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very high but the growth stops and the mortality increases as soon as the resources are depleted, which gives the resources a chance to recover and so on. At a growth rate slightly higher than the value giving maximum exergy, the model starts to show deterministic chaos: a minor difference in the initial value causes exponentially increasing changes as the time increases. Figure 1 illustrates the exergy as function of the zooplankton growth rate in the model referred to above, focusing on the time when the model starts to show deterministic chaos. These results are consistent with Kaufmann's statement: biological systems tend to operate at the edge of chaos to be able to utilize the resources at the optimum. In response to constraints, systems move as far away from thermodynamic equilibrium as possible under the prevailing conditions, but this will imply that the system has a high probability to avoid chaos, although the system is operating close to chaos. Considering the enormous complexity of natural ecosystems, and the many interacting processes, it is surprising that chaos is not frequently observed in nature, but it can be explained by an operation at 'the edge' of chaos to ensure a high utilization of the resources – to move as far away from thermodynamic equilibrium as possible at the prevailing conditions.

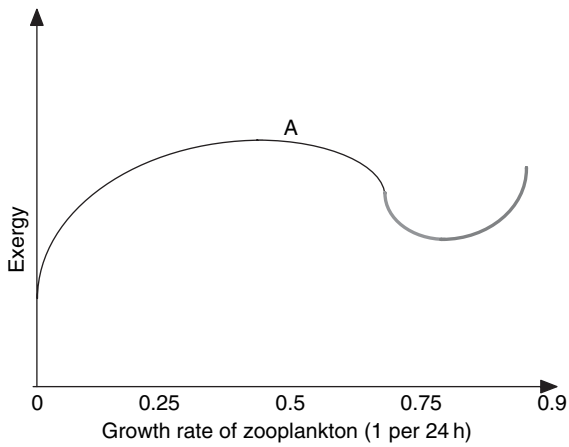

Figure 1 Exergy is plotted versus maximum growth rate for zooplankton in a well-calibrated and validated eutrophication model. The shaded line corresponds to chaotic behavior of the model, i.e., violent fluctuations of the state variables and the exergy. The shown values of the exergy above a maximum growth rate of about 0.65–0.7 d^{-1} are therefore average values. By a minor change of the initial value of phytoplankton or zooplankton in the model, significant changes are obtained after 2 months of simulations as an indication of deterministic chaos.

See also: Catastrophe Theory.

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Chaparral

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Introduction

Chaparral is the name applied to the evergreen sclerophyllous (hard-leaved) shrub vegetation of southwestern North America, largely concentrated in the coastal zone of California and adjacent Baja California. It is a dense vegetation often retaining many dead spiny branches making it nearly impenetrable (Figure 1). It dominates the foothills of central and southern California but is replaced at higher elevations by forests. On the most

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Figure 1 Chaparral shrubland in California. Photo by J. E. Keeley.

arid sites at lower elevations evergreen chaparral is replaced with a lower-stature summer deciduous 'soft chaparral' or sage scrub.

Chaparral owes much of its character to the Mediterranean climate of winter rain and summer drought. The severe summer drought, often lasting 6 months or more, inhibits tree growth and enforces the shrub growth form. Intense winter rains coincide with moderate temperatures that allow for rapid plant growth, producing dense shrublands. These factors combine to make this one of the most fire-prone ecosystems in the world. This Mediterranean climate is the result of a subtropical high-pressure cell that forms over the Pacific Ocean. During the summer, this air mass moves northward and blocks water-laden air masses from reaching land, and in winter this high-pressure cell moves toward the equator and allows winter storms to pass onto land. On the Pacific Coast it is wettest in the north, where the effect of the Pacific High is least, and becomes progressively drier to the south, and consequently chaparral dominates more of the landscape in the southern part. Interestingly, these synoptic weather conditions form globally at this same latitude (30–38° north or south) and on the western sides of continents. As a result similar Mediterranean-climate shrublands occur in the Mediterranean Basin of Europe, central Chile, South Africa, and southern Australia.

