FIRE IN MEDITERRANEAN CLIMATE ECOSYSTEMS—A COMPARATIVE OVERVIEW

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ABSTRACT

Four regions of the world share a similar climate and structurally similar plant communities with the Mediterranean Basin. These five areas, known collectively as "mediterranean-type climate (MTC) regions", are dominated by evergreen sclerophyllous-leaved shrublands, semi-deciduous scrub, and woodlands, all of which are prone to widespread crown fires. Summer droughts produce an annual fire hazard that contributes to a highly predictable fire regime. Fire has been an important factor driving the convergence of these systems and is reflected in plant traits such as lignotubers in resprouting shrubs and delayed reproduction that restricts recruitment to a postfire pulse of seedlings. On fertile soils where postfire resprouting is very rapid, opportunities for postfire seedling recruitment are limited and thus these woody taxa have not opted for delaying reproduction. Such *fire-independent recruitment* is widespread in the floras of MTC regions of the Mediterranean Basin and California and *postfire seeding* tends to dominate at the more arid end of the gradient. Due to very different geological histories in South Africa and Western Australia, substrates are nutrient poor and thus postfire resprouters do not pose a similar competitive challenge to seedlings and thus postfire seeding is very widespread in these floras. Although circumstantial evidence suggests that the MTC region of Chile had fire-prone landscapes in the Tertiary, these were lost with the late Miocene completion of the Andean uplift, which now blocks summer lightning storms from moving into the region. Today these five regions pose a significant fire management challenge due to the annual fire hazard and metropolitan centers juxtaposed with highly flammable vegetation. This challenge varies across the five MTC landscapes as a function of differences in regional fuel loads and population density.

Keywords: chaparral , convergent evolution, fire, fynbos, heathlands, matorral, postfire seeders, resprouters, serotiny

INTRODUCTION

Fire is a global ecosystem process, with approximately a third of the land mass experiencing frequent intensive burning (Chuvieco et al., 2008). A growing recognition of the importance of fire is the emerging discipline of *pyrogeography*, which considers fire not only as a local factor driving the assembly of ecological communities (Keeley et al., 2012), but also as a global Earth System process (Bowman et al., 2009) of varying importance since the first land plants spread sufficiently to create contiguous fuels (Pausas and Keeley, 2009).

Ecosystems in the Mediterranean Basin are highly fire-prone, and this is also true of the other four mediterranean-type climate (MTC) regions in the world (Fig. 1). These landscapes share a similar climatic regime of winter precipitation with mild temperatures, alternating with summer drought under high temperatures. A key feature of MTC regions is that precipitation exceeds potential evapotranspiration during the rainy season, resulting in plant growth sufficient to produce contiguous fuel loads that are highly flammable during the summer drought. Thus, on an annual basis they are highly flammable and prone to high-intensity fires resulting in common ecological responses
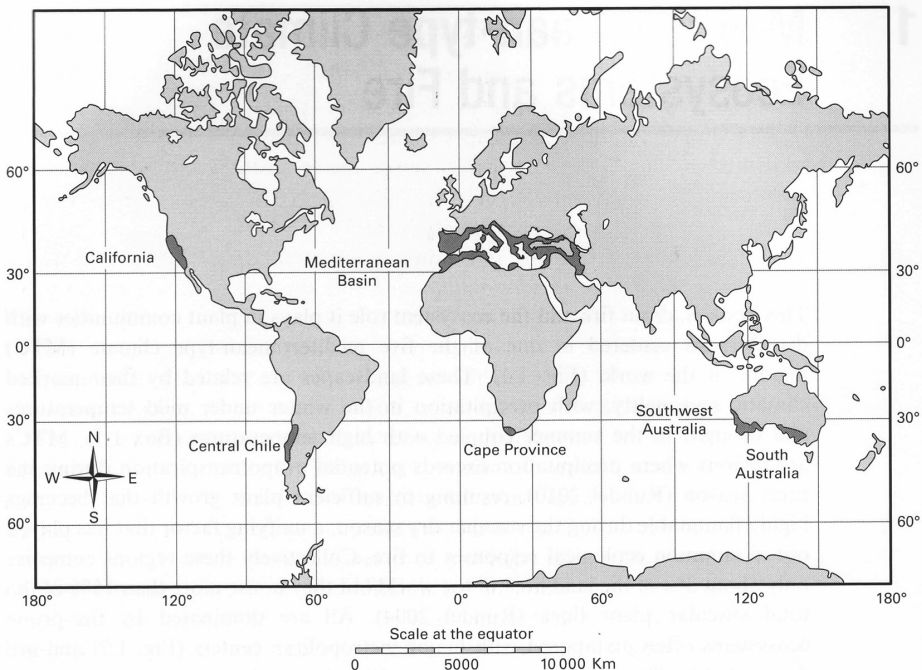

