Recovery of Lepidoptera (Moths and Butterflies) Following a Wildfire at Inverness Ridge in Central Coastal California

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Abstract

In numbers of species, Lepidoptera (butterflies and moths) make up the largest group of plant-feeding animals in North America. Caterpillars of nearly all species feed on plants, and most of them are specialists on one or a few kinds of plants. Therefore they are liable to be severely affected by wildfires, and secondarily, their parasites and predators, including birds, bats, lizards, and rodents suffer losses of a major food resource. In October 1995, a wildfire swept over part of Point Reyes National Seashore, burning more than 12,300 acres (5,000 hectares) of public and private land, following a fire-free period of several decades. I tracked survival and recolonization by moths and butterflies during the subsequent five seasons. I made daytime searches for adults and caterpillars approximately monthly from March through October and collected blacklight trap samples, mostly in May and September-October. More than 600 species of Lepidoptera have been recorded in the Inverness Ridge area, and about 375 of them were recorded during the post-fire survey, including larvae of 31% of them. Plants in a Bishop pine forest higher on the ridge, where the fire was most intense, accumulated their caterpillar faunas slowly, while Lepidoptera feeding on plants typical of riparian woods in the lower canyons reestablished sooner and more completely. Recolonization varied markedly among different plant species,

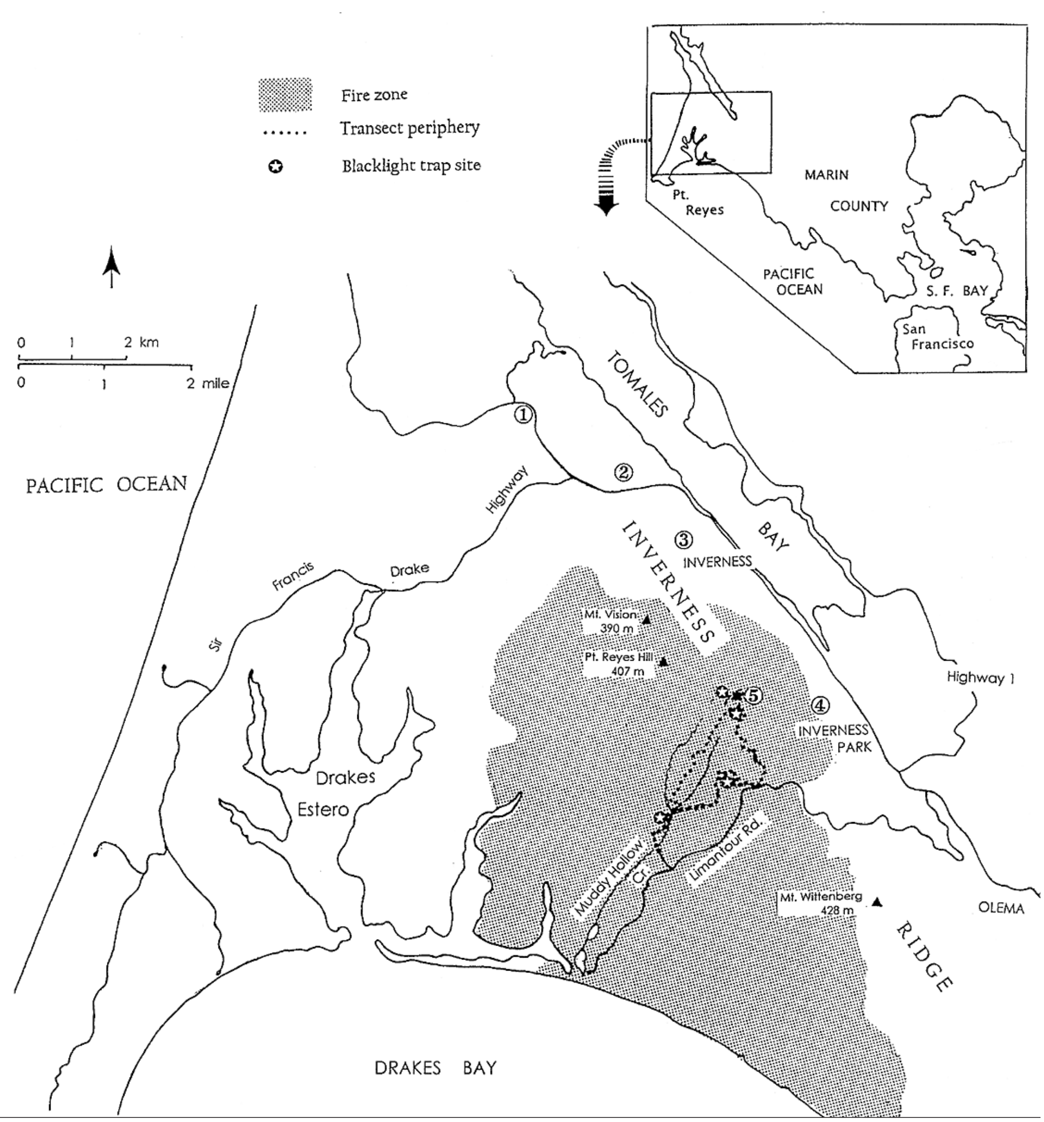


Fig. 1
Map of Inverness Ridge and lower Tomales Bay, 30 miles northwest of San Francisco. Shaded area depicts the extent of the October 1995 fire, which burned 12,300 acres along the crest and southwest slopes of the ridge in Pt. Reyes National Seashore and into private land in Inverness Park. Historical and recent sites of Lepidoptera inventory are indicated by circled numbers:

1) Pierce Pt. Road, 3 miles west of Inverness (Bauer and Buckett, 1940s -1965;

2) Sea Haven district (Powell, 1994-95);

3) Inverness (Bauer & Buckett, 1940s-50s; Patterson, 1950s-present; Toschi, 1950s- 1963; Powell 2000);

4) Inverness Park (O'Brien, 1959-61, Powell 1995-99);

5) Summit area at terminus of Drakes View Rd. (U.C. Berkeley Field Entomology classes, 1970-82).

in marked contrast to generalizations about effects of fire on arthropods derived from fire management of grasslands.

