Braconid Wasp (Hymenoptera: Braconidae) Diversity in Forest Plots Under Different Silvicultural Methods

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ABSTRACT Braconid wasps were used as an indicator group to test the hypothesis that the degree of disturbance in silvicultural treatments will change the total abundance and composition of species. Wasps were collected with Malaise traps on undisturbed (control), moderately disturbed (pine single-tree selection) and highly disturbed (pine-hardwood seed-tree) research plots of the USDA Forest Service in the Ouachita National Forest of Western Arkansas. We used 3 measures of wasp diversity: (1) numbers of individuals and numbers of species, (2) estimated total species richness and abundance, and (3) observed and estimated complementarity (proportions of species shared or not shared) among treatment types. In all, 1,300 wasps were collected, representing 23 subfamilies, 84 genera, and 251 morphospecies. Raw numbers of individuals and species suggested little difference among treatments. Total species richness estimates projected that the disturbed treatments have twice the number of species as the undisturbed. However, measures of complementarity revealed strongly different species complexes between treatments: undisturbed and highly disturbed treatments had just 24% of their species in common, whereas moderately and highly disturbed treatments shared 42%. Thus, some species in undisturbed forests are lost after disturbance, even though actual diversity appears to increase. Braconid wasps show promise as sensitive indicators of faunal changes during disturbance. These changes are best perceived through species comparisons between treatments when patterns of relative abundance and faunal complementarity are incorporated.

KEY WORDS Braconidae, forest management, species richness, biodiversity, complementarity

SUSTAINING BIOLOGICAL DIVERSITY has become one of the principal goals of conservation. Gradually the goals have moved from concern for specifically threatened species to the broader desire to protect ecosystems, thereby allowing many more species to benefit. As a result, a variety of methods has been devised for quantifying the diversity of species within an ecosystem. The most thorough analysis of biodiversity in an ecosystem would be an inventory of all taxa and their relative abundances. Such inventories are prohibited by the ultimate size of the data sets, as well as the time requirement and the difficulty in getting sufficient scientific and financial support (Kim 1993). Researchers have thus been looking for ways to assess biological diversity by using a single species or a small indicator group to represent the overall set of species in a community.

We have focused on insects because they provide many critically important ecosystem services (Wilson 1987, Kim 1993, Samways 1994, Hammond 1995). Insects are well suited to monitoring landscape changes because of they are abundant, species rich, and ubiquitous in occurrence (Rosenberg et al. 1986). Among the insects, the Hymenoptera, and in particular the parasitoid wasps, are among the most species rich and biologically diverse taxa (LaSalle and Gauld 1993).

This study explored the use of braconid parasitoid wasps (Hymenoptera: Braconidae) as biological indicators. We posed the following questions: First, will the degree of disturbance in silvicultural practices affect the abundance and diversity of the local braconid wasps, and if so, how? Second, do braconid wasps have characteristics that make them useful indicators of local diversity? Third, if so, which measures of diversity are most effective in capturing the indicator potential of the wasps?

We sampled wasps with standard Malaise traps in undisturbed, moderately disturbed, and highly disturbed silvicultural treatment sites. The wasps could then be compared among treatments by 3 methods: comparisons of total numbers of individuals and total species, estimations of total species for each treatment from the sample distributions, and finally, the faunal disparity (complementarity) between treatments. The usefulness of braconids as diversity indicators can then be evaluated from these combined data.

Why Braconidae? Braconid wasps represent one of the most diverse and abundant of the parasitoid groups (Shaw and Huddleston 1991, LaSalle and Gauld 1993). They are typically parasitoids of other insects, parasitizing and ultimately killing their hosts. Their most common hosts are the larvae of Lepidoptera, Coleoptera, and Diptera (Wharton et al. 1997). They occur in very diverse habitats and are highly abundant in cool temperate regions (LaSalle and Gauld 1993, Wharton 1993, Quicke and Kruft 1995). Braconid species tend to attack and feed on a very narrow range of hosts, and they are limited by specialized biological

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and behavioral adaptations (Whitfield and Wagner 1988, Shaw and Huddleston 1991, Wharton 1993, Shaw 1994). Such a high degree of specialization gives braconid wasps strong potential to be sensitive indicators of environmental richness and stability (Shaw and Huddleston 1991).

