DIVERSITY AND MANAGEMENT OF RARE ARCTOSTAPHYLOS AND CEANOTHUS SPECIES IN CHAPARRAL

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ABSTRACT

Arctostaphylos (manzanita) and Ceanothus (California lilac) have diversified within California and most of their species occur in coastal regions. These are the only two shrub genera in California that have evolved an obligate seeding life form that are generally considered fire-dependent for regeneration. The high species diversity within the obligate seeders also includes most of the rare, threatened or endangered woody species in California. Because of their differential presence in coastal regions of California and the Sierra Nevada foothills, these species and the chaparral they inhabit are in conflict with human development and expansion. Both conservation and management in the context of human developments are difficult. Prescribed burning is a poor technique and often fails to reestablish populations while 'fuel' removal or chipping destroys populations and opens habitats to invasive annuals. High intensity fire, on the other hand, is not an acceptable management option. While wildfires may occur regardless of management style, too frequent fires, or fires with too short a between-fire interval can eliminate obligate seeding species. This paper focuses principally on the diversity of these taxa and the difficulty of managing species dependent on soil seed banks and high intensity fire.

Key words: Arctostaphylos, California, California lilac, Ceanothus, chaparral, fire, fire management, manzanita, obligate seeders.

INTRODUCTION

Chaparral is the most common native vegetation type in California. Chaparral contains a large number of rare species and represents a special, but surprisingly difficult vegetation to conserve. Here I focus on the concentration of rare or restricted species in the two genera Arctostaphylos Adans. and Ceanothus L. Arctostaphylos (Ericaceae) is the most diverse woody genus in California with almost 100 different species and subspecies; Ceanothus (Rhamnaceae) is similar in its diversity with over 50 species and varieties. Both have their centers of species diversity within the California floristic province.

I concentrate on these two genera because they contain species with an unusual type of response to fire. Most species within these genera are obligate seeders, which means the adults are killed by fire and the population recovers from the germination of seed stored in the soil. The seeds can be dormant for long time periods and accumulate to a variety of densities, depending on the size of seed and the density of rodents or other caching seed predators. Germination of Arctostaphylos seeds are cued complexly and involve chemicals found in smoke (Keeley and Fotheringham 1998), while Ceanothus seeds require a heat pulse to permit water to flow into the seed (Keeley 1987, 1991; Parker 1987; Parker and Kelly 1989; Kelly and Parker 1990). Species found in other genera are also obligate seeders, such as the closed-cone pines and cypresses characteristic of chaparral areas, but they store their seed within cones; the cones enforce dormancy and after fire opens the cones, the seeds are released and germinate readily.

Obligate seeding species require special attention at this point because of the context of recent large-scale fires and aggressive fuel modification activities. While both small and large-scale fires have been a historic constant, the movement of people into wildland areas in greater numbers has increased the loss of human property and lives. Such losses also have increased the recognition of the potential magnitude of these fires and consequently the emphasis on human safety. Maximizing fire protection comes at the cost of destruction of wildland habitat in the name of fuel management. Ironically, the increasing density of humans in wildland areas correlates with the increased numbers of fires in areas because humans are the source of most ignitions (Keeley and Fotheringham 2001; Syphard et al. 2007).
FIRE AND PATTERNS OF CHAPARRAL SHRUB RECRUITMENT

Chaparral contains a variety of shrub types with respect to fire response: obligate sprouters, facultative sprouters, and obligate seeders (Parker and Kelly 1989). A common shrub type, obligate sprouters are species that lose above-ground parts during fire and subsequently resprout from buds, root crowns or rhizomes to reestablish individuals. Recruitment of new individuals does not occur in the post-fire environment, but actually takes place slowly in old-growth chaparral. Facultative sprouters, or facultative seeders, resprout following the burning of the stems and leaves, but have a persistent soil seed bank. Seeds stored long-term in the soil or the persistent soil seed bank are stimulated to germinate by the fire, and new individuals establish the spring following a fire. Obligate seeders also store seeds in persistent soil seed banks, but the adults are killed completely by fire. The populations of obligate seeders are completely dependent on the germination and establishment of new individuals from the soil seed bank. Because almost all the seeds germinate in a single pulse that first spring, obligate seeders have a life style closer to annual plants lacking seed dormancy than to other woody plants (Parker and Kelly 1989), except that in obligate seeders, the “year” is the between-fire interval. Thus within chaparral, shrub recruitment is spread out; some life histories specialize in recruitment in the first year or two after fires, while others recruit later in older chaparral.