Introduction

A wildfire in early October 1995, at the end of California's long dry season, burned an extensive portion of Inverness Ridge, from Mt. Vision eastward into private land, where more than 40 homes were destroyed the first day, then southward to Drakes Bay (Fig. 1). Its effects were most dramatic higher on the ridge, where the pine forest and its understory vegetation were destroyed, and ground litter was burned to bare soil. The fire was less intense down slope, where vegetation in chaparral and grassland burned, but most plants were not killed, diminishing to an understory fire in the canyons, where alder- and willow-dominated riparian woods partially survived.

There is a wealth of literature on effects of fire on insects and spiders, but most studies deal with managed fires in prairie and other grasslands habitats where rotational plots can be compared — that is, they assess communities of insects that are fire-tolerant and persist where periodic burning has been practiced. Most have involved short term monitoring, i. e., a few months or a year, and often the insects have been recorded by biomass or order and family level taxa, not species. No study has comprehensively assessed Lepidoptera, the major group of plant feeding insects, recording species of all kinds, from tiny leaf miners to large moths and butterflies, and none has attempted to correlate colonization by larval host plants. I proposed a 3-year study to document the recovery of all Lepidoptera and their hosts and extended it to 5 seasons.

Background

The fire history on Inverness Ridge is not documented in detail. There had been no fires in the area I monitored for 30 years prior to 1995, after ownership of the land shifted from private ranchers to the National Park Service. Earlier records are fragmentary. Large fires occurred in the area in the 1880's and 1927, and ranchers routinely used fire management to suppress brush in grazed grasslands (Sugnet 1985, based on newspaper articles and other sources). Robert Ornduff estimated Bishop pines killed in the 1995 fire to be 30-45 years old, from counts of tree rings in stumps on private land (Ornduff and Norris 1997). However, there was a mature pine forest in 1970, when I first visited and photographed that area, indicating no major fire for at least 25-30 years before that time. Probably the Bishop pine community was at least 50 to 68 years old (dating to the 1927 fire). The chaparral community and grassland of the lower slopes and riparian woods along Muddy Hollow Creek were fire free for 30 years or more, in a mosaic pattern.

There was no comprehensive baseline inventory of the moths and butterflies that lived in the Pt. Reyes National Seashore. Pre-fire insect survey of the ridge top and seaward slopes of Inverness Ridge that burned was limited to that conducted during annual 2-day visits by a field entomology class from the University of California, Berkeley, in late April or May during the 1970s, in the area of the western terminus of Drakes View Road. Hence, a post-fire census of species could not be compared directly to a pre-fire community, and I tracked recolonization of selected plants, especially woody shrubs and trees, which harbor the richest communities of Lepidoptera.

Methods

Inventory of insects presents several problems: most species are present in life cycle stages that are easily sampled for only short seasonal periods; many populations undergo enormous fluctuations in individual numbers so may be overlooked or considered rare in a given year; and the success of most sampling methods is dependent upon insect activity and therefore local weather, especially temperature. Predicting weather conditions at Pt. Reyes is inexact, so sampling consistently in ideal conditions was not possible. Strong, cold onshore winds are prevalent, with coastal fog persisting unpredictably on the seaward, burned side of the ridge, especially in spring and summer. Warm conditions in the region, even at Inverness on the east side of Inverness Ridge, often give way to cold, blowing fog on the ridge top and west slope.

Area sampled

The area selected is defined on the west side by the Drakes View trail, on the south by Bayview trail from Inverness Ridge trail to Muddy Hollow Road, and to the east along Inverness Ridge trail from Limantour Road to Drakes View Road, a perimeter distance of about 6 miles (9.6 km) (Fig. 1). The triangulate plot thus defined provides a transect from the more severely burned pine forest at 1,000 ft. (300 m) elevation on the ridge top, descending through chaparral and grassland, to riparian gallery forests along Muddy Hollow Creek at 100 ft.

(30 m). Most of the sampling after two years following the fire was done along the perimeter trails, because much of the area became impenetrable thickets of dense vegetation growing over fallen trees, dominated by pine, blue blossom, blackberry, and poison oak on the ridges, and nettle and blackberry in the canyons. By years 4 and 5 some chaparral and canyon areas became more accessible, with willow saplings or shrubs replacing the dense low thickets, but on the ridges incredibly dense stands of young pine, often 12-18 trees per square m, which had grown to 4-4.5 m (12-14 ft.) high, rendered many areas inaccessible and crowded out more varied post fire vegetation.

Sampling techniques

Monitoring was designed to maximize observations of diversity rather than to monitor single sites or standardized transects. The goal was to record colonists of plant species as vegetation reappeared and grew to stabilized structure, the diversity, occurrence, and succession of which could not be predicted. Observations and collections were made by three approaches: diurnally, either 1) by observing or netting adults, and 2) visual search and beating sheet sampling of selected plants for caterpillars and larval mines or galls; and 3) by nocturnal attraction of adult moths to 8- or 15-watt ultraviolet lights ("blacklight") powered by small rechargeable batteries. Adult butterflies were recorded mostly by sight, adult moths mostly by net or blacklight trap collection. Caterpillars were transported to Berkeley for lab rearing.

Abandoned leaf mines were pressed and dried. If host plant identifications were required, small samples were pressed and submitted to the University of California Herbarium. In general, plant feeding insects occur in greater species richness on woody plants of high architecture, i. e., trees, larger shrubs, then successively fewer on smaller perennials, herbs, and monocots (Lawton 1983), although grasses as a group harbor many Lepidoptera. Our sampling emphasized trees and shrubs, including pine (*Pinus*), alder (*Alnus*), willow (*Salix*), blackberry and thimbleberry (*Rubus*), currant and gooseberry (*Ribes*), coyote brush (*Baccharis*), oak (*Quercus*), madrone (*Arbutus*), manzanita (*Arctostaphylos*), huckleberry (*Vaccinium*), blue blossom (*Ceanothus*), coffeeberry (*Rhamnus*), and poison oak (*Toxicodendron*).