The Ecological Community

Chaparral is a shrub-dominated vegetation with other growth forms playing minor or temporary successional roles after fire. More than 100 evergreen shrub species occur in chaparral, although sites may have as few as one or more than 20 species, depending on available moisture, slope aspect, and elevation. The most widely distributed shrub is chamise (*Adenostoma fasciculatum*), ranging from Baja to northern California, occurring in either pure chamise chaparral or in mixed stands. It often dominates at low elevations and on xeric south-facing slopes. The short needle-like leaves produce a sparse foliage, and soil litter layers are poorly developed and result in weak soil horizons. Chamise often forms mixed stands of vegetation with a number of species. These include the bright smooth red-barked manzanita (*Arctostaphylos* spp.), the sometimes spiny ceanothus, also known as buckbrush or California lilac (*Ceanothus* spp.). On more mesic north-facing slopes chaparral is commonly dominated by broader-leaved shrubs, including the acorn-producing scrub oak (*Quercus* spp.), the cathartic coffeeberry (*Rhamnus californica*), redberry (*R. crocea*), the rather bitter chaparral cherry (*Prunus ilicifolia*), and chaparral holly (*Heteromeles arbutifolia*), from whence the film capital Hollywood derives its name.

The most common shrub species and the majority of herbaceous species have fire-dependent regeneration, meaning that seeds remain dormant in the soil until stimulated to germinate after fire (see the section titled 'Fire' below). These include chamise, manzanita, and ceanothus shrubs, which flower and produce seed most years but seldom produce seedlings without fire. Some ceanothus species are relatively short-lived or are easily shaded out by other shrubs and die after several decades. They, however, persist as a living seed pool in the soil. In addition, a large number of annual species live most of their life as dormant seeds in the soil, perhaps as long as a century or more. Also, many perennial herbs with underground bulbs, known as geophytes, may remain dormant for long periods of time between fires.

All of the other shrub species listed above are not fire dependent and produce seeds that germinate soon after dispersal; however, successful reproduction is relatively uncommon. This is because their seedlings are very sensitive to summer drought and because there are a number of herbivores that live in the chaparral understory and prey on seedlings and other herbaceous vegetation. These include deer mice (*Peromyscus maniculatus*), woodrats (*Neotoma fuscipes*), and brush rabbits (*Sylvilagus bachmani*). Both rodents (mice and rats) are nocturnal; however, evidence of woodrats, or packrats as they are sometimes called, is very evident in many older chaparral stands because of the several foot high nests of twigs they make under the shrub canopy. These animals not only affect community structure by consuming most seedlings and herbaceous species, but also are important vectors for disease and other health threats. For example, deer mice are host to the deadly hanta-virus and woodrats are a critical host for kissing bugs (family Reduviidae) that can cause lethal allergic responses in humans. All animals including reptiles act as hosts for Lyme disease-carrying ticks (*Ixodes pacificus*). The browser of mature shrubs is the black-tailed deer (*Odocoileus hemionus*), although many are attacked by specific gall-forming wasps and aphids. Often scrub oak will have large fruit-like structures produced by

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gall wasp (family Cynipidae). The adult wasp oviposits on a twig, leaf, or flower and the developing larvae hijack the metabolic activities of the plant cells and force it to produce a highly nutritious spongy parenchymous tissue for the developing wasp larva.

These shrubs that reproduce in the absence of fire have successful seedling establishment largely restricted to more mesic plant communities such as adjacent woodlands, or to very old chaparral with deep litter layers that enhance the moisture holding capacity of the soil. When seedlings do establish under the shrub canopy, they typically persist for decades as stunted saplings in the understory. These saplings are heavily browsed by rodents and rabbits and often will produce a swollen woody basal burl that survives browsing and continually sprouts new shoots. If these saplings survive until fire, they are capable of resprouting from their basal burl after fire and exhibit a growth release that enhances their chances of recruiting into the mature canopy during early succession. Thus, in some sense these shrubs may be indirectly fire dependent for completion of their life cycle.

Chaparral has a number of herbaceous or woody (lianas) vines, including manroot (*Marah macrocarpus*) and chaparral honeysuckle (*Lonicera* spp.). These vines overtop the canopy of the shrubs and flower on an annual or near-annual frequency. The former produce fleshy spiny fruits with very large seeds that are highly vulnerable to predation and the latter dry capsules with light seeds that may be wind borne. Both have weak seed dormancy and often establish seedlings in the understory.