Why Sample with Malaise Traps? Malaise traps work well for collecting braconid wasps because most species are fliers, and because the herb-shrub (0–3 m) layer sampled by this trap has been found to be richer in braconid wasps than other parts of the canopy (Papp 1994). The traps are tent-like structures made of fine mesh fabric netting. The version we used has a matte black, vertical center panel that reduces its visibility, and blocks the passage of flying insects. The top of the trap is roof-shaped and higher at one end. The insects gather at the highest point in the "roof" and then exit into a collecting chamber with a removable container filled with killing agent (Townes 1972, Gauld and Bolton 1988). We used identical standardized traps so the samples were replicates (Matthews and Matthews 1983, Owen 1983).

Materials and Methods

Study Area. Sampling was conducted in the Ouachita National Forest of western Arkansas, a pine-hardwood forest covering 610,500 ha (USDA 1984). In the overstory of the average stand in this forest, the most numerous species were shortleaf pine, *Pinus echinata* Mill. (Pinaceae), followed by postoak, *Quercus stellata* Wang. (Fagaceae), white oak, *Q. alba* L., black hickory, *Carya texana* Buckl. (Juglandaceae), mockernut hickory, *C. tomentosa* (Poir.) Nutt., and winged elm, *Ulmus alata* Michx. (Ulmaceae) (Guldin et al. 1994). The dominant species in the understory were predominantly: Northern red oak, *Q. rubra* L., flowering dogwood, *Cornus florida* L. (Cornaceae), blackjack oak, *Q. marilandica* Muench., and winged elm. The prominent ground cover species included panic grasses, *Panicum boscii* Poir, *P. dichotomum* L. (Gramineae), tick trefoil species, *Desmodium nudiflorum* (L.) DC., *D. rotundifolium* DC., and *Desmodium* spp. (Leguminosae), dittany, *Cunila origanoides* (L.) Britt (Labiatae), pipe-vine, *Aristolochia serpentaria* (Aristolochiaceae), wild licorice, *Galium circaezans* Michx. (Rubiaceae), bird's foot violet, *Viola pedata* L. (Violaceae), downy phlox, *Phlox pilosa* L. (Polemoniaceae), stiff Coreopsis, *Coreopsis palmata* Nutt. (Asteraceae), poverty oatgrass, *Danthonia spicata* (L.) Beauv. ex Roem. and Schult. (Gramineae), and moss cover. These plants occur in communities that differ depending on the predominant oak species in the overstory (Foti and Guldin 1994).

USDA-Forest Service Silvicultural Experimental Design. This study was carried out within ecosystem management plots of the USDA Forest Service (USDA-FS) in the Ouachita National Forest. The research design implemented alternative silvicultural methods that included partial cutting techniques that retained pine and hardwoods in various densities, compositions, and structures in even and uneven-aged forests. Tree harvesting to implement the silvicultural treatments was completed in September 1993 (Baker 1994). The research stands were on south or west facing slopes that contained ≥14 ha of mature, pine-dominated forest, with trees averaging >70 yr old. The average stand basal area of pine was 13.8–25.2 m^2/ha, whereas that of hardwoods was 4.6–11.5 m^2/ha (Baker 1994).

Braconid Study Treatments. From the USDA-FS research design we chose 3 treatments for our study: undisturbed, moderately disturbed, and highly disturbed sites that reflected the original pine-hardwood forest community. The following 3 treatments were replicated 3 times, so wasps were collected at 9 sites.

Undisturbed, Unmanaged Control. This treatment contained 13.8–25.2 m^2/ha pine basal area and 4.6–11.5 m^2/ha hardwood basal area with no harvesting or stand management for the past 30 yr except for wildfire protection (Baker 1994).

Moderately Disturbed, Pine Single-Tree Selection, Uneven-Aged. Some pines were harvested on a 10-yr cutting cycle based on single-tree selection. Residual basal area in pines varied from 10.3 to 15.0 m^2/ha. The hardwoods were harvested except for a remnant for wildlife use (0.5–1.1 m^2/ha) (Baker 1994).

Highly Disturbed, Pine-Hardwood Seed-Tree. In this disturbed treatment, 25–35 of the largest pines and hardwoods were cut leaving a total basal area of 2.3–4.6 m^2/ha, of which 1.1–3.4 m^2/ha were hardwoods, with all others having been harvested or otherwise removed (Baker 1994).

