IMPACT OF INSECT HERBIVORES ON COMPETITION BETWEEN BIRDS AND MAMMALS FOR PINYON PINE SEEDS[1]

KERRY M. CHRISTENSEN AND THOMAS G. WHITHAM
Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA

Abstract. Few studies have considered impacts of insect cone herbivores on bird and mammal seed consumers. Harvests of pinyon pine (*Pinus edulis*) cones by insects, birds, and mammals were negatively correlated both within and across sites. Birds and mammals significantly increased their cone harvest when the other group was experimentally prevented access to trees, and mammals harvested more cones when insects were removed from trees with an insecticide. These results suggest that stem- and cone-boring insects (primarily *Dioryctria albovittella*), birds (Clark's Nutcrackers, Pinyon Jays, and Scrub Jays), and mammals (cliff chipmunks and rock squirrels) compete for pinyon pine seeds. Additionally, insects affected the interaction between birds and mammals because the ratio of mammal to bird harvest increased up to 350-fold as insect cone consumption increased. Because insect-infested and uninfested pinyon pines are genetically different, these observations and experiments suggest that genetic interactions between plants and herbivores can affect the structure of a seed-consumer community.

Key words: community structure; herbivory; interspecific competition; meta-analysis; Pinus edulis; *plant genetics; randomization tests; removal experiments; seed dispersal; seed predation.*

INTRODUCTION

Many studies have examined how herbivores impact plants and plant communities (see Huntly 1991), but only a few have examined the impact of an herbivore (or granivore) on the interactions among other herbivores or seed consumers (Davidson et al. 1984, Brown and Heske 1990, Thompson et al. 1991, Hunter 1992). Existing long-term studies demonstrate that community responses to herbivory can be great. For example, removal of seed-eating kangaroo rats from Chihuahuan desert shrub vegetation for 12 yr resulted in dramatic changes in the plant and mammal community (Brown and Heske 1990). This study and others (e.g., Paine 1966, Estes and Palmisano 1974, Kerbes et al. 1990) show how species' abundance in the community can be affected by a "keystone species," but rarely examine how a keystone species might affect interactions between other species in the community.

The stem- and cone-boring moth *Dioryctria albovittella* has the potential to act as a keystone species due to its diverse impacts on pinyon pine (*Pinus edulis*). Heavily attacked trees averaged 47% less annual trunk growth, lost their upright growth form, assumed a shrub-like architecture, failed to produce female cones (Whitham and Mopper 1985), and lost 33% of their mycorrhizal mutualists compared to nearby lightly attacked trees (Gehring and Whitham 1991). Insect-removal experiments demonstrated that these phenotypic effects were caused by the moth.

Because pinyon pines and their avian seed dispersers

are thought to be coadapted (Vander Wall and Balda 1977, Ligon 1978), any agent that affects pinyon pine fecundity is likely to affect this mutualism. For example, because *D. albovittella* reduced pinyon pine cone crops by an average of 57%, avian seed dispersers abandoned infested individuals and populations, thereby altering the local avian community (Christensen and Whitham 1991, Christensen et al. 1991).

Here, we examine pinyon pine community interactions by addressing the hypothesis that stem- and cone-boring insects (*Dioryctria albovittella* and *Conopthorus* sp.), mammals (cliff chipmunks, *Eutamias dorsalis*; and rock squirrels, *Spermophilus variegatus*), and birds (Clark's Nutcracker, *Nucifraga columbiana;* Pinyon Jays, *Gymnorhinus cyanocephalus;* and Scrub Jays, *Aphelocoma courelescens*) compete for pinyon pine seeds, and that insects affect the competitive interactions between birds and mammals. The following specific questions are addressed: (1) Is cone harvest by one group of consumers negatively correlated with that of other groups? (2) When each taxon is experimentally prevented access to the seed resource, does another consumer increase its harvest relative to controls? (3) Do insects influence the relative harvest of mammals and birds?

To address these questions, we examined interactions between insect, bird, and mammal resource utilization at four levels: (1) within-site correlations of resource use, (2) among-site correlations of mean resource use, (3) patterns of cone harvest from single trees when each group was naturally or experimentally excluded from resources, and (4) a regression of the ratio of mammal to bird harvest across sites as a func-

tion of mean insect infestation of cones. For the exclusion experiments, we compared both the absolute number and the percentage of the crop used by treatment and control groups. For the correlation analyses, cone harvest was expressed as the percent of the crop used as described below.