Yucca (*Yucca whipplei*) is a fibrous-leaved species that persists as an aboveground rosette of evergreen leaves. It often survives fire because it prefers open rocky sites with very little vegetation to fuel intense fires. Because they are monocotyledonous species they have a central meristem that is protected by the outside leaves, which can withstand severe scorching. This species flowers prolifically after fire and exhibits a remarkable mutualism with the tiny yucca moth (*Tegiticula maculata*). Moth pupae survive in the soil and emerge in the growing season as adults that fly to yucca flowers where they collect pollen. They then instinctively fly to another yucca plant and pollinate the flower, ensuring cross-pollination, and then oviposit an egg in the base of the ovary. This egg soon hatches and the larva feeds on the developing seeds. Yucca moths only reproduce on yucca flowers and yuccas apparently require the pollinator services of this moth for successful seed production, a classic example of symbiosis.

Community Succession

Chaparral succession following some form of disturbance such as fire is somewhat different than in many other ecological communities. Generally all of the species present before fire in chaparral will be present in the first growing season after fire, and thus chaparral has been described as being 'auto-successional', meaning it replaces itself. In the absence of disturbance chaparral composition appears to remain somewhat static with relatively few changes in species composition or colonization by new species. In part because of the rather static nature of chaparral, old stands have been described with rather pejorative terms such as 'senescent', 'senile', 'decadent', and 'trashy', and considered to be very unproductive with little annual growth. This notion derives largely from wildlife studies done in the mid-twentieth century that concluded, due to the height of shrubs in older stands, there was very little browse production for wildlife. However, if total stand productivity is used as a measure, very old stands of chaparral appear to be very productive and are not justly described as senescent. Also, these older communities appear to retain their resilience to fires and other disturbances, as illustrated by the fact that recovery after fire (see below) in ancient stands (150 years old) recover as well as much younger stands.

Allelopathy

The lack of shrub seedlings and herbaceous plants in the understory of chaparral and related shrublands has led to extensive research on the potential role of allelopathy, which is the chemical suppression by the overstory shrubs of germination (known as enforced dormancy) or growth of understory plants. Often this lack of growth extends to the edge where these shrublands meet grasslands, and forms a distinct bare zone (**Figure 2**). The importance of allelopathy has long been disputed, with some scientists arguing that animals in the shrub understory are the primary mechanism limiting seedlings and herbaceous

Figure 2 Bare zone between chaparral and grassland. Photo by J. E. Keeley.

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species from establishing. While research has not completely ruled out the possibility of chemical inhibition, it is known that for a large portion of the flora, allelopathy has no role in seed dormancy but rather dormancy is due to innate characteristics that require signals such as heat and smoke to cue germination to postfire environments rich in nutrients and light.

Fire

The marked seasonal change in climate is conducive to massive wildfires, which are spawned by the very dry shrub foliage in the summer and fall and spread by the dense contiguous nature of these shrublands. Fires have likely been an important ecosystem process since the origin of this vegetation in the late Tertiary Period, more than 10 Ma, if not earlier. Until relatively recently the primary source of ignitions was lightning from summer thunderstorms. Fires would largely have been ignited in high interior mountains and coastal areas would have burned less frequently and only when these interior fires were driven by high winds with an offshore flow. In many parts of California such winds occur every autumn and are called Santa Ana winds in southern California and Diablo winds or Mono winds in northern California. When Native Americans colonized California at the end of the Pleistocene Epoch around 12 000 years ago, they too became a source of fires, and as their populations greatly increased over the past few thousand years humans likely surpassed lightning as a source of fire, at least in coastal California. Today humans account for over 95% of all fires along the coast and foothills of California.

Chaparral fires are described as crown fires because the fires are spread through the shrub canopies and usually kill all aboveground foliage. Normally, following a wet winter, high fuel moisture in chaparral shrubs makes them relatively resistant to fire. The amount of dead branches is important to determining fire spread because they respond rapidly to dry weather and combust more readily than living foliage. As a consequence, fires spread readily in older vegetation with a greater accumulation of dead biomass. However, there is a complex interaction between live and dead fuels, wind, humidity, temperature, and topography. In particular, wind accelerates fire spread primarily by heating living fuels and often can result in rapid fire spread in young vegetation with relatively little dead biomass. Fires burning up steep terrain also spread faster for similar reasons.

Community Recovery from Wildfires

Rate of shrub recovery varies with elevation, slope aspect, inclination, degree of coastal influence, and patterns of precipitation. Recovery of shrub biomass is from basal resprouts (**Figure 3**) and seedling recruitment from a dormant soil-stored seed bank. After a spring or early summer burn, sprouts may arise within a few weeks, whereas after a fall burn, sprout production may be delayed until winter. Regardless of the timing of fire, seed germination is delayed until late winter or early spring and is less common after the first year. Resilience of chaparral to fire disturbance is exemplified by the marked tendency for communities to return rapidly to prefire composition.

