

The Ecology of
FYNBOS

Nutrients, Fire and Diversity

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A Californian's view of fynbos

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Convergent evolution is a hypothesis that predicts similar environments will select for similar structures and functions in phylogenetically unrelated organisms. Remarkable similarities in the physiognomy of vegetations in mediterranean climate regions of the world have resulted in a great deal of interchange between scientists interested in evolutionary convergence. One ambition of mediterranean climate ecosystem comparisons has been the expectation of using information on ecosystem function in one region to make predictions in the other systems. The focus of this chapter is to consider to what extent conclusions drawn from Californian chaparral apply to the structure and function of South African fynbos.

Mooney (1977) provided a detailed comparison of Californian chaparral and Chilean matorral that revealed remarkable levels of convergence in both structure and function at the primary producer level. Non-convergence between vegetations on these two continents was attributable to subtle differences in the environments. Thus, we might conclude that deviations from convergence between California and South Africa should be attributable to deviations in ambient conditions. I suggest that much of the difference observed in vegetation structure and function between Californian chaparral and South African fynbos can be related, in large part, to differences between these two regions in stresses induced by deficits of water and inorganic nutrients.

FYNBOS VERSUS CHAPARRAL ENVIRONMENTS

Cody and Mooney (1978) summarized the major differences between chaparral and fynbos and pointed out that soil anomalies are undoubtedly an important factor accounting for much of the non-convergence between

these mediterranean climate vegetations. The nutrient deficient nature of fynbos soils is well known, in particular the deficiency of nitrogen and phosphorous. To a southern Californian it was surprising to hear chaparral soils characterized as 'high fertility', relative to fynbos soils.

Differences in water stress between these regions, however, are potentially as important as soil nutrition in accounting for degrees of non-convergence. A comparison of fynbos and chaparral sites at similar latitudes and elevations reveals several indicators of more severe summer water stress in California (Table 15.1). At similar latitudes, elevations, and distances from the coast, southern Californian chaparral sites have substantially less precipitation and a greater proportion of it concentrated in winter. On most chaparral sites summer quarter precipitation seldom exceeds 1–4% and interior sites typically have summer temperatures above 30°C. Rutherford and Westfall (1986) compared the distribution of fynbos and other more arid vegetations relative to the percentage of winter-half rainfall and summer aridity (Figure 15.1). Californian chaparral sites all fall on the border between fynbos and the more arid succulent karoo vegetation. Sites with annual precipitation comparable to many fynbos sites are forested in California.

In addition to differences in precipitation, temperature extremes are more severe in chaparral relative to fynbos (Table 15.1). Although the temperature differences may not seem particularly great, Axelrod (1981) maintains that Holocene climate changes of only 1°C in mean temperature of the warmest or coldest month have had a profound impact on vegetation distributions. Another indication of greater extremes in California is the unpredictability of precipitation; for example,

TABLE 15.1 A climatic comparison between typical South African fynbos stations and southern Californian chaparral stations.

	South Africa			Southern California		
	Paarl	Ceres	Swartboskloof	La Mesa	Echo Valley	San Dimas
Latitude	33° 43'S	33° 22'S	34° 00'S	32° 46'N	32° 54'N	34° 12'N
Longitude	18° 57'E	19° 18'E	18° 57'E	117° 01'W	116° 39'W	117° 46'W
Elevation (m)	166	456	305	162	1 070	850
Distance to coast (km)	45	89	20	20	55	66
Precipitation:						
Annual mean (mm)	933	1 276	1 553	304	449	670
% wettest quarter	44	39	42	51	46	59
% driest quarter	9	7	11	2	4	1
Driest month (mm)	22	14	50	1	4	0
Mean temperature:						
Coollest month (°C)	6.2	2.9	6	12.2	1	2.6
Warmest month (°C)	29.7	29.9	27.6	22.3	32	30.7