METHODS

In 1985, we counted the number of mature cones, and quantified insect cone infestation and bird and mammal cone harvest for trees at two sites near Flagstaff, Arizona, USA (Sunset Crater, $n = 33$ trees; Winona, $n = 11$) using the methods described below. In 1986 through 1988, we counted the number of emergent conelets (cones are initiated within the branch 1 yr prior to emergence, and emerge 1 yr prior to maturation) on 9–33 trees at eight sites (including the two sites from 1985). All sites were within 25 km of each other at elevations between 1759 and 1887 m. Each site was separated from others by habitat lacking pinyon pine, and so was considered a separate population. All trees were mature with a trunk circumference 1 m from the ground between 79 and 108 cm. There were no significant differences among populations in mean tree circumference (ANOVA; $F = 1.87, P > .05$, df = 7, 126). To quantify cone crop size, conelets were visually counted, branch by branch, each fall following their emergence. We initially repeated counts and found that they were within 5% of each other, indicating a high degree of consistency. For each site, conelet number was averaged across trees for use in population comparisons.

Because insects, birds, and mammals leave distinctive signs of their cone use, we could identify which group had infested or harvested seeds from a cone. To quantify infestation by insects, 20 conelets on each tree were tagged in the late summer following emergence. Monthly examinations of conelets showed what proportion had been consumed by insects (as evidenced by the presence of insect frass). The censuses ceased when mammals and/or birds began harvesting mature cones the following summer. We determined avian seed harvest by counting the number of cones whose scales had been pried open by a bird's bill (Christensen and Whitham 1991). No attempt was made to separate harvest levels of Clark's Nutcrackers, Pinyon Jays, and Scrub Jays. Chipmunks and rock squirrels typically remove the seeds by chewing through the cone scales. We counted and removed bird- and mammal-opened cones in and under each tree at ≈14-d intervals. We averaged the cumulative number of cones harvested by each group for each site and year for use in population comparisons.

To describe general patterns of resource-use interaction, we examined correlations (Spearman rank correlation; Conover 1980) between insect and mammal, insect and bird, and bird and mammal cone use (per-

cent of the emergent crop utilized by each group) for individual trees within sites and for the averages of these harvests across sites. We examined these interactions within and across sites because birds are known to react to cone availabilities at these two levels (Christensen and Whitham 1991). We used percent of the crop utilized by each group, and not the absolute numbers of cones used, for the correlation analyses. This was done because cone crop sizes vary greatly among trees (from 1 to 1491 cones per tree), and spurious positive correlations would result if absolute numbers were used. For example, if birds and mammals each harvest 5 cones from a tree with 10 cones, and birds harvest 900 cones while mammals harvest 100 cones from a tree with 1000 cones at the same site, there would be a positive correlation between the absolute harvests of birds and mammals because both of their harvests increased. Using percent, however, there would be a negative correlation because as the percent of the crop harvested by birds goes up (from 50 to 90%), the percent harvest by mammals goes down (from 50 to 10%). The latter analysis more accurately reflects the nature of the interaction because the increase in relative harvest of birds is associated with a relative decline in the harvest of mammals.

Because the magnitude of one group's harvest can often be predicted by knowing the harvests of the two other groups, we used a randomization test (Edgington 1980) to incorporate dependency among harvests into the calculation of the significance level of an observed correlation coefficient. Here, we created distributions of the correlation statistics under the null hypotheses of no correlation by using random permutations of the observed data (Mitchell-Olds 1987). Consider tossing a coin; the exact probability of obtaining heads and tails is 0.50, but if a coin is repeatedly tossed 100 times, rarely is a 50 : 50 ratio obtained. A distribution of ratios centered at the 50 : 50 ratio, however, is obtained. In the present case, the proportion of cones harvested by each group was known, and we simulated the harvest of cone crops at each site 2000 times to get distributions of harvest correlations based on the observed harvest proportions. Thus, for each tree, each cone was assigned to a consumer group with the probability equal to the overall proportion harvested by each group for that site. This was achieved by dividing a number line from zero to one into the observed proportions of harvest by each group, and a random number between zero and one determined in which segment and therefore which group that cone was assigned. The numbers of cones falling into each group were tallied for each tree, and translated back into the percentage of the crop harvested. We calculated correlation coefficients for each pair (insect–mammal, insect–bird, bird–mammal) of harvest percentages in each iteration (2000 total), yielding three distributions of correlation coefficients. The probability of obtaining the actual correlation coefficient given the appropriate null distri-