Data Collection. Insects were collected in Malaise traps for 1 wk each month during June, July, and August of 1994, ≈1 yr after silvicultural treatments were initiated. The Malaise trap model used was a bidirectional Townes style with 203 cm front height, 112 cm back height, and 122 cm wide by 183 cm long (Townes 1972). Trap collection jars were filled with 95% ethanol. All traps were set up on the same day and collected 7 d later. Data collected for the 3 treatments were control (9 samples), pine single-tree selection (6 samples), and pine-hardwood seed-tree (5 samples). We lost 4 samples in 2 remote locations because of interference by bears, in all we collected 23 of the 27 samples in the design.

The braconid wasps were sorted from the raw samples, stored in 95% ethanol, later pinned or pointed, and labeled. Specimens resulting from this study were deposited as vouchers in the University of Arkansas Arthropod Museum. The wasps were identified to genus using Marsh et al. (1987) and the Manual of the New World Genera of the Family Braconidae (Hymenoptera) (Wharton et al. 1997), then sorted to morphospecies.

The comparison of wasp abundance and diversity between treatments was analyzed in the following three ways: (1) Treatments were compared for total numbers of individuals and total numbers of species during the monthly sampling periods; (2) diversity estimators were used to predict the estimated total species in each treatment; and (3) complementarity comparisons were made of species compositional dif-

Table 1. Analysis of total numbers of wasps by treatment (mean ± SE)

Treatment	Avg no. of wasps per trap			
	June	July	Aug	Overall
Control	46.4aA ± 6.1	31.0bA ± 6.6	59.5aB ± 9.2	44.1 ± 7.1
Pine single-tree selection	54.4bA ± 10.8	44.4bA ± 9.7	136.3aA ± 17.1	69.1 ± 11.1
Pine-hardwood seed-tree	40.4bA ± 7.6	39.7bA ± 7.5	66.4aB ± 13.0	47.4 ± 8.3

For a treatment, monthly values with different lowercase scripts are significantly different ($P > 0.05$). For a month and overall, treatment values with different uppercase scripts are significantly different ($P > 0.05$).

ference and similarity between selected pairs of treatments. The shared species for the pairs of treatments were estimated and compared with the raw data.

Statistical Analyses. (1) The model for the analyses of data on number of individuals and number of species was a generalized linear model (McCullagh and Nelder 1989). The error distribution for insect and species counts was chosen as the Poisson distribution because this distribution is often appropriate for such counts; the analysis can accommodate the situation in which the variance is proportional to the mean. In the analysis, the log of the true mean is fit by a linear model consisting of the main effects and interaction effects of treatment and month; nested effects of location within treatment were also included. The residual was used as the error for comparing months and the location source of variation was used as the error for treatment comparisons. When the interaction of treatment and month was significant at the 10% level of probability, treatments were compared at the 5% level of probability per comparison within each month, and months were similarly compared within each treatment. When the main effect of treatment was significant at the 10% level of probability, treatment means over months were compared at the 5% level of probability per comparison. All tests and comparisons were carried out for means on the log scale. Estimates of means on the log scale were back-transformed by the anti-log for presentation as mean counts. The standard errors, estimated from the model analysis, were added and subtracted to the mean estimates on the log scale; these values were then back-transformed, and one-half of their difference was reported as the standard error for the reported mean counts. The analysis was done using the GENMOD procedure of SAS (SAS Institute 1996).