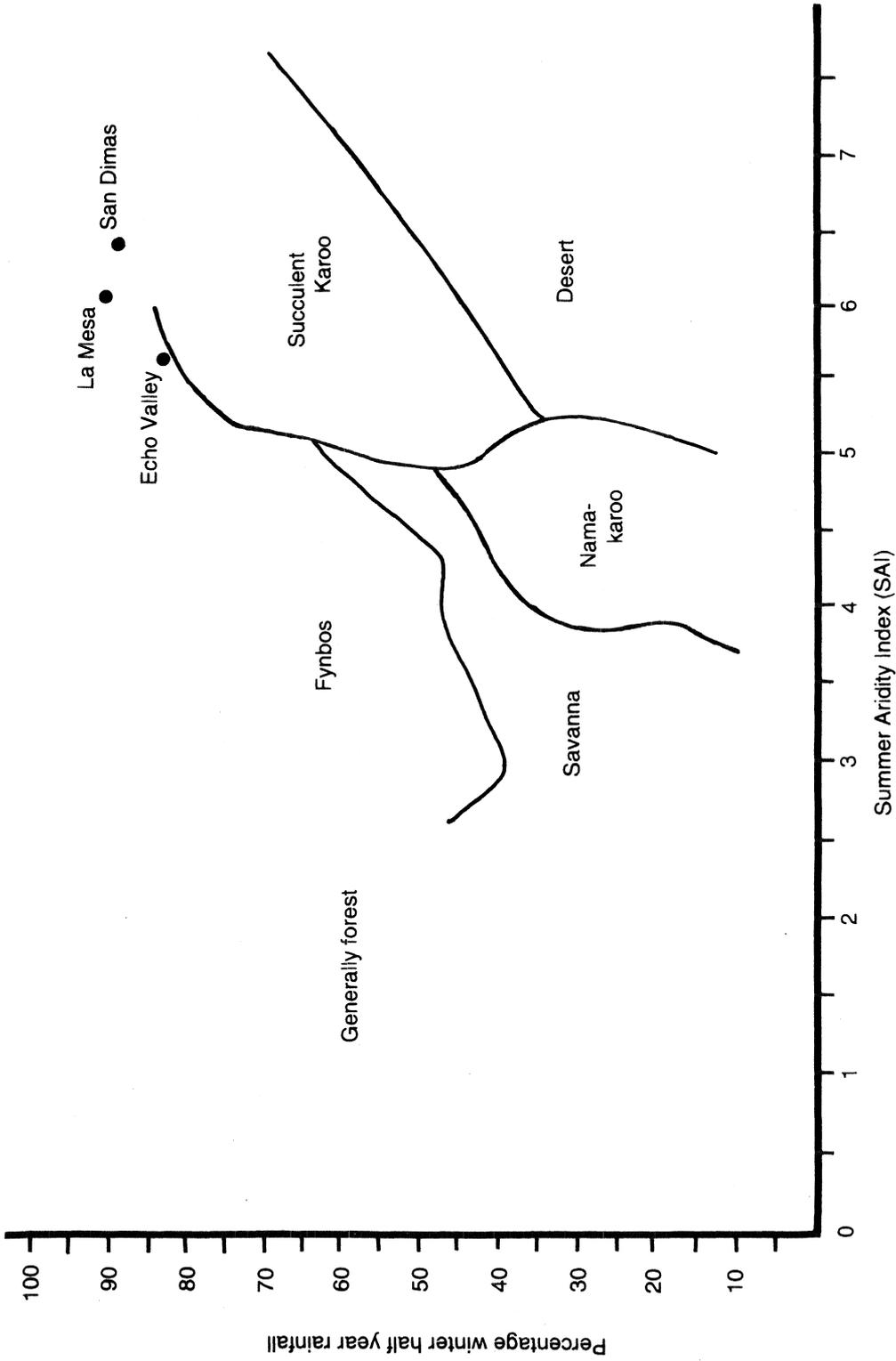


FIGURE 15.1 The distribution of the fynbos biome relative to the summer aridity index and the percentage of winter half year rainfall (redrawn from Rutherford and Westfall 1986). The relative position of southern Californian chaparral sites from Table 15.1 is indicated.

➤ : 200% (Keeley and Keeley 1988) whereas most fynbos sites seldom exceed 100% (Le Maitre 1984). In many respects, fynbos could be described as having a much more equable climate.

In summary, abiotic stresses are different in these regions, and their potential for inducing structural and functional differences in the communities is a function of the time scale over which they operate. Water stress is a greater bottleneck to survival than nutrient stress; brief periods of several months of intense water stress may result in extirpation of a species from a site, whereas longer time scales may be required for nutrient stress to have a similar impact.

CHAPARRAL/FYNBOS COMPARISONS

Community structure

A comparison of community attributes of chaparral and fynbos is shown in Table 15.2.

STRATA

At a rather gross level, these vegetations are readily separable by the fact that chaparral sites are typically dominated by one to a few shrubs that form a mono-layer of overlapping branches often exceeding 100% ground surface cover and commonly 2.5–4 m high (Figure 15.2). This contrasts markedly with the multi-layer restioid-ericoid-proteoid mix in fynbos communities in which several growth forms share dominance and cover is generally less than 80% (Kruger 1979, 1985). Undisturbed mature chaparral has no component comparable to the restioid and ericoid strata.