bution was obtained by calculating the proportion of simulated correlations to the left (negative direction) of the observed correlation coefficient (a one-tailed test of the null hypothesis that $r \geq 0$).

We used the method developed by Fisher (1954) and described in Sokal and Rohlf (1981) to combine probabilities of the correlation analyses across sites and years to obtain an overall P value for each set of cone harvest correlations (i.e., insect–mammal, bird–mammal, and insect–bird). This method (a form of meta-analysis; Glass 1976) allowed us to test the hypothesis of an overall negative correlation (one-tailed test) between groups in cone harvest. Because we are testing a one-tailed hypothesis for a negative correlation, we adjusted the P values for positive correlation coefficients by subtracting them from one. This adjustment causes positive correlations to add only slightly to the test statistic while it increases the critical chi-square value such that positive correlations reduce the likelihood of rejecting the null hypothesis that $r \geq 0$. The test statistic, $X^2 = -2 \sum_{i=1}^{k} \ln P_i$, is distributed as a chi-square with $2k$ (k = the number of correlations) degrees of freedom.

For a negative correlation between percent harvest by different groups to reflect resource-use competition, it is necessary for groups to increase their absolute harvest in the absence of their potential competitor. To test this assumption, we performed exclusion experiments as detailed below.

Exclusion experiments

To examine mammal responses to insect exclusion, we first sprayed relatively small trees (<2 m tall) at the Sunset Crater site with a systemic insecticide (Cygon) from 1984 to 1988. In 1988, we monitored conelet number and subsequent mammalian harvest for these trees and 10 paired (for equal size) control trees. We compared the mean number and mean percentage of cones harvested by mammals between treatment and control trees using the Wilcoxon signed-ranks test (Conover 1980). We could not examine bird use of these trees because birds did not visit small trees with relatively small cone crops (Christensen et al. 1991).

To determine the effect of mammals on birds, we excluded mammals by fitting 25 trees (10, 8, and 7 trees at three sites) with barriers made of sheets of aluminum 1.07 m high wrapped completely around the base of each tree. We also removed low-hanging branches and branches from adjacent trees that might also provide access to the canopy. We counted the number of surviving (insect-free) cones on each tree, and matched each treatment tree with a control tree of similar cone number. We monitored avian harvest, and compared mean number and the mean percentage of cones harvested between treatment and controls using the Wilcoxon signed-ranks test.

To determine the effect of birds on small mammals, in 1988 we covered 10 trees with polypropylene netting of 1.5 cm mesh diameter at a site where birds were harvesting. Nets, measuring 10 m wide, were fastened to the trees with wire and covered the tree down to ≈60 cm above the ground. With the netting, mammals still had access to the cones, but birds did not. We matched each covered tree with a control tree with a similar number of cones. We used the Wilcoxon signed-ranks test to compare mean number and mean percentage of the crop harvested by mammals between treatment and control trees.

Natural removal experiments

Although trees at the Sunset Crater site produced similar numbers of cones per tree in both 1985 and 1986 ($\bar{X} = 141.2 \pm 4.6$ and 148.3 ± 6.1 cones, respectively [mean $\pm$ 1 [SE]), absence of birds in 1986 provided us with a natural removal experiment. We compared mean percent mammal harvest for each of these years using the Mann–Whitney test (Conover 1980). We also used this test to compare mean mammal harvest for all trees that were and were not harvested by birds at all the sites across the 4 yr.

Insect impact on the relative harvest by birds and mammals

To examine the influence of insect-caused cone mortality on the relative seed harvest by birds and mammals, we regressed the ratio of mammal to bird cone harvest (mean percentage of the crop harvested at a site by each group) on mean insect-caused cone mortality (percent of crop at each site). A positive slope would indicate that mammal harvest increases relative to bird harvest with increasing insect infestation of the cones, and a negative slope would indicate that bird harvest is positively associated with insect infestation.

