

**Impact of Timber Harvest on Species Accumulation Curves
for Oak Herbivore Communities of the Missouri Ozarks**

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Abstract.—We report the effects of two timber harvest methods, even-aged and uneven-aged harvest, versus no harvest on species accumulation curves for leaf-chewing herbivores of *Quercus alba* and *Q. velutina* in the Missouri Ozarks. The study was part of a larger project, the Missouri Ozark Forest Ecosystem Project (MOFEP). Herbivores were sampled four times during the year (early May, June, July, and late August) for each of 4 years after cutting. Species accumulation curves were generated by plotting the total number of species recorded per leaf area sampled in all stands (N=6 stands/site) within a site in May 1997, the first census of the first year following cutting, and then adding the number of new species encountered in each subsequent census through the end of 2000. Treatment effects first became apparent in 1998. Uneven-aged management tended to reduce the rate of species accumulation across years for *Q. alba* compared to no harvest (control) and even-aged management, although marginally so. In contrast, even-aged management significantly increased the rate of species accumulation on *Q. velutina* compared to no harvest, with uneven-aged curves lower than no harvest. The May and June censuses contributed most to the treatment effect for *Q. alba* and *Q. velutina*, respectively. We interpret these results to mean that the treatments either increased or decreased population size relative to controls, thus resulting in an increased or decreased probability, respectively, of sampling a species. Species accumulation curves were lower for younger forests, suggesting that continued cutting, regardless of harvesting method, will reduce species richness of this herbivore fauna.

A major concern for natural area managers is the impact that management will have on the biodiversity of managed areas. One component of biodiversity is the total number of species (i.e., species richness) found in any one location. Changing the nature of the habitat through active management (e.g., harvesting timber), or in some cases absence of manipulation (e.g., protection as old growth), can lead to changes in the ability of species to use that

habitat. Whether an individual species increases or decreases in abundance as a result of some management option will depend on the ecology and life history of the particular species involved. When the effects on communities of organisms are considered, changes in total species richness will be the sum of the reactions of all individual species making up the community, with some species perhaps showing positive population responses to management, and

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others showing negative responses. Because species have intrinsic value unto themselves (Wilson 1988) and changes in species richness can be linked to changes in various ecosystem functions (Hart *et al.* 2001), an important goal of managers is to define management regimes that limit loss of native species.

Species accumulation curves provide one way to assess the effects of management on species richness. Such curves represent the cumulative number of species encountered as sample size is increased in either time or space. When management has a negative effect on species richness, the species accumulation curve should be shallower or level off at a lower number of samples compared to that for unmanaged habitats. When management has a positive effect on species richness, more new species will be accumulated with fewer number of samples compared to control locations. Species accumulation curves have been used to compare the effectiveness of different sampling techniques to estimate arthropod diversity (Longino and Colwell 1997), to compare canopy versus understory insect diversity (DeVries *et al.* 1997, Le Corff and Marquis 1999), and to determine the effects of natural disturbance on plant community diversity (Vandermeer *et al.* 2000).

During the years 1993-2000, we assessed the impact of two alternative forest harvesting regimes on the community structure and abundance of leaf-chewing insects feeding on white (*Quercus alba*) and black oak (*Quercus velutina*) in the southeastern portion of the Missouri Ozarks. This study is part of a larger multi-collaborator experiment, the Missouri Ozark Forest Ecosystem Project (MOFEP) (Sheriff, this proceedings), designed to determine the impacts of alternative forest harvesting regimes on the overall biodiversity and long-term productivity of these oak-hickory forests. The first harvest entry was completed; it was the first of a continuing series of periodic harvests to be implemented on a 15-year cycle in the even-aged and uneven-aged harvest units. We sampled the herbivore communities of the same stands, and the same trees within those stands, 3 years before cutting and 4 years after cutting. In each year, we sampled four times to account for predictable changes in community composition as the season progressed. Because the specific stands we sampled were not harvested, our sampling results reveal the landscape-level effects of harvesting on species accumulation.

We present here species accumulation curves for stands within regions undergoing two harvesting regimes (even-aged versus uneven-aged management) and a no-harvest (control) treatment. First, we determined the degree to which the species accumulation curves differed among the three treatments, with increasing numbers of samples over time (censuses and years), and we did so separately for the two host plants, *Q. alba* and *Q. velutina*. Second, we asked whether different times of year (different censuses) contributed differentially to treatment effects and to the overall 4-year pattern. The herbivore faunas of these oak species change dramatically in composition across the season, particularly between May and the rest of the the year. It is of interest to know, therefore, whether different portions of the fauna contribute equally to any observed treatment effects. Impacts on species richness *per se* and species turnover will be described in another publication (Marquis *et al.*, in rev.).

We predicted that both treatments would decrease species richness, resulting in lower species accumulation curves compared to unharvested forest regions. Three results from our initial pre-treatment sampling led us to predict a decrease. First, we found that total abundance of insect herbivores was greatest on trees located on north- and east-facing slopes as compared to trees on south- and west-facing slopes, for both *Q. alba* and *Q. velutina* (Marquis and Le Corff 1997). Thinning of the forest (uneven-aged management) would open the canopy, and increased proximity to clearcuts (even-aged management) would expose sampled trees and their insects to more open abiotic conditions. Both would be similar to the abiotic conditions of south- and west-facing slopes. Fewer individual insects would result in fewer species sampled. Second, prior to cutting, we found fewer species in the canopy of oaks than in the understory on saplings and low-hanging branches of mature trees (Le Corff and Marquis 1999). The canopy environment should be more similar to a thinned forest or clearcut edge than closed understory. Third, we found some evidence that younger forests have fewer insects (Marquis and Le Corff 1997). If opening up the forest simulates earlier successional stages, then fewer insects would be expected, and in turn, fewer species would be sampled. Finally, we expected the greatest decline in the uneven-aged management forest tracts, because a larger portion of their area was affected by cutting, and many stands that we sampled in

uneven-aged sites were thinned whereas none of our sampled even-aged stands were within a clearcut.