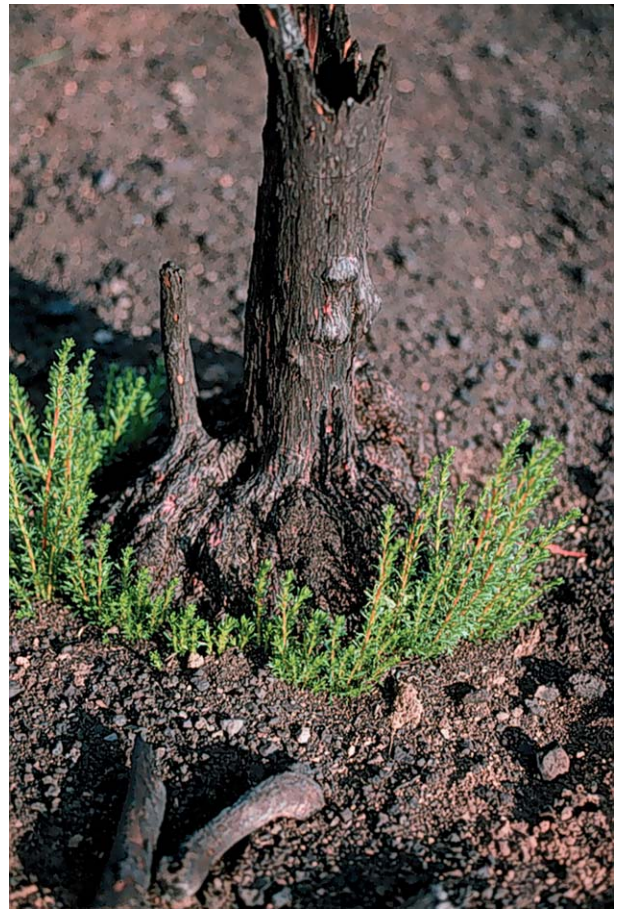

Figure 3 Postfire resprouts from basal burl of chamise with meter stick. Photo by J. E. Keeley.

Shrub species differ in the extent of postfire regeneration from resprouting versus reproduction from dormant seed banks. Most species of manzanita and ceanothus have no ability to resprout from the base of the dead stem and thus are entirely dependent on seed germination. Such shrubs are termed 'obligate-seeders'. A few species of manzanita and ceanothus as well as chamise resprout and reproduce from seeds, and these are referred to as 'facultative-seeders'. The majority of shrubs listed above, however, regenerate after fire entirely from resprouts and are 'obligate-resprouters'.

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In the immediate postfire environment the bulk of plant cover is usually made up of herbaceous species present prior to the fire only as a dormant seed bank or as underground bulbs or corms. This postfire community comprises a rich diversity of herbaceous and weakly woody species, the bulk of which form an ephemeral postfire-successional flora. This 'temporary' vegetation is relatively short-lived, and by the fifth year shrubs will have regained dominance of the site and most of the herbaceous species will return to their dormant state. These postfire endemics arise from dormant seed banks that were generated after the previous fire and typically spend most of their life as dormant seeds. These are termed 'postfire endemics' and they retain viable seed banks for more than a century without fire until germination is triggered by heat or smoke of a fire. Postfire endemics are highly restricted to the immediate postfire conditions and if the second year has sufficient precipitation may persist a second year but usually disappear in subsequent years.

Not all of the postfire annuals are so restricted, rather some are quite opportunistic, taking advantage of the open conditions after fire but persisting in other openings in mature chaparral. Such species often produce polymorphic seed pools with both deeply dormant seeds that remain dormant until fire and nondormant seeds capable of establishing in or around mature chaparral. These species fluctuate in relation to annual precipitation patterns, often not appearing at all in dry years.

Herbaceous perennials that live most of their lives as dormant bulbs in the soil commonly comprise a quarter of the postfire species diversity. Nearly all are obligate resprouters, arising from dormant bulbs, corms, or rhizomes and flowering in unison in the first postfire year. Almost none of them produce fire-dependent seeds; however, reproduction is fire dependent because postfire flowering leads to produce nondormant seeds that readily germinate in the second year.

Diversity in chaparral reaches its highest level in the first year or two after fire. It is made up of a large number of relatively minor species and a few very dominant species and is illustrated by dominance–diversity curves (**Figure 4**). Dominance in chaparral is driven by the fact that a substantial portion of resources are taken by vigorous resprouting shrubs and much less is available for the many annual species regenerating from seed.