RESULTS

Within-site correlations of cone use

In 11 of the 14 site–year comparisons there was a negative correlation between insect and mammal percent cone use, although the correlation was significant in only 7 of the 14 cases (Table 1). Combining probabilities, there was an overall significant negative correlation between insect and mammal percent cone use ($\chi^2 = 105.9$, critical χ^2 with 28 df at the .001 level = 56.9).

In 9 of the 10 site–year comparisons there was a negative correlation between insect and bird percent cone use, although the correlation was significant in only 4 of 10 cases (Table 2). Combining probabilities, there was an overall significant negative correlation between insect and bird percent cone use (combined probabilities; $\chi^2 = 59.7$, critical χ^2 with 20 df at the .001 level = 45.3). Because insects begin consuming

TABLE 1. Correlations between percent cone harvest by insects and mammals for individual trees within sites and years.

Year	Site	r	P value	Number of trees
1986	Sunset	−0.367	.046*	33
1987	Sunset	−0.431	.072	20
1988	Sunset	−0.945	<.0005*	12
1986	Winona	+0.606	.999	9
1988	Winona	−0.191	.198	11
1987	FS419	+0.476	.944	11
1987	NewPks	−0.682	.0015*	11
1988	NewPks	−0.593	.0075*	15
1987	FS420	−0.444	.0625	10
1988	FS420	−0.829	.003*	10
1987	Steller	−0.646	.00135*	10
1988	Steller	−0.894	<.0005*	13
1987	Walnut	−0.298	.238	8
1988	Walnut	+0.411	.988	8

* Results significant at the .05 level (one-tailed P values testing for a negative correlation based on the randomization test).

TABLE 3. Correlations between percent cone harvest by birds and mammals for individual trees within sites and years.

Year	Site	r	P value	Number of trees
1985	Sunset	−0.649	.0005*	33
1985	Winona	−0.989	.0005*	13
1986	Winona	−0.202	.2855	9
1988	Winona	−0.387	.024*	18
1986	FS420	−0.991	.0005*	9
1987	FS420	+0.399	.914	9
1988	FS420	−0.495	.0735	9
1987	FS419	+0.207	.8605	11
1987	NewPks	−0.921	.0005*	11
1988	NewPks	−0.450	.0235*	16
1987	Walnut	−0.202	.2855	9
1988	Walnut	−0.176	.1865	8
1988	Stellers	−0.447	.0245*	13

* Results significant at the .05 level (one-tailed P values testing for a negative correlation based on the randomization test).

cones >1 yr prior to birds and mammals, it appears they negatively influence later seed consumers.

In 11 of 13 site–year comparisons there was a negative correlation between bird and mammal percent cone harvests, and the correlation was significant in 7 of the 13 cases (Table 3). Combining probabilities, there was an overall significant negative correlation between bird and mammal percent cone harvest ($\chi^2 = 109.1$, critical χ^2 with 26 df at the .001 level = 54.1). These generally negative pairwise associations between insect, mammal, and bird utilization of pinyon pine cones, coupled with the fact that 81.9% of all pinyon cones examined were harvested, suggest that seeds are in short supply much of the time.

Among-site correlations of cone use

The relationship between insect and mammal cone use across sites differed between 1987 and 1988; they were negatively correlated in 1987, but positively correlated in 1988 (Table 4). This may have been a result

of cone availability; not only were fewer cones produced in 1987 than 1988 ($\bar{X} = 211 \pm 31.7$, 148.1 ± 16.4 cones respectively [mean ± 1 SE], $P = .043$, Mann–Whitney), but a greater percentage of those cones was consumed by insects as well ($\bar{X} = 69.5 \pm 9.9$, 43.9 ± 5.8%; $P = .022$; Mann–Whitney). Consequently, the number of cones available to mammals was much reduced in 1987, producing a negative correlation coefficient. The positive correlation in 1988 may have resulted from more cones being available to mammals because birds avoided areas with greater insect populations (as evidenced by the significant negative correlation between bird and insect cone use described below), leaving all the remaining cones to mammals. These data did not yield an overall negative correlation between insect and mammal mean percent cone harvest (combined probabilities; $\chi^2 = 8.7$, critical χ^2 with 4 df at the .05 level = 9.488, .10 > P > .05).