(2) Species richness estimations were generated using *EstimateS* 5. Richness Estimator program version 5.0.1 (Colwell 1997). The program incorporates total observed species, total individuals, singletons (species represented by 1 individual), doubletons (species represented by 2 individuals), uniques (species occurring in only 1 sample), and duplicates (species occurring in only 2 samples) to compute species richness estimates (Colwell 1994, 1995; Colwell and Coddington 1994). The program has specialized estimators for applications to different types and sizes of data sets. Our data were characterized by large numbers of singletons and species containing <10 individuals. The following 5 estimators were chosen as most applicable to our data: (1) The incidence-based coverage estimator bases predictions on species found in 10 or fewer sampling units (Lee and Chao 1994, Chazdon et al. 1998). (2) The Chao 2 estimator is an incidence-based predictor of population size based on capture-recapture data (Chao 1987). (3) The 2nd-order jackknife (Jackknife 2) bases estimates on numbers of uniques and duplicates and the number of sites sampled (Burnham and Overton 1978, 1979; Heltshe and Forrester 1983; Smith and van Belle 1984; Coddington et al. 1990; Chazdon et al. 1998; Landau et al. 1999). (4) The bootstrap estimator of species richness based on the proportion of sites containing each species (Smith and van Belle 1984, Colwell and Coddington 1994). (5) The Michaelis–Menten equation, originally developed for use in enzyme kinetics (Raaijmakers 1987); the equation makes use of maximum likelihood to estimate the parameters and their variances (Landau et al. 1999). The most useful estimators for our data were projected to be Chao 2 and the 2nd-order jackknife, because they can make estimations of species based on small samples that include uniques and duplicates. All estimates were based on 1,000 randomized replications.

(3) Complementarity was used as a diversity estimator to compare the species lists of 2 selected treatments (Price 1984, Williams 1993). Complementarity is a simple heterogeneity measurement with biological significance, because it is the proportion of all species in the 2 treatments that occur in one treatment or the other only (Colwell and Coddington 1994). Species

Table 2. Analysis of total numbers of morphospecies by treatment (mean ± SE)

Treatment	Avg no. of morphospecies per trap			
	June	July	Aug	Overall
Control	21.2aB ± 3.9	20.6aA ± 3.5	25.7aB ± 4.3	22.4B ± 3.5
Pine single-tree selection	38.4bA ± 6.5	30.5bA ± 5.8	67.4aA ± 5.6	42.9A ± 5.9
Pine-hardwood seed-tree	31.3aAB ± 4.8	29.7aA ± 4.6	35.1aB ± 6.5	32.0AB ± 4.7

For a treatment, monthly values with different lowercase scripts are significantly different ($P > 0.05$). For a month and overall, treatment values with different uppercase scripts are significantly different ($P > 0.05$).

lists for each treatment were used to calculate richness. The total species (S_j) in one treatment were added to the total species (S_k) in a 2nd treatment, then species (V_{jk}) common to both treatments were subtracted, leaving the total richness (S_{jk}) for the 2 treatments.

$$S_{jk} = S_j + S_k - V_{jk}$$

Species common to only 1 of the 2 treatments, (i.e., unique (Ujk) to either site) were found by totaling species in both treatments and then subtracting twice the number of species common to the 2 treatments.

$$U_{jk} = S_j + S_k - 2\,V_{jk}$$

Finally, the complementarity of the 2 sites is found by dividing unique species by the total species richness.

$$C_{jk} = U_{jk}/S_{jk}$$

The complementary figures are expressed as the percentage of species that are different between the 2 treatments (Colwell and Coddington 1994). The comparisons are proportionalities drawn from the presence-absence data collected in each treatment.

In addition to the raw data comparisons, we compared treatment pairs using the coverage-based estimator of shared species (V_{jk}) (Chen et al. 1995) computed by the *EstimateS* 5 program. The estimator (V) is a shared species estimator that augments the observed number of shared species by a correction term based on the relative abundance of shared, rare species (Colwell 1997).

Results

We collected 1,300 braconid wasps representing 23 subfamilies and 84 genera. These were separated into 251 morphospecies. A complete listing of morphospecies designation, location, and month collected is provided in *Appendix 1*.

Comparison of Treatments. Analysis of the total number of individuals from each site showed no significant differences between treatments over the 3 mo collection period ($P > 0.05$). Comparisons between June, July, and August showed a highly significant month effect (df = 2, 9; $P < 0.001$), plus a significant treatment and month interaction (df = 4, 9; $P = 0.035$) (Table 1). The total number of species collected among treatments (df = 2, 5; $P = 0.064$) and the interaction of treatment and month (df = 4, 9; $P = 0.084$) were marginally insignificant among months (Table 2). The total number of species collected varied significantly among months with August collections more species rich than those in June and July, which were similar to each other in number of species. The treatment effect was nearly significant.