We recorded Lepidoptera on 82 dates from March 14, 1996 to November 1, 2000, during which we made 45 diurnal visits, 263 larval and leaf mine collections, and 54 blacklight samples on 45 dates. Daytime survey, usually of 2.5-6.5 hours, was conducted approximately monthly from mid March to late October, with sporadic additional visits, mostly in May and October. After initial trials, I used four light trap sites at different elevations, situated 0.8-1.2 miles (1.3 to 2.0 km) inside the perimeter of the fire zone, at spots sheltered from sight of unburned areas by intervening hills (Fig. 1). Additionally, in 1999 M. Hart, made six evening visits to collect at light sheets, mostly during January to April, when we had few records. Blacklight samples were initiated one year after the fire and were made in all months except December and June, 75% of them in May or September-October.

Estimating expected species richness

To provide a basis for estimating potential caterpillar guilds of individual plants, I compiled a list of lepidopteran species that had been collected historically and recently on Inverness Ridge, including areas outside the fire. In addition to our collections with entomology students in the 1970s, sporadic collections had been made by amateur collectors and university students from 1940 to present, in and near Inverness (see Acknowledgments and Fig. 1). I sampled moths at lights on about 175 dates between July 1994 and November 2000, mostly in Inverness Park (Fig. 1). In total, there have been moth collections at lights in all months of the year, more extensively in May-October, but there had been few larval collections prior to my post-fire survey. From the collection data, I abstracted lists of Lepidoptera known to be larval host plant specialists of selected plant taxa. As the study progressed I added specialist species that had not been recorded in the Inverness area previously, as well as generalists that were found feeding on each plant in the burn zone, to derive potential lepidopteran communities for each plant. For example, I found larvae of 6 species feeding on nettle (*Urtica*), 4 specialists and 2 generalists, adults of one additional *Urtica* specialist were trapped at blacklight in the fire zone, and another specialist was collected in Inverness Park = total expected guild of 8. Lists of species recorded at Inverness Ridge and their larval host plants are posted on our Essig Museum website (http://essig.berkeley.edu/doc/invernessleps.htm.

Results

In early October most insects are dormant, in mines or larval galleries in plants, or buried in ground litter or soil. Therefore, many species were not affected by temporary loss of larval foods, and some were protected, but where the fire was most intense, as in the pine forest, even ground dwellers were destroyed. As might be expected, few Lepidoptera survived or quickly colonized the fire zone — we found adults or larvae of only 16 species during our first visit in March 1996, five months following the fire. As native vegetation returned, many moths and butterflies reappeared, and numbers of lepidopteran species observed steadily climbed during five seasons (Fig. 2). We recorded 376 species, 33 butterflies, 343 moths (+ ca. 10 species of uncertain taxonomic status), of which we found caterpillars or larval leaf mines of 118 (31%). Among species observed only as adults, 121 are known to be larval host plant specialists (32% of the total), so larval food associations were projected for 63% of the species recorded. These feed on 65 plant taxa. Most of the remainder are generalist plant feeders, fungivores, or detritivores, or their larval habits are unknown.

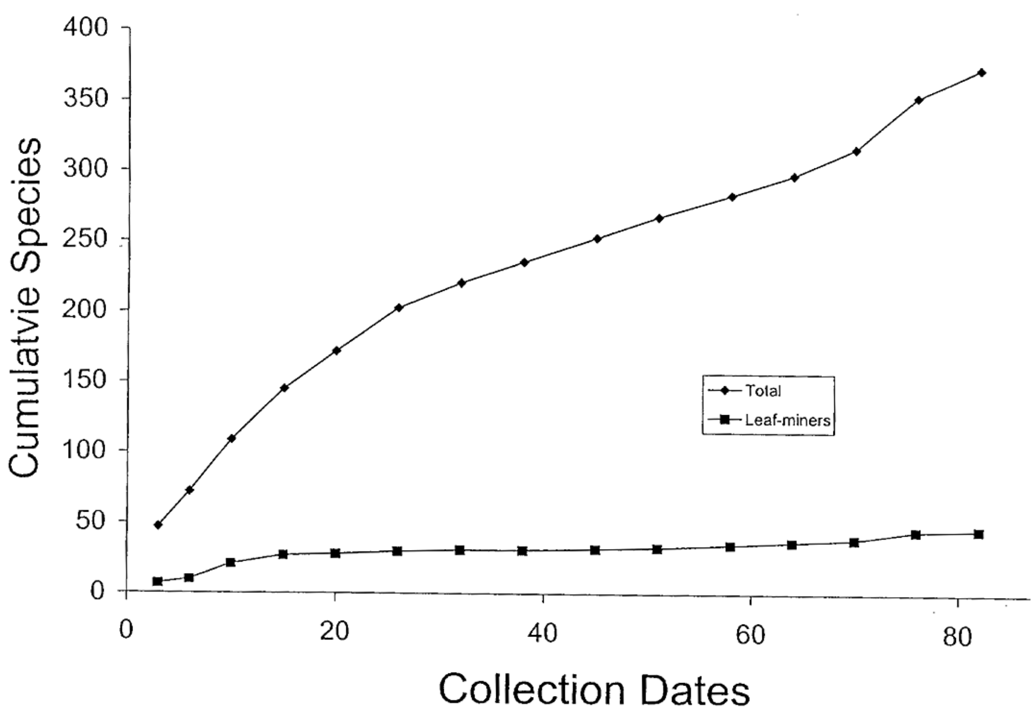
The observed species accumulation was continuous, enhanced by increased blacklight sampling effort in years 4 and 5; 50% of the 5-year total were recorded by May 1998 (24 sampling dates) and 75% by September 1999 (58 dates), nearly four years after the fire (Fig. 2). Butterflies were recorded sooner than moths, 48% by the third survey date, 64% by the end of year 1 (6 dates), and 75% within 18 months following the fire (9 dates) (Fig. 3). Leaf mining and gall causing species, all of which are tiny moths believed to be of limited dispersal tendencies, were recorded at a faster rate than larger, presumably stronger flying moths: 50% by the end of year 2 (20 dates) and 75% by the end of year 3 (38 dates) (Fig. 2).

