INSECT COMMUNITY STRUCTURE IN A SPECIES OF YELLOW ASTER

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Abstract: Insects use flowers for a variety of reasons, including food, shelter, and oviposition sites. While many studies have tested how insect communities within a flower affect the flower's fitness, we aimed to measure the effect that the flower's life cycle has on insect community structure. We predicted that insect community abundance, richness, and evenness would vary across four flower age classes, being highest in the mature flowers because these would have the most floral resources available to insect inhabitants. We found the greatest number of individuals and the greatest richness and evenness of insect morphotypes in mature flowers. However, once we rarefied our data to equalize the numbers of individuals in each flower age class, we found no difference among age classes in richness or evenness.

Key Words: Asteraceae, florivory, succession, rarefaction, diversity

INTRODUCTION

Many insect species are closely associated with flowers as pollinators, florivores, or as a combination of both (Armbruster 1997). From the insects' perspective, a flower is an environment that provides not only food, but also habitat for entire communities of invertebrates. While many studies that explore the relationship between plants and their insect inhabitants have looked at the effect of insect florivory on the plant (Irwin *et al.* 2003, McCall and Irwin 2006), few have examined the complementary effects that the flower has on resident insect communities.

In the family Asteraceae, a flower develops from a closed bud to an open disk. Disk florets open and produce pollen and nectar, and ovules may be fertilized. The flower then withers and the plant begins to allocate resources to the developing seeds (Heywood 1993). For invertebrate inhabitants, these changes over time in flower morphology, size, and chemical secretions might represent important changes in the quality and quantity of available resources and habitat.

Florivorous insect species commonly consume particular flower parts or a combination of parts (e.g., sepals, petals, stamens, pistils, pollen, and ovules) (McCall and Irwin 2006). In addition, other insects associated with flowers are carnivorous and prey on different kinds of florivores. Because many insects are specialized with regard to the resources they obtain from the flower, different amounts of these resources over the life of the flower could drive corresponding changes in the resident invertebrate community composition. Furthermore, because we expect total resource availability in the flower habitat to be positively correlated with invertebrate abundance, and

because higher numbers of individuals are more likely to contain more species (Fisher *et al.* 1943), changes in total resource abundance in the flower could drive corresponding changes in invertebrate community richness.

We measured invertebrate abundance, richness, and evenness in Asteraceae flowers of four age classes within one species to understand how flower development affects the invertebrate communities living in flowers. Because mature flowers are at the height of their resource production (of nectar, dehisced pollen, and developing ovules), we predicted that mature flowers would have higher abundance, richness, and evenness of insects than other age classes.

METHODS

Study system.

We collected our data on 28-30 January, 2007 at the Estacion Biologica Cuerici, San Jose Province, Costa Rica (elevation 2600 m). We chose to use an Asteraceae species because we found many invertebrates in Asteraceae flowers and because Asteraceae flowers can be easily categorized into age classes by examining the numbers of closed, open and spent disk florets. The species we studied, referred to as "yellow aster" in this paper, is a scandent shrub which produces abundant clusters of yellow composite flowers about 4 cm in diameter. It is common around the field station, occurring in open sunny gaps along either side of the road between the stream and the farmhouse belonging to Abel, the uncle of the director of the station, Carlos Solano.

Field methods.

We studied ten clusters of the yellow aster that were all at least three meters apart from each other. The clusters were located on either side of the road between the stream and Abel's farmhouse. In each cluster, we chose four individual flower heads representing young, mature, old, and very old age classes (Table 1). The proportions of florets at each stage represent both flower age and available resources, and petal number may represent flower attractiveness. We cut each flower and placed it in a separate bag. In the laboratory, for each flower, we measured the diameter of the disk, the numbers of closed, open, and spent disk florets, the numbers of closed, open, and withered ray florets, and the number and kinds of invertebrates. We identified the invertebrates to the lowest taxonomic level possible with the resources available (Table 2).

Table 1. Yellow aster flowers were grouped by age class according to the criteria defined below. Values represent mean ± 1 SE (n=10 flowers per age class). Different letters represent significantly different age classes (=0.05).