METHODS

Overall MOFEP Design

The MOFEP design (Brookshire *et al.* 1997, Sheriff, this proceedings) includes nine sites of approximately 400 ha each. At the onset of the study (1993), each of these sites was assigned to one of three cutting treatments: control, even-aged, or uneven-aged (N=3 sites/treatment). Pre-treatment sampling was conducted from 1993 to 1995, and cutting occurred in 1996, during which no data were collected. Post-treatment sampling began in 1997 and has continued through 2000. Sites were blocked by geographic proximity and other general characteristics (Sheriff and He 1997). The results presented here are for the post-treatment years only. We are testing whether these treatments affect species accumulation curves at the landscape scale, that is, across entire sites, since none of the stands in the control and even-aged sites, and only a portion of the uneven-aged sites, were altered directly by the cutting.

General Census Methods

Data presented here are for ground-level censusing (0.5 to 2.5 m) on a mixture of saplings and low-hanging branches of sub-canopy to canopy *Q. alba* and *Q. velutina* trees. The same trees and the same stands were censused each year and across years. Five trees each of *Q. alba* and *Q. velutina* were chosen haphazardly from those available within a stand, given a minimum leaf number criterion of 600 leaves per *Q. alba* individual and 200 leaves per *Q. velutina* individual, and a total of 3,000 and 1,000 leaves per stand for *Q. alba* and *Q. velutina*, respectively. When only trees with fewer numbers of leaves were available, more trees were marked. Trees that died within the time span of this study were replaced with nearby neighbors of the same species to maintain a comparable sample size. Sampled trees were spread over approximately 0.2 to 0.8 ha per stand.

To measure insect species richness, leaves on saplings or marked branches of trees were searched both top and bottom, as were associated branches and the main stem of the tree. The number of leaves on marked branches of each tree or sapling was counted in June of each year to estimate the amount of leaf area searched each census. Leaf-chewing insects encountered were classified to species or morphospecies, using a combination of photographs and detailed species descriptions. Each field worker was given training in identification prior to sampling and had a list of descriptions for all species sampled. At no time were leaves collected. All insects were left intact on the plant unless individuals could not be positively identified to species; these unknowns were taken back to the laboratory for rearing and photographing. Each unknown was given a unique sample number and description, and this information was entered into a database. An insect of unknown species was photographed and then observed throughout development until it could be verified as a previously-recognized species or classified as a species new to our inventory.

Post-treatment Censuses (1997-2000)

Leaf, Tree, and Stand Sample Size

During the four post-treatment years, we sampled an average (± 1 SE) of 855 ± 54 and $2,296 \pm 109$ leaves per stand on *Q. velutina* (N=43 stands) and *Q. alba* (N=54 stands), respectively. Using the average leaf size for *Q. velutina* (96.7 cm^2) and *Q. alba* (58.7 cm^2) (N=200 undamaged leaves for each species, each from a different tree), we sampled an average of $\text{ca } 8.3 \text{ m}^2$ and 13.5 m^2 of foliage/stand on *Q. velutina* and *Q. alba*, respectively. Within each stand, the leaves were distributed among 5-12 trees per oak species. For *Q. alba*, we sampled six stands in each of the nine sites. For *Q. velutina*, it was not always possible to locate appropriate sized trees in every stand, so the number of stands/site ranges from 3 to 6 (N=43 total stands). The location of stands within each site was chosen randomly, except that in even-aged sites, we restricted the list of potential sites to the area scheduled to be cut in the second round of cutting in 2011; in so doing, we ensured that our stands were not located within clearcuts.



Number of Samples and Site Sampling Schedule

Due to changes in herbivore abundance and composition through the year (Marquis and Whelan 1994), trees were censused four times per year: early May, late June, late July, and late August-early September. Each census required 2 weeks to complete. In 1997 and 1998, the order of sampling of sites was the same as in pre-treatment sampling: sites 6, 5, and 4 of block 2; sites 3, 2, and 1 of block 2; and sites 7, 8, and 9 of block 3 (see Sheriff, this proceedings). Because we were concerned that the order of sampling might affect census results, especially in the May census when species are rapidly completing their life cycle before leaf hardening, we randomized the order in which we sampled blocks in the May censuses of 1999 (3, 2, 1) and 2000 (1, 2, 3), keeping the order of sites within blocks the same as in previous years.

Data Analysis

Species accumulation curves were generated by plotting the total number of species recorded in all stands within a site in the first census (May) of 1997 and then adding the number of new

species encountered for each successive census through the last census (August) of the year 2000. Although we sampled multiple trees within stands and multiple stands within sites, we chose to calculate species accumulation at the site level because site was the level at which treatments were actually applied. For each census, data were pooled across all stands within each site and cumulative species richness values were weighted by the leaf area sampled. Because the amount of leaf area/site varied slightly among years, data points for 1998-2000 were weighted by the running average of leaf area sampled (e.g., cumulative richness values for 1998 censuses were divided by the mean area sampled in 1997 and 1998). Separate curves were generated for *Q. alba* and *Q. velutina*. To examine the effect of the cutting treatments, block, year, and census on the pattern of species accumulation, we used repeated-measures analysis of variance (Littell *et al.* 1991). Treatment and block were the between-subject fixed effects, and year and census and their interactions with treatment and block were the within-subjects effects. Profile analyses (Littell *et al.* 1991, von Ende 1993) were conducted to determine when effects were significant (i.e., between which pairs of successive censuses and years). We estimated

Table 1.—Repeated measures ANOVA testing for treatment and block effects on the cumulative number of species per square meter of leaf area. F-approximations are based on Wilk's-Lambda test statistic. Ndf and Ddf are numbers of degrees of freedom in the numerator and denominator, respectively, for calculating the F-statistic for within subject effects.

