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POSTFIRE INSECT SUCCESSION IN SOUTHERN CALIFORNIA CHAPARRAL

There is a renewed interest in ecological succession within natural communities. It is curious how problems like this are all but forgotten—perhaps even considered solved—only to emerge again when someone questions the validity of the entire concept. For a time most ecologists were convinced that succession was the orderly progression of developmental stages in a community beginning with a very pristine, simple, perhaps harsh situation with few or no organisms. Development was thought to proceed, step by step, to a final stage called the "climax," where certain species dominated, and which was more complex (contained more species) and less physically rigorous than earlier stages, more organized, permanent, and stable. These successional changes appeared to be directional and predictable.

Recently Drury and Nisbet (1973), Colinvaux (1973), Horn (1974, 1976), Connell and Slatyer (1977), and others have made an effort to clarify this classical, stereotyped image of community development. Horn (1976), especially, has attempted to analyze succession from available data (most of which involves temperate-climate plants), and suggests that (1) the process of succession shows a variety of patterns; (2) succession occurs because of adaptations of individuals or populations within a community, and not because of any intrinsic properties that communities themselves may have; (3) the concept of the establishment or reestablishment of convergent, stable communities as a matter of course in nature is more often than not illusory. Concerning secondary succession, Horn (1974) concludes that (1) no single theory of the process fits all cases; (2) the pattern of species replacement appears to follow the r-selected (early) to K-selected (late) sequence; (3) as succession progresses productivity tends to decline, diversity increases for a time but must eventually decrease again, and stability depends upon how one defines the term. It appears, then, that the "new" succession may have certain directional characteristics, but that it is certainly not as predictable as once envisioned.

Postfire succession of plants in California chaparral has been studied by a number of authors (Horton and Kraebel 1955; Sweeney 1956; Patric and Hanes 1964; Hanes and Jones 1967; Hanes 1971; Vogl and Schorr 1972; Biswell 1974; Keeley 1977; Keeley and Zedler 1978). Most of these studies have dealt with shrub species only, but several have involved the herbaceous element as well. Although Hanes (1971) commented on the unusual qualities of postfire succession in the shrub component of chaparral, the fact that the total flora (both shrubs and herbs) exhibits unusual replacement characteristics has largely been ignored, especially in literature pertaining to succession as a process. Fires in California chaparral appear to conform with what Horn (1976) refers to as regular devastation-type disturbances. Horn explains, "this schedule gives a competitive advantage to early successional species whose lifespans match the intervals between catastrophes" (p. 199). This description fits the shrublike flora in this type

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of chaparral completely. These shrubs reappear quickly either from undamaged underground parts of burned plants or from seeds, and eventually form most of the flora until the next fire. More interesting, perhaps, is the "fire-type" herbaceous flora that appears profusely the first spring after a fire and often for a very few years thereafter. This particular flora is thought to be confined exclusively to chaparral found in California (Mooney and Parsons 1973; Cody and Mooney 1978). Horton and Kraebel (1955), Vogl and Schorr (1972), and Keeley (1977) have studied this flora at several locations in southern California, whereas Sweeney (1956) collected data from northern California. Including both the herbaceous and shrubby flora, all found a very large number of plant species appearing the first year after fire. Their findings point out a type of floral succession that is rather uncommon but is prevalent in California chaparral and certain other Mediterranean-climate, sclerophyll scrub floras (Specht et al. 1958; Russell and Parsons 1978); that is, a very high species richness (number of species) and possibly diversity (index of richness and relative abundance) as well is attained immediately after fire disturbance, instead of the poverty of species normally found in a postdisturbance situation. Moreover, plant richness begins to decline very early (as early as the second year after a fire) and continues to decline instead of increasing to some later maximum, as appears to be the almost universal rule in succession, and as exemplified recently by postfire studies in other kinds of vegetation by Shafi and Yarranton (1973) and Smith and James (1978).

This unique successional character raises some questions and presents several intriguing implications concerning other organisms living within the California chaparral system. For example, if floral richness and diversity follow a declining pattern after a disturbance, would one also expect the insects, which are closely dependent upon plants for resources to display the same pattern? And if the insects do indeed show this pattern, then what about the chaparral birds and perhaps other animals, many of which are dependent upon insects for food?

Animal succession in chaparral burn areas is less well known than that of plants, and therefore more difficult to describe and analyze. Practically nothing is known about insect succession after a chaparral burn. This paper describes the findings from the first 3 yr of a postfire study of insect succession in a southern California chaparral area, especially those gross changes in insects that have occurred annually in relation to the plant changes. The ecological and evolutionary processes that must have led to this particular successional system are discussed.