The species can be grouped in three cohorts: 1) *Transitional species*, those that colonize early vegetational components, then disappear or become rare as plant succession proceeds; 2) *Long term residents*, species that colonize later stage plants, especially woody shrubs and trees; and 3) *Vagrants*, non resident individuals that migrate through or immigrate as temporary residents or casual visitors.

Transitional species

Characteristically in California, herbaceous vegetation appears profusely in the first spring following a fire, diminishing in succeeding years. This flora has been documented by several authors (e.g. Cosy and Mooney 1978, Keeley and Zedler 1978). In chaparral communities the first year post-fire flora attains a higher species richness than normally found in other post-disturbance, such as flooding or landslides. This richness begins to decline by the second year and does not increase to a later maximum, shown by post-fire studies in some other vegetation types (Smith and James 1978). In spring following the fire at Inverness Ridge, there was an impressive flush of new growth, especially herbaceous vegetation, dominated by weedy grasses, vetch (*Vicia*), poison hemlock (*Conium*) and other exotics, as well as cow parsnip (*Heracleum*) and other native plants. This set the stage for opportunistic colonization and abundance of some Lepidoptera

Fig. 2
Species accumulation during 1996-2000 in the fire zone at Inverness Ridge. Upper graph: all Lepidoptera (n=376); lower: leaf-mining species only (n=46)



during the first two or three years, until this community of rapid growth plants was succeeded by the more slowly developing shrubs and trees.

The most spectacular examples of short-lived, fire-adapted plants at Inverness Ridge were several legumes, including a bush lupine and extensive mats of bird's-foot trefoils (*Lotus*) and clovers (*Trifolium*), mixed with broom-rose (*Helianthemum scoparium,* Cistaceae). All of these grew from seeds that evidently had been dormant in the soil for several decades, and in a "Big Bang" kind of reproductive strategy, the legumes flowered for one or two seasons, leaving a replenished seed bank, then disappeared.

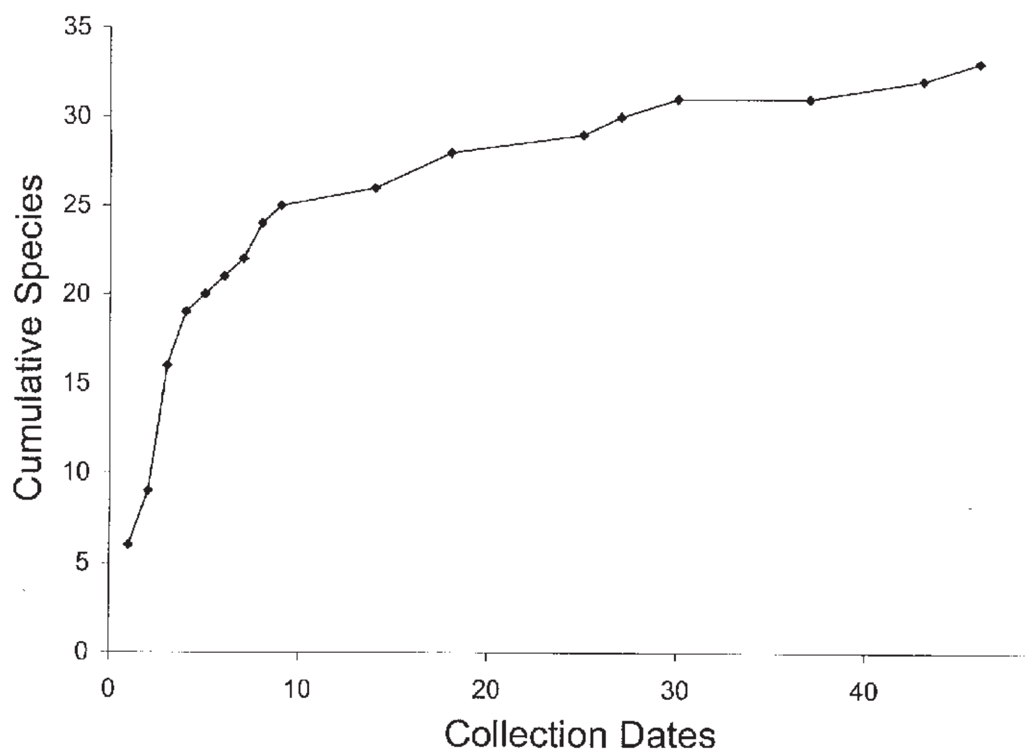
The bush lupine was judged by Ornduff (1998) to be a form of *Lupinus arboreus*, although it differs from nearby beach dune populations of that species in having blue flowers rather than yellow, short inflorescence stems, and by its fire-adapted life history. Although this lupine had been absent or very rare in recent decades (Ornduff & Norris 1997, Ornduff 1998), it appeared in an almost continuous stands in deeper soils of the former pine forest and much of the subtending chaparral slopes, becoming 1-1.5 m (4-5 ft.) high shrubs by the end of the first year, and flowering in unison in the second spring in a tremendous display that painted the hills in vivid blue, after which every plant that set seed died. A few plants or parts of plants that failed to bloom did so in year 3 then died, leaving only scattered new plants, mostly in disturbed spots along the trails.

The legume mats, determined by Ornduff to consist of 5 species of *Lotus* and 2 of *Trifolium*, occupied all the ridge areas characterized by poor soils. *Lotus hiermanni* var. *orbiculatus*, which was judged to be the most abundant species, had not been known in the National Seashore (Fellers et al. 1990). Except for sporadic *L. junceus* in disturbed soil along the paths, all the native *Lotus* disappeared after the second year.