Age	Description	Open Florets		Petal Number	
Young	Contains mostly closed florets; petals open or closed	B	2 ± 1.0	A	9 ± 0.4
Mature	Contains mostly open florets; petals open	A	32 ± 3.2	A	9.4 ± 0.4
Old	Contains mostly spent florets; petals open or withered	B	5.3 ± 3.4	B	6.7 ± 0.9
Very Old	Contains mostly spent florets; petals mostly withered or fallen off	B	0.6 ± 0.43	C	2.2 ± 0.6

Table 2. Insects found in the yellow aster flowers, identified to the lowest possible taxonomic level.

Common Name	Taxon Level	Latin Name
weevil	family	Curculionidae
thrip	family	Thripidae
fly	family	Drosophilidae
chigger	family	Trombiculidae
crab spider	family	Thomisidae
leafhopper	family	Cicadellidae
ant	family	Formicidae
tent worm	order	Lepidoptera
inchworm	order	Lepidoptera
gnat	order	Diptera
unidentified spider	order	Araneae
unidentified grub	class	Insecta
unidentified nymph	class	Insecta
unidentified gall larva	class	Insecta

Statistical analysis.

We verified that our flower age classes differed by comparing the number of open florets and the number of petals among age classes, with two separate ANOVAs. Next, to control for possible effects of disk size on abundance, we examined the relationship between disk area and invertebrate abundance with a correlation analysis. We calculated evenness, J, for each flower as the Shannon-Weiner diversity divided by the natural log of richness:

$$J = -\sum_{i=1}^{S} (P_i \times \ln P_i)/\log(S),$$

where P_i equals the proportion of total individuals in the ith species and S equals species richness in the sample.

We log-transformed total insect abundance and arcsine square-root transformed evenness to approach normality, because the raw data were left-skewed. We compared the abundance, richness, and evenness of invertebrate flower inhabitants across the four age classes using three separate ANOVAs. To account for variation among clusters, we used a randomized block design, using flower cluster as the blocking factor for each ANOVA. After finding significant differences in invertebrate abundance, richness, and evenness among age classes, we tested which classes were different from each other with Tukey Highly Significant Difference multiple comparisons tests with α=0.05. Statistical analyses were performed using JMP 5.1.2.

We then rarefied the richness and evenness data to determine how these response variables were affected by unequal abundances among age classes. We calculated evenness J as the rarefied Shannon-Weiner diversity H, divided by the natural log of rarefied richness.

Because many flowers had very low abundances of invertebrates (25% of the flowers contained less than three individuals), we could not rarefy our data at the level of the individual flower sample. Instead, we summed the number of individuals of each species for each age class (pooling all flowers in an age class), and from those data we rarefied richness and evenness down to 60 individuals (the lowest number of insects found in any age class, after pooling replicates) using EcoSim (Gotelli and Entsminger 2001). Because we grouped our replicate flowers for the rarefaction, we could not perform significance tests on our rarefied richness or evenness.

RESULTS

The number of open florets varied with flower age ($F_{3,36}$=38.5, P<0.0001); on average, mature flowers had more open florets than all other stages (Fig. 1, Table 1). Petal number also varied with flower age ($F_{3,36}$= 31.7, P<0.0001, Table 1). Mature and young flowers had the most petals, followed by old, and very old flowers had the least (Table 1).

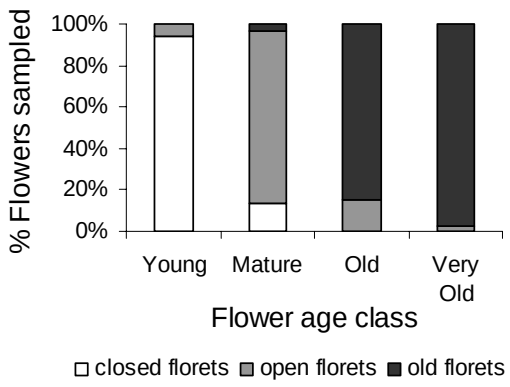

Figure 1. The proportions of closed (white), open (gray), and old (black) disk florets found in yellow aster flowers, in each of four age classes (Table 1).