While these results suggest that in some years mammals indirectly benefited from insect infestation, avian seed harvest was significantly negatively correlated with

TABLE 2. Correlations between percent cone harvest by insects and birds for individual trees within sites and years.

Year	Site	r	P value	Number of trees
1986	Winona	−0.634	.2385	9
1988	Winona	−0.187	.088	11
1987	FS419	−0.750	.0165*	11
1987	NewPks	+0.387	.921	11
1988	NewPks	−0.100	.143	16
1987	FS420	−0.730	.0075*	10
1988	FS420	−0.870	.0015*	10
1988	Steller	−0.332	.0045*	13
1987	Walnut	−0.700	.054	9
1988	Walnut	−0.337	.086	9

* Results significant at the .05 level (one-tailed P values testing for a negative correlation based on the randomization test).

TABLE 4. Correlations of insect–mammal, insect–bird, and bird–mammal percent cone harvest for site averages across years (1986, 1987, and 1988).

Comparison	Year	r	P value	Number of sites
Insect–mammal	1987	−0.832	.0065*	7
	1988	+0.795	.975	6
Insect–bird	1987	−0.822	.01*	7
	1988	−0.596	.045*	6
Mammal–bird	1986	−0.392	.105	8
	1987	+0.077	.73	7
	1988	−0.833	.015*	6

* Results significant at the .05 level (one-tailed P values testing for a negative correlation based on the randomization test).

insect cone use in both 1987 and 1988 (Table 4). There was also an overall significant negative correlation between percent insect and bird harvest (Table 4; combined probabilities, $\chi^2 = 15.41$, critical χ^2 with 4 df at the .025 level $= 11.14$).

Mammal and bird mean percent harvest were also overall significantly negatively correlated across sites ($\chi^2 = 13.54$, critical χ^2 with 6 df at the .05 level $= 12.59$). Although the above correlation analyses suggest competitive interactions among these seed consumers both within and across sites, the following pairwise exclusion experiments were employed to discriminate between this and alternative hypotheses.

Exclusion experiments

When we removed insects from individual trees, mammals harvested 2.3 times more cones relative to control trees (Fig. 1). Because more cones matured when insects were removed, more cones were available for mammals. This suggests that seeds were in short supply. The percentage of the cone crop harvested by mammals, however, was not affected by insect removal (Wilcoxon signed-ranks, $P = .298$), indicating that mammal harvest was proportional to cone availability.

Consistent with the hypothesis that birds and mammals compete for pinyon pine seeds was the result that birds harvested 2.5 times more cones from trees where mammals had been excluded compared to controls (Fig. 2a). Mammals apparently reduced the availability of resources to birds, and birds responded to a release from competition with mammals by increasing their harvest.

Birds also harvested a fivefold greater percentage of the crop from trees without mammals relative to controls (Fig. 2b). Thus, in the absence of mammals, trees received disproportionately greater harvest by birds, and caching by birds is known to enhance seed germination (Vander Wall and Balda 1977, Ligon 1978).

