

Postburn Insect Fauna in Southern California Chaparral¹

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Ecological studies of chaparral insects have been badly neglected. With the exception of a handful of papers (see Force 1981b) stimulated by the Mediterranean Scrub Project of the International Biological Program (IBP), there is a dearth of published information on the subject. Those studies that are in print deal largely with comparisons between certain matorral insects from Chile and chaparral insects from California. This neglect is somewhat surprising in that a variety of chaparral plant and vertebrate animal investigations have been published. It appears that more interest might have been shown in the insect fauna since, ostensibly, it is so intimately involved with these other groups of organisms. Certainly we should be interested in how and how much insects affect such things as (a) the pollination of chaparral flora, (b) the growth of this flora by their feeding, (c) the disposition of chaparral plant seeds, (d) the postfire succession of the chaparral community and (e) the food chains of higher animals found in chaparral. Conversely, we would like to know how insects are themselves affected by various other chaparral elements. As it is, we know very little about variations in even such fundamental elements as insect identities, abundance, biomass, richness and diversity in chaparral of various kinds and of different ages.

I have reviewed what literature I could find pertaining to the relationships of chaparral insects with the community ecology of this vegetation (Force 1981b). Also, I have reviewed the postfire floral and faunal succession of chaparral, including certain aspects of my own study on the early (first 3 years) postfire succession of insects in the San Gabriel Mountains of southern California

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Abstract: Extremely little is known about succession of insects in postfire chaparral. This 4-year postfire study in the San Gabriel Mountains of southern California showed that pollen-nectar feeders and predatory insects can be very abundant beginning the first spring after a burn. Annual plants in bloom appeared to entice flower feeders, and hence predators, into the area. Phytophagous insects (other than flower feeders) and parasitic insects more slowly established in the burn. Insect biomass tended to peak annually in June and July. There was no obvious correlation between insect biomass and yearly rainfall. Fourth-year insect richness and diversity showed a dramatic increase after an overall 3-year decreasing trend.

(Force 1981a,b). The present report will cover other aspects of the same study and extend previously reported data to a total of 4 years, when the project was terminated.

STUDY AREA: METHODS

From May 1976 to December 1979 I conducted a study of postfire insect succession within the San Dimas Experimental Forest located in the south-central San Gabriel Mountains, approximately 45 km east of Los Angeles. The actual study site was in the northeast section of the Forest (see Mooney and Parsons 1973) that burned November 1975. Specifically, I measured those gross insect changes that occurred annually in relation to the plant changes. Insect sampling consisted of periodic net collections and observations of insects (numbers of families and individuals) along a 1.5 km section of unmaintained contour trail at 1250 m elevation, as well as collections and observations from a series of 100 m² plots situated along the trail. Plant sampling was undertaken only once a year (early summer) and consisted of line intercept counts (numbers of species and individuals) in addition to plot counts (Force 1981a,b).

RESULTS

Trophic Groups

Figure 1 shows the relative abundances of various insect trophic groups during the 4-year period of postfire succession at San Dimas. These data can tell us something about the availability of resources for, and the utilization of resources by insects, as well as availability of insects as resources themselves for other animals. Another part of the story can be observed from biomass calculations, which will be treated later.

Predators tended to peak each year some time during the spring months (samples were not taken until May in 1976), mainly because of the great