Colonization by Lepidoptera quickly followed. Two species of widespread native butterflies, the orange sulphur (*Colias eurytheme*) and the acmon blue (*Plebejus acmon*), appeared abundantly in association with the *Lotus* by the end of year 1, along with several inconspicuous moth species, all of which declined in numbers as the colonies of *Lotus* were replaced by pine and manzanita thickets in later years (Table 1). *Acmon* persists, dependent upon the introduced *Lotus* corniculatus that grows along the disturbed trail edges. Similarly, nettle (*Urtica*) was abundant in the canyons the first two years following the fire, then declined as it was crowded out by young alders and other riparian growth. Four species of Lepidoptera that feed on nettle were numerous in early years of succession but rare in later years (Table 1).

The most remarkable example of such succession is *Helianthemum* and a tiny black moth of the genus *Mompha*. This plant, which had been listed of doubtful occurrence in the National Seashore (Fellers et al. 1990), formed extensive turf-like patches by the thousands, interspersed

Fig. 3
Accumulation of butterfly species (n= 33) during 1996-2000 in the fire zone at Inverness Ridge.



with *Lotus*, and after five years persisted on decomposed sandstone soils where not supplanted by manzanita and pine. In mid 1997 I began to find the *Mompha* associated with this plant and discovered its larvae feeding in the seeds. I had not seen this moth before, and a specialist has determined it to be an undescribed species. Its populations occurred in enormous numbers, sometimes 300-600 specimens in a single 8-watt blacklight trap, and did not diminish appreciably through year 5. Based on past behavior of *Helianthemum* (Howell 1949) following large fires, in time the plant and its seed predator will become very rare again.

Numerous other lepidopteran species passed through stages of abundance then became rare in later years (Table 1), either because they used weedy early succession plants (e.g. the noctuid moth *Heliothis phloxiphaga*, which is a generalist often feeding in flowers of herbs), or their native plant host was crowded out. For example, the mustard white butterfly, *Pieris napi*, feeding on milk maids, *Cardamine*, which was abundant in year 1, and the butterflies flourished through three or more generations, flying until October, highly unusual for this species. But its habitat changed as dense ground cover replaced the shaded understory of the riparian alder-willow woods, and butterfly numbers declined abruptly to only a few seen in years 4 and 5 (Table 1). In some instances the initial abundance may have resulted from a release from natural parasites and predators that normally regulate insect populations. Later host moths diminished in abundance biotic controls reestablished . Examples include the gracillariid leaf miners, *Caloptilia* and *Phyllonorycter* on *Ribes sanguineum*, and *Epermenia* on cow parsnip (*Heracleum*). Tiny larvae of *Epermenia*, which feed gregariously on undersides of the leaves and create conspicuous skeletonized patches, were already abundant in March 1996, five months after the fire, and remained so for two seasons, then gradually became scarce (Table 1), although the host plant remained abundant.

Long term resident species

Recovery of species believed to be long term residents was tracked by searching selected plant species for larvae. Collection of adults of species known to be host specific on those plant species provided additional evidence of colonization. Plants that support guilds of numerous caterpillar species, emphasized during this survey, are grouped as characteristic of three communities: *Riparian*, *Chaparral*, and *Bishop pine forest* (Tables 2-4).

Table 1. Transitional Species — moths (m) and butterflies (b) that were observed multiple times during years 1, 2, or 3 then became rare in years 3-5, 4-5, or 5. Numbers designate number of dates observed; * designates numerous individuals.

	'96	'97	'98	'99	'00
Lotus, *Lupinus* feeders:					
Aristotelia sp. (m)	2	0	1	1	0
Syncopacma sp. (m)	2	5	0	0	2
Epinotia infuscana (m)	-	4	4	1	2
Uresiphita reversalis (m)	-	2	0	0	0
Semiothisa californiata (m)	-	9	6	0	0
Colias eurytheme (b)	5*	8*	5*	0	0
Plebejus acmon (b)	5*	9*	6	7	3
Urtica feeders:					
Anthophila alpinella (m)	2	6*	0	1	0
Hypena californica (m)	2	4	2	3	1
Polygonia satyrus (b)	5	7	3	4	1
Vanessa atalanta (b)	4*	5	7	2	1
Brassicaceae feeders:					
Euchloe ausonides (b)	-	3	1	0	0
Pieris napi (b)	4*	3	2	2	1
Pieris rapae (b)	1	2	5	0	0
Heracleum feeder:					
Epermenia californica (m)	4	3	1	2	1
Generalists:					
Amblyptila pica (m)	2	0	1	0	0
Heliothis phloxiphaga (m)	2	3	0	0	0

The Riparian Community along Muddy Hollow Creek experienced a comprehensive burn, but its intensity was considerably lower than on the ridges and was mosaic in distribution. Hence, there was an understory fire in some areas, with most buckeye (*Aesculus*), bay trees (*Umbellularia*), and some alders surviving, while willows and most low-growing vegetation burned to the ground. The former shaded, riparian corridor mostly disappeared, and a rich mixture of herbaceous vegetation, including stump sprouted willows, alder seedlings, blackberry and other species of *Rubus*, nettle, cow parsnip, and adventive weeds such as poison hemlock flourished.

Regrowth of willow and alder to nearly full stature was much more rapid than for trees and shrubs of the ridges, such as the pine, oak, and manzanita. As a result, many Lepidoptera adapted to canyon plants survived or quickly recolonized (Table 2). Nearly all expected nettle feeders were established by the end of year 1, and species associated with other riparian plants reestablished relatively quickly, 67% of the expected total by year 3, 87% by year 4, and 92% after 5 years (Table 2).