Intense competition for scarce nutrients has been suggested as a factor leading to growth form diversity in fynbos (Tilman 1983). Another factor favouring low-growing, shallow-rooted restioid and ericoid growth forms would be the equable seasonal distribution of precipitation. In chaparral, brief intense storms concentrated in winter would, as horticulturists have long known, result in 'deep watering' which favours deep-rooted shrubs and trees.

BIOMASS

The multi-strata, more open nature of shrub distribution in fynbos is reflected in lower biomass relative to chaparral; mature fynbos sites are typically between 15 000 to 26 000 kg per ha (Kruger 1977; Rutherford 1978; Kathan 1981; Stock and Allsopp this volume) whereas mature chaparral is often double that amount (Schlesinger and Gill 1980; Ehleringer and Mooney 1982). Some fynbos sites — e.g. ones dominated by *Widdringtonia* (Cupressaceae) or other trees — may have biomass levels comparable to chaparral (Van Wilgen 1982).

SPECIES DIVERSITY

Species richness is significantly greater in fynbos than in chaparral and possibly greater, at a regional level, than the richest tropical rain forests (Cowling et al. this volume). This conclusion is, however, dependent upon the particular measure of diversity and the scale of focus (Bond 1989). In terms of landscape level comparisons, the Cape Floristic Region is markedly richer in species than the California Floristic Province (Cowling et al. this volume).

A precise comparison of community or alpha diversity is difficult because Californian ecologists have not collected the detailed information on species richness at different scales as is widely available for fynbos; the data on chaparral cited in Specht (1988) or in Naveh and Whittaker (1979) is incomplete by fynbos standards.

One of the complications in comparing alpha diversity in fynbos and chaparral is that species richness is usually reported for a single point in time. Species richness is often a function of time since fire and is greatest after fire (Campbell and Van der Meulen 1980; Keeley et al. 1981; Cowling 1983). Several factors would tend to inflate, relative to chaparral, the species richness reported for fynbos. Due to the higher fire frequency (see below), most fynbos stands are younger than chaparral stands. In fynbos, diversity peaks in the second year and may remain at that level for many years (Kruger 1986). In fact, it appears that the species richness values for mature fynbos (Cowling et al. this volume) are not markedly lower than values for post-fire fyn-

TABLE 15.2 A comparison of Californian chaparral and South African fynbos, based on literature discussed in the text and personal observation.

	California		South Africa
Vegetation structure	Mono-layer		Multi-layer
Shrub dominants	Few species		Many species
Shrub coverage	80–150%		< 80%
Community diversity		<<	
Shrub structure and function			
Branching		>>	
Spinescence		>>	
Summer xylem water potentials	Low		Moderate
Foliage nutrients (N and P)		>>	
Sclerophyll index		<<	
Consumers			
Phytophagous		>?	
Granivory		<?	
Termites		<	
Shrub reproduction			
Flowering phenology	Largely spring		Spring and summer
Flower size	Small–medium		Medium–large
Dioecy	Rare		Frequent
Wind pollination	Rare		Frequent
Bird and mammal pollination	Rare–uncommon		Frequent
Insect pollination	Hymenoptera		Coleoptera
	Lepidoptera		
Seed production	Water limited ?	>?	Pollinator limited ? Nutrient limited ?
Seed banks			
Transient	Many species		Few species
Persistent	Soil-stored		Canopy-stored and soil-stored
Seed dispersal			
Ornithochory	Frequent		Rare
Myrmecochory	Rare		Very common
Anemochory	Uncommon		Common
Telochory	Common		Common
Fire regime			
Frequency		<<	
Intensity		>	
Post-fire response			
Temporary flora	Annuals		Geophytes
Shrub resprouters	Facultative and obligate		Mostly facultative
Seeders	Facultative and obligate		Facultative and obligate
Plant resilience			
Short fire-free periods		<<	
Long fire-free periods		>>	