Plants are not the only part of the biota that has specialized its life cycle to fire. Smoke beetles (*Melanophila* spp.) are widely distributed in the western US and are attracted by the infrared heat given off by fires. Often while stems are still smoldering they will bore into the scorched wood and lay their eggs.

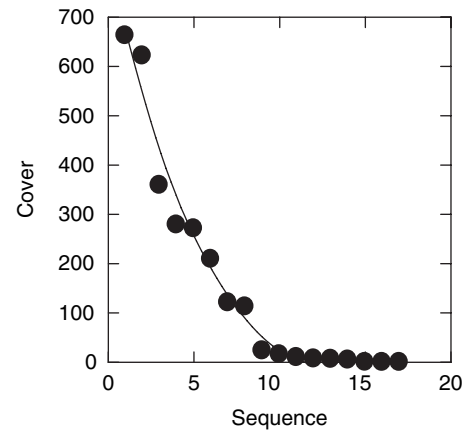

Figure 4 Dominance–diversity curve based on cover of species in sequence from highest to lowest from postfire chaparral.

Seed Germination

Many chaparral species have fire-dependent regeneration, meaning that dormant seeds in the soil require a stimulus from fire for germination. A few species have hard seeds that are cracked by the heat of fire and this stimulates germination. Ceanothus seeds are a good example of this germination mode. However, for the majority of species, seeds do not respond to heat but rather to chemicals generated by the burning of plant matter. This can result from exposure to smoke or charred wood. In many of these species seeds will not germinate when placed at room temperature and watered, unless they are first exposed to smoke or charred wood. In natural environments the seeds remain dormant for decades until fire. There is evidence that a variety of chemicals in smoke and charred wood may be responsible for stimulating germination of postfire species, and both inorganic and organic compounds may be involved.

Seeds of many species have a requirement for cold temperatures (<5 °C), which is interpreted as a seasonal cue, but in these chaparral species this requirement is not like the cold stratification requirement of many species from colder climates, where the seeds require a certain duration of cold in order to prevent winter germination. In California species just a short burst of cold often will trigger germination; thus, cold is not a cue that winter is over (as with more northern latitude species) but rather that winter has arrived, which is consistent with the winter germination behavior of these Mediterranean-climate species.

Seed Dispersal

Shrubs can be divided into those with temporal dispersal versus those with strong spatial dispersal. The former are the fire-dependent species that accumulate dormant seed

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banks, which in essence disperse these shrubs in time, from one fire cycle to the next. Within this group there is limited spatial dispersal. Ceanothus have explosive capsules that shoot seeds a short distance of a meter or two from the parent shrub. Manzanitas drop most of their seeds beneath the parent plant because their small dry fruits are not attractive to birds, although a small number of the seeds are distributed further by coyotes (*Canis latrans*) and bears (*Ursus americans*, historically also included *U. horribilis*). Chamise produces small light fruits that may be carried tens of meters or more by the wind but it appears that most are distributed around the parent shrub.

The postfire endemic annuals also have seeds that are largely dispersed in time rather than in space. Most do not have characteristics suggestive of widespread dispersal. For example, the fire-following whispering bells (*Emmenanthe penduliflora*) derives its name because the flowers and fruits are pendulous and drop seeds directly beneath the parent plant. Postfire endemics in the sunflower family (Asteraceae), a family noted for well-developed dispersal with dandelion-like pappus, commonly have deciduous pappus, which ensures dispersal in time rather than in space.

Shrub species that exhibit fire-free (nonfire-dependent) reproduction have fruits highly attractive to birds and mammals, and the bulk of the seed crop appears to be dispersed by these vectors. Seedling recruitment is sensitive to desiccation and thus it is of some significance that one of the main dispersers of these fruits, the scrub jay (*Aphelocoma californica*), preferentially caches seeds in the shade.

Regional Variation in Fire Regime

California chaparral exhibits regional differences in burning patterns and largely due to regional variation in winds. In much of coastal California autumn winds create severe fire conditions. These occur every year and result in 5–10 days of strong offshore flow with windspeeds of 100 kph or more. These winds result from a high-pressure system in the interior West, and are known as Santa Ana winds in southern California and Diablo or Mono winds in northern California. As these air masses move from the high-pressure cell in the interior to a low-pressure trough off the coast, the air descends and dries adiabatically, resulting in relative humidity below 10%. The fact that these winds occur every year and arrive at the end of an extended drought results in one of the most severe fire conditions in the world. As a consequence only a small portion of southern California landscape has escaped fire during the last century, and much of the lower-elevation chaparral has burned at an unnaturally high frequency.