Source	Between subjects							
	<i>Quercus alba</i>				<i>Quercus velutina</i>			
	df	MS	F	P	df	MS	F	P
Treatment (T)	2	0.62	3.48	0.1331	2	2.86	13.67	0.0163
Block (B)	2	1.49	8.43	0.0368	2	13.28	62.92	0.0009
Error	4	0.17			4	0.21		
Source	Within subjects							
	<i>Quercus alba</i>			<i>Quercus velutina</i>				
	Ndf/Ddf	F	P	Ndf/Ddf	F	P		
Year (Y)	3/2	140.31	0.0071	3/2	101.00	0.0098		
Census (C)	3/2	87.52	0.0113	3/2	98.56	0.0101		
Y X C ¹	9/36	49.16	0.0001	9/36	26.92	0.0007		
Y X T	6/4	1.48	0.3676	6/4	1.02	0.5157		
Y X B	6/4	4.00	0.1005	6/4	3.00	0.1532		
C X T	6/4	0.62	0.7157	6/4	1.50	0.3627		
C X B	6/4	1.98	0.2644	6/4	2.48	0.1994		
Y X C X T ¹	18/36	0.70	0.2529	18/36	1.67	0.2610		
Y X C X B ¹	18/36	1.55	0.7853	18/36	2.98	0.1053		

¹Insufficient degrees of freedom to calculate values in MANOVA; univariate results reported.

the contribution of individual censuses to the overall 4-year pattern by graphically comparing the mean effect of each census on species accumulation. Sufficient degrees of freedom were not available to test some interactions in these profile analyses (see table 1). The α -level was considered to be $P \leq 0.05$ unless otherwise indicated.

RESULTS

Species Accumulation Across Years

For both *Q. alba* and *Q. velutina* (fig. 1), the number of species sampled per leaf area in 1997, the first year following timber harvest, was approximately equal across treatments. For