There was a weak positive correlation between the log total abundance of invertebrates and disk area (r_{34}=0.38, P=0.02). Additionally, the mean difference between young and mature flowers in average disk diameter was 1 mm, which represents a 14.0% increase in disk diameter between young and mature flowers.

Age class, but not flower cluster, affected invertebrate abundance (Age: $F_{3,27}$=7.92, P<0.002, Fig. 2; Cluster: $F_{9,27}$=1.81, P>0.2). Mature flowers had more invertebrate individuals than very old and young flowers, while mean invertebrate abundance for old flowers did not differ significantly from the other age categories (Fig. 2). Eighty-three percent of the total abundance across all age classes was thrips (Thripidae), 13% was weevils (Curculionidae), and 4% was other invertebrates.

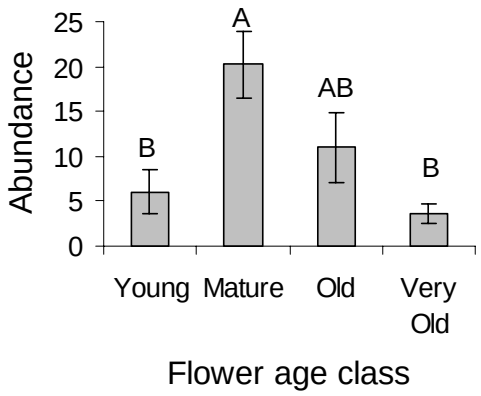

Figure 2. Average abundance of insects across four yellow aster flower age classes (means ± 1 SE; n=10 flowers per age class). Different letters represent groups with significantly different mean abundances.

As with abundance, invertebrate morphotype richness varied with age class, but not cluster (Age: $F_{3,27}$=4.76, P<0.02, Fig. 3; Cluster: $F_{9,27}$=1.07, P>0.5). Mature flowers had significantly higher richness than very old and young age classes, and richness for old flowers did not differ significantly among the three other age categories (Fig. 3). Invertebrate evenness also varied among age classes, but not flower clusters (Age: $F_{3,27}$=4.43, P<0.05, Fig. 4; Cluster: $F_{9,27}$=1.29, P>0.50). Mature flowers had higher evenness than the young flowers, but mature flower invertebrate evenness was not significantly different from the old or very old.

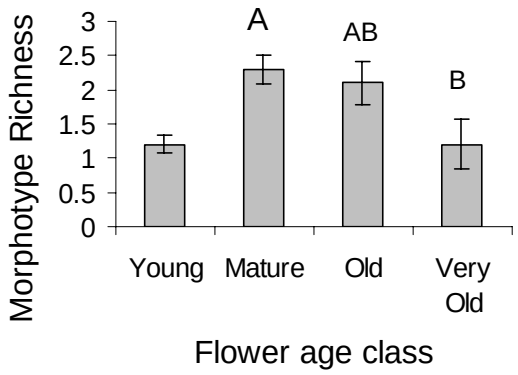

Figure 3. Average unrarefied morphotype richness across the four flower age classes of yellow asters with error bars showing ± 1 SE (n=10 flowers per age class). Different letters represent groups with significantly different mean richness.

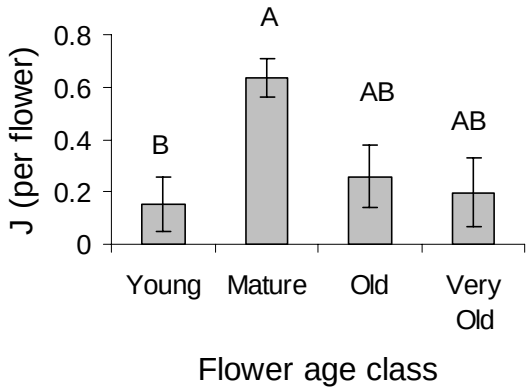

Figure 4. Average unrarefied invertebrate evenness in yellow aster flowers, with error bars showing ± 1 SE (n=10 flowers per age class). Different letters represent groups with significantly different mean evenness.