Facultative sprouters and obligate seeders are of particular importance to chaparral management and conservation because they only recruit the spring after fire, which is an issue because they are adapted only to a particular fire regime. In southern California, repeated burning in some sites resulting from overlapping wildfires has eliminated obligate seeders completely (Zedler et al. 1983; Haiginger and Keeley 1993); in these cases, the between-fire interval was much too short for the plants to mature and produce sufficient seed to reestablish a successful persistent soil seed bank.

The vulnerability of obligate seeders, and in the long-term of any plant relying on soil seed banks with humans modifying fire regimes, is a critical issue for conservation of large numbers of restricted, threatened or endangered plant species. In the San Francisco Bay Area, a number of species are surrounded by—or adjacent to—human development. For example, Arctostaphylos pallida Eastw. survives in only a few small populations in the East Bay Hills, A. imbricata Eastw., and A. pacifica Roof are restricted to San Bruno Mountain while A. montana subsp. ravenii (P.V.Wells) V.T.Parker, M.C.Vasey and J.E.Keeley and A. franciscana Eastw. The ten counties of the immediate San Francisco Bay Area have over 50 different manzanita taxa alone, the majority of which are endemic to the region. Human encroachment into wildland areas with chaparral, whether in the Coast Ranges or Sierra Nevada foothills, not only eliminates or fragments habitat, but also modifies fire frequencies and other dimensions of fire regimes (Zedler et al. 1983; Parker 1987, 1990, 1993). Emphasis only on fire safety will result in the loss of this diverse and important ecosystem (Parker 1990, 1993).

HIGH DIVERSITY IN CHAPARRAL: A CONSERVATION PRIORITY

One characteristic of obligate seeders is that they have differentially radiated into a number of different species or subspecies (Nobs 1963; Wells 1969; Fross and Wilken 2006; Parker et al. in press). About two thirds of both Arctostaphylos and Ceanothus are species of limited distribution or high rarity. The diversity of Arctostaphylos, for example, is principally in the Coast Ranges, peaking in central California. Most of these species have only a limited spatial range. For example, fifteen Arctostaphylos species are found in the Santa Cruz Mountains that run through the San Francisco peninsula into the Monterey Bay area; eleven of these are restricted to some limited portion of the range (for example, A. andersonii A.Gray, A. glutinosa B.Schreib., A. ohloneana M.C.Vasey & V.T.Parker, A. regismonata Eastw.), while only four are found outside the Santa Cruz Mountains.

Marin County provides another example of endemic species. For the county as a whole, chaparral can be found in three types, a maritime chaparral characteristic of areas receiving summer fog, a serpentine chaparral on that soil type, and a mixed chaparral, generally with species of broad distribution. Seventeen Arctostaphylos and Ceanothus species are found in Marin County. Of those, fifteen are obligate seeders, six are only found in Marin County, and an additional six reach their southern or northern limits in or near Marin County. Endemics to Marin County include Ceanothus
gloriosus J.T.Howell var. gloriosus, C. gloriosus var. porrectus J.T.Howell, C. jepsonii Greene var. jepsonii, C. masonii McMinn, A. montana, and A. virgata Eastw. This is an incredible degree of diversity that challenges any other vegetation type in the state.

Species diversity is a dramatic aspect of chaparral, and here I am only emphasizing two woody genera. Close to a hundred species combined for Arctostaphylos and Ceanothus are of limited distribution, which is the majority of woody species found in chaparral. Chaparral is a vegetation not only wonderfully rich in plant and animal species, but also one that functions in ways to support our lifestyles in California by limiting erosion, filtering water, and moderating local temperature regimes among other processes. At the same time, most Californians do not see chaparral as something worthy of conservation. Conservationists have not adequately made the general public aware of its diversity and services, but the public is well aware of chaparral as a constraint on development and a fire hazard. Similarly, we have poorly described the services chaparral ecosystems inadvertently provide to our human society.