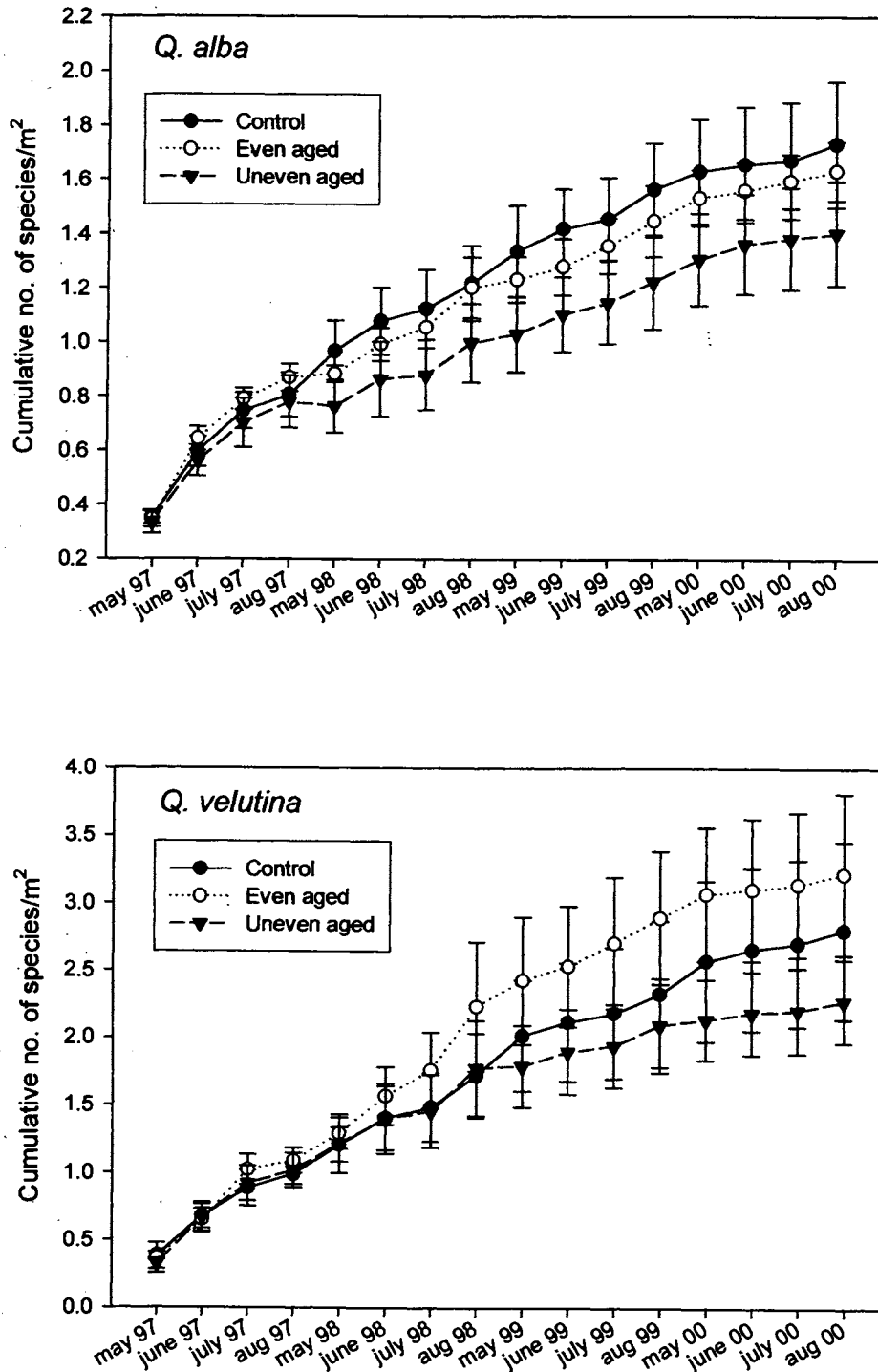


Figure 1.—Effect of harvest treatments on species accumulation curves across all four censuses for the years 1997–2000 on *Quercus alba* and *Q. velutina*. Values are the mean number of new species ($\pm$ SE) accumulated per square meter of leaf area since the previous census.



Q. alba, mean numbers of new species sampled per square meter of leaf area searched at the end of the August 1997 census were 0.79 ± 0.08 , 0.86 ± 0.05 , and 0.7 ± 0.10 for control, even-aged, and uneven-aged treatments, respectively, while for *Q. velutina* these values were 0.98 ± 0.08 , 1.08 ± 0.09 , and 0.90 ± 0.02 , respectively. Thereafter, treatments diverged for both species. Both the significant census ($P < 0.011$) and year ($P < 0.0098$) effects for both species (table 1) and the shape of the curves (fig. 1) indicate that a significant number of new species continued to be added to the list in both *Q. alba* and *Q. velutina* throughout the 4-year period. By the end of 2000, we had recorded a total of 174 and 195 species of leaf-chewing insects on *Q. velutina* and *Q. alba*, respectively. A large majority of these species were rare: 12 percent were represented by a single individual and 16 percent were represented by only two to five individuals. Only one species was exotic, the Asiatic oak weevil, *Crytepistomus castaneus* Roelofs.

Control and even-aged treatments had higher species accumulation over time for *Q. alba*, but not significantly so for the entire study period (fig. 1) (table 1, $P = 0.133$). For *Q. velutina*, treatment ($P = 0.016$) was significant. For this species, control sites had intermediate numbers of new species compared to even-aged treatment (highest) and uneven-aged treatment (lowest) (fig. 1, table 2). Profile analysis showed that contrasts between years were not significant ($P > 0.13$).

Table 2.—Adjusted least squared means ($\pm$ standard error) of cumulative number of species per square meter of leaf area for *Q. alba* and *Q. velutina* in August 2000. Means with different letters are significantly different.

Block	<i>Quercus alba</i>	<i>Quercus velutina</i>
1	$1.62 \pm 0.096ab$	$2.54 \pm 0.22a$
2	$1.86 \pm 0.096a$	$3.74 \pm 0.22b$
3	$1.29 \pm 0.096b$	$2.02 \pm 0.22a$
Treatment	<i>Quercus alba</i>	<i>Quercus velutina</i>
Control	$1.73 \pm 0.096a$	$2.80 \pm 0.22ab$
Even-aged	$1.63 \pm 0.096a$	$3.22 \pm 0.22a$
Uneven-aged	$1.40 \pm 0.096a$	$2.26 \pm 0.22b$

Species accumulation curves varied significantly by block for both *Q. alba* ($P = 0.037$) and *Q. velutina* ($P = 0.0009$) (table 1, fig. 2). For each species, block 2 had the highest curve, with blocks 1 and 3 similar in average number of accumulated species at the end of the 4 years (fig. 2, table 2). Profile analyses by year showed that the majority of the block effect for both species occurred after 1997, as only the contrast between 1997 and 1998 was significant for each species ($P = 0.032$ and 0.031 , for *Q. alba* and *Q. velutina*, respectively).

These block differences appear to be due in part to the differences in management histories of the sites, with individual blocks containing sites of similar ages. The total number of species accumulated per site at the end of 2000 was significantly negatively correlated with the year in which the sites came under the protection of the Missouri Department of Conservation (i.e., site acquisition year). This correlation was significant for 3 of 4 years for *Quercus alba* ($r = -0.77$ to -0.82 , $P = 0.006-0.01$) and for all 4 years for *Q. velutina* ($r = -0.74$ to -0.79 , $P = 0.01-0.02$) (fig. 3). Repeated-measures ANOVA showed that the effect of site acquisition year on total number of accumulated species at the end of each year was marginally significant for both *Q. alba* ($P = 0.103$) and *Q. velutina* ($P = 0.086$).

Species Accumulation by Census Across Years

For both *Q. alba* ($P = 0.011$) and *Q. velutina* ($P = 0.010$), censuses varied significantly in the rate at which species accumulated over time (table 1). Profile analysis showed that the significant treatment effect in *Q. velutina* was due mainly to the difference in treatments between the June and July censuses (fig. 3, $P = 0.036$, all other contrasts $P > 0.41$). In contrast, the strongest treatment effect in *Q. alba* occurred in the May census (fig. 4). Block differences in *Q. alba* were significant between the June and July censuses ($P = 0.01$), and marginally so between the July and August censuses ($P = 0.06$). For *Q. velutina*, block differences were significant between May and June ($P = 0.009$), between June and July ($P = 0.04$), and marginally so between July and August ($P = 0.06$).