PROCEDURES

This study was located in the San Dimas Experimental Forest, a U.S. Forest Service research area in the south-central San Gabriel Mountains of southern California, approximately 45 km east of Los Angeles. The characteristics of this area have been thoroughly discussed by Mooney and Parsons (1973). Briefly, the area is of steep topography and is dominated by evergreen sclerophyll scrub or chaparral. The study site itself was located in the forest's northeastern part, which burned November 26, 1975. Insect and plant sampling was undertaken along and adjacent to an approximately 1.5-km section of unmaintained contour trail at an elevation of 1,250 m. This trail winds and turns to such an extent that nearly every directional exposure is provided by the slopes lying adjacent to the trail. Insect sampling followed two methods. One method consisted of timed (usually 2–4 h) excursions along the trail several times monthly during the warmer seasons and at least once a month during the winter. Sweep net samples were taken along both sides of the trail during these excursions for permanent collections, and counts were tallied of insects (particularly insect families) observed but not collected. The other method utilized 10 plots (10 m × 10 m each) situated along the trail at various directional exposures. These plots were sampled once a year (early summer) by dividing each plot into 100 1-m square quadrats of which 20% were sampled randomly. Each quadrat sampled was carefully observed for numbers and families of insects. Those insects beneath the soil surface were ignored.

Plant sampling was done only during the height of the growing season (early summer at this elevation) and was less detailed than the insect sampling procedures. Ten 7.6-m line intercepts were placed at intervals parallel to and above the trail, making sure that various directional exposures were included. The numbers and species of both shrubby and herbaceous plants intercepting each line were recorded. Also the numbers and species of plants were recorded from each quadrat observed during the plot sampling of insects described above.

RESULTS

The findings are reported in three ways: (1) the richness or number of taxonomic categories of insects and plants observed; (2) the diversity (richness and relative abundances) of taxonomic categories of insects and plants observed using Simpson's index, $D = 1/\Sigma p_i^2$ (Simpson 1949); and (3) the average number of individual insects observed per unit time. The insects were analyzed according to their respective family taxa because of the intractability of making species or even genus identifications from observations of insects in the field. The plants, however, were identified to species (Graminae excluded). Table 1 gives the richness and diversity indices for both insects and plants, and the abundance (all families) index for insects only, for each year of the 3-yr period of study. Since the sweep net collections and field observation tallies were timed procedures, all of the insect data, before being analyzed, were transformed into numbers of individual insects collected or observed by insect family per observer or collector hour. The plant data were analyzed on the basis of actual numbers of species and individuals observed in the sample.

Richness and diversity for both insects and plants were highest the first year (1976) after fire (table 1). There was a moderate decline in insect richness and diversity and in plant richness the second year (1977); however, plant diversity dropped precipitously. This low plant diversity index was caused by the unevenness in abundances of the various species rather than a significant lowering of species numbers. The third year (1978) indicates another moderate decline in plant richness and insect diversity; however, both plant diversity and insect richness increased above the level of the second year, although not to the level of the first

TABLE 1

RICHNESS, DIVERSITY, AND ABUNDANCE INDICES FOR INSECTS AND PLANTS IN SOUTHERN CALIFORNIA CHAPARRAL THE FIRST THREE YEARS AFTER A FIRE

	1976	1977	1978
Insect family richness*	85	72	82
Insect family diversity†	13.3	10.9	9.1
Plant species richness*	29	26	23
Plant species diversity†	7.6	2.4	6.0
Insect abundance‡	90.0	80.2	77.9

*Total no. of insect families; plant species.

† Calculated from $D = 1/\Sigma p_i^2$ (Simpson 1949).

‡ Average no. insects collected/observed per man h.

year. This higher level of plant diversity in 1978 was the result of a much more even distribution of species abundance than was observed the second year, and may have been related to a much higher rainfall in 1978 than in 1977 (Keeley 1977). The higher level of insect richness may have been also directly weather related, although it is possible that insect richness was simply tracking changes in plant diversity. The average number of insects collected and observed per man hour declined slightly each year.

DISCUSSION

Although 3 yr may be a short period of time to observe successional trends, it appears from this study that the early successional statistics of chaparral insects tend to parallel those of chaparral plants. There is an overall declining trend in richness, diversity, and abundance of both kinds of organisms during the early years of postfire succession. Or, if one prefers to be skeptical concerning the reality of certain of these trends, at the very least one has to concede that there is no apparent tendency for any of these statistics to increase as would normally be expected from the classical concept of succession. Of course, these data apply to only one postfire successional sequence, and therefore need to be supported with additional cases. Elevated trends in plant richness after chaparral burns have been reported for many years, although diversity indices have not been calculated. As long ago as 1891, Brandegee noted the abundance and variety of annual plants in Marin County, California, the first spring after a burn. Now generally called "fire annuals," this flora was at first thought to develop in the disturbed area because of a lack of competition (Daubenmire 1947; Went et al. 1952). The implication was that this flora moved quickly into the burn from the surrounding undisturbed area. Sweeney (1956) showed conclusively that this interpretation was incorrect and that these plants actually germinate from seeds produced by the fire annuals which were prevalent following the preceding fire. The seeds of these plants may lie dormant in the soil for many years and do not germinate until exposed to the heat of fire. These annual plants have evolved a system whereby they are dependent upon fire for their survival. Moreover, the seeds must wait relatively long periods of time between fires from one reproductive period to the next. Vogl and Schorr (1972) estimated that fires occur only once or twice a century in southern California's "higher" chaparral (their study was located at 1,219 m), somewhat more often at lower elevations. Perhaps fires were more frequent in chaparral before the advent of modern man and his fire suppression policies, although Byrne et al. (1977) and Zedler (1977) conclude that chaparral fires may have been less frequent before modern times.