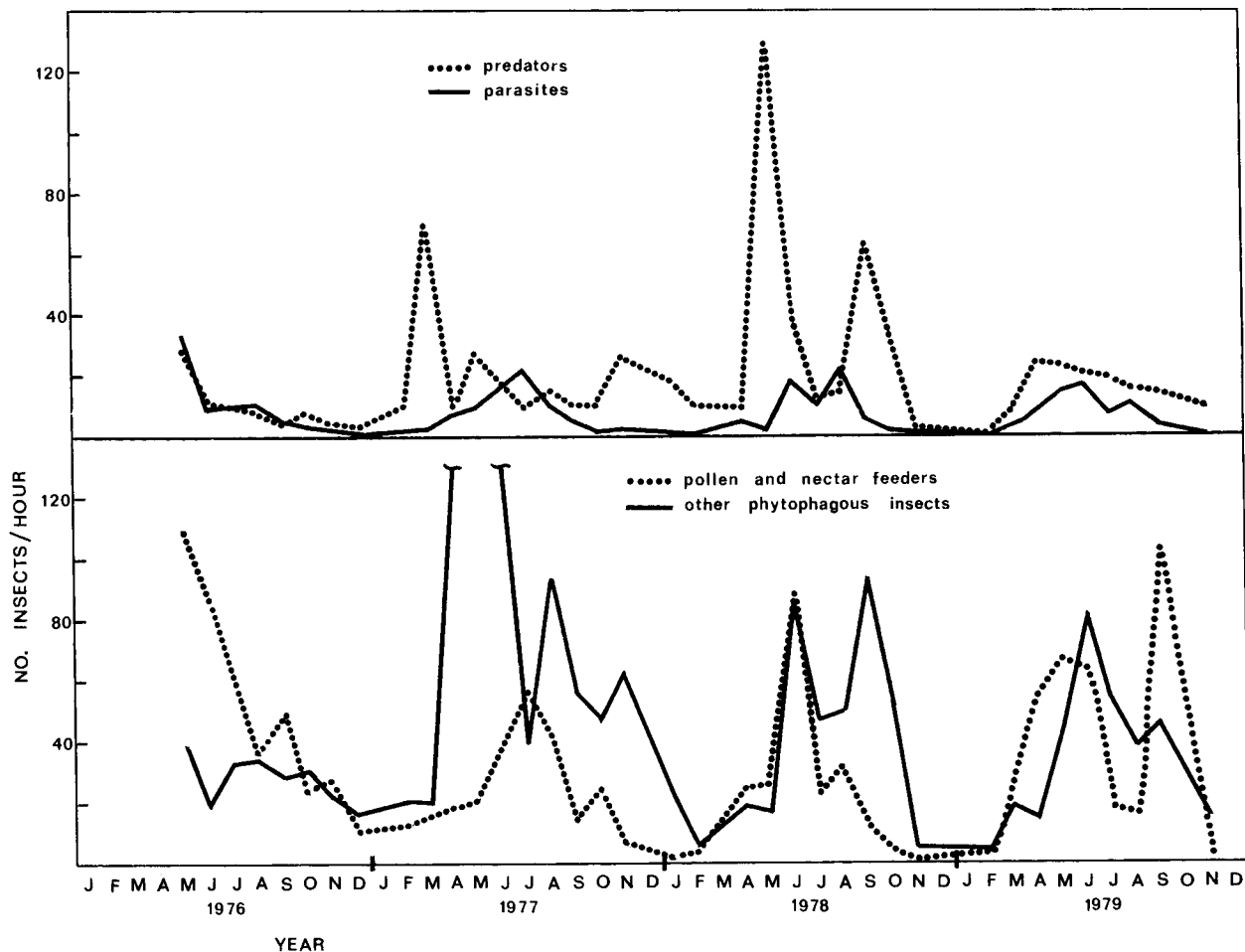


Figure 1--Relative abundances of various insect trophic groups during 4 years of postfire chaparral succession in the San Dimas Experimental Forest. The data are in numbers of insects collected and/or observed per man/hour.

numbers of Coccinellidae that emerged from hibernation in the lower mountains at this time. Many of these beetles began to feed immediately if prey were available, whereas others appeared to be migrating to lower altitudes. The earlier activity in 1977 (numbers peaked in March) as compared to 1978 (numbers peaked in May) was possibly related to weather. The winter of 1976-77 was very dry with an abundance of warm weather in early spring; whereas in 1977-78 precipitation was much above normal and early spring temperatures were low. The beetles may, therefore, have been stimulated into emerging from hibernation earlier in 1976-77. Coccinellids were much less numerous in 1979 than in the two preceding years. The secondary peaks of predators seen in November 1977 and September 1978 reflect the abundance of vespid wasps, which gather prey to stock their nests. These particular wasps, however, were interested primarily in what appeared to be extrafloral nectaries of oak (*Quercus*), and perhaps were not acting as predators at this time. They were most numerous in 1978. Asilid flies were abundant in May 1976 and

were never so abundant again. These insects must have migrated into the burn in great numbers from outside sources. They were observed preying on the extraordinary numbers of flower-visiting insects (especially Hymenoptera) that were also attracted to the burn to take advantage of the extensive bloom of annual plants that normally occurs the first spring following fire.