Fig. 1. On the western sides of continents between 30-40° latitude are located the five mediterranean-type climate (MTC) regions discussed here (from Keeley et al., 2012).

to fire. From a fire management perspective MTC ecosystems present major challenges, since they are often juxtaposed with large metropolitan centers. This creates substantial fire risks to local inhabitants and challenges to the balance between resource protection and fire risk.

In addition to producing conditions conducive to an annual fire hazard, the MTC is dominated by species that share a great many similarities in growth form and life history. The largest expanse of landscape in each region is dominated by evergreen sclerophyllous-leaved shrubs. Although this has historically been viewed as a demonstration of climatically driven ecosystem convergence (e.g., Mooney, 1977), similar fire regimes are an equally important driver of convergence across these MTC regions (Keeley et al., 2012). Common to all regions are shrubs with basal lignotubers that resprout vigorously after fire and, to all but one, a postfire pulse of seedling recruitment. Nonetheless, each region has unique characteristics relative to the range of plant responses to fires, due to different phylogenetic histories, subtle climatic variations, and not so subtle geological differences.

Although all MTC regions are dominated by evergreen sclerophyllous-leaved shrubs, this growth form is widely distributed in isolated patches under other climatic regimes, suggesting the growth form is a response not to synoptic weather patterns that drive the MTC, but rather to a range of conditions that generate soil drought (Keeley et al., 2012). The contribution of the MTC is that, by coupling seasonal drought with high summer temperatures, it has resulted in a significant expansion of suitable habitat for this type.

The Mediterranean Basin is the nominate MTC landscape and comprises the largest east–west expanse of all the MTC regions, followed by Australia, while South Africa represents the smallest. Broad-leaved evergreen sclerophyll woodlands are abundant in the Mediterranean Basin, California, and Australia, of lesser importance in central Chile, and rather depauperate in the Cape Region. Taller stature forests are abundant in California and South Australia. The fire regime in shrublands is one of high-intensity crown fires, but depending on tree density and understory vegetation, woodlands and forests may burn in crown fires or low-intensity surface fires.

PLANT RESPONSES TO FIRE

Crown fires result from a continuity of fuels both vertically and horizontally, killing all aboveground biomass over vast portions of the landscape. Plant recovery by colonization from outside the burn perimeter is very limited, due in part to the large area/perimeter ratio for most burns. In all likelihood this has been a factor in the selection for endogenous regeneration of most shrubs, which means they recover in situ by resprouts or from a postfire pulse of seedlings from dormant seed banks. Although some animals survive fires in burrows, many populations are extirpated by fire and depend on recolonization from meta-populations outside the burned area.

POSTFIRE RESPROUTING

Common to all MTC shrublands are woody species that resprout vegetatively after

fire, from stems or roots, and thus individual genets may survive through many fire cycles. Resprouting is a rather ubiquitous trait in woody dicots (Wells, 1969; Pausas et al., 2004), so there is nothing unique to MTC regions in this regard. However, MTC shrublands are unique in that many of the dominant species resprout from basal lignotubers (Fig. 2) that are produced as a normal part of development (Canadell and Zedler, 1995). These taxa generally comprise a subset of all resprouting species (Keeley et al., 2012). For example, in the Mediterranean Basin almost all evergreen shrub taxa resprout but only species of *Erica, Phyllyrea*, and *Arbutus* produce lignotubers. Also unique to some MTC ecosystems are shrub species that completely lack the capacity for resprouting (Wells, 1969), contrary to the supposition that all species resprout but differ in level of resprouting (Vesk and Westoby, 2004).