FIG. 2. (a) Number of cones harvested by birds from trees where mammals had been excluded compared to the harvest from control trees (means and 1 SE). Wilcoxon signed-ranks test, $P = .003$. (b) Percentage of a tree's cone crop harvested from trees where mammals had been excluded compared to the harvest from control trees (means and 1 SE). Wilcoxon signed-ranks test, $P < .0001$.
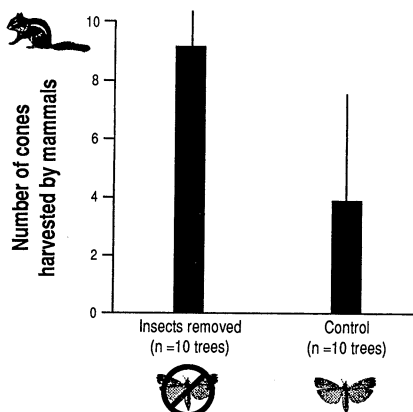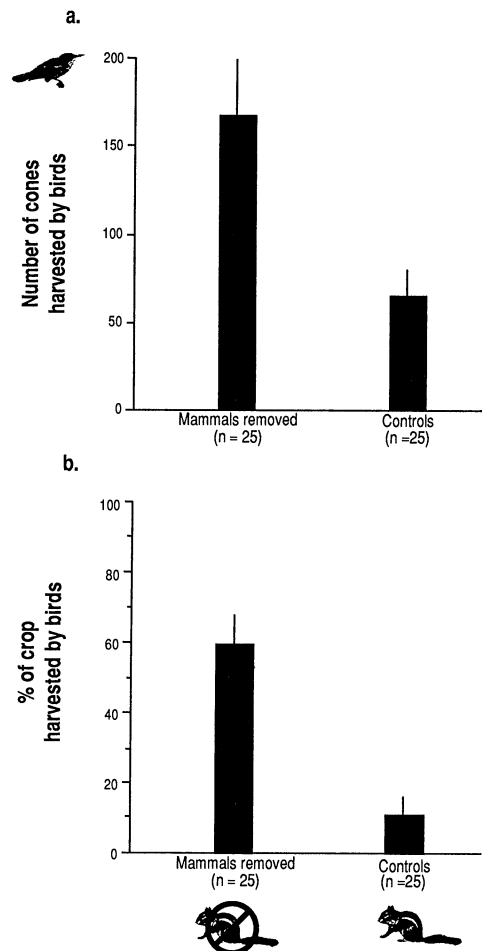

FIG. 1. Number of cones harvested by mammals from trees where insects had been removed compared to the harvest from control trees (means and 1 SE). Wilcoxon signed-ranks test, $P = .017$.

The reciprocal exclusion experiment also suggests that birds and mammals compete for seeds. When birds were prevented access to trees, mammals harvested 3.2 times more cones compared to controls (Fig. 3a). Thus, mammals also responded to greater seed availability by increasing their harvest when released from resource competition with birds. Mammals also harvested a 2.6 times greater percentage of the cone crop from trees without birds relative to controls, exhibiting a similar response to that of birds (Fig. 3b).

Similar results were obtained when we compared cone harvest by mammals from trees when birds were naturally present and absent. When birds were absent from the Sunset Crater site in 1986, mammals harvested twice the percentage of cones compared to 1985 when birds also harvested (Fig. 4a). Similarly, for trees at all sites all years, mammals harvested a 1.3 times greater percentage of cones in the absence of birds com-
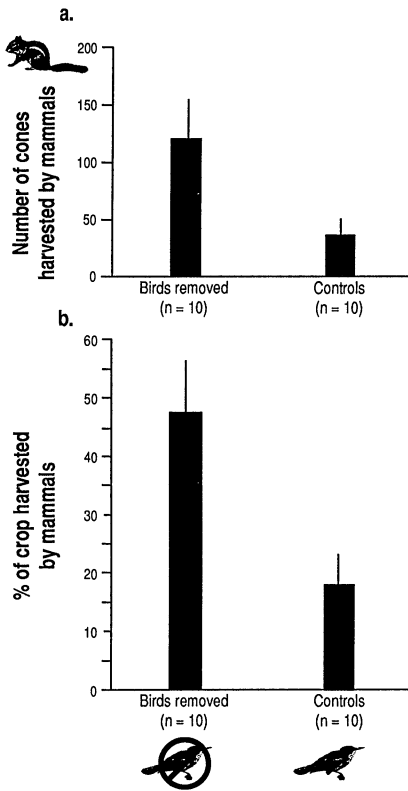
FIG. 3. (a) Number of cones harvested by mammals from trees where birds had been excluded compared to the harvest from control trees (means and 1 SE). Wilcoxon signed-ranks test, $P = .017$. (b) Percentage of a tree's cone crop harvested from trees where birds had been excluded compared to the harvest from control trees (means and 1 SE). Wilcoxon signed-ranks test, $P = .018$.

pared to when birds were present (Fig. 4b). These results are consistent with those obtained in our bird removal experiments, and further document the competitive nature of this interaction.

