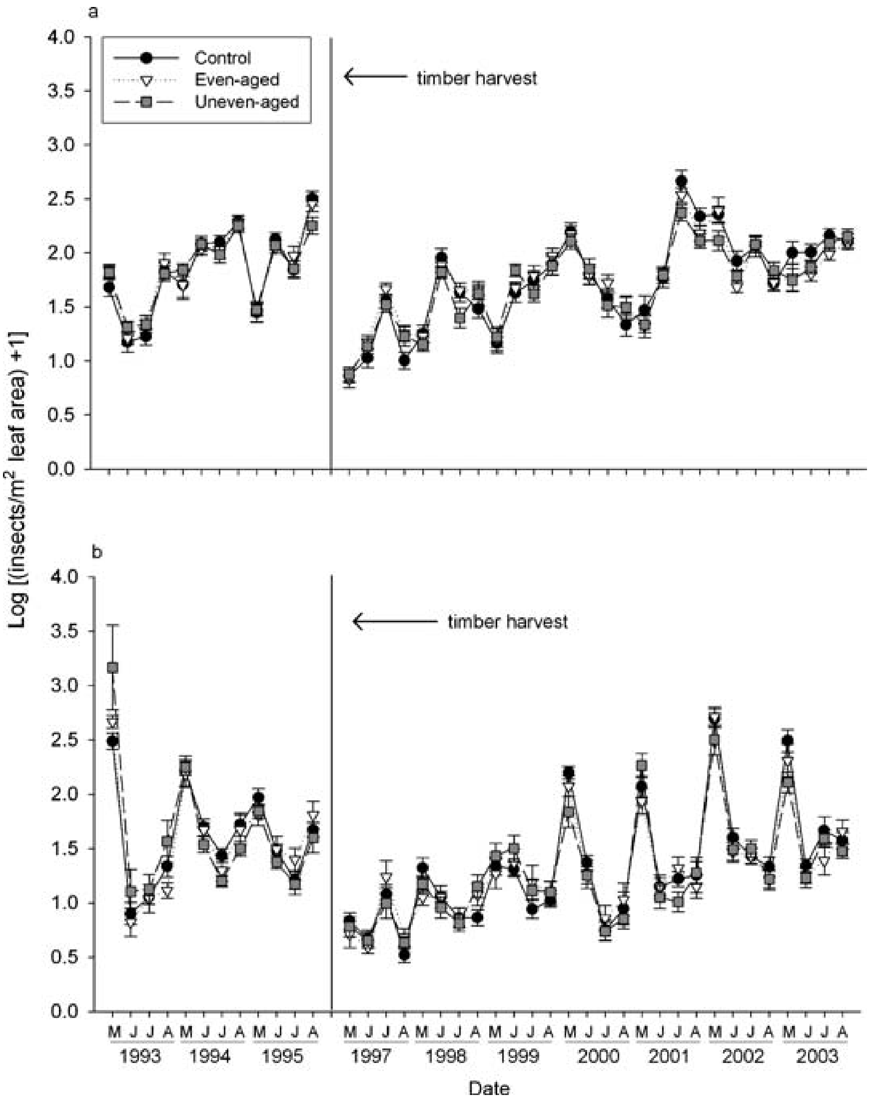

Figure 2. Mean total abundance (log [(insects/m^2 leaf area) +1] ± 1 SE) of leaf-chewing herbivores on (a) white oak and (b) black oak in control and timber-harvest treatments (even-aged and uneven-aged harvest).

in richness were marginally higher in May (census × treatment: $F_{6,14} = 2.98, p = 0.0958$). In contrast, species richness and total density did not differ on white oaks in gaps versus intact stands (species richness: $F_{2,8} = 1.00$, $p = 0.4085$; total density: $F_{2,8} = 0.70, p = 0.5244$).

Community structure differed between trees in intact stands versus clearcut gaps (Fig. 6). Differences in community structure on white oak were due to the absence in gaps of species such as the copper underwing (Noctuidae: *Amphipyra pyramidoides* Guenee) and Edward's hairstreak and to lower abundances of the girlfriend underwing (Noctuidae: *Catacola amica* Hübner), the common oak moth (Noctuidae: *Phoberia atomaris* Hübner), and two Geometridae (*Phigalia titea* Cramer and *P. strigitaria* Minot). Differences in community structure on black oak were due to the absence in gaps of Geometridae such as the linden looper (*Erannis tiliaria* Harris) and the one-spotted variant (*Hypagyrtis unipunctata* Haworth), and to higher abundances in gaps of common species such as oblique-banded leaf rollers (Tortricidae: *Choristoneura rosaceana* Harris [Tortricidae]) and pale tussock moths (*Halysidota tessellaris* Smith [Arctiidae]).