Diversity Measures. The *EstimateS* 5 diversity estimators produced fairly wide ranges of species estimates for each treatment. The bootstrap estimations were in the low end of the range for all treatments. For example, the bootstrap estimated the control treatment to have 112 species. The high end of the range of estimations was produced by the incidence-based coverage estimator and by the Michaelis-Menten means, which produced the overall highest estimate of 365 species for the pine single-tree selection treatment (Table 3). The Chao 2 and 2nd-order jackknife estimators were more realistic for this data set, and they produced similar estimates for each treatment. These 2 estimators suggest that ≈60–70% of the actual total species were sampled in the 2 disturbed treatments, whereas only 53% were sampled in the control treatment. Thus, the control treatment appeared to be less fully sampled than the 2 disturbed treatments. These 2 estimators were plotted along with the species accumulation curve for each treatment in Fig. 1. The total number of singletons, doubletons and species represented by ten or less is shown for each treatment site in Table 4.

Table 3. Species richness estimates for all treatments

Value	Control	Pine single-tree selection	Pine-hardwood seed-tree
Bootstrap	112	206	192
Chao1	162	276	222
Chao2	143	313	293
ICE	172	350	325
First-order jackknife	135	258	239
Second-order jackknife	156	313	289
Michaelis-Menten means	145	365	313

Faunal Complementarity Among Treatments. Comparisons between control and pine single-tree selection treatment sites showed 70% complementarity between the treatments, with 60 species shared by both. The 2 extreme treatments, control and pine-hardwood seed-tree, had the highest complementarity of 76%, where 153 species were found in only 1 of the 2 treatments. Between the pine single-tree selection and pine-hardwood seed-tree treatments, the complementarity was lower at 58%, with fewer species thus found in only 1 treatment and more shared species. Table 5 lists the total and shared species for each comparison.

The coverage-based estimator of shared species (V) was used to project estimations of what would be found if the samples were complete for the treatment pairs. The control and pine single-tree selection treatments were estimated to have 107 shared species. The control and pine-hardwood seed-tree treatments were predicted to have 94 common species. The treatments, pine single-tree selection and pine-hardwood seed-tree were estimated to have 198 shared species. The estimates of shared species for each pair of treatments were thus approximately twice that of the observed complementarity calculations. (Table 5

Discussion

We began this study by asking whether degree of disturbance in forestry practices would affect braconid wasp populations. The alpha diversity or species richness revealed little about the effect of forest disturbance on the wasps. When the species lists from the