Even for resprouting species, not all members of a population resprout after fire, and the proportion failing to resprout may range from 0–100% (Keeley et al., 2012). Resprouting capacity is a function of species-specific and age-specific traits, fire intensity, and the quantity and timing of pre- and postfire precipitation, among other factors. Long fire-free intervals potentially inhibit resprouting by generating higher fire intensity (Moreno and Oechel, 1994). Antecedent drought may also play a role in that it leads to die-back of canopy foliage, which contributes to higher fire intensity, and postfire drought can inhibit survival of resprouts. Shorter fire intervals, and fires in certain seasons, can deplete storage carbohydrate reserves and reduce resprouting as well (Rundel

Fig. 2. Resprouting lignotuber of *Arbutus andrachne* (Ericaceae) from southern Turkey in the eastern Mediterranean Basin (photo by J. Keeley).

et al., 1987; Canadell and López-Soria, 1998; but cf. Cruz et al., 2003). In California chaparral, evergreen shrubs are more likely to resprout if they are larger, whereas semi-deciduous sage scrub species have a much greater capacity for resprouting when young, and this has been attributed to different phylogenetic histories (Keeley, 2006). Moreira et al. (2012) have proposed a model of the ecological factors driving intraspecific variability in postfire respouting that considers three sequential steps: initial ability to resprout, resprouing vigor, and post-resprouting survival.

Arborescent growth forms often posses the capacity for epicormic sprouting from buds underneath the bark along the main stems and branches. This is widespread in the genus *Quercus* in the northern hemisphere and *Eucalyptus* in Australia. In the latter case, entire forests burned in high intensity crown fires may resprout and stand as an exception to the northern hemisphere generalization that crown fires in forests can be equated with stand-replacing fires (Keeley et al. 2012).

POSTFIRE SEEDING

In all of the MTC regions except Chile, there are shrub species that have evolved delayed reproduction, where, despite more or less continuous seed production, seedling recruitment is nil throughout the life of the plant and occurs as a single pulse after fire. These species either produce seeds that are deeply dormant and require a cue from fire to trigger germination (Keeley and Fotheringham, 2000) or they produce serotinous cones or fruits that only open after fire (Lamont et al., 1991; Ne'eman, 1997). Delaying reproduction for decades or longer has considerable costs in terms of potential lifetime reproduction (e.g., Cole 1954), and thus conditions suitable for seedling recruitment must be rather poor in mature shrublands, but greatly improved after fire.

In many species with postfire seedling recruitment the parent shrubs have retained the capacity for resprouting after fire, and these species have been termed *postfire facultative seeders*. There are other species, however, that have no capacity for resprouting and they are *postfire obligate seeders*. In a few cases there is intra-specific variation such that some populations are facultative seeders and others are obligate seeders. In addition to the cumulative effect of lost reproductive opportunities considered by Cole (1954), obligate seeders face an additional risk in that they are highly sensitive to short fire return intervals, termed *immaturity risk* (Zedler, 1995).

In the Mediterranean Basin, postfire seeders are in diverse families including the Cistaceae, Ericaceae, Fabaceae, Lamiaceae, Rosaceae, and Pinaceae (Paula et al., 2009). Particularly common are the largely obligate seeders *Cistus* and the facultative seeders such as *Erica, Genista*, and *Ulex*. In California, seeders are in all of these families plus the Rhamnaceae. Postfire seeding in southern hemisphere fynbos and heathlands occurs in members of most of these families plus the Myrtaceae and Proteaceae.

Modes of seed storage

Species with a postfire pulse of seedling recruitment differ in mode of seed storage between fires. The majority of species accumulate seeds in the soil, where seeds lie dormant until germination is triggered by fire. Also a substantial fraction of the flora in

some ecosystems accumulate seeds in serotinous cones or fruits that are retained within the canopy of the parent plant until fire triggers the opening of the cones and dispersal of largely non-dormant seeds.