The steeper slopes for the May censuses, followed by the August census, for both *Q. alba* (fig. 4) and *Q. velutina* (fig. 5) indicate that these

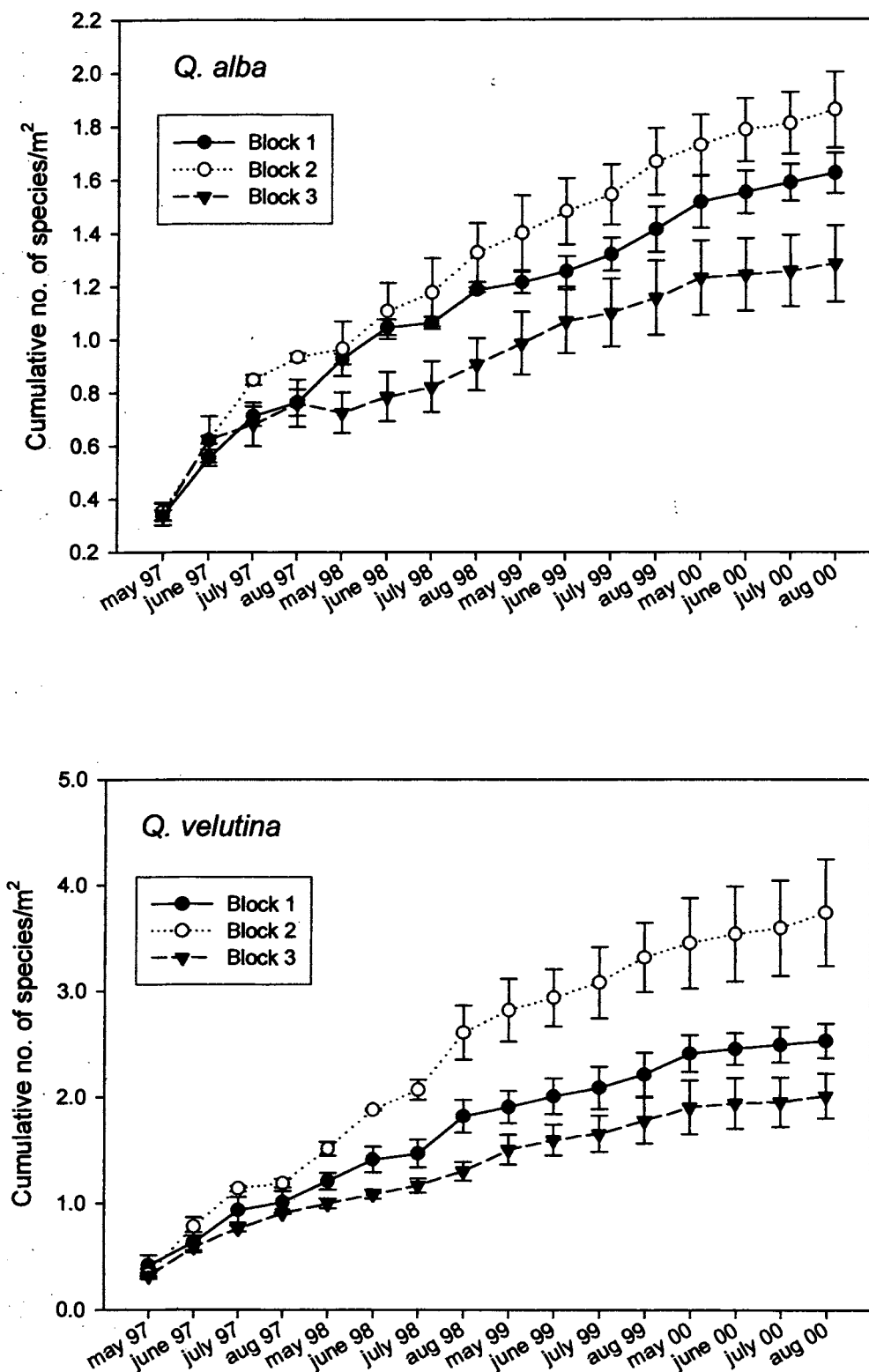


Figure 2.—Effect of block on species accumulation curves across all four censuses for the years 1997-2000 on *Quercus alba* and *Q. velutina*. Values are the mean number of new species ($\pm$ SE) accumulated per square meter of leaf area since the previous census.