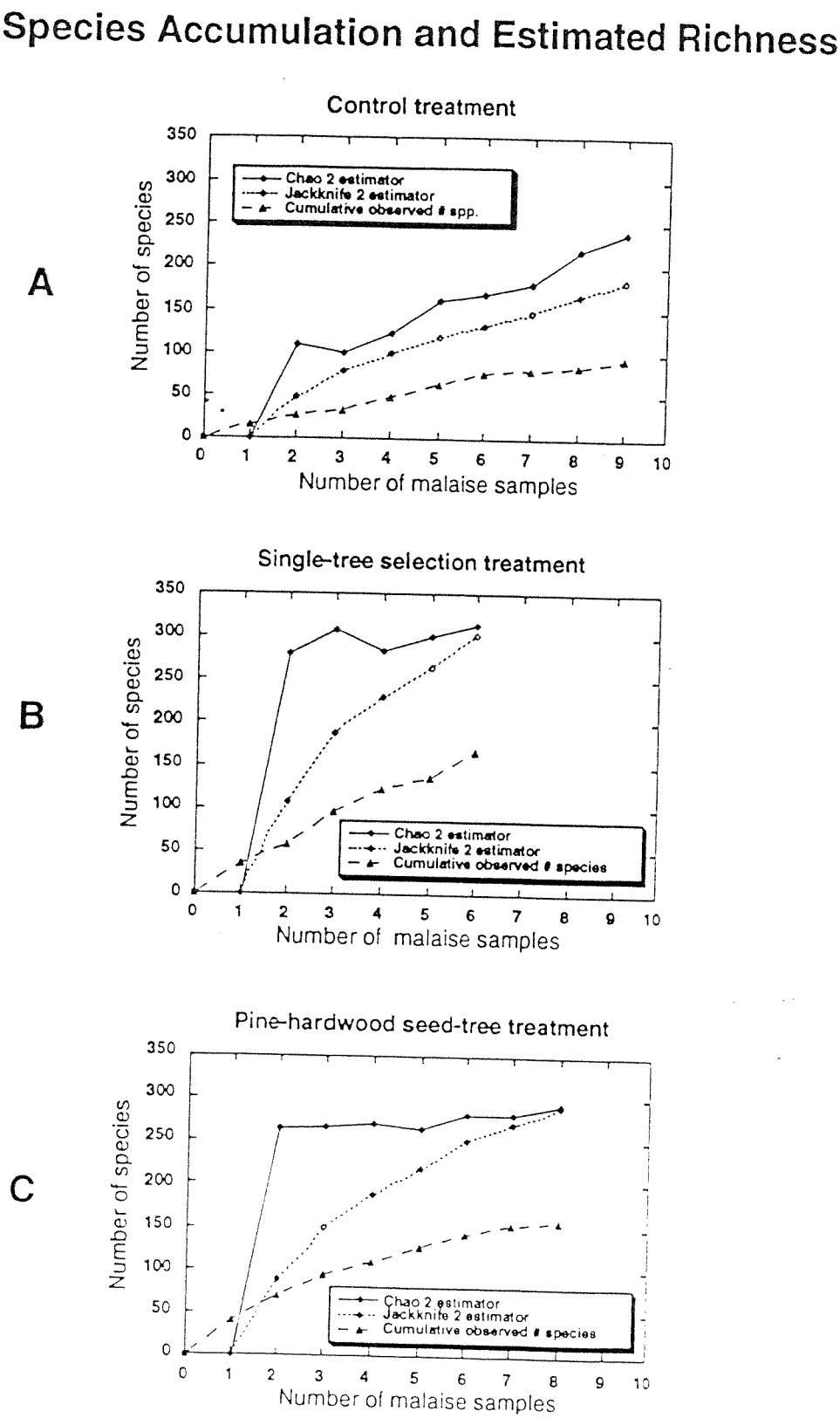

Fig. 1. Chao 2 and 2nd-order jackknife (Jackknife 2) estimator calculations of species richness in each treatment, plotted with the actual cumulative observed species found in each treatment.

Table 4. Overview of singletons, doubletons, and species information on all sites

Treatment location, 1994	Control										Pine single-tree selection										Pine-hardwood seed-tree									
	Site 1			Site 2			Site 3				Site 1			Site 2			Site 3				Site 1			Site 2			Site 3			
	June	July	Aug.	June	July	Aug.	June	July	Aug.	Total	June	July	Aug.	June	July	Aug.	June	July	Aug.	Total	June	July	Aug.	June	July	Aug.	June	July	Aug.	Total
Species																														
Singletons	8	12	10	17	20	21	13	12	17	44	-	-	-	29	27	36	30	20	44	84	31	32	23	21	26	28	25	11	-	70
Doubletons	3	5	2	8	3	4	3	4	6	14	-	-	-	3	2	12	7	4	15	32	4	6	7	4	7	5	4	4	-	37
Uniques										47										103										95
Duplicates										22										36										33
<10	14	18	15	29	26	33	20	18	30	82	-	-	-	35	31	62	42	30	72	158	40	39	38	27	35	42	29	17	-	152
Individuals	38	25	34	71	45	80	36	27	72	428	-	-	-	48	39	137	61	50	136	471	55	47	81	36	49	74	33	26	-	401

-, Samples were destroyed by bears.

respective treatments were compared, the beta diversity showed marked differences. Among the treatments, the distributions of rare and common species were also very different, and this may provide the most insight into what happens to braconid wasps when the forest is disturbed. For this discussion, *rare* species were defined narrowly as singletons found in only 1 treatment, and *common* ones as species found in all treatments. Using these definitions, there were 25 rare species in the control treatment, whereas the 2 disturbed treatments contained 50 rare species each. Over half of all wasp species collected were singleton species found in only 1 treatment. However, individuals of common species made up more than half of all individual wasps collected. In the control treatment, common species made up 42% of species and 72% of all individuals. In the disturbed treatments, common species represented 23% of species and 45% of individuals in pine single-tree selection and in pine-hardwood seed-tree they were 25% of species and 40% of individuals.