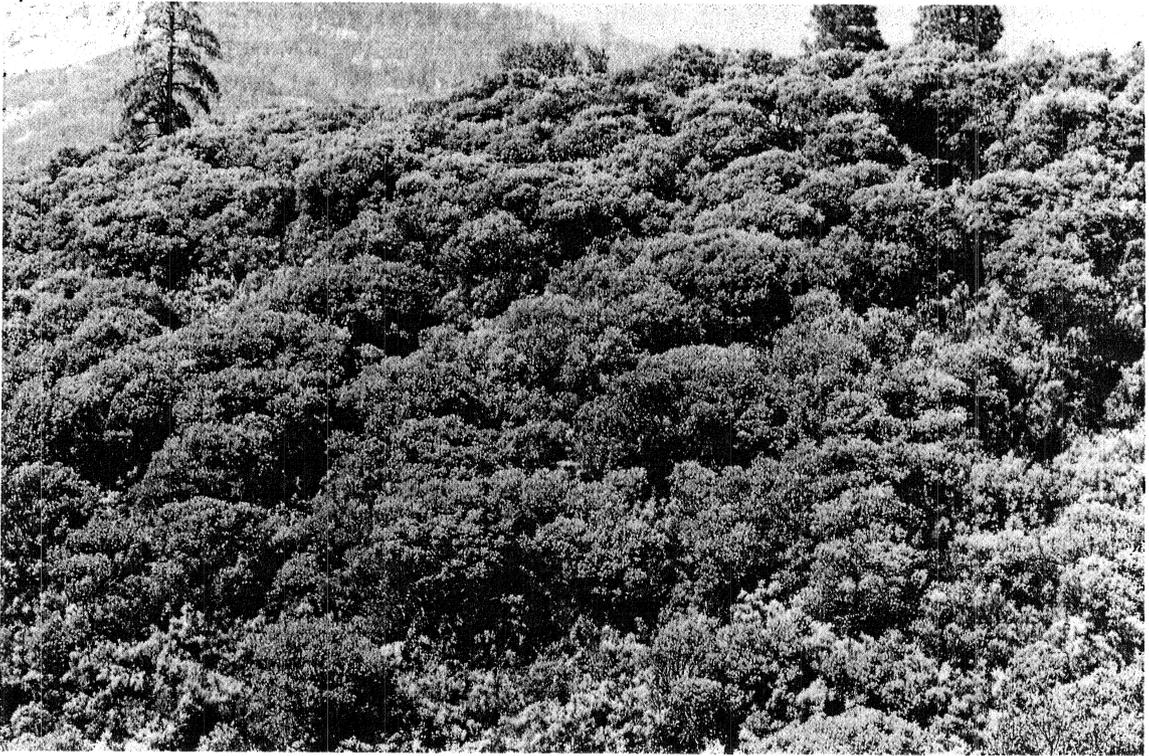


FIGURE 15.2 The typical single stratum of shrub dominants in Californian chaparral.

bos (reported in Specht 1988). This pattern would not be observed in chaparral. Due to the ephemeral nature of the chaparral post-fire flora, the decrease in species diversity is more rapid; peak species richness in chaparral occurs in the first post-fire year and declines rapidly over the next several years (Keeley et al. 1981; Davis et al. 1988). In chaparral more than half of the flora may be composed of these post-fire annuals, many of which are present between fires only as dormant seed; most studies fail to include these species. Even annuals that establish between fires are often not included due to their very ephemeral nature. Clearly, a detailed comparison of species diversity at different successional stages in chaparral and fynbos is needed.

Although precise numbers are lacking for a comparison of chaparral and fynbos, it is clear that species richness in fynbos is extraordinarily high, as is the diversity of theories on the causes. Nutrient stress in fynbos has been suggested as a mechanism for pre-

venting dominance by any single species and selecting for a diversity of growth forms with competing modes of nutrient capture (Tilman 1983). This theory may account for differences in species richness between chaparral and fynbos. Habitats with low nutrients have low plant biomass and high light penetration (Tilman 1988). More nutrient-rich chaparral sites with higher plant biomass have greater light extinction by the shrub canopy, a factor potentially limiting understorey diversity. In fynbos, Campbell and Van der Meulen (1980) noted that after fire, species diversity declined the most in fynbos that attained the greater biomass, and this was linked to loss of species from the lower strata. Others have also noted a decline in understorey species richness as the overstorey proteoid dominance increased in fynbos (Cowling and Gxaba 1990; J Midgley personal communication).

In addition, greater summer moisture stress in chaparral may limit the diversity of successful physiological modes and increase

the extirpation of species from a site. Testing this hypothesis is problematical. However, regional comparisons provide circumstantial evidence that such a factor may be important. Today species-rich pockets of palaeoendemics in California are positively correlated with warm season precipitation (Raven and Axelrod 1978), suggesting that increasing summer aridity, although contributing to accelerated speciation in some annual taxa, may have contributed to decreased species richness in other groups. More extreme winter and summer temperatures may also limit the options available to chaparral taxa. Axelrod (1973) maintains that a gradual decrease in equability of the Californian climate has resulted in a decrease in species richness during the Quaternary.