Species with soil-stored seeds are vulnerable to granivores and this can be very significant, often with a large portion of the annual seed crop being consumed (Parker and Kelly, 1989). In order to accumulate seeds it is only necessary that some portion of the seed pool is dormant. Non-dormant seeds will germinate in the first growing season and their fate is a function of their location. If germinating under or near the shrub canopy, there is a good possibility the seedlings will not survive. Seeds arriving on more open sites stand a better chance of successful recruitment. For example, the Californian *Adenostoma fasciculatum*, a prominent postfire seeder, has a portion of each annual seed crop that germinates in the understory and in gaps in the shrub canopy but these recruits are short-lived, due to herbivory and other factors. However, if dispersed to an open site somewhat removed from the vegetation they often will grow to maturity, and these patterns are likely true of many "postfire seeders" in other MTC ecosystems. Longevity of dormant seeds is largely unstudied, but various pieces of circumstantial evidence would suggest it is on the order of many decades or even centuries (Keeley and Fotheringham, 2000; Keeley et al., 2005).

Serotiny is found in both northern and southern hemisphere MTC ecosystems but there is a major asymmetry in importance (Lamont et al., 1991). In the Mediterranean Basin it is found in a few species of gymnosperms, in *Cupressus, Tetraclinis*, and *Pinus*, and in California in *Hesperocyparis* (formerly *Cupressus*) and *Pinus*. In South Africa and Australia it is also found in several gymnosperm genera, *Widdringtonia, Actinstrobus*, and *Callitris,* but also in hundreds of angiosperm, in families such as the Asteraceae, Bruniaceae, Casuarinaceae, Ericaceae, Rosaceae, Myrtaceae, and Proteaceae.

There are a number of ecological trade-offs associated with canopy vs. soil seed storage. Canopy seed storage provides protection of seeds from ground-dwelling granivores, although in order to avoid aerial predators it requires greater expenditure of energy on fruit and cone structures (Lamont and Enright, 2000; Hanley and Lamont, 2001). In addition, total seed storage is limited by the canopy architecture, and such species typically produce smaller postfire seedling populations than species with soil-stored seeds (Keeley et al., 2012).

Germination of dormant soil-stored seeds

Heat-shock and chemicals released from biomass combustion are two cues that trigger postfire germination of species in MTC ecosystems (Bell et al., 1993; Gonzalez-Rabanal and Casal, 1995; Keeley and Fotheringham, 2000). There are clear phylogenetic patterns in the distribution of germination cues and typically species within a lineage will respond to one but not both of these cues, although there are exceptions. Heat as a germination cue is widespread in species outside MTC ecosystems, whereas in natural ecosystems germination by chemicals from combustion is largely restricted to MTC vegetation (Keeley et al., 2012).

Species with heat-shock stimulated germination are hard-seeded species with wa-

ter-impermeable seed coats, and germination requires rupturing of the seed coat, which induces imbibition. This is widespread in plant families such as the Fabaceae, Cistaceae, Convolvulaceae, and Rhamnaceae, among others (Thanos et al., 1992; Keeley and Fotheringham, 2000; Luna et al., 2007).

Chemicals released by combustion are present in smoke and charred wood and are clear triggers to postfire germination in a great many species in MTC vegetation, with the exception of Chilean vegetation. In the Mediterranean Basin there are a number of species that are stimulated by smoke (Moreira et al., 2010), but the dependence on this cue by postfire seeder species is most widely developed in Californian, South African and Australian MTC vegetation (Keeley, 1991; Brown, 1993; Dixon et. al., 1995; Enright et al., 1997). The mechanism for smoke-stimulated germination is unclear. It is known that the chemical in smoke can be transferred to seeds as a gas, as a liquid, or by binding to soil particles with secondary release at a later time (Keeley and Fotheringham, 1997). There is growing evidence that there are a number of combustion products that stimulate germination of these species (Keeley and Fotheringham, 1997; Flematti et al., 2004, 2011; Downes et al., 2010), which is to be expected in what is likely a case of convergent evolution (but cf. Bradshaw et al., 2011).