It appears that disturbance in the forest caused displacement of many of the common wasps, while at the same time drawing in species not normally found there. Disturbance may increase the species diversity and overall numbers of braconid wasps, at least in the short run. This may be caused in part by the increased primary productivity of disturbed systems, which is usually greater than that of climax associations. Current theory suggests that the highest species diversities should be found in relatively undisturbed to moderately disturbed habitats (Petraitis et al. 1989). Some level of disturbance may act to increase species diversity, but if the disturbance is too severe or too frequent, species may be lost from the community. The levels of disturbance in these forest systems, at least at the local level, appears to be relatively extreme, especially in the pine-hardwood seed-tree treatment.

Other factors may be influencing the wasp community. First, the undisturbed areas may naturally have lower total wasp population densities that are more difficult to sample by Malaise trap. In undisturbed forests, braconid wasps and their natural host populations may be low in numbers but high in overall species diversity (Huffaker and Messenger 1964, LaSalle 1993). Wasps in undisturbed forests may also be more fully stratified vertically, and thus more difficult to completely sample by Malaise trap.

Second, in more disturbed treatments, open areas become covered with early succession flowering plants and weeds that attract pollinators and phytophagous insects. Some species of braconid wasps normally not common in these forests may be drawn to clearings by an exploitable temporary host population on successional plants. The flowering plants themselves are also attractive to many adult braconid wasps, and both males and females of a variety of species have been observed to visit flowers for nectar and (especially) pollen (Shaw and Huddleston 1991, Jervis et al. 1993).

Several questions then emerge. In disturbed areas, where are the increased numbers of braconid wasps coming from? Are they drawn out of nearby forests or,

Table 5. Complimentarity (comp) calculations and estimates of shared species

Treatment pairs	Complimentary calculations					Estimated species	Shared species
	Species collected	Unique species	Shared species	Total species	Comp. %		
Control	93					155	
and		139	60	199	70		107
Pine single-tree selection	166					289	
Control	93					155	
and		153	48	201	76		94
Pine-hardwood seed-tree	156					246	
Pine single-tree selection	166					289	
and		130	95	226	57		198
Pine-hardwood seed-tree	156					246	

alternatively, from open field communities? If there is no mature forest in the vicinity for recolonization, are some species then lost in the long run? We might then predict that, if extensive disturbance is too widespread, it may be detrimental, whereas small-scale disturbance might be temporarily "beneficial," as suggested by the results obtained in this study.

How did the braconids fare as biodiversity indicators? This study has shown that braconids can be useful as diversity indicators. The family has many species, with wide variation in abundance, which we collected quite easily in Malaise traps in all treatments. Their species distributions underscored interesting and sometimes peculiar differences among the treatments. However, braconids are slow to process and identify because of their small size and high diversity, and identification to the species level may not always be possible because many groups need taxonomic revision.

The indicator potential of the braconids was best expressed through the combination of diversity measurements used above, rather than through any single measurement. In particular, we found that the simple comparison of species richness did not reveal anything about how species were affected by differences among treatments. Instead, we required the beta diversity, or complementarity, to highlight the differences among the species composition of the treatments.

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Appendix 1. Braconid Morphospecies Collected from Each Treatment Site. Alphabetical list of braconid wasp morphospecies identified according to treatment, site, and month collected. Numbers indicate wasp collections in each site, morphospecies totals are listed in the right-hand column, and site totals are at the bottom of the appendix.