The rarefied richness for the four age classes (pooled data across replicate flowers) had large 95% confidence intervals, and we were unable to conclude that richness differed across age classes (Fig. 5). Since the 95% confidence intervals for rarefied Shannon-Weiner diversity were also very large, there were no significant

differences in evenness among age classes (Fig. 6).

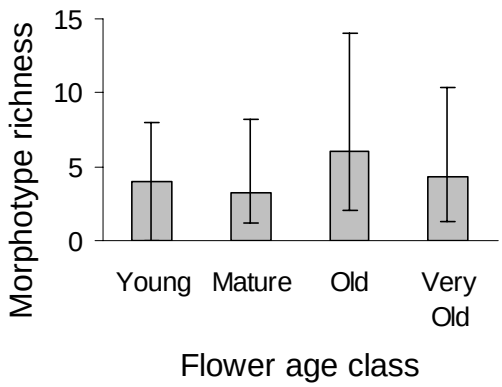

Figure 5. Rarefied invertebrate richness in yellow aster flowers and 95% confidence intervals, combining all flower samples within each age class.

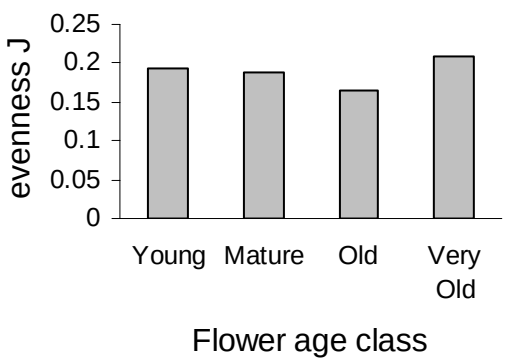

Figure 6. Yellow aster invertebrate evenness calculated from rarefied Shannon-Weiner diversity and richness among age classes.

DISCUSSION

Our data supported our prediction that mature flowers would have the highest insect abundance. However, abundance did not differ significantly between mature and old flowers, which may indicate a time lag in the response of invertebrate populations to decreases in flower resources.

Disk diameter was weakly but significantly correlated with invertebrate abundance disk diameter increased by 14% from young to mature flower stages. Since larger habitat area is correlated with higher abundance and species diversity (Denslow 1995), this difference in disk size may be responsible for some of the increases in invertebrate abundance and richness observed between young and mature flowers.

The higher invertebrate abundance in mature flowers may have also influenced the observed richness patterns (Fisher *et al.* 1943). Because our study used entire flower habitats as replicate units, and because we took absolute censuses of those habitats, the variability in abundance among age classes represents an intrinsic property of the study system, rather than an artifact of sampling effort. However, the natural variability in invertebrate abundance among flower age classes meant that flowers of different ages contained different numbers of total individuals from which to calculate richness. Rarefaction is a useful tool for comparing species richness while controlling for unequal numbers of individuals sampled. However, not all data sets are equally suitable for rarefaction. For example, the low invertebrate abundance found in some flowers forced us to pool our replicates for each age class, and thus prevented us from performing significance tests on

the rarefied richness and evenness. Furthermore, because many of the morphospecies we found were represented by a very few individuals, the rarefied values for richness in any age class were highly variable, producing large confidence intervals around our richness estimates (Fig. 5) and preventing us from drawing a satisfying conclusion about the results. These complications in our analysis of richness and evenness demonstrate some of the difficulties of comparing diversity between habitats, especially when the realities of the natural study system produce a data set whose characteristics are not ideal for analysis by rarefaction models.

Although our study's main conclusive results were limited to invertebrate abundance, further studies in this system might reveal interesting patterns in species diversity, functional group diversity, food web structure, and other community characteristics of flower-dwelling invertebrates. Further studies could address broader ecological questions about the dynamics of community succession occurring in biotic habitats. Community succession in newly available abiotic habitats, such as recently cleared ground, is generally viewed as being driven entirely by endogenous community dynamics, such as differential dispersal and competitive abilities of colonizing organisms. In contrast, in newly opened biotic habitats, such as a flower bud, colonization and community succession are further affected by the biological growth and development of the living habitat.

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