FIRE-INDEPENDENT SEEDLING RECRUITMENT

Despite the apparent advantages of postfire seedling recruitment, a great many taxa have not modified their reproductive cycle to restrict recruitment to a single postfire pulse of seedlings. Indeed, these species produce seeds with little or no dormancy and thus fail to accumulate a seed bank for recruitment after fire. Seedling recruitment by such species is largely restricted to the understory of the shrub canopy or in open sites such as abandoned agricultural fields (Pausas et al., 2006). These species persist after fire entirely from resprouts and thus are termed *postfire obligate resprouters*. There are a number of genera of obligate resprouters that are shared between the Mediterranean Basin and California, including *Arbutus, Clematis, Lonicera, Prunus, Quercus, Rhamnus*, and *Styrax*, and many other woody taxa restricted to one or the other regions. In Chilean matorral all woody taxa are obligate resprouters and in South African fynbos there are five such taxa, but none in Australian heathlands (Keeley et al., 2012). These shrubs that recruit during the inter-fire interval all share a number of reproductive features, including animal-dispersed fruits and weakly dormant short-lived seeds with transient soil seedbanks.

DISTRIBUTION PATTERNS OF RESPROUTERS AND SEEDERS

The question of factors favoring resprouters over seeders has been addressed at many different scales. Bellingham and Sparrow (2000) attacked this question at a global scale but their predictions of how, under severe disturbance regimes, resprouting should decrease when disturbance frequency is low has many exceptions. One reason is that the factors favoring seeding over resprouting vary a great deal depending on the fire regime, e.g., crown fire vs. surface fire regimes, both between and within species. By focusing within crown fire regimes, for example, one can come much closer to consistent, broadly

applicable rules favoring one or the other strategy (Pausas et al., 2004).

One complication in understanding patterns is the failure to distinguish between obligate resprouters and facultative resprouters (here termed facultative seeders). Some studies have contrasted the distribution pattern of obligate seeders vs. congeneric facultative seeders, but this is not strictly a comparison of seeders vs. resprouters since both types have postfire seedling recruitment. A clearer comparison would be between obligate seeders and obligate resprouters. In these comparisons one general rule is that seeders dominate at the more arid end of the gradient, and resprouters at the more mesic end of the gradient. A number of authors (e.g., Wells, 1969; Herrera, 1992; Verdú, 2000; Ackerly, 2004) have interpreted this in terms of rate of adaptation to the arid conditions of the MTC. The implication of this argument is that these obligate resprouters are Tertiary "relicts" that have failed to adapt to the contemporary MTC conditions. Setting aside the fact that many postfire seeders have early Tertiary origins, there are good ecological reasons for the presence of obligate resprouters on fire-prone landscapes (Keeley et al., 2012). On mesic sites resprouters have high survival and they rapidly dominate a site after fire, leaving relatively limited space for seedling recruitment. As site aridity increases there is much greater spacing between postfire resprouts and more resources available for successful seedling recruitment. In this view obligate resprouters and seeders are subdividing resources in ways that enhance contemporary patterns of community assembly.

COMMUNITY RESPONSES TO FIRE

In the first growing season after fire, a rich flora of herbaceous and short-lived woody species establish from long-dormant soil-stored seed banks. This ephemeral "successional" flora differs in many respects between the five MTC regions. In the Mediterranean Basin it comprises many annual forbs and grasses, although most all are species that are also found on other open sites disturbed by livestock grazing, agriculture, etc. (Naveh and Whittaker, 1980; Kazanis and Arianoutsou, 2004). In California the immediate postfire environment is dominated by a near synchronous germination of native annual forbs, many of which are largely if not entirely restricted to recently burned sites. So specific to postfire conditions are these species that the majority of species have deeply dormant seeds that are mostly cued by smoke and they are referred to as *fire endemics* (Keeley et al., 2006). Both of these northern hemisphere MTC ecosystems have many short-lived sub-ligneous taxa that may persist depending on how open the site remains. In Chilean MTC shrublands there are few if any species that regularly recruit after fire from dormant seed banks (Keeley and Johnson, 1977).

Southern hemisphere shrublands have a more depauperate annual flora, and those few fire endemic annuals they have are very diminutive (Pate et al., 1985). Much more prominent in postfire environments are herbaceous perennials that were present prior to the fire but suddenly burst forth in full flower, making for a spectacular floral display on many sites (Le Maitre and Brown, 1992). These life history differences result in important differences in species diversity patterns (Keeley and Fotheringham, 2003). Postfire chaparral has the highest diversity in the immediate postfire years and then as

the shrub canopy closes in diversity is greatly reduced. Matorral and garrigue in the Mediterranean Basin follow a similar pattern unless past disturbance has opened the shrub canopy such that a closed canopy shrubland is not achieved after fire. In South African and Australian MTC ecosystems there is an increase in diversity, but many of those species persist long after fire and thus diversity stays high in mature stands (Keeley and Fotheringham, 2003).