Discussion

Uneven-aged management had a negative effect on the species richness of insects feeding on white oak in intact stands. White oaks in stands within these sites had 32% fewer herbivore species per square meter leaf area relative to stands within even-aged and control sites from 2000–2003, and there was a trend for lower richness in uneven-aged sites for all years after harvest. In contrast to white oak, black oaks in uneven-aged sites had lower richness than those in even-aged sites, with intermediate richness in controls. This difference appears to be the result of an elevation (approximately 8–9%) of herbivore species richness on black oak relative to levels before harvest under both extraction methods (cf. before and after treatment, Fig. 1). These results for both oak species

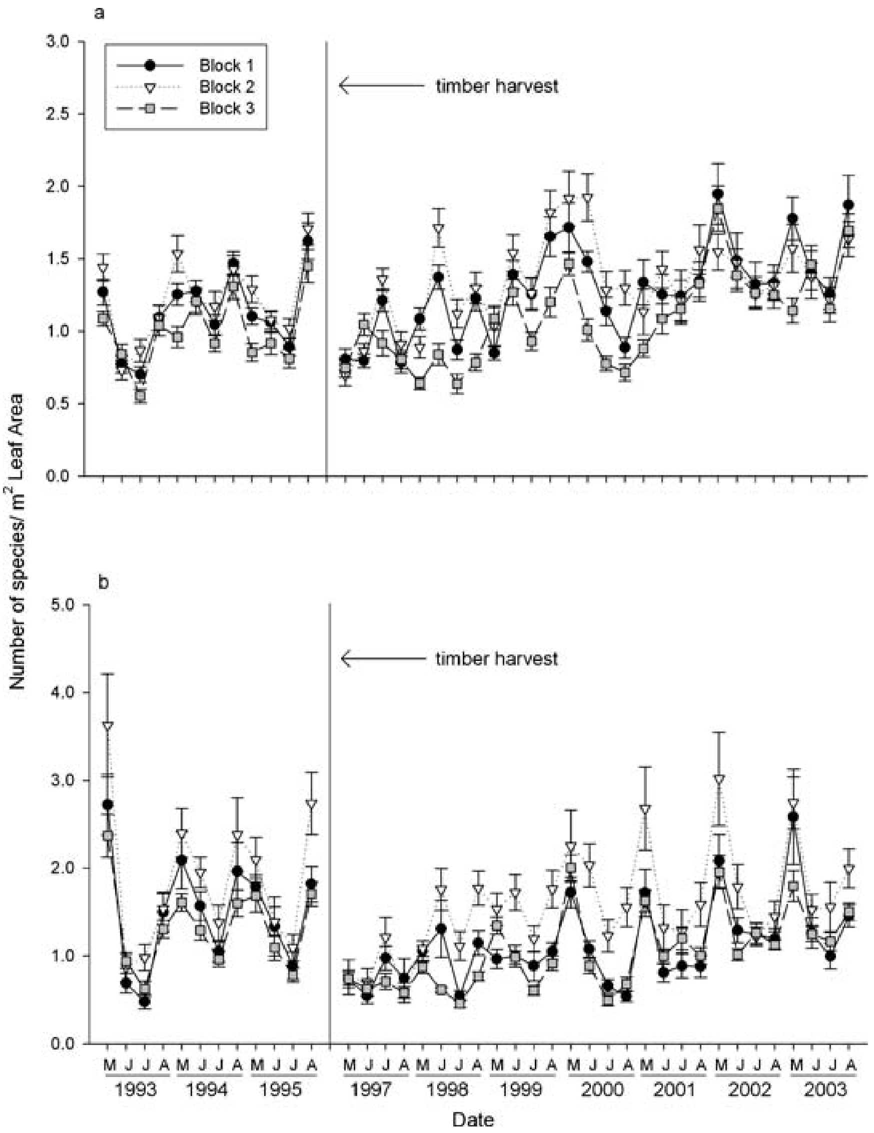

Figure 3. Mean species richness (number of species/m^2 leaf area ± 1 SE) of leaf-chewing herbivores on (a) white oak and (b) black oak in forest blocks 1, 2 (older forest), and 3 (date is month and year).

mirror the effects of treatments on the accumulation of new herbivore species over time, analyzed for 1997–2000 (Marquis et al. 2002).