MANAGEMENT ISSUES WITH OBLIGATE SEEDERS: CONFLICTS

Because California’s human population continues to expand into hazardous vegetation types near population centers or in the foothills of the Sierra Nevada, currently there is a rush to modify “fuel” (i.e., natural vegetation) by thinning or completely removing it, chipping or other actions (Keeley 2005). These fuel management actions need cost-benefit analyses and environmental impact assessments because they are not fire surrogates. In southern California, high winds driving fires through modified fuel regions or recent burns challenges the claims of effectiveness of current fire management practices. While most people recognize that living in natural areas contains a risk of wildfire, the pace and rate of expansion suggests that the degree of risk is underappreciated and indicates too great a reliance on fuel management, perfect fire fighting and control of wildfires. Policy makers seem to be unaware of the hazards of development in certain areas, and that their policies burden firefighters with increasing risk of their lives in increasingly dangerous conditions, and burden the homeowners with property losses that are often irreplaceable. Human developments in chaparral require differential investment of limited state resources in infrastructure and fire safety personnel, costs that all residents end up bearing for the few. At the same time, fuel management generally conflicts with processes that support chaparral regeneration.

The management issue involved in the conservation of chaparral arises due to two principal issues: 1) most plant species require wildfire to complete their life cycles, and 2) most chaparral plant species store seed in persistent soil seed banks. Management of chaparral only becomes much of a concern in areas where humans have expanded developments, either as a wildland-urban interface, or more commonly, as a wildland-urban intermix. Problems are tremendous for managers because first, appropriate wildfires are not controllable, and therefore are generally not part of a manager’s “toolbox.” Secondly, soil seed banks are incredibly difficult to control and manage.

An additional management problem is that because these plants use different germination cues, except for high intensity fire, nearly every management action can inhibit maintenance and conservation of some or all of these plants (Table 1). Southern California demonstrates that one vegetation management issue is the failure to suppress fires arising at too short an interval. Too short a time between fires will limit the abilities of obligate seeders to mature and create a new soil seed bank (e.g., Zedler et al. 1983). Permitting too many fires will result in the loss of the natural resource. To artificially stimulate seed banks, somehow managers will need to heat the soil and in addition, provide chemical cues. If this is done without any fire, then there is no elimination of potential pathogens, no fire mineralization of biomass freeing nutrients or other beneficial processes that result from natural fire. Prescribed fires in this vegetation type, however, are almost always out of the natural fire regime (Parker 1987, 1990, 1993), differentially impacting their recovery.

At the other extreme, effective long-term fire suppression can also be problematic. In northern California, for example, Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) has been rapidly expanding into forests and chaparral. Because Douglas-fir shares fungal mutualists with Arctostaphylos, mycorrhizal root symbionts of a large diversity of fungi, Arctostaphylos differentially facilitates the invasion of chaparral by Douglas-fir (Horton et al. 1999). As the trees grow and as more trees establish and fill in gaps, suddenly chaparral is shaded out and plants are killed off. Should the stand of trees remain long enough, any remaining seeds of chaparral species in
the soil will lose viability and the site will have been converted.

Other management actions are similarly problematic. Attempts to stabilize recently burned areas by seeding in a variety of different species or covering with straw generally suppress or reduce recovery by species dependent on seedlings arising from soil seed banks (Conard et al. 1995; Beyers et al. 1998; Robichaud et al. 2000; Beyers 2004). Manipulating “fuel” by thinning, clearing, grinding, chaining, chipping or other processes are devastating to species with soil seed banks. Not only are the adults killed, but the soils are disturbed without stimulating recovery. Disturbance opens the sites to invasion by introduced annual grasses or weeds (Keeley 2005). Fuel breaks, whether as large open areas in Southern California or as shaded fuel breaks in Northern California, become highways for invasive species (Keeley 2006; Merriam et al. 2006). Following fire, these species rapidly invade chaparral, reducing or eliminating recovery.

All of these management actions restrict production of Arctostaphylos and Ceanothus seed and its incorporation into a seed bank, inhibit re-establishment, cause mortality of seeds in the seed bank, or facilitate invasive species and type conversion of sites (Table 1). This means conservationists have a major job influencing policies governing the spread of development into hazardous areas and also subsequent activities thought to increase fire safety. Because the two most diverse woody genera found in California are at stake, as is the vegetation type that characterizes California, conservation of these species needs to become a priority.