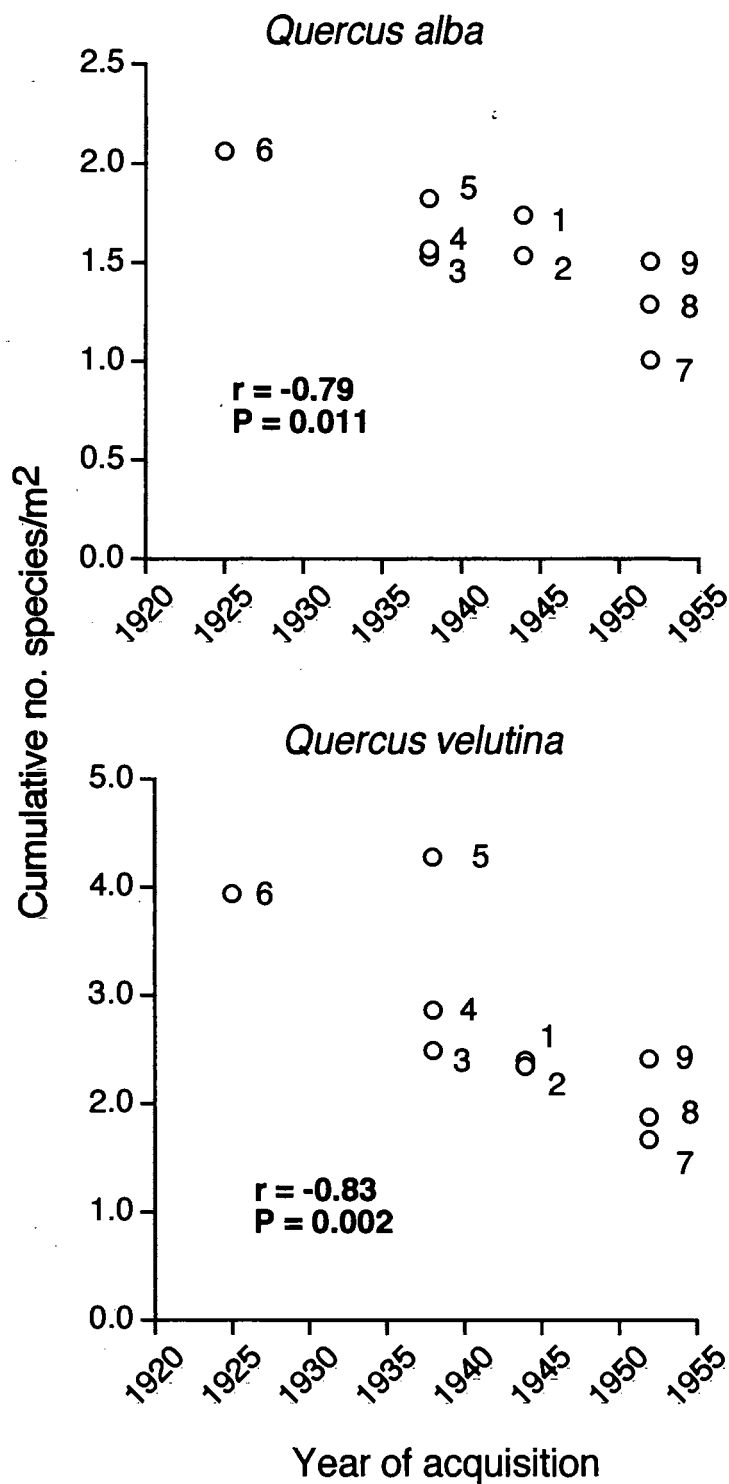


Figure 3.—Effect of time since acquisition under the auspices of the Missouri Department of Conservation on total number of species accumulated per square meter of leaf area up to the end of 2000 since the beginning of 1997 for both *Quercus alba* and *Q. velutina*. Number labels for the points are the MOFEP site numbers (see Sheriff, this proceedings).