FACTORS BEHIND NON-CONVERGENCES IN FIRE RESPONSE

Convergence theory is based on the premise that similar environments select for similar characteristics and this comes about through both evolutionary adaptation and ecological sorting. The five MTC regions have long been noted as examples of convergence in the dominance of evergreen sclerophyllous-leaved woody plant communities, and this has largely been attributed to climatic similarities (Mooney, 1977). However, subtle differences in climate, not so subtle differences in geology, and substantial differences in phylogenetic histories, have all contributed to differences in plant traits, community composition, and fire regimes. It should be taken as axiomatic that convergence is to be expected, but since no two environments are identical a more appropriate question is, "which environmental factors have played the greatest role in driving non-convergences?"

In all likelihood many of the differences in fire response between these five MTC regions are tied to different geological histories and origins of fire-prone sclerophyllous shrublands (Keeley et al., 2012). It is hypothesized that in the northern hemisphere these shrublands originated in the mid-Tertiary in isolated pockets of drought-prone substrate such as on ridgetops or rocky pole-facing slopes within a landscape dominated by more mesic and less fire-prone woodlands. The island-like patches of such fire-prone vegetation likely favored species with animal-dispersed propagules and the lower probability of fire would have favored fire-independent recruitment. These Miocene climates may have had some degree of seasonal drought, but fire hazard was likely tied to decadal climatic oscillations that would have led to large fires and expansion of shrublands into the edges of more mesic environments. Periodic but not highly predictable fires on these landscapes would have favored vigorous postfire resprouters. With the late Tertiary development of a MTC, the amount of drought prone landscape favoring these fire-adapted communities would have contributed to expansion of sclerophyll shrublands and increased predictability of fires, all of which would have selected for fire-adapted seedling recruitment.

In the southern hemisphere, evergreen sclerophyllous shrublands dominate on very nutrient-poor substrates that cover vast expanses of the landscape. Such landscapes have been present since the Cretaceous and many of the present day MTC vegetation traces origins back to at least the early Tertiary (Hopper, 2009). Regardless of climate these coarse soils would have been drought-prone and the oligotrophic nature of these substrates would have favored evergreen sclerophyllous-leaved shrubs, characteristics that contributed to their fire-prone nature. The lack of an island-like patchwork of shrub-

lands as hypothesized for the early northern hemisphere sclerophyll communities may account for the general lack of importance of obligate resprouters with animal-dispersed fruits in southern hemisphere shrublands (Keeley et al., 2012). The highly oligotrophic substrates in the southern hemisphere are thought to contribute to the high incidence of serotiny as a means of reducing seed predation (Keeley et al., 2011, 2012). Chilean landscapes tell a very different story. Their geological history was much more similar to California and during the middle Tertiary fire prone vegetation likely developed on the more drought-prone portions of the landscape. This would account for the presence of lignotuberous resprouters in their matorral vegetation (Montenegro et al., 1983). However, by late Miocene the Andean uplift had blocked summer storms from bringing summer lightning ignitions into central and northern Chile, and that pattern persists to the present. This late Miocene loss of fire-prone landscapes would have rapidly selected against postfire seedling recruitment, and would explain the absence of that functional type in present-day MTC ecosystems of Chile (Keeley et al., 2012).

LIVING WITH FIRES IN MTC REGIONS

The combination of annual fire risk and high intensity crown fires in shrublands and woodlands binds all of the MTC regions. Since these are also human population centers they share many of the same fire management concerns. Fire risk, however, varies in response to variations in fuel loads and population density between regions (Keeley et al., 2012). For example, Mediterranean Basin pine forests and Californian chaparral contrast markedly with South African fynbos and Western Australian heathlands in terms of fuel load. The much greater fire hazard in the two northern hemisphere landscapes, coupled with substantially higher human population densities, makes these landscapes particularly risky. As a consequence, catastrophic wildfires with large losses of homes and human lives are relatively unknown in MTC regions such as the Cape Region of South Africa or Southwestern Australia, but all too common in the northern hemisphere landscapes of California and the Mediterranean Basin.

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