Nutrient stress, coupled with very frequent disturbance from fire, may maintain the fynbos in a non-equilibrium condition that prevents a few species from dominating a site such as in mature chaparral (Huston 1979; Tilman 1983; Cowling 1987). Cowling (1987) has suggested that fire has played an important role in disruptive selection leading to high species diversity in fynbos, although it is not clear if this could account for differences in species richness between fynbos and chaparral.

To summarize, in fynbos, the more equable climate with less stressful summer drought, reduces the potential abiotic weeding-out of species, and the nutrient-poor soils, by limiting biomass production and thus areal competition, reduce the potential biotic weeding-out of species. Although there are no community level tests of these ideas, regional patterns in California are consistent with these hypotheses. For example, in California, species richness increases with equability of the climate (Moldenke 1975; Richerson and Lum 1980) and the most diverse and endemic-rich chaparral communities are on oligotrophic Quaternary aeolian sands with a marked marine influence in central coastal California (Griffin 1978; Raven and Axelrod 1978; Axelrod 1982; Davis et al. 1988). Species richness on these sites is several times greater than areas of comparable size on more fertile sites under a less equable climate in the interior parts of the California Floristic Province (Richerson and Lum 1980).

Shrub structure and function

Relatively detailed structural comparisons of chaparral and fynbos have revealed marked differences (Cowling and Campbell 1980) and similarities (Cody and Mooney 1978).

MORPHOLOGY

The branching of the dominant woody species is distinctly greater in chaparral species, although the reasons for this are not obvious. Possibly nutrient allocation patterns are different in morphologies which grow from fewer more robust shoots, with lower surface to volume ratio, than in morphologies that proliferate many side shoots. Another possibility is that there are allometric explanations tied to the size of flowers, such as Bond and Midgley (1988) have suggested for *Leucadendron*.

DECIDUOUSNESS

Cowling and Campbell (1980) pointed out a marked difference in growth forms; low elevation summer-deciduous elements and high elevation winter-deciduous elements are largely lacking in fynbos. The greater summer rainfall and higher winter temperatures in the fynbos biome (Table 15.1) may play a role, although low nutrient soils would also select for evergreenness (Campbell and Werger 1988).

WATER POTENTIALS

Summer water stress is generally much greater in chaparral than in fynbos species (Stock et al. this volume). Dominant fynbos shrubs seldom reach xylem water potentials below -3 MPa (Miller et al. 1983; Miller et al. 1984; Moll and Sommerville 1985; Smith and Richardson 1990), whereas chaparral shrubs in summer routinely reach levels twice as low as these (Dunn et al. 1976; Miller and Poole 1979; Mooney and Miller 1985). Lack of intense drought stress is also suggested by the fact that fynbos shrubs reach zero stomatal conductance at substantially higher water potentials than observed for chaparral species (Miller 1985; Poole et al. 1981).

These differences may be attributable to greater total precipitation and greater summer rainfall coupled with lower summer temperatures on most fynbos sites. Richardson and Kruger (1990), however, suggest that sparse canopies of fynbos communities may be insufficient to dry the soils. If true, then the greater

coverage typical of chaparral communities may account for a more rapid exhaustion of soil moisture leading to greater water stress. Richardson and Kruger's suggestion seems to contradict the prediction of Poole and Miller (1981) that communities should converge in total transpiration. However, Poole and Miller did not consider sites of radically different nutrient status.

Despite these differences, photosynthetic characteristics are remarkably similar between fynbos and chaparral taxa (Mooney et al. 1983; Van der Heyden and Lewis 1989; Von Willert et al. 1989; Stock et al. this volume).

FOLIAGE NUTRIENTS

Foliage nutrients, in particular N and P, are generally substantially lower in fynbos than in chaparral species (Rundel 1988). This results in much higher sclerophyll indices (lignin + cellulose/protein) in fynbos; 391–1 885 with 50% of the taxa reported as over 1 000 in fynbos, whereas in chaparral reports range from 266–688 with 50% less than 500 (Specht 1988). These differences are undoubtedly related to the greater nitrogen use efficiency of fynbos taxa, which is to be expected in plants from nutrient-poor sites (Rundel 1982; Field et al. 1983).

Additionally, the more equable climate may also contribute to a higher sclerophyll index in fynbos species. Favourable soil moisture conditions during the summer and higher air temperatures during the winter (Table 15.1) allow fynbos shrubs to maintain positive carbon balances throughout the year (Stock et al. this volume).

It is of interest that the level of foliage nutrients in chaparral from oligotrophic soils in central coastal California is more similar to fynbos than to chaparral on other sites (Rundel 1988).