Quercus alba

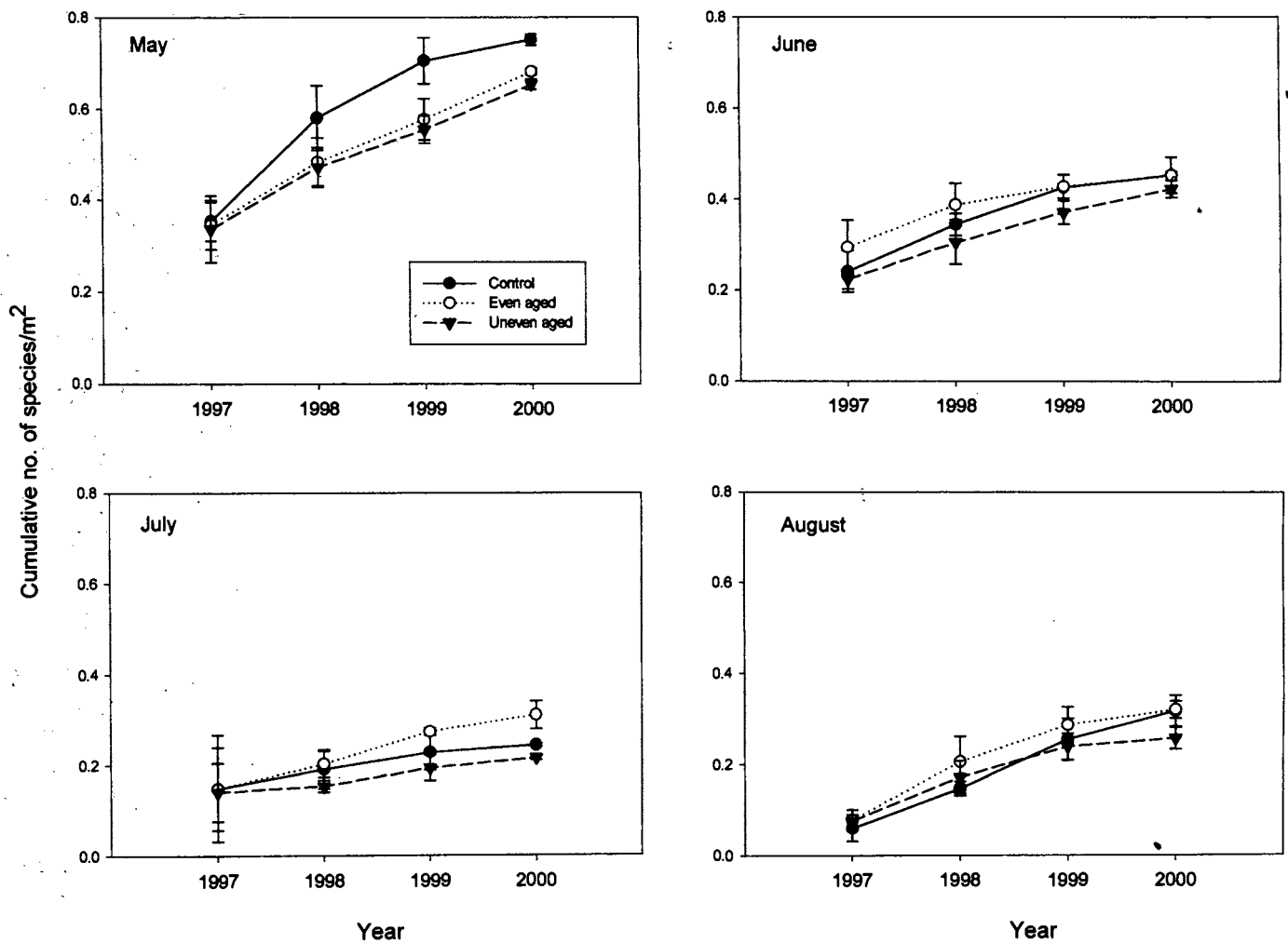


Figure 4.—Effect of treatment on species accumulation curves by individual census for *Quercus alba*. Values are the mean number of new species ($\pm$ SE) accumulated per square meter of leaf area since the previous census.

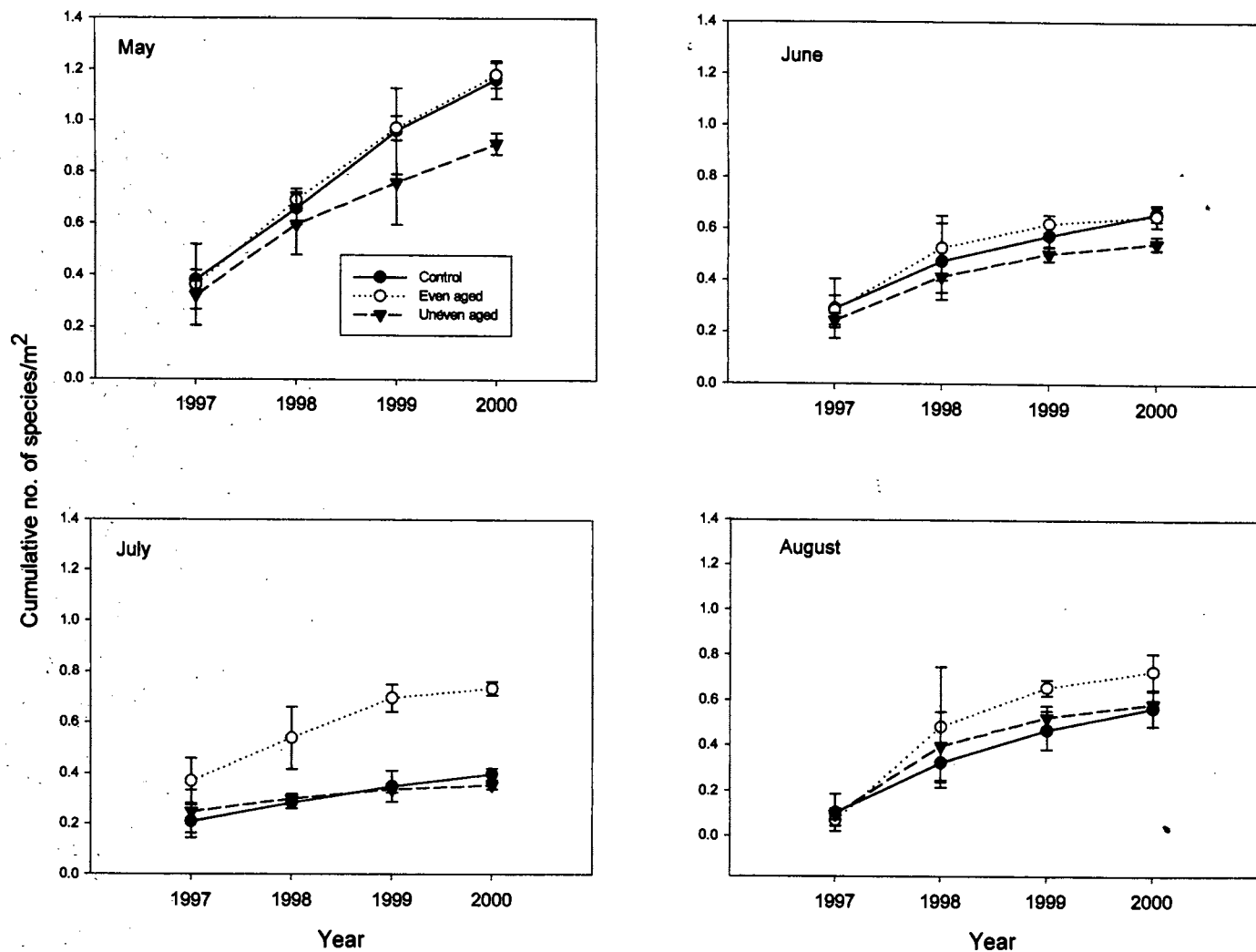
*Quercus velutina*

Figure 5.—Effect of treatment on species accumulation curves by individual census for *Quercus velutina*. Values are the mean number of new species ($\pm$ SE) accumulated per square meter of leaf area since the previous census.

two censuses contributed the most to the overall pattern of species accumulation (fig. 1). May censuses continued to contribute almost twice as many new species compared to the other three censuses throughout the 4-year study period.