	Treatment	Control									Pine single-tree selection									Pine-hardwood seed-tree								
	Location 1994	Site 1			Site 2			Site 3			Site 1			Site 2			Site 3			Site 1			Site 2			Site 3		
		June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	Total
Subfamily	Genus																											
Adeliinae	Adelius					1																						1
Agathadinae	Alabagrus														1	1						1					2	5
	sp2				1					1																		2
	sp3														1							3						4
	Bassus					1	1								1	3			2						2			10
	sp2													2				1	1		1		1					6
	sp3													2			2											4
	sp4																1			1								2
	sp5																1											1
	sp6																		1									1
	Cremnops																		1			3						4
Alysiinae	Aphaereta						2			2						1	1		1	1					2			10
	sp2															1	1		1	2					1			6
	Aspilota				1	3	1		2	1				1	1	9			2				1	1	6	1		30
	sp2		2	6	2	1	5	4		2				1		7			2			1		1	7			41
	sp3		1	1			2									3						1						8
	sp4		1		3	1	1		1	5						2									1			15
	sp5	4	3	9	11	3	12	6	4	14				3	1	10	3		4	1		1	1		4			94
	sp6	5	1	5	11	4	1	1		1				3		1		1	1	3		1	1		4			44
	sp7	3	1	1	2		7	2		3				1		3			2						2	1	1	29
	sp8	1			2	1	1	1		5						3				1					1			16
	sp9	1	1	1	1	6	3	2	1	2						5							1		3			27
	Chorebus															1												1
	sp2																						1					1
	Cratospila						1																					1
	sp2		1																									1
	Dapsilarthra								1	4						1												6
	sp2									1						1												2
	Orthostigma		2							2						8												12
	sp2								1																			1
	sp3					1									1	1												3
	sp4	2			2		6		3	1				1		2			3	3								23
	sp5						2			2																		4
	sp6													1					1	1								3
	Pneumosema							3		1														2				6
Aphidiinae	Aphidius																			1		5			3			9
	sp2																					5						5
	sp3																					2				1		3
	Binodoxys																								1			1
	Boreogalba																							1				1
	Ephedrus														1					1			4		1			7
	sp2														1				1				2					4
	Lysaphidus																		1									1
	sp2																			1								1
	Lysiphlebus													1						1		1			1	1		5
	sp2																1								1			2
	sp3																								1			1
	Pauesia																									1		1
	Praon																		2			11			1			14
	sp2																						1					1
	sp3																		1			2						3
Blacinae	Blacus							1																				1
	sp2		1				1																					2
	sp3			1																								1
	sp4						1			1						2												4
Braconinae	Atanycolus																							1				1
	sp2													1			1				2					1		5
	Bracon																			1								1
	sp2																1											1
	sp3															1					1			1				3
	sp4																				1	1						2
	sp5																		2		1	1				1		5
	sp6																1											1
	sp7																		1	1							1	3
	sp8									1						1		2						1				5
	Cyanopterus																				1				1			2

	Treatment	Control									Pine single-tree selection									Pine-hardwood seed-tree									
	Location 1994	Site 1			Site 2			Site 3			Site 1			Site 2			Site 3			Site 1			Site 2			Site 3			
		June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	June	July	Aug.	
Microgastrinae	Diolcogaster sp6																1		5	1		1							8
	sp7																2		1										3
	sp8																								1				1
	Dolichogenidae							1																		1			2
	Glyptapanteles															2											3		5
	sp2																		1										1
	sp3														1			1	1										3
	sp4															1										1			2
	Microgaster	1			1			4						1	1									1			1		10
	sp2																		1										1
	Microplitis				5	1		1									1	1		1	1								11
	sp2																			1	1			1					3
	sp3														1				1		1			1					4
	sp4																1												1
	sp5																					1							1
	sp6														1														1
	sp7														1	2			5		2								10
	sp8																3		1		2		1	1		1			9
	Pholetesor ornigis				1																			1					2
	Pholetesor bedelliae																					1				1			2
	Protomicroplitis																	4	2	1		4					1		12
	sp2																	1		4									5
	Rygoplitis															1													1
	sp2																		1										1
Miracinae	Mirax				1		1																						2
	sp2																				1		1			1			3
Opiinae	Opius				1									1			2												4
	sp2													1		2		4	1		1								9
	sp3													1					1				1						3
	sp4																			1						1			2
	sp5													1	1	1	2			1		1	1	2		1			11
	sp6																	3		1	2								6
Orgilinae	Orgilus				2											1	1	1			1								6
	sp2																	1											1
	sp3																1				1								2
	sp4							1																					1
	sp5		1																					1					2
	sp6																				1								1
Rogadinae	Aleiodes						1		1							1			1						3				7
	sp2				1			1								1				1									4
	Clinocentrus														1	3								4	1				9
	Rogas						1															1							2
	sp2						1											1	1										3
	sp3				1																								1
Sigalphinae	Sigalphus																								1				1
	Total	38	25	34	71	45	80	36	27	72	0	0	0	48	39	137	61	50	136	55	47	81	36	49	74	33	26	0	1300