In contrast, Santa Ana winds are absent from the southern Sierra Nevada and parts of the central coast, in part to mountain barriers that fail to funnel these winds coastward. This, coupled with lower human population density, has resulted in many fewer fires. As a consequence nearly half of the landscape in the southern Sierra Nevada has not had a fire for well over a century. This condition places these landscapes at the upper end of the historical range of variability. Nonetheless, these older stands of chaparral appear to maintain natural ecosystem processes and exhibit no sign of dying out or replacement by other vegetation types. This is particularly evident, following fires in ancient stands of chaparral from the region, that it exhibits vegetative recovery in cover and diversity indistinguishable from postfire recovery in younger stands.

Future Threats and Management

Degradation and type conversion of native shrublands to alien-dominated grasslands has been noted by numerous investigators, some of whom contend that increased frequency of disturbance is the primary factor that favors non-native annuals over woody native species. In the absence of fire, seeds of non-natives have a low residence time in the soil; thus, the presence of these species on burned sites is more often due to colonization after fire. Typically a repeat fire within the first postfire decade is sufficient to provide an initial foothold for aliens. In addition to outcompeting native plant species, non-native grasses alter the fire regime from a crown-fire regime to a mixture of surface- and crown-fires, where highly combustible grass fuels carry fire between shrub patches. This increases the likelihood of fires and ultimately increases fire frequency. As fire frequency increases there is a threshold beyond which the native shrub cover cannot recover.

Fire management practices potentially conflict with natural resource needs. These landscapes currently experience an unnaturally high frequency of fire; thus, much of it is at risk for alien invasion. When fire managers add to this by using prescription burning and other fuel manipulations, they open up these shrublands and expose them to invasion and potential type conversion to non-native grasslands. In managing these landscapes it might be helpful to consider the fact that the vast majority of alien species in California are opportunistic species that capitalize on disturbance. Adding additional disturbance through prescription burning (or grazing) will only exacerbate the alien problem.

Very little chaparral landscape is protected in parks or wilderness areas. Much of it is in private hands or under federal jurisdiction. Historically, it has largely been managed as rangeland by frequent burning to destroy the

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chaparral cover, or burned to reduce fuels perceived to be hazardous to more desirable forests or urban environments. Today the expansion of urban development has resulted in large portions of urban communities being juxtaposed with watersheds of potentially dangerous chaparral fuels. Historical studies show that large high-intensity crown fires are a natural part of this ecosystem and there is little reason to believe there will not be more such fires in the future. Fire management has always worked under the philosophy that they can change the vulnerability of communities to wildfires through manipulation of fuels. However, over the past century of such management, every decade has been followed by one of increasing losses to wildfires. Californians need to embrace a different model of how to view fires on these landscapes. Our response needs to be tempered by the realization that these are natural events that cannot be eliminated from the southern California landscape. We can learn much from the science of earthquake or other natural hazard management. No one pretends they can stop earthquakes; rather, they engineer infrastructure to minimize impacts. In the future, living safely with fire is not going to be achieved solely by fire management practices, but will require close integration with urban planning.

See also: Ecological Niche; Fire; Invasive Species; Mediterranean; Plant Demography.

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Chemical Communication

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Introduction
Semiochemicals
Pheromones
Allelochemicals
Further Reading

Introduction

Communication, broadly defined, is the transfer of information from one individual (signal emitter) to another (signal receiver). The signals used to transmit the information through the surrounding environment involve multiple sensory modalities. Based on the sensory capabilities of the receiver, the medium, which is used to convey information, and the distance, which has to be covered, signals can be considered to fall into three main categories.

The first group covers acoustic or vibrational signals which are transmitted through a medium such as air, water, or solid materials over short (e.g., vibration signals organize labor in honeybee colonies), medium (e.g., airborne songs of birds and frogs), and very long distances (e.g., infrasound communication of whales and elephants). The second type of signals involves a variety of visual signals such as the bright plumage coloration of birds, aposematic coloration of toxic insects and reptiles, and bioluminescence used by deep-sea fish to attract prey. Despite their striking appearance, these signals can only