Parasitic insects reached their 1977 and 1978 peak abundances in midsummer. In 1976, however, the peak was in May, and in 1979 in May and June. The great majority of these parasites were bombyliid flies, the larvae of which are parasitic on wild bees for the most part, whereas the adults are flower visitors and good pollinators. It is difficult to know for certain what these flies were doing at various times in chaparral. It is my guess, however, that at the time of their highest numbers (May 1976) they were responding to the abundance and variety of blooming annual plants, since they were observed feeding on this resource extensively. They were also likely drawn from

outside the burn by the profuseness of blooming. Of course, numerous wild bees were also present and the bombyliids may have later parasitized bee nests within the burn. (The Bombyliidae was included in both the parasitic and the flower visiting trophic groups.) In June 1978 a moderate number of blood-feeding rhagionid flies was present. The number of Chalcidoidea and Ichneumonoidea (Hymenoptera) whose larvae are parasitic on other insects was extremely small in 1976 and 1977. The Ichneumonoidea were more abundant in 1978 but the Chalcidoidea were still very sparse. In 1979 both groups were slightly more numerous. They appeared to respond slowly to the abundant host resources that were available in the early postfire years.

I am aware of no other published data on chaparral insect predators and parasites that are directly comparable with those reported here. Atkins (1977) published a 1-year (1973) survey of chaparral insects from San Diego County, California; but he combined predators with parasites, reported the data as diversity indices, and sampled in a completely different manner.

Flower visitors (pollen and nectar feeders) are naturally influenced by plant-blooming periods. These insects were extremely abundant in May 1976 when sampling was first initiated and at a time when blooming of annual plants was very profuse. Some flower visitors were in the burn area even earlier before regular sampling was begun; bombyliid flies and honey bees (*Apis mellifera*) were moderately common early in February. By late February wild bees and wasps of several families were present. These insects also must have been attracted into the burn by the profuse bloom of annual plants. Many honey bees were probably originating from domestic colonies maintained within several km of the area by apiculturalists; however, wild colonies are not uncommon in these mountains. The majority of flower visitors in May and June of 1976 were bombyliid flies, honey bees, and anthophorid bees. Flower visitors subsequently declined greatly during the summer months as blooming subsided. By midsummer bees of all kinds were less common but more families were represented. Butterflies became more abundant at this time, especially the families Nymphalidae and Pieridae. By October and November of 1976 syrphid flies were the most common flower visitors along with a number of honey bees. In 1977 a few syrphid flies were present early in the spring. Syrphids appear to be important early spring pollinators, but there was very little blooming in 1977 until well into June. By July bombyliid flies were common flower visitors, honey bees were even more abundant, and anthophorid bees were common in early August. These three groups represented the majority of flower visitors in 1977. By September and October about the only flower insects remaining were a few honey bees. The very late, and seemingly rather poor, bloom this year may have been caused by the greatly subnormal amount of precipitation that fell during the 1976-77 winter. Again in 1978 syrphid flies were the earliest flower visitors, appearing in April and becoming even more abundant in May.

In June bombyliid flies were abundant and several butterfly families were common (Hesperiidae, Lycaenidae, and Pieridae), but by far the most abundant insect (and the one responsible to a large degree for the height of the June peak) was the Chalcidon checkerspot butterfly (*Euphydryas chalcedona*), a common nymphalid species. Honey bees, bumble bees, and anthophorid bees were common in June and July and several other bee families were represented in lesser numbers. Bombyliid flies, anthophorid bees, and honey bees were still common in August of 1978. The April-May-June peak of flower visitors in 1979 was dominated by bombyliid flies, anthophorid bees, honey bees, lycaenid butterflies and nymphalid butterflies. Megachilid bees and bumble bees were also common. The later peak in September and October was caused by great numbers of honey bees and more moderate numbers of syrphid flies; however, they were not visiting flowers but rather were interested in extrafloral nectaries on scrub oak. Bombyliid flies were abundant throughout the season. Flower visiting Hymenoptera were more abundant and diverse in 1976 and 1979 than in 1977 and 1978.