Since plant richness and diversity are high after a chaparral fire, it follows that insect richness and diversity are also high. A large food resource potential is available for plant sap- and foliage-feeding insects, as well as for nectar and pollen feeders. This is a situation that great numbers and kinds of opportunist insects can use to their advantage. Perhaps the most surprising aspect of the phenomenon is the suddenness with which these large numbers and diversities of insects appear the first spring after a fire; it seems almost as if they too (like the seeds of the annual plants) had been lying dormant in the ground since the preceding fire, but nothing like this condition has ever been observed. Of course, many ground-inhabiting insects do apparently survive chaparral fires. Soil samples taken from this study site 3 mo after the 1975 fire revealed live Collembola, Diplura, and other nonflying arthropods that clearly could not have moved in from surrounding unburned areas so quickly. This particular fire was in November; many insects were undoubtedly in diapause by this time and those diapausing in the ground may have survived. Sweeney (1956) demonstrated the high heat insulating properties of soil, and probably most insects can survive temperatures at a very few centimeters below the soil surface during a chaparral fire. However, large numbers of insects that are present the first year after fire appear to migrate into burns from the surrounding area—not only from surrounding chaparral but from other kinds of flora as well. A number of years ago, Paul D. Hurd, Jr., of the National Museum of Natural History made observations of flight distances of ground-nesting bees (personal communication). He found that marked bees were flying into chaparral from distances of nearly 5 km. The study site of the project reported here was approximately 2 km from the closest perimeter of the burn—well within the migrating range of bees and many other insects—and there were several small "islands" of various kinds of unburned flora even closer. Because insect successional data are scarce, the rapid movement of large numbers of insects into disturbed areas (setting up high initial densities, richness, and diversities) may be more common than presently realized. Hawkins (1980) studied the reestablishment of insects in a strip-mined area during the first five postmining years. He found that although no trends were evident for the plants, the insects showed declining abundance, richness, and diversity as the pioneer plants were replaced. He felt, however, that these trends might be temporary.

It may be assumed that migration of insects into a burn must dilute the insect density in the surrounding unburned areas. But it is also probably safe to speculate that larger burns have fewer insects migrating inward per area burned than smaller ones, simply because of the longer distances and the much greater dilution factor that would be involved. Perhaps this partly explains why Moldenke (1977) found a somewhat different postfire situation in San Diego County than I did at San Dimas. Moldenke, reporting on pollinators only, presents data indicating much lower ratios of insect numbers in burned chaparral than in unburned (1:4), and also a somewhat lower species richness in burned (254) compared to unburned (309). From his findings one might expect an increasing trend in abundance and richness as succession proceeds; my own data indicate a decreasing trend, at least early in the process. But the burned area Moldenke sampled was 70,000 ha in extent, whereas the San Dimas burn covered 8,000 ha. Moldenke's nearest unburned source area was 7 km distant and mine was 2 km. So it is possible that the statistics reported by both Moldenke and myself from postburn situations were influenced by the size of the burn and the distance from sources. Another possibility is that the decreasing trends shown by my own data are only temporary, and that these statistics begin increasing later in succession as, for example, more parasitic insects (which were extremely scarce the first 3 yr) move in and food web complexity increases. A still unresolved problem is the effect the weather may have had on our two sets of data, since they were collected in different years. Keeley (1977) has found that precipitation greatly affects postfire flora in chaparral areas, which in turn would be expected to affect the insect fauna. Clearly, a long-term study (in planning) involving several postfire situations is required to resolve these problems.

Much data from vertebrate animal studies reinforce the general picture of either declining diversity, richness, and abundance, or of no overall change in these numbers as postfire succession proceeds. Lawrence (1966), for example, found no significant change in total bird numbers before and after a controlled burn, although species composition shifted in response to greater availability of insects and seeds after the burn. Wirtz (1977) reported a higher breeding bird diversity and greater numbers of individuals in 1-yr-old (postburn) chaparral than in 17-yr-old, although species numbers did not change. He found no significant change in rodent diversity in the same study. Lillywhite (1977), comparing chaparral and grassland habitats, reported lizard abundance and rodent species diversity were highest in chaparral opened by fire. Quinn (1980), however, provides evidence for increasing richness and abundance of rodents the first 5 yr postfire.

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