Consumers

Based on differences in the sclerophyll index, the foliage of fynbos plants could be expected to be of lower nutritive value and thus I would predict that foliage herbivores would play a greater role in chaparral.

Although precise data on primary consumers are unavailable to test this hypothesis, Johnson (this volume) concludes that certain

herbivore guilds are poorly developed in fynbos. However, the degree of similarity in the foraging ecology of birds in fynbos and chaparral (Cody and Mooney 1978) indicates a strong degree of convergence in the trophic and foraging levels of these secondary consumers, suggesting the primary consumer faunas may be similar. On the other hand, spines are developed to a much greater degree in chaparral (Cowling and Campbell 1980) and this would be expected if chaparral had evolved under greater selective pressure by browsing animals. Much more comparative work between these two regions is needed before this problem is adequately addressed.

Fynbos communities are markedly different from chaparral with respect to termite faunas. Although numbers are lacking, certainly termite presence is far more impressive in fynbos, as evidenced by the numbers of termite mounds. Possibly the more equable climate, higher winter temperatures, and higher summer moisture favour termite faunas. Also, fynbos is rich in fine twigs and stems produced by the restioid and ericoid layers, and these resources would be more readily available to termites than the bulky wood products available in chaparral.

Reproductive biology

PHENOLOGY

Phenological studies suggest that flowering is more synchronized to spring in chaparral, although a few species do extend into the summer e.g. *Adenostoma sparsifolium*, *Heteromeles arbutifolia* (Cody and Mooney 1978). Also, in chaparral there are many taxa that flower (prior to growth) in late winter and early spring on 'old wood' from buds initiated in the previous growing season e.g. all *Ceanothus*, *Arctostaphylos*, and *Rhus* spp. (not *Malosma*). It has been suggested that this pattern allows these plants to speed up their spring flowering and possibly 'beat' the summer drought (Keeley and Keeley 1988).

Fynbos taxa flower over a more extended duration well into summer (Pierce 1984; Moll 1987) probably because of the greater xylem water potentials. Spreading out the duration of flowering over the year may be an important means of reducing competition for pollinators and could be a factor promoting species rich-

ness. Summer flowering and fruiting in myrmecochorous species (see below) may have been selected in order to disperse seeds at the time of maximum ant activity (Pierce 1984). Le Maitre (cited in Pierce 1984) notes that *Leucospermum* species flower on the previous year's twigs prior to vegetative growth, although these taxa typically flower in summer, and, therefore, this phenological pattern does not result in a speeding up of flowering, as is the case with Californian taxa that flower on old growth.

Although no published data are available, it seems to me that seed maturation is a much more extended process in fynbos species than in chaparral. One advantage of this would be to increase the period of time for nutrient capture, a luxury allowed by the better summer moisture conditions in fynbos.

POLLINATION

Differences in pollinating strategies are apparent. Most striking is the high incidence of anemophily (wind pollination) in the fynbos flora (Johnson this volume). In chaparral this syndrome is absent; perhaps the more closed nature of chaparral, resulting from less structural variation, may hinder the free movement of pollen. Also, wind is not nearly as predictable as in the Cape during the summer. Mammal pollination is present in fynbos but missing from chaparral. Furthermore, bird pollinators are less common and not responsible for the pollination of any major shrub species in chaparral. Although phylogenetic constraints cannot be ruled out, it is possible that the shorter duration of flower availability in chaparral may represent a bottleneck in resources that large animals are unable to survive.

Additionally, for the same reasons that fynbos shrubs have a high sclerophyll index, it is expected that carbon-rich products, e.g. nectar and flowers, are more readily available for pollinators than nutrient-rich products such as pollen (see Le Maitre and Midgley this volume). Consequently, larger pollinators, which require a carbon-rich nectar reward, may be selected for, whereas pollen-gatherers such as bees would play a subsidiary role. To me, it seemed as though bees were much less common in fynbos than in chaparral and apparently there is some data to support this

observation (see Johnson this volume). In place of bees, flower-feeding Coleoptera seemed to be much more common in fynbos than in chaparral, and this would be expected if carbon-rich compounds are more readily available. One consequence of this guild of fynbos pollinators may be that it has selected for larger flowers than are typical of chaparral species.

POLLINATION LIMITATION

Although there is little evidence (see Johnson this volume), there are reasons for suspecting that seed production in fynbos is more pollinator-limited than in chaparral; in the latter vegetation, there is good reason to believe that seed set is more often water-limited (Keeley and Keeley 1988). One phenomenon that needs closer scrutiny is the very high number of unfilled non-viable seeds reported for several fynbos species (see references in Pierce 1990). I also observed this in several taxa I collected. If true, it could reflect pollinator limitation although other reasons are possible e.g. nutrient limitations and inbreeding depression. Alternatively, a strategy of unpredictable resource availability may have selected this characteristic in order to disguise good seeds from predators or satiate them with empty seeds.