Moldenke (1976, 1977) has reported richness (number of species) and abundance (number of individuals) of flower-visiting insects in chaparral. He found bees especially rich and abundant in both mature and burned chaparral, perhaps because of the sparseness of low ground cover, thus providing ample space for ground nesting. Bees are also by far the most important chaparral pollinators, followed by bombyliid flies. Moldenke (1976) reports, however, that much of the postburn annual flora is self-compatible and, therefore, not dependent on pollinators for reproduction. It is interesting, then, that in the San Dimas study such a large influx of pollinators (both bees and bombyliid flies) occurred the first year postfire. Apparently the annual plants were providing ample nectar and pollen for these flower feeders in order to draw them from outside sources. But why should these plants expend so much energy for this purpose if they are self-compatible? Perhaps self-compatibility is a mechanism to insure their reproductive capabilities just in case pollinating insects are not available for one reason or another. Since many of these annual plants bloom for only one season between fires, perhaps they cannot afford to depend upon insects for their continued survival. However, cross pollination by insects may substantially increase seed set over self-pollination. If this is the case, these plants would benefit by producing large quantities of high quality nectar to attract pollinators into burn areas. If seed set is increased by cross pollination, then it is clear that pollinating insects could be affecting the plant population dynamics of the chaparral ecosystem, in addition to producing more food for all kinds of seed-feeding animals.

The other phytophagous insects (all those except nectar and pollen feeders) were less abundant in 1976 than in the following years. This group in 1976 comprised a large number of families, but none was very large in numbers of individuals. In 1977

a tremendous outbreak of Aphididae occurred on Lupinus from March to June. Counts of these insects were hopeless because of their excessive numbers; the broken peak in figure 1 represents how their numbers might look when graphed. By May of 1977 many Lupinus plants in the area were wilting from the effects of aphid feeding. Coccinellid beetles were moderately numerous also (see predators in fig. 1) and were feeding on the aphids, but the former could not begin to affect the aphid numbers. Acridid grasshoppers were abundant throughout most of 1977, possibly because of the extremely dry, warm spring weather. The high numbers of phytophagous insects from August to November were largely because of acridid grasshoppers, although the family Miridae (Hemiptera) was also very common in August, and vespid wasps became abundant in November. These vespids appeared to be feeding on extrafloral nectaries on scrub oak. (Vespids were arbitrarily put into both the predator and phytophagous groups since they feed their young on animal material, whereas adults feed on various plant material. Extremely few vespids were observed visiting flowers, however.) Again, in 1978, the phytophagous insect fauna was quite varied. Most abundant in midsummer were chrysomelid beetles and acridid grasshoppers. The peak in September was caused mostly by anthomyiid flies, vespid wasps, and acridid grasshoppers. These grasshoppers were scarce in 1979, however. The peak in June and July of that year was largely the consequence of large numbers of chrysomelid beetles and butterflies in the families Nymphalidae and Lycaenidae. (Butterflies were put into both the pollen-nectar feeding group because of adult habits, and the "other" phytophagous group because of larval habits.) Vespid wasps were common in September. Phytophagous ants were more common in 1978 than in the two previous years and became still more abundant in 1979.

Overall, there may be certain structural characteristics that one can discern in the early development of trophic groups within the chaparral insect community after fire. In general, parasitic forms are scarce except for bombyliid flies, whose members may be more interested at this stage of floral development in gathering nectar than parasitizing bee nests. Parasitic hymenopterans are extremely scarce at first, but become more numerous by the fourth postfire year. Biting flies (e.g., Tabanidae, Hippoboscidae) that are reported to be fairly common in mature chaparral are very scarce after fire. Predatory insects are much more abundant and active than parasitic forms. This observation reinforces the hypothesis that predators are more *r*-selected than parasites and, therefore, naturally tend to be more abundant and important immediately after a habitat disturbance. Flower visitors are mostly bombyliid flies and bees of various families. They appear in numbers that match the profuseness of blooming and probably migrate into burn areas to take advantage of the nectar and pollen provided by the "fire annuals" especially. The nonflower visiting phytophagous insects may be greatly influenced by year to year weather changes. Aphids may explode in numbers

during a warm, dry spring; acridid grasshoppers are perhaps abundant following a dry winter and spring. More data are needed before any of the above observations can be verified.

Biomass

Figure 2 shows the relationship of insect biomass (below) to rainfall (above) at the project site in the San Dimas Experimental Forest for the 4-postfire years, 1976-1979. Biomass is shown as dry weight of the total insects collected and/or observed per man/hour each month; these weights were estimated from the weight of a representative sample of each variety of insect. The rainfall data (centimeters/month) were taken from Forest Service records gathered at Tanbark Flat near the project site.