Plants of the intermediate elevation Chaparral Community are mostly shared with the pine or riparian communities (e.g. *Baccharis, Rhamnus, Lotus, Rubus ursinus, Toxicodendron*); Lepidoptera feeding on those that are most characteristic of the dry, open westerly facing slopes are summarized in Table 3. These species were slower to colonize than those on riparian plants. Particularly surprising was the *Baccharis*-feeding guild because coyote brush grew rapidly from stump sprouts and is dominant over large areas, forming a seemingly ideal island for recolonization. Yet none of its numerous Lepidoptera was observed in year 1, and fewer than half the expected total until year 4. One-third of potential grass (*Poaceae*)-feeding species were not recorded. Possibly following 30+ fire- and grazing-free years of brush intrusion the grassland is too limited in size, species richness, or habitat diversity, to support more of the region's grass feeders. Overall, nearly half the expected caterpillar fauna of the chaparral and grassland plants had established by the end of year 3, and 76% after year 5 (Table 3).

Reestablishment was even slower in the Bishop pine community. As noted, much of the formerly forested ridge crest was covered at first by legumes growing from seed banks. Later stage plants are adapted to survive fire in different ways, and most either grew from stump sprouts, e.g., coffeeberry (*Rhamnus*), huckleberry (*Vaccinium*), madrone (*Arbutus*), tanbark oak (*Lithocarpus*), or the mature plants were replaced by fire-adapted seed germination, notably Bishop pine (*Pinus muricata*), and Marin manzanita (*Arctostaphylos virgata*). These require much longer growth periods to reach stages suitable for support of insect populations. For example, *Arctostaphylos* seedlings were not in evidence until late spring 1996, when many other plants already had been colonized by caterpillars, and did not achieve appreciable standing as shrubs until year 3. Coast live oak (*Quercus agrifolia*) survived the fire in another way. Entire trees burned, but the trunks and larger limbs survived, giving rise to epicormic vegetative growth. The new foliage was subject to mildew during the first season, and trees did not develop appreciable canopy foliage until the 2nd or 3rd year. Therefore, reestablishment of the caterpillar guilds of the ridge plants lagged behind that of other communities: only 12% of the expected fauna were recorded in year 1, 47% by year 3, and 61% after 5 years (Table 4).

Vagrants and short-term resident species

Census of Lepidoptera, many of which possess strong dispersal tendencies, inevitably encounters individuals that are not resident in the local area. Transients often are difficult to identify as such because one or a few records may result from migrants or vagrants, or they

Table 2. Post fire recovery of Lepidoptera guilds on Riparian plants: Cumulative larval host plant use, based on larvae, mines, and projected from adults of specialist species.

Year:	1	2	3	4	5	Expected
Alnus	2	7	7	10	10	11+
Salix	5	9	11	14	17	17+
Ribes	0	3	4	5	5	7
Rubus	1	3	4	5	5	5+
Urtica	6	6	6	7	7	5
Heracleum	1	3	3	4	4	4
Total	**15** **27%**				**48** **86%**	**52+**

may be resident species that escape notice because their seasonal activity is primarily restricted to times other than the survey effort, or they may have small populations located away from transects sampled. In general, I regarded all species for which I found larval activity as resident, as well as those seen as adults on multiple dates, and smaller microlepidoptera were assumed to be non-migrant. Larger moths and butterflies recorded only once are suspect vagrants, but those seen only in year 4 or 5 may be new colonists. At least 15 of the 376 species recorded likely were non-resident.

Discussion

Recovery of plant-feeding insect populations following an extensive wildfire is a function of several factors, especially intensity of the fire, its seasonal timing, and the size of the area burned in relation to availability of nearby plant/insect communities that can serve as recolonization sources. If the fire is intense, occurs during a season when many insect species are most vulnerable as adults or larvae, many species likely will be eradicated from the site. If the burn area is sufficiently large to support insect populations that depend on plants that are unique in the region (i.e., no access to colonization sources nearby), the time to recovery may be very long. Conversely, insects may survive in local spots if the fire is variable in intensity and affects the habitats in a mosaic pattern, as is typical of wildfires in diverse topography, and/or it occurs at a season when most insects are dormant (e.g., as pupae on the ground). If the burn zone is adjacent to or surrounded by similar habitat harboring colonies of the insects, recovery likely will occur relatively rapidly through immigration and colonization.

The fire at Inverness Ridge, while moderately large (5,000 ha) and extremely intense on the higher ridges, occurred with attributes generally favorable for recovery of its herbivorous insects. As the fire proceeded downslope during days 2-5, it diminished in intensity and varied, becoming only an understory burn in places, and many trees and larger shrubs survived. Moreover, the area is bordered on all sides except along Drakes Bay by extensive areas of native vegetation, including all major communities in the burn area (Fig. 1). Hence, the situation was favorable for recovery of vegetation and associated insect populations.

Recovery of the pre-fire community

Except for butterflies, species accumulation did not stabilize after 5 years (Figs. 2, 3), although recorded recovery rates are partly artifacts of sampling error. Butterflies are more easily observed than moths, so they are detected more readily. Inventory of larger moths is primarily dependent upon attraction of adults to lights, and effectiveness of sampling varies with seasonal flight period, temperature and wind conditions, moon phase, positioning of traps, and activity of vertebrate predators at the traps. Adults of some microlepidoptera are diurnal, and those of tiny nocturnal species are not reliably sampled by light traps. However, larvae of shelter makers in foliage are readily discovered, and leaf mines and plant galls induced by some microlepidoptera can be recorded by experienced observers because they persist throughout the season and can be recognized long after the larval feeding period.

Recolonization of particular plant species by larval Lepidoptera was more rapid in less intensely burned habitats. Species feeding on plants in the riparian community recovered sooner and more completely, compared to their projected caterpillar guilds (92%), than in chaparral and grassland (76%), and the more severely burned bishop pine community (61%) (Tables 2, 3, 4). Pooling data from these three plant lists yields an estimate of 74% of the expected total Lepidoptera fauna as a baseline estimate of the proportion of pre-fire species that colonized within 5 years.