For the herbivore faunas of both oaks, spring-feeding species appeared to be affected more than late-season species, which points to a possible treatment effect on plant phenology. Spring-feeding species are generally more sensitive than late-feeding species to small changes in plant phenology (Parry et al. 1998). In addition to potential phenological effects, the microclimates (e.g., levels of insolation and temperature) of the stands within uneven-aged sites were more likely to be directly altered than those in even-aged sites because the uneven-aged treatments encompassed a much larger total area of each site. Changes in light levels or temperature resulting from uneven-aged treatments may have altered food quality and/or patterns of habitat selection for some insect herbivores, decreasing their attraction to or survival on trees.

The degree to which our results for intact stands are due to herbivore, plant, or predator responses to gaps generated by timber extraction depends on how far gap- and edge-related changes propagate through the understory. Paired comparisons of clearcut gaps with uncut stands within even-aged sites showed effects of timber extraction on richness, abundance, and community structure for black oak and effects on community structure for white oak. The overall weak effects on richness and lack of differences in community structure in intact stands within treated landscapes, however, suggest that logging effects on leaf-chewing herbivores are highly localized. Significant before and after harvest treatment × block interactions in both between- and within-subject effects also suggest that population dynamics are localized (that is, the treatment effects differed among sites) for the herbivores we examined.

Effects of management treatments are likely to be influenced by site history (Schowalter 1995; Progar et al. 1999). Blocks in our study represent forests of different age, land-use history, and host-plant density. The combination of increased insect density on black oaks in older

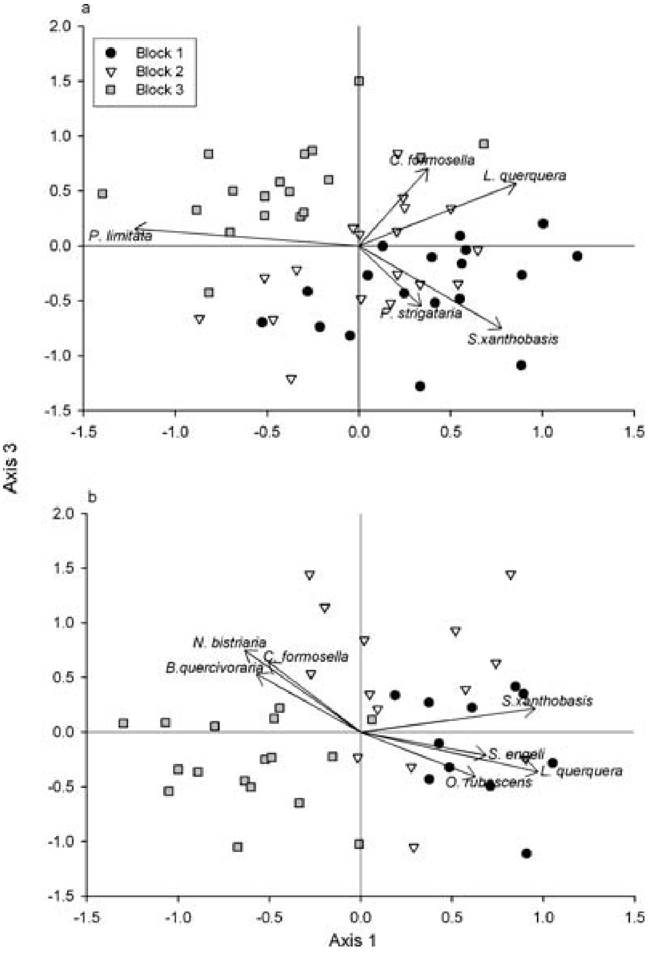

Figure 4. Nonmetric multidimensional scaling results for variation in insect community structure among experimental forest blocks for (a) white oak (stress = 18.78, R^2: axis 1 = 0.152, axis 2 = 0.291, axis 3 = 0.268) and (b) black oak (stress = 18.34, R^2: axis 1 = 0.252, axis 2 = 0.107, axis 3 = 0.343) in 2000. Refer to text for common names of species.