The 1976 peak in biomass occurred in May when sampling was first initiated. An average of about half of the total insect biomass during the months of May through September was composed of hymenopterans--especially the families Apidae and Anthophoridae. Nearly a quarter of the total biomass in May was comprised of bombyliid flies. These figures, along with the trophic group statistics given earlier, indicate the dominance of flower visitors during the spring and summer months of the first postfire year. Almost the entire bloom consisted of annual plants, which apparently enticed these flower visitors into the burn with their reward of nectar and pollen. By the last three months of 1976, acridid grasshoppers made up the greater part of the biomass and continued to comprise most of the biomass through the early months of 1977, augmented by coccinellid beetles in March. The broken peak from March through June of 1977 is the estimated contribution to biomass made by a massive buildup of aphids on Lupinus. These insects were neither counted nor weighed, but I estimate their weight easily doubled the total biomass of other insects during these months. The 1977 biomass peak in August and September was due largely to acridid grasshoppers, although anthophorid bees and a variety of Lepidoptera contributed significantly in August to the total. Acridids and vespid wasps contributed the main biomass from September through November.

There is a slightly bimodal biomass peak in 1978 and a very definite one in 1979. However, the insects contributing the main biomass in the two years are somewhat different. In 1978 the June-July peak was because of nymphalid butterflies and bumble bees, and the August-September-October high was mainly vespid wasps and acridid grasshoppers. The 1979 May-June peak was caused partially by nymphalid butterflies again, and also a mixture of Hymenoptera, particularly anthophorid bees. The well-differentiated September peak was comprised of vespid wasps, honey bees, and syrphid flies. Surprisingly, acridid grasshoppers were a very small part of the biomass the second half of 1979 from July until the end of the year.