DIOECY

Dioecy is markedly more common in fynbos than in chaparral (Le Maitre and Midgley this volume). This is true both in the percentage of the flora and the percentage cover of vegetation at a site; dioecious species, e.g. *Garrya* spp., are uncommon in chaparral, whereas dioecious *Leucadendron* spp. are dominant on many fynbos sites. Curiously, *Garrya* spp. and the dioecious *Simmondsia chinensis* are more common on the arid margin of chaparral, extending into desert environments.

Theories attempting to account for dioecy are widely published and none is overly compelling for fynbos. Selective pressure for dioecy may increase in environments where there are barriers to outcrossing. Perhaps in fynbos there are indirect barriers to outcrossing such as limited seed set; *vis-à-vis* if outcrossed seeds constitute a smaller proportion of the potential seed pool and few seeds ever

mature, this may result in a proportionately greater adverse impact on outcrossed seeds. In the case of the chaparral shrub *Simmondsia*, the barrier may be the precarious situation of successfully maturing a particularly large 'nut' in a rather arid environment.

Alternatively, as Midgley (1987) and others have suggested, there may be nutrient limitations that would select for dioecy. By eliminating the male function, female shrubs are able to devote all of the nutrients sequestered by their roots to seed production. This argument may also account for the incidence of dioecy on nutrient-deficient sites in chaparral.

Seed dispersal

Seed dispersal patterns are markedly different in fynbos and chaparral.

ORNITHOCHORY

Bird-dispersed fruits are relatively common in chaparral but much rarer in fynbos where they are present in only a few taxa (e.g. *Rhus*, *Heeria*, and *Myrica*) (see Le Maitre and Midgley this volume; Johnson this volume). In chaparral species, this mode of dispersal is coupled with other reproductive characteristics (Keeley 1991a); seeds are non-dormant at dispersal, thus bird-dispersed taxa do not accumulate a persistent seed bank and consequently do not have post-fire seedling recruitment. In chaparral, ornithochory does not seem to be important as a means of dispersing seeds to gaps, since successful seedling recruitment in these species is generally confined to shaded understoreys of very old (> 50 yrs.) chaparral (Keeley 1991b). Seedlings of these species are more drought-sensitive than other chaparral species and it has been suggested that establishment requires shady sites with a well-developed soil litter layer, conditions that have selected for larger seeds which necessitate ornithochory. The lack of old fynbos sites (see below), except perhaps along river courses, may have selected against ornithochorous species.

Interestingly, many forest species in the Cape are bird-dispersed and share many of the same characteristics described above for such chaparral taxa (Manders 1990, 1991).

MYRMECOCHORY

California has at most three myrmecochorous, or ant-dispersed, plant species (Keeley and Keeley 1988), whereas approximately 2 500 fynbos species are myrmecochorous (Breytenbach 1988). Hypotheses on the selective advantage to myrmecochory are:

Dispersal to reduce intra- or inter-specific competition

I suggest this is an unlikely explanation for the high incidence of myrmecochory in fynbos because it does not result in particularly widespread dispersal and also concentrates seeds much more than other forms of dispersal. If the hypothesis were true, one would predict a higher incidence of myrmecochory in chaparral where higher shrub cover would generate greater shrub competition than in fynbos.

Burial to avoid destruction by fire

This hypothesis seems unlikely because soil-stored seeds of chaparral species are not obviously better protected against fire than seeds of fynbos species, and fire intensities are greater in chaparral than in fynbos (B W van Wilgen personal communication).

Dispersal to nutrient-rich microsites

Empirical data fail to support this hypothesis (Westoby et al. 1982; Bond and Stock 1989).

A dispersal alternative to ornithochory on phosphorous-poor soils

One observation that weakens this hypothesis (Milewski 1982) is that most myrmecochorous species are obligate reseeder recruiting post-fire from persistent seed banks; in other mediterranean climate regions, this mode of regeneration is never ornithochorous (Keeley 1991a). Apparently the 'character syndrome' associated with ornithochory is not compatible with post-fire seedling recruitment. Thus, myrmecochory should not be viewed as a potential dispersal alternative to ornithochory.

Rapid removal and burial to reduce predation

This is supported from studies in fynbos (Bond and Breytenbach 1985). However, in order for this hypothesis to have much

explanatory power, it must account for why predatory pressure is greater in fynbos than in chaparral. I support the suggestion made by others that the high incidence of myrmecochory in fynbos is tied to the nutrient-deficient soils (e.g. Breytenbach 1987) and suggest it has the following consequences.