Insect impact on the relative harvest by birds and mammals

Even though pairwise experiments showed that insects negatively affected mammals, insects might indirectly benefit mammals through their negative influence on bird foraging. Across pinyon pine populations, as insect utilization of cones increased, the ratio of mammal to bird consumption also increased from 0.34 to 120 (i.e., 350-fold; Fig. 5). Thus, even though insects reduced the cone crop, the decline in attractiveness of stands to birds allowed mammals access to those cones that did survive insect attack.

DISCUSSION

We empirically and experimentally demonstrated two major patterns in the interactions among insect, mammal, and bird seed consumers of pinyon pine. First, results of exclusion experiments and correlation analyses support the hypothesis that resource competition

occurs among these taxa. Second, insect seed predation was found to enhance the relative consumption of seeds by mammals compared to birds due to the larger negative effects of insects on birds than mammals. These patterns have general implications to three conceptual areas of ecology: (1) competition among distantly related taxa, (2) herbivore mediation of species interactions, and (3) herbivore impacts on plants and the community. Each of these areas will be discussed separately below.

Competition among taxa

Examples of competition among distantly related taxa are now common (Connell 1983, Schoener 1983, Davidson et al. 1985, Brown et al. 1986, Karban et al. 1987, Morin et al. 1988). While we did not perform all of the possible reciprocal exclusion experiments, we did do all that are feasible and biologically relevant, and the results of each of our experiments are consistent with resource competition. We do not argue that competition among these groups always occurs; only when crops are naturally low or when insect infestation is particularly high do we expect this interaction.

Increasing attention toward competition between unrelated taxa (Karban et al. 1987, Morin et al. 1988,
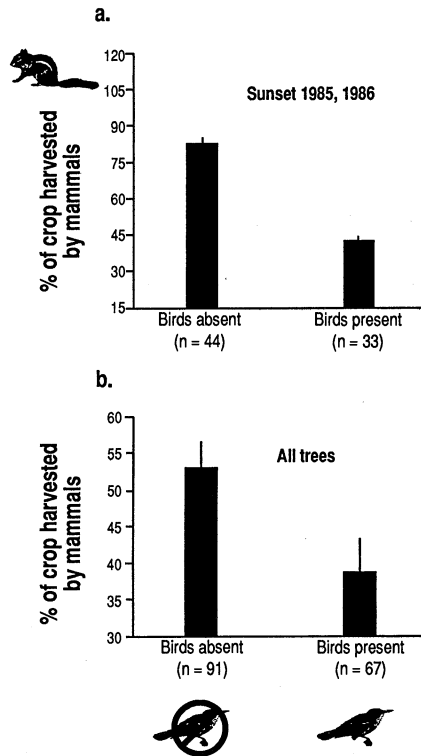

FIG. 4. (a) Percent of crop harvested by mammals at the Sunset Crater site in a year when birds also harvested (1985) to when birds did not harvest there (1986) (means and 1 SE). Mann–Whitney test, $P = .003$. (b) Percent of crop harvested by mammals for all trees that were harvested by birds to those trees not harvested by birds (means ± 1 SE). Mann–Whitney test, $P = .014$.

Thompson et al. 1991) has heuristic value in that it may broaden the way in which we perceive communities and community interactions. Competition studies now examine direct and indirect competition among community constituents regardless of their taxonomic affinity. To better understand community interactions and dynamics, it may be important to examine competition between even more distantly related organisms such as mycorrhizae and herbivores for photosynthate or between fruit fungi and avian frugivores for fruit.

Herbivore mediation of competition

Recently, studies have shown that one species, or a group of species, can indirectly mediate interactions between two other species (Davidson et al. 1985, Karban et al. 1987, Morin 1987, Morin et al. 1988, Moran and Whitham 1990, Safina 1990, Christensen and Whitham 1991, Thompson et al. 1991). With pinyon pines, we found that insect herbivores indirectly affected relative resource use by birds and mammals through their influence on pinyon pine cone crop sizes. Because insects reduce crop sizes by an average of 57% (frequently up to 100%; Christensen and Whitham 1991), and because at least three species of birds and three species of mammals use pinyon pine seeds for food, herbivory directly affects their resource base and indirectly the interactions between them.