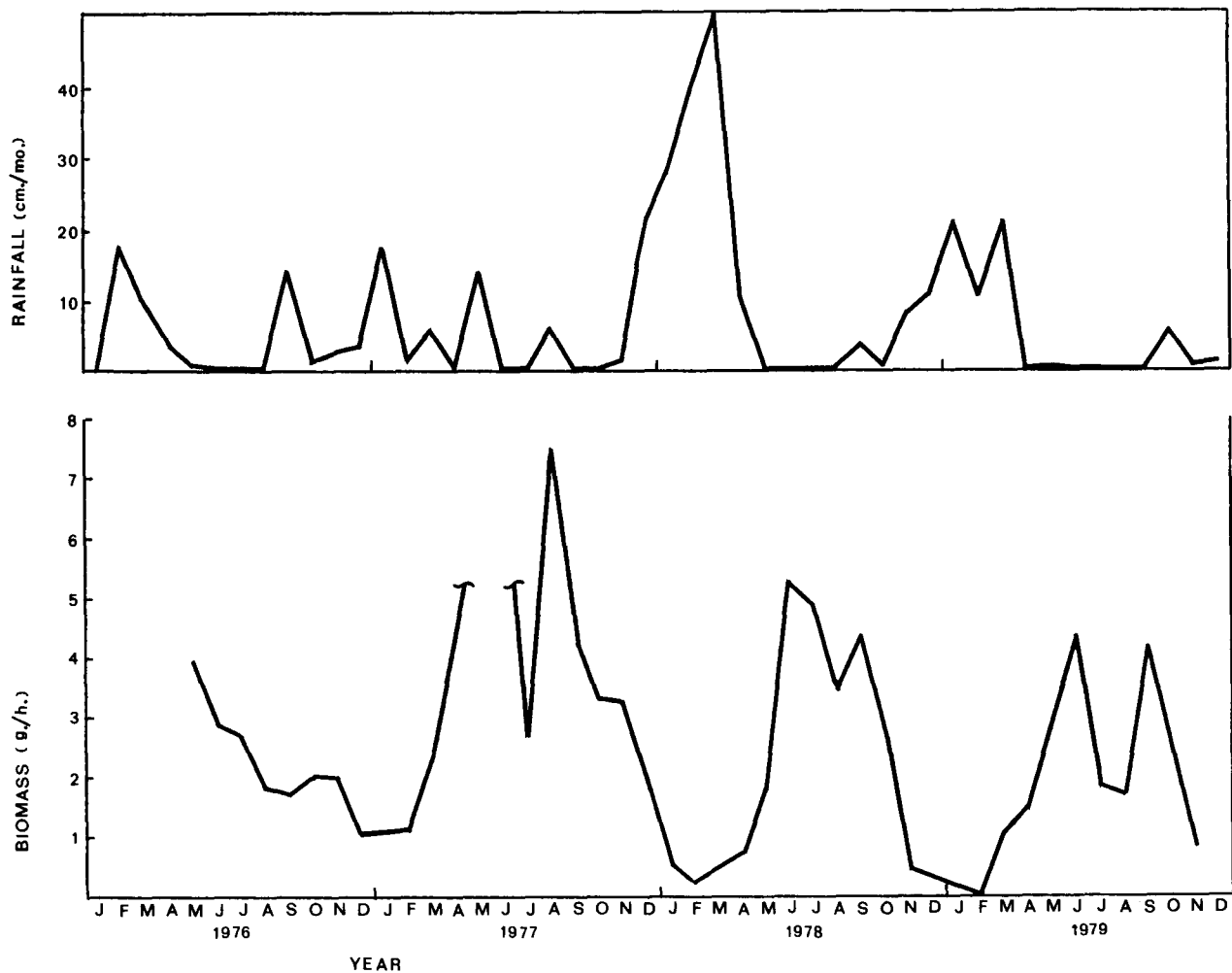


Figure 2--Seasonal distribution of rainfall and insect biomass during 4 years of postfire chaparral succession in the San Dimas Experimental Forest. The biomass data are shown as dry weight of the total insects collected and/or observed per man/hour each month.

A comparison of insect biomass found by Atkins (1977) in San Diego County with that at San Dimas indicates certain differences. Of course, the sites and conditions were also quite different. Atkins' location (Echo Valley) is considerably south of San Dimas, and at a lower elevation than the San Dimas research site. His sampling was done in mature rather than postfire chaparral, his sampling methods were completely different, and he sampled for only one year (1973). The Echo Valley biomass peaks at a much earlier date (March-April) in 1973 than any year at San Dimas (June-July), a difference that would probably be expected because of latitudinal and altitudinal differences. Additionally, the "fall" biomass (September-October) appears to be proportionally much lower at Echo Valley than at San Dimas.

The effect of weather on chaparral insects is still to be determined. A search for correlations between rainfall and biomass in figure 2 is largely enigmatic. (Temperature data were not available for the immediate research area.) The winter of 1976-77 was comparatively dry with rather warm temperatures. Whether this weather had anything to do with the mass buildup of aphids and grasshoppers that ensued during 1977 is uncertain. The winters of 1977-78 and 1978-79 were quite different in the amount of rain that fell, and yet there appeared to be no great difference in the total biomass pattern, although the insects comprising the larger part of the biomass were rather different each year. Further analysis of the effects of weather on chaparral insects will have to await additional data from other studies.

Richness, Diversity, and Abundance

I have reported elsewhere (Force 1981a,b) richness and diversity changes in plants and insects, and abundance changes in insects only, for the first 3 postfire years (1976-78) at the San Dimas study site. Richness was reported as number of insect families and plant species, diversity as

Simpson's Diversity Index, $\underline{D} = \frac{1}{\sum p_i^2}$ (Simpson

1949), using insect families and plant species, and abundance as average number of insects observed per unit of time. A general decline in all categories was observed over the 3-year period, and it was noted that the successional trends of insects appeared to parallel those of chaparral plants. It was also noted that declining trends in these kinds of statistics are unusual in successional sequences; usually richness, diversity, and abundance increase during the early years after a disturbance. Also discussed in those papers were the following hypotheses: (1) that the comparatively high richness and abundances of insects in a chaparral area the first year following a burn are due to immigration from outside sources, (2) that the size of the burn influences the magnitude of these numbers because of the variable dilution factor involved, (3) that the decreasing trends shown in my data could be temporary, and (4) that various kinds of weather may influence trends of this sort.

For comparative purposes, table 1 gives the same statistics as reported in earlier papers (Force 1981a,b) for the first 3 postfire years (1976-78), but also incorporates recently analyzed data for the fourth year (1979). It is obvious from table 1 that the overall decreasing trends seen the first 3 years are dramatically broken the fourth year. Insect family richness rises even higher than during the first postfire year, which presumably means that by the fourth year additional slow-to-colonize insect families were finding their way into the burn. Insect diversity also makes a large gain partly because of the increase in richness, but mostly because of the more balanced numbers of individuals among the various families. There were no disproportionate number increases among any of the insects in 1979, and this more equitable distribution greatly influenced the calculation of diversity. Average insect abundance, on the other hand, was no different in 1979 from the preceding 2 years and was only slightly less than in 1976. In fact, it is surprising that abundance changed so little in the course of the 4-year study. Abundance was greatest the first postfire year with the large influx of opportunistic feeders that apparently migrated into the burn to take advantage of the annual plant bloom.