DISCUSSION

Species accumulation curves differed significantly by timber harvest method for *Quercus velutina* (fig. 1). For *Q. alba*, there is a trend for continued deviation in species accumulation curves over time, but the curves were not significantly different at the end of 2000. These results suggest that when a species accumulation curve for a particular harvest method and host tree species was lower than that for control sites (e.g., uneven-aged treatment on *Q. velutina*, fig. 1), harvesting reduced population size in a significant number of species such that they were no longer sampled. In turn, when a species accumulation curve in a harvest treatment was higher than that of the control (e.g., even-aged treatment on *Q. velutina*, fig. 1), we suggest that tree harvest increased the population size of a significant number of species such that they were sampled, while in control sites they were not.

Treatments did not affect species accumulation curves for *Q. velutina* immediately, as indicated by the marginally significant year effects in profile analysis (1997 vs. 1998: $P=0.13$; 1998 vs. 1999: $P=0.18$) and the very similar means in 1997. A delayed time course of block effects on species accumulation was seen for both *Q. alba* and *Q. velutina* (fig. 2), with profile analysis supporting this conclusion. The degree to which there was a real delay in treatment and block effects is not clear, as population sizes were very low in 1997 across all censuses and for both host plant species (Gram *et al.* 2001; Marquis *et al.*, in prep.). Reduced population sizes across the insect community might reduce our ability to detect treatment effects on species accumulation curves. Possible spill over effects from neighboring sites of contrasting treatments also might reduce our ability to discern treatment effects. The results of analysis of spatial effects are forthcoming in which we can test whether treatment effects are due to spill over effects from harvested areas into neighboring intact forest versus whole site effects resulting from changes in the composition and structure of the entire forest matrix.

The effects of the treatments in *Q. velutina* varied somewhat depending on census. Although there was no significant overall treatment X census interaction for either host species (table 1), there was a significant contrast between the June and July censuses in the profile analysis for *Q. velutina*. This result indicates a significant change in treatment effect across these censuses, with the greatest effect coming in June and less of an effect in July (fig. 5). Over and above the treatment effect, the May census contributed most to the overall pattern of species accumulation for both host species across the 4 years (figs. 4 and 5). This result suggests that the composition of the May fauna is more variable from year to year than is that of the later season.

The observed trend for effect of harvesting on species accumulation curves for *Quercus alba* was similar to our initial prediction, i.e., both harvesting treatments reduced the rate of species accumulation and uneven-aged treatment had the greatest effect. In contrast, the even-aged treatment actually increased the rate of species accumulation on *Q. velutina* compared to non-harvested, control sites, which were intermediate among the three treatments. Why the treatment effect was stronger in *Q. velutina* than in *Q. alba*, and why even-aged harvesting should increase the rate of species accumulation is not clear. The two tree species share a number of herbivore species, but each also has a set of unique species (34 and 14 unique species for *Q. alba* and *Q. velutina*, respectively). Perhaps the species unique to *Q. velutina* are adapted to plants growing under more open conditions, and as a result, their abundances increased with cutting. *Quercus velutina* grows on drier and more open sites than *Q. alba* does throughout its range (Fowells 1965). Spatial analysis of the treatment effects and analysis of individual insect species patterns will be necessary to resolve this question. Unfortunately, little is known at this time of the ecology of individual herbivore species in this system.

Similar to the pattern for overall abundance based on pre-treatment sampling (Marquis and Le Corff 1997), we found a significant negative relationship between the total number of species encountered in a site and the year the site was acquired by the Missouri Department of Conservation. This pattern held true for both host plant species and was found at both the



beginning and end of the post-treatment sampling period. One possible confounding factor is that through 1998, we sampled sites in the approximate order of their acquisition, oldest to most recent. This might be a problem for the spring census, for at the end of that census many species are beginning to pupate, and as a result would not be censused. However, we still see significant correlations for species accumulated for each of the individual censuses, suggesting that as these forests age, either insect species accumulate and/or population sizes increase across many or most species so that more species are sampled with increasing forest age. Block 3 (sites 7, 8, and 9) had 30 to 50 percent lower number of large *Q. alba* trees ≥ 4.5 in. d.b.h. than the other blocks (Kabrick *et al.* 1997), although the abundance of large *Q. velutina* trees does not differ by block or site. Another possible confounding factor is that sites of the same age tend to be close in proximity. To clarify the role of forest age on herbivore species richness, future sampling should include other sites of known age outside of the MOFEP design (and therefore not spatially confounded with them).

Our preliminary conclusion, based on the analysis of species accumulation curves for 4 post-treatment years, is that timber harvest affects either population size and/or the presence-absence of a number of leaf-chewing herbivore species on *Q. alba* and *Q. velutina*. These effects result in changes in species accumulation curves. Both harvesting techniques had a negative but weak effect on the number of species sampled on *Q. alba*, while even-aged management significantly increased the number of species sampled on *Q. velutina*. However, there was a strongly significant effect of the date of acquisition by the Missouri Department of Conservation on the number of observed species for both *Q. alba* and *Q. velutina*. Sites not disturbed by fire, cattle grazing, and tree harvest had more observed species. This result suggests that after additional timber harvests in the MOFEP experiment, population sizes and the number of sampled species will decline on *Q. alba* and *Q. velutina* in both even-aged and uneven-aged treatments. A corollary of this prediction would be that insect numbers and species diversity would be much lower in clearcuts than in intact forest. Comparative sampling of clearcuts and understory is underway.

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