Table 3. Post-fire recovery of Lepidoptera Guilds on Chaparral and Grassland plants: Cumulative larval host plant use, based on larvae, mines, and projected from adults of specialist species

Year:	1	2	3	4	5	Expected
Anaphalis/Gnaphalium	3	5	7	7	7	7
Rhamnus	3	5	5	6	6	7
Baccharis	-	4	5	9	11	14
Toxicodendron	-	-	-	-	3	4
Poaceae	10	11	13	17	20	30
Total	**16** **26%**				**47** **76%**	**62**

A total of 602 species of Lepidoptera, 40 butterflies and 562 moths (+ about 30 of uncertain species status) have been recorded during the past 60 years in the Inverness Ridge area, whereas 376 (+10 ?) species were found in the fire zone during the 5 seasons. Obviously not all the species in the region are expected to have lived in the area sampled because small portions of any area harbor fewer habitats and species than the whole area. For example, the east slope of the ridge has a dense, shaded, and, more diverse forest type, dominated by Douglas-fir (*Pseudotsuga*) and tanbark oak (*Lithocarpus*), both of which were rare in the burn area I monitored. If we assume butterflies are completely censussed, we can project a percent recovery based on them. Of the total in the region, 34 species likely are resident on Inverness Ridge (several others live in adjacent marsh and beach habitats), and 28 of 33 species observed in the fire zone are assumed to be resident (82% of the resident ridge fauna). If moth diversity is comparably distributed, 480 species (80% of 600) might have comprised the pre-fire community, and the observed 376 species recorded make up 77% of the expect fauna (Table 5). Probably this is an optimistic projection because inventory of the region as a whole is incomplete — there has been minimal effort to collect and rear larvae other than in the fire zone — 650-700 species is a more realistic estimate of the fauna. If true, 80% of the total projects to 520-560 species expected in the fire zone, of which 60-65% were recovered.

Post-fire recovery of Lepidoptera contrasted with insects in other habitats

This study demonstrates dramatic differences in the effects of fire on insect herbivores among plant species and vegetation types within complex plant communities. Contrasting the recovery at Inverness Ridge with other post-fire studies of arthropods is problematic because none has attempted to comprehensively assess moth species, which make up 95% of the Lepidoptera. Traditional fire management for various uses has been contentious (e.g., in prairie grasslands in the midwestern U.S., pine plantations in the southeast, heaths in Europe, eucalypt forests in Australia), and there have been many studies of the effects of prescribed burning on arthropods (reviews by Warren et al. 1987, Folkerts et al. 1993, Swengel 2001, Panzer 2002). Such studies usually compare recently or annually burned with unburned and/or less frequently burned, comparable small plots of habitat in areas that have been subjected historically to periodic burning. Therefore, they assess recovery response among arthropod communities that tolerate periodic fires and exist in spite of or even because of them. Typically, standard sampling methods have been used in order to make statistical comparisons between burned and unburned plots, primarily by pitfall traps, flight intercept traps, or sweep net samples along fixed transects. Most have identified insects only to order or family level. Those that have listed insect species usually focus on Orthoptera (grasshoppers), Hemiptera (true bugs, leafhoppers) or butterflies as herbivores, and spiders or carabid beetles as predators. Evaluations often assess short (0-2 months) or intermediate term (2-12 months) effects.

In general, the pattern revealed by numerous such studies is high species richness and abundance, or biomass (often dominated by grasshoppers), during the first season following prescribed fires, as compared to unburned plots or second and third year post-fire samples. Because prescribed burning aims to suppress invasive shrub and understory growth, short-term studies following them measure primarily the rapidly developing cohort I have termed Transitional Species. Managed grasslands, savanna, and pine plantations are prevented from evolving in stages to shrub dominated communities and wood lots, which would support more diverse, long-term Lepidoptera communities. As might be expected, these sam-

Table 4. Post-fire recovery of Lepidoptera Guilds on Bishop Pine forest plants: Cumulative larval host plant use, based on larvae, mines, and projected from adults of specialist species.

Year:	1	2	3	4	5	Expected
Pinus	3	3	5	5	6	15+
Arbutus	-	2	3	3	3	5
Arctostaphylos	-	1	7	9	10	14
Vaccinium	1	3	5	5	5	5
Quercus	4	11	16	19	22	37+
Ceanothus	4	11	13	15	16	18+
Total	**12**				**62**	**94+**
	13%				**66%**	

pling regimes recover insignificant numbers of Lepidoptera relative to other arthropods tallied (e.g., 2% of all arthropods sampled by Nagel 1973 and Siemann et al. 1997).

Nonetheless, generalizations are offered for arthropods as a whole. For example, Nagel (1973) found significantly greater numbers and biomass of herbivore arthropods on a burned site than on unburned, but the difference in Lepidoptera was insignificant and 9% higher in the unburned plot. Siemann et al. (1997) concluded that burns necessary to maintain grassland and oak savanna do not appear to be harmful or to greatly impact the arthropod fauna; yet a visual count averaged 47 butterflies per unburned and infrequently burned vs. 18 per frequently burned plot, and light traps produced 22 moth species/sample in unburned and infrequently burned vs. 16/sample in frequently burned plots.

Moreover, there are contradictory results from some studies of grassland-,soil-, and litter-dwelling invertebrates. Buffington (1967) found fewer taxa and individuals of soil arthropods one year after a wildfire in New Jersey pine barrens, and litter arthropods studied by Metz and Farrier (1973) were less abundant in annually burned loblolly pine woods in South Carolina than in unburned or less frequently burned plots. Research by Nekola (2002) clearly showed that fire management causes significant reduction in land snail richness and abundance and most significantly impacts the rarest species. Panzer (2002) assessed effects of prescribed burning in 21 tallgrass prairie reserves in Indiana, Illinois and Wisconsin. He found negative post fire responses in 40% of 151 species representing 33 families of insects, positive responses in 26%. Among negatively affected populations, all recovered within two years. Butterflies and *Papaipema* (Noctuidae) moth species, which are stem borers in herbs, comprised an appreciable proportion of the remnant-dependent species examined.