### Table 1. Problems managing persistent soil seed banks in high intensity fire chaparral vegetation.

<table>
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<th>Management action</th>
<th>Seed bank response</th>
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| Failure to suppress fires at too short a time interval | * Failure of seed production  
* Loss of obligate seeders  
* Inhibition of facultative sprouter recruitment  
* Invasive species displacement of natives |
| Post-fire seeding of grasses or other species | * Inhibition of chaparral reestablishment  
* Invasive species displacement of native |
| Fuel manipulation                  | * Loss of seed production  
* Loss of vegetation  
* Invasive species displacement of natives |
| Effective long-term suppression of fires | * Mortality of seed in soil seed bank  
* Displacement of chaparral by forest or other vegetation |
| Fuel breaks                        | * Physical loss of persistent soil seed banks  
* Invasive species displacement of natives |
| Prescribed fires                   | * Fires at conflict with natural fire regime can reduce seed bank response, even inhibit sprouting  
* Invasive species displacement of natives  
* Too small an area can impact recovery due to excessive seed and seedling predation |
| Non-fire manipulation of seed bank | * Reduced emergence and loss of species  
* Conflict in germination cues leading to reduced emergence in one or more groups of species |

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### CONCLUSIONS AND RECOMMENDATIONS

Obligate seedling species of Arctostaphylos and Ceanothus are adapted to a particular fire regime of hot, dry-season wildfires that have sufficient between-fire timing to permit seed bank development. Because of that, these plants are sensitive to:

* too frequent fires: cannot form seed banks (becoming common in southern California)
* too infrequent fires, especially in northern California or the Sierran foothills, conifers can invade and extinguish chaparral
* off-season, poor intensity, or small prescribed burns all result in mortality in the seed bank or failure of seedling establishment

Ironically, currently in California, almost all obligate seeders can be divided into two groups, populations declining slowly, or populations declining rapidly.

The current rush to create fuel breaks and fuel manipulations in chaparral is leading to a rapid decline in the health and distribution of a large variety of chaparral types. As a typical politically driven management action, the general public feel safer while natural resources decline, yet safety is not actually improved. Given that fuel manipulations do not stop fires in this vegetation type, fuel breaks and
fuel manipulations need to be challenged for their true costs and benefits and weighed against the permanent loss of natural resources. Our current pattern of development and response to wildfires threatens the persistence of chaparral in many parts of California. We not only lose a diverse and endemic vegetation with a high number of rare or restricted species, but we facilitate this loss by supporting an expanding fire fighting effort without evaluating the societal costs and the long-term loss of these species.

The increased human population size in California and differential expansion into wildfire zones provides much of the impetus for this essay, but these problems will only worsen in the future without some type of action. Providing management and policy recommendations are beyond my expertise, yet obviously policies should encourage urban infill rather than low-density development in wildfire zones. Others emphasize limiting development in fire-prone chaparral areas as well (Moritz and Stephens 2008) due to the complexities of wildfires and evacuating residents, especially in the context of our uncertainty about how climate change will impact fire regimes in California (Price and Rind 1994; Westerling and Bryant 2008; Miller et al. 2009). Because Americans have a distinct perspective on private property, restricting development is particularly difficult. However, the desired effect of restricting development often can be achieved voluntarily by providing appropriate information to the public and to the property buyer. Similar to earthquake fault warnings, titles to property in wildfire hazard areas should have warnings; this was once recommended by a former head of the Department of Fire and Forestry Protection and was quickly defeated in the state legislature.

Meanwhile, the costs of developing in these areas are imposed on all of us. Policy changes that restrict development would be helped by insurance regulation that truly reflects differential wildfire hazards rather than spreading the costs among all of us. Meanwhile, the proportion of the state budget dedicated to the California Department of Fire and Forestry Protection (CalFire) continues to increase, requiring urban dwellers to subsidize these essentially wildland developments; regional fire management plans should be completed and implementation locally subsidized prior to any further development. This also suggests there should be a differential tax rate on property in wildfire hazard areas; otherwise, taxes on urban dwellers represent a “confiscatory take” on private money to support the development and protection of other people’s private property. An ideal solution is for expansion of public property in chaparral areas, especially in sites with rare or geographically restricted obligate seeders; national parks in chaparral habitat can provide critical educational opportunities. Ultimately, conservationists, ecologists and other scientists have to promote more environmental literacy; otherwise, little will be left to conserve.

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LITERATURE CITED


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