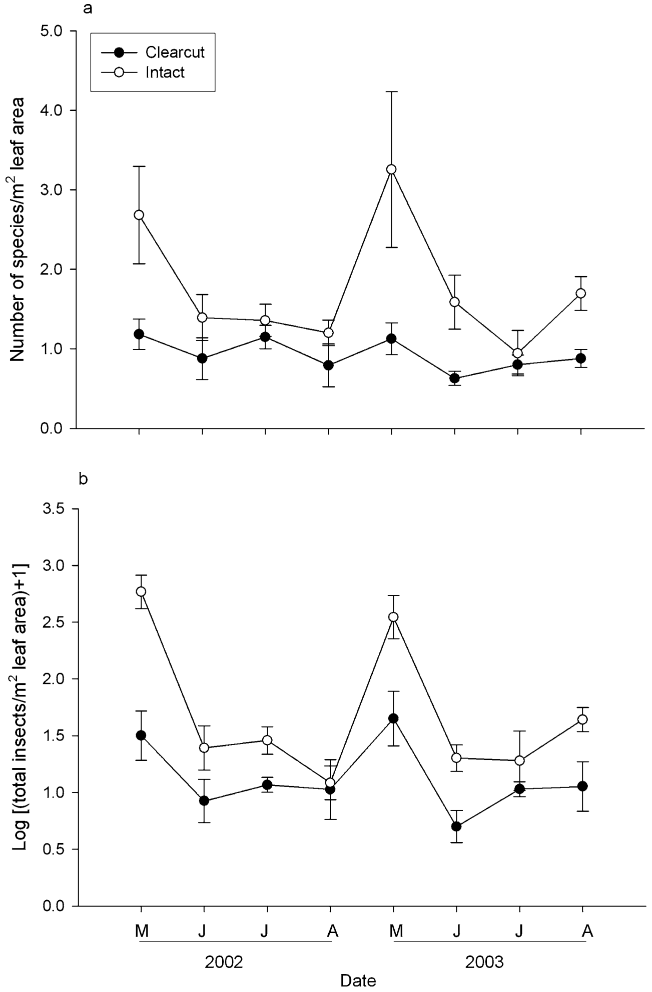

Figure 5. (a) Mean species richness (no. species/m^2 leaf area ± 1 SE) and (b) mean total density (log [insects/m^2 leaf area) +1] ± 1 SE) of leaf-chewing herbivores on black oak in clearcut gaps and intact stands within even-aged sites in 2002 and 2003.

forests (block 2) and higher densities of out-breaking species (the oblique-banded leaf-roller and the variable oakleaf caterpillar) in clearcut gaps suggests that clearcutting older forests may increase their susceptibility to large-scale defoliation. In a previous analysis we found that blocks accumulated species at different rates after harvest (Marquis et al. 2002), with block 3 having the lowest rates of accumulation of new herbivore species. Mathematical models of extinction and population dynamics show that responses to disturbance (i.e., extinction probabilities) are sensitive to initial population densities or starting conditions (Primack 1993), suggesting that historical factors were likely to have played an important role in determining current patterns of spatial variation and responses to treatment.

Timber extraction did not affect community structure in intact stands. If the insect fauna in unlogged portions of harvested landscapes is resilient to timber extraction, these habitats may provide source populations for recolonization. Reduced species richness and density on black oaks in stands regenerating from the 1996 clearcutting, however, suggest that if the cutting cycle is too short for clearcuts within even-aged sites to return to pretreatment conditions, we may see large reductions in richness or changes in community composition in even-aged landscapes in the long term. That community ordinations included densities of nearly 100 species makes it difficult to describe differences in community structure. Because of the nature of rare species (i.e., extremely low population densities and infrequent occurrences), it is difficult to ascertain whether any species was unique to a particular harvest treatment. When we analyzed common or rare species separately, however, we found no significant differences in community structure among intact stands in