The most surprising observations from the 1979 data are the increases from 1978 in plant richness and diversity. These statistics would be expected to decline with the continued disappearance of annual plant species as succession proceeds. However the small difference in plant richness could

easily have been sample error, and most of the gain in diversity was, as in the case of the insects, because of more equitable distribution of individuals among plant species. Several questions immediately come to mind at this juncture. (1) The insect data appear to parallel the plant data throughout the study; i.e., insect richness and diversity rise or fall in correlation with plant data. The question is whether this correlation was cause and effect or merely coincidental.

(2) Does the abrupt switch in direction of statistics the fourth year indicate that the decline in richness and diversity were temporary and that, henceforth, increases would prevail? This condition would tend to agree better with conventional theories of succession and would perhaps explain Moldenke's (1977) finding of higher insect pollinator richness and abundance in mature chaparral than in postfire chaparral (see Force 1981a,b).

(3) Do weather conditions have any deciding influence on chaparral successional events? None of these questions can be answered without additional studies in chaparral burn situations.

Table 1--Richness, diversity, and abundance indices for insects and plants in southern California chaparral the first three years following fire

	1976	1977	1978	1979
Insect family richness ¹	85	72	82	90
Insect family diversity ²	13.3	10.9	9.1	16.0
Plant species richness ¹	29	26	23	26
Plant species diversity ²	7.6	2.4	6.0	9.5
Insect abundance ³	90.0	80.2	77.9	80.6

¹Total no. of insect families; plant species.

²Calculated from $\underline{D} = \frac{1}{\sum p_i^2}$ (Simpson 1949).

³Avg. no. insects collected/observed per man/hr.

WHAT NEEDS TO BE DONE

Research on chaparral insects is still in its infancy. Because of the attributes of chaparral (e.g., pulse stable perturbation by fire, unique plant recovery characteristics), there are undoubtedly new and bizarre phenomena to be discovered about how insects deal with it. At present, however, we do not know even such basic things as what insects are there in what numbers at what times. After we have these answers, perhaps it will be easier to determine why the insects are where they are and what they are doing there. More exploratory questions concern (1) the amount of movement of insects from outside sources into new burns of various sizes, (2) what factors (floral or otherwise) are responsible for this immigration into burns, (3) whether the trends I have found in insect richness, diversity, and abundance during one postfire succession are commonplace, (4) whether insect feeding and pollination significantly affect chaparral postburn succession, (5) whether floral or vegetational characteristics significantly affect insect succession in chaparral, and (6) what effect weather perturbations have on insect populations and insect community structure in chaparral.

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LITERATURE CITED

- Atkins, Michael D. Insect biomass and diversity. *In*: Thrower, Norman J.W.; Bradbury, David E., eds. *Chile-California Mediterranean scrub atlas*. Stroudsburg, Pennsylvania; Dowden, Hutchinson and Ross, Inc.; 1977; 180-183.
- Force, Don C. Postfire insect succession in southern California chaparral. *Am. Nat.*; 1981a; 117:575-582.
- Force, Don C. Ecology of insects in California chaparral. *In*: Symposium on the classification and distribution of California chaparral ecosystems. Sixtieth annual meeting of the Western Soc. of Naturalists; 1979; December 28; Pomona, Calif.: USDA, Forest Service; 1981b in prep.
- Moldenke, Andrew R. California pollination ecology and vegetation types. *Phytologia*; 1976; 34:305-361.
- Moldenke, Andrew R. Insect-plant relations. *In*: Thrower, Norman J.W.; Bradbury, David E., eds. *Chile-California Mediterranean scrub atlas*. Stroudsburg, Pennsylvania; Dowden, Hutchinson and Ross, Inc.; 1977; 199-217.
- Mooney, Harold A.; Parsons, David J. Structure and function of the California chaparral--an example from San Dimas. *In*: di Castri, F.; Mooney, Harold A., eds. *Mediterranean-type ecosystems: origin and structure*. New York; Springer-Verlag; 1973; 83-112.
- Simpson, E. H. Measurement of diversity. *Nature*; 1949; 163:688.