Herbivore impacts on plants and the community

Herbivores impact communities in that they can affect plant community structure (Brown and Heske 1990), other herbivores (Faeth 1986, Moran and Whitham 1990, Hunter 1992), predators (Price et al. 1980), and mutualists (Cushman and Whitham 1990, Gehring and Whitham 1991). Several impacts of *Dioryctria albovittella* on pinyon pine have already been documented. For example, Whitham and Mopper (1985) found that chronic herbivory by these moths resulted in slower tree growth rates, greatly reduced female function, and altered architecture. When released from herbivory, trees resumed normal growth patterns and reproductive effort, demonstrating that herbivory caused the phenotypic effects. Christensen and Whitham (1991) found that even those cones that survived insect attack had reduced probabilities of being dispersed because avian seed dispersers ignored trees and stands of trees with herbivore-reduced crops. The present study found that seeds that do survive insect infestation can be 350 times as likely to be harvested by mammals as birds, and it is unknown if mammals are effective dispersal agents of pinyon pines. Additionally, insect impacts reported here are conservative because our studies only deal with the cones that survive to be attacked by cone borers or harvested by vertebrates. Because *D. albovittella* kills terminal shoots that would have produced conelets and stimulates the production
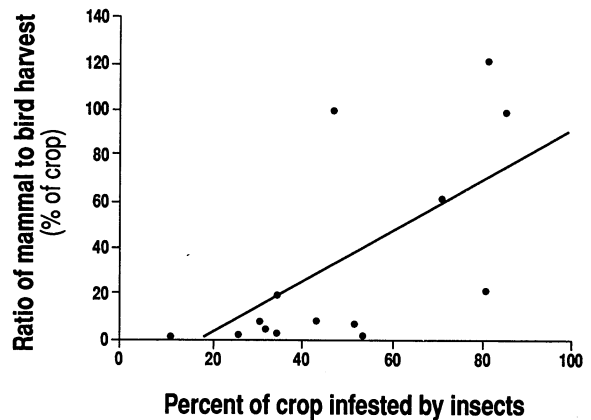

FIG. 5. Regression predicting the ratio of mammals to bird percent crop harvest as a function of insect-caused cone mortality. Each point represents the mean for one site in one year ($Y = -30.6 + 1.28X$, $r^2 = 0.46$, $P < .02$, $n = 14$).

of lateral shoots that have no female function (Whitham and Mopper 1985), these other direct and indirect effects further reduce the potential cone crop.

Genetic effects at the community level

Few studies have examined genetic interactions between plants and their herbivorous insect community (Moran 1981, Fritz and Price 1988, Maddox and Root 1988, Paige et al. 1990, Boecklen and Price 1991). In the pinyon pine system, there are links between plant genetics, insect and mammalian herbivory, and mycorrhizal and avian mutualists. Allozyme studies of Mopper et al. (1991) found that insect-resistant and -susceptible pinyon pines exhibited significant differences in both allelic frequencies and heterozygosity. Additionally, Gehring and Whitham (1991) found that insect-susceptible trees had 33% fewer ectomycorrhizae than resistant trees. When insects were removed, the densities of these mutualists rebounded to levels comparable to uninfested trees. Thus, the underlying genetic structure of a pinyon pine population affected the distribution of a major herbivore, which in turn affected the belowground fungal community.

A second genetic link between host plant resistance to *D. abovittella* and community structure is through the impact of herbivory on the avian seed dispersal agents of pinyon pine. Christensen et al. (1991) and Christensen and Whitham (1991) found that avian seed dispersers of pinyon pine (primarily Clark's Nutcrackers and Pinyon Jays) selectively foraged where cone crops were greatest, both within and among pinyon pine stands. Because chronic insect herbivory reduced the cone crop by an average of 57%, and completely eliminated the crop of susceptible individuals (Whitham and Mopper 1985), the local presence of these avian mutualists is also linked to the genetically based insect-resistance traits of pinyon pines. The data presented here also suggest a third link in which resistance and susceptibility to insect attack influences mam-

malian seed harvest as well as their interactions with avian seed harvesters. Thus, these studies suggest that the distribution and/or foraging behavior of diverse organisms may map onto the underlying genetic structure of the plant population.

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