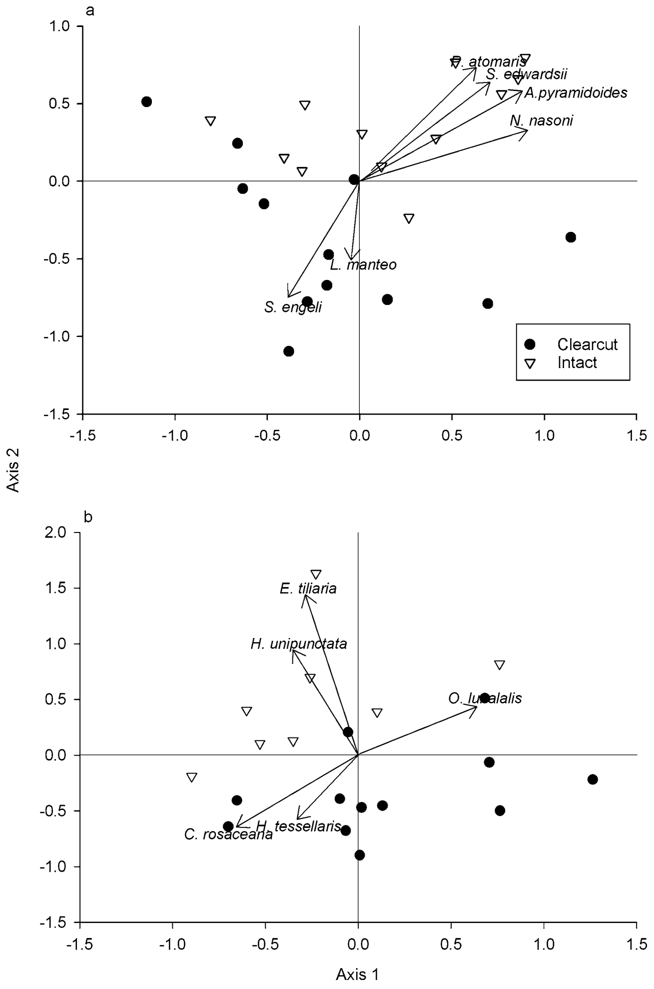

Figure 6. Nonmetric multidimensional scaling results for variation in insect community structure of leaf-chewing herbivores on (a) white oak (stress = 8.28, R^2*: axis 1 = 0.361, axis 2 = 0.267, axis 3 = 0.298) and (b) black oak (stress = 13.70,* R^2*: axis 1 = 0.147, axis 2 = 0.328, axis 3 = 0.296) in clearcut gaps and uncut stands within even-aged sites in 2002 and 2003. Refer to text for common names of species.*

logged sites compared with stands in control sites for either oak species. Continued monitoring of clearcut gaps is needed to determine whether a 15-year cutting cycle is sufficient for gaps to return to pre-harvest community composition, density, and richness.

Yearly fluctuations in insect abundance complicate studies of management impacts. Richness, density, and community structure varied dramatically before and after treatment. We observed particularly low levels of richness and abundance in 1997 across all treatments. Across-the-board declines may have been due to climatic factors (Roy et al. 2001). We observed a premature warming of temperatures in March followed by late April frosts in both 1996 and 1997. Late April frosts in 1997 occurred after leaf flush and damaged leaves. Other MOFEP studies on birds and herpetofauna also showed population declines across all treatments for this time period (Gram et al. 2001; Renken et al. 2004). In a study of logging and butterfly diversity, Hill (1999) found that populations became fragmented in dry years, complicating the interpretation of logging effects. Our ability to detect differences among treatments may have been reduced if regional factors such as climate constrained species densities to low levels or created large yearly variation in means.

Our study is in its early stages: only one round of cutting has taken place. Sampling intact stands within treated sites may further diminish discernible impacts of timber extraction. Others have suggested that low intensities of logging may not alter species richness in logged sites close to intact forest (Usher & Keiller 1998; Willott et al. 2000). The effects we observed in intact areas of treated sites were subtle. Future rounds of timber extraction and continued censusing will be necessary to ascertain more completely the relative landscape-level effects of even-aged versus uneven-aged logging on communities of leaf-chewing herbivores.

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Supplementary Material

The following supplementary material is available as part of the online article from http://www.blackwell-synergy.com:

Appendix S1. Analysis of variance tables for differences in mean number of understory species per square meter leaf area on white and black oak before and after timber harvest.

Appendix S2. Differences in total number of leaf-chewing insects per square meter leaf area on white and black oak before and after timber harvest.

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