Force (1981) tracked insect succession in a chaparral community in southern California for 3 seasons following a wildfire in November. He conducted observational transects along a 1.5 km trail, similar to my sampling approach, several times monthly, augmented by thorough census of 10 plots annually. He found insect family richness and diversity and species richness to be highest in year 1, declining in years 2 and 3, while species diversity was highest in year 1, lowest in year 2. He did not differentiate among detritivore, herbivore, parasitoid, and predator taxa in the analysis and did not report the insect families tallied, so the representation of Lepidoptera is unknown. Force believed the large food resource available to foliage-, sap-, and pollen and nectar-feeding insects attracted many vagrants from outside the burn.

Implications for fire-management policy

A fallacy in assuming that diverse and lush post-fire vegetation and the accompanying richness of some insects represents richness of all insects lies in the nature of the early post fire vegetation. Much of it consists of weedy herbs and native annuals, which serve as larval food for few Lepidoptera, whereas the later succession shrubs and trees provide resources for the great majority of moth larvae. Although post-fire vegetation was lush at Inverness Ridge initially, Lepidoptera were low in species richness and diversity in year 1, then gradually increased as the long-term, high-architecture vegetation became established. Lepidoptera make up the most diverse group of plant-feeding insects, and more state and federally protected species in the U.S. are Lepidoptera than any other insects. The adults and caterpillars provide an important food resource for many vertebrates, including lizards, rodents, bats, and birds. The fate of these herbivores should not be subsumed within management decisions made on the basis of generalists (e.g. grasshoppers) and other early succession insects (leafhoppers, spittlebugs), or carabid beetles, spiders, and soil arthropods in fire-adapted communities. In addition, at Inverness, butterflies were recovered appreciably sooner than leaf mining taxa or Lepidoptera as a whole (Figs. 2, 3), which suggests that they comprise a group that

Table 5. Summary of Lepidoptera recovery five years after the Mt. Vision Fire.

	Species Observed	% of Area total	% of Projected
microlep	148	67	84
pyraloid	28	51	65
macro moth	167	55	70
butterfly	33	80	100
Total	**376**	**60**	**77**

includes Transitional Species and is easily censussed but is not an indicator of typical rates of recolonization by other plant-feeding insects.

Caution should be exercised in application of generalizations produced from study of post-fire recovery in periodically burned grasslands and savannas, based on pooled data from diverse arthropod taxa (detritivores, herbivores, predators). Policy decisions concerning use of prescribed burning for weed suppression or other management, such as in national wildlife refuges, national parks, need careful consideration of long-term goals and effects on the native insect fauna.

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Literature Cited

Buffington, J. D. 1967. Soil arthropod populations of the New Jersey pine barrens as affected by fire. Annals of the Entomological Society of America 60: 530-535

Cody, M. L. and H. A. Mooney 1978. Convergence vs. nonconvergence in Mediterranean Ecosystems. Annual Review of Ecology and Systematics 9: 265-321.

Fellers, G. M., V. Norris, and W. Follette 1990. Point Reyes National Seashore Plant Checklist. Pt. Reyes National Seashore Association, Pt. Reyes, CA; 41 pp.

Folkerts, G. W., M.. A. Deyrup, and D. C. Sisson 1993. Arthropods associated with xeric longleaf pine habitats in the southeastern United States: A brief overview. Proceedings of the Tall Timbers Fire Ecology Conference, 18: 159-192.

Force, D. C. 1981. Postfire insect succession in southern California chaparral. American Naturalist 117:575-582.

Howell, J. T. 1949. Marin Flora. University of California Press, Berkeley and Los Angeles; vii + 323 pp.

Keeley, J. E. and P. H. Zedler 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. American Midland Naturalist 99: 142-161.

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology 28: 23-39.

Metz, L. J. and M. H. Farrier 1973. Prescribed burning and populations of soil mesofauna. Environmental Entomology 2: 433-440.

Nagel, H. G. 1973. Effect of spring prairie burning on herbivorous and non-herbivorous arthropod populations. Journal of the Kansas Entomological Society 46: 485-496.

Nekola, J. C. 2002. Effects of fire management on the richness and abundance of central North American grassland land snail faunas. Animal Biodiversity and Conservation 25: 53-66.

Ornduff, R. 1998. Three years after the Vision Fire in Point Reyes. Fremontia 26(3): 26-27.

Ornduff, R. and V. Norris 1997. Rebirth of a Bishop Pine forest: First year after the Mount Vision fire. Fremontia 25(3): 22-28.

Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. Conservation Biology 16: 1296-1307

Powell, J. A. 1995. Lepidoptera inventories in the continental United States. pp. 168-170 in: LaRoe, E. et al., (eds.) Our Living Resources.

A Report to the Nation on the Distribution, Abundance, and Health of U. S. Plants, Animals, and Ecosystems. U. S. Department of Interior, National Biological Service, Washington, D.C.

Siemann, E., J. Haarstad, and D. Tilman 1997. Short-term and long-term effects of burning on oak savanna arthropods. American Midland Naturalist 137: 349-361.

Smith, D. W. and T. D. W. James 1978. Changes in the shrub and herb layers of vegetation after prescribed burning in *Populus tremuloides* woodland in southern Ontario. Canadian Journal of Botany 56: 1792-1797.

Sugnet, P. W. 1985. Fire history and post-fire stand dynamics of Inverness Bishop Pine populations. M. S. Thesis, University of California, Berkeley; v + 82 pp., tables.

Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodiversity & Conservation 19:1141-1169.

Warren, S. D., C. J. Scifres, and P. D. Teel 1987. Response of grassland arthropods to burning: a review. Agriculture, Ecosystems, and Environment 19: 105-130.