One result of nutrient-deficient soils is that they give rise to foliage with a very high sclerophyll index, making leaves a less desirable food source than other plant parts such as seeds (e.g. see Johnson this volume). Seed predation would be intensified by the fact that low nutrient soils would make seedling establishment more precarious and select for seeds that are nutrient sinks (Jongens-Roberts and Mitchell 1986; Stock et al. 1990; Stock and Allsopp this volume). Since, within the 'herbivore guild', seeds are one of the few high quality nutrient (N and P) sources for consumers, granivory may constitute a greater selective pressure in fynbos than in chaparral. Low nutrient fynbos soils may also generate lower seed production over that observed for chaparral shrubs (Le Maitre and Midgley this volume) and possibly more empty seeds than typical of chaparral species; both of which could exacerbate the predation intensity in fynbos and increase the selective pressure for myrmecochory.

Myrmecochory reduces seed predation in two ways. The obvious means is by collecting and burying seeds, thus making them unavailable to seed predators. The less obvious means is through the competitive displacement of seed predators i.e. myrmecochorous ants competitively displace harvester ants in much the same way harvester ants displace other seed-consuming guilds e.g. Brown and Davidson (1977). In effect, myrmecochorous ants are being 'bribed' with a carbon-rich reward for not destroying the nutrient-rich seed. The non-destructive dispersal of myrmecochorous seeds by normally predaceous harvester ants (Bullock 1974) suggests they are bribable and is consistent with the presumed evolution of this behaviour from a seed-harvesting ancestor (Holldobler and Wilson 1990).

Several observations are consistent with the predator-avoidance hypothesis. One is the rarity of myrmecochory in post-fire flowering geophytes (Le Maitre and Midgley this volume). Most of these species sprout and flower

profusely after fire (Le Maitre and Midgley this volume) and since most seeds are dispersed at the end of the first post-fire growing season, I would speculate that the main seedling recruitment stage is in subsequent years after fire, a period when animal predation is low (Breytenbach 1987). Another observation supporting the predation hypothesis is the rarity of myrmecochorous species in renoster shrubland, a vegetation juxtaposed with fynbos but with a soil nutrient status more similar to chaparral (Specht 1988). Also, consistent with this hypothesis is the high number of myrmecochorous species on nutrient-poor sites in Australia (Bond and Slingsby 1983; Westoby et al. 1982).

It has been suggested that the presence of vertebrate predators in chaparral, and depauperate small mammal fauna on myrmecochorous-rich sites in Australia, is evidence against this hypothesis (Midgley 1987). These facts alone are insufficient to disregard the hypothesis since the loss of vertebrate predators from the 'granivorous guild' is readily compensated for by increased invertebrate predation (Brown and Davidson 1977).

Post-fire regeneration

FIRE REGIME

One environmental factor that is less readily quantifiable is fire regime. There are several reasons for believing that fires are much more frequent in fynbos. Fynbos stands over 20 years of age are uncommon and areas over 40 years are essentially non-existent. In fact, fynbos stands have a 90–100% probability of burning before they reach the age of 25 years (Kruger 1983; Van Wilgen and Van Hensbergen 1991). This contrasts with Californian chaparral where many stands are over 20 years old and sites over 50 years are present throughout the region (Black 1987; Keeley 1991b). One reason for this difference is that prescribed burning is practised to a greater degree in South Africa and wildfires are only suppressed if they are an immediate threat (B W van Wilgen personal communication). Also, even though most fires in both regions are anthropogenic, there is evidence that natural lightning-caused fires may be more important in the Cape (Kruger 1979; Van Wilgen 1981; Horne 1981; Keeley 1982; Le Maitre and Midgley this volume).

One observation that suggests a greater fire frequency in fynbos is the much more rapid developmental rates of the dominant fynbos species. The juvenile period in many fynbos shrubs is less than seven years (Kruger 1986; Van Wilgen et al. this volume) whereas in many chaparral species it may be substantially greater than that (personal observation).

One factor that could increase fire frequency is the relentless summer southeasterly winds in the Cape that make suppression more precarious and play a significant role in the fynbos fire regime (Van Wilgen 1981). Another factor is the difference in vegetation structure between chaparral and fynbos, which generates very different fuel characteristics. Finer fuels generated by restioids and ericoids make fynbos susceptible to burning at any time of the year, possibly contributing to higher fire frequency.

Historically, fire frequency may have been increased by human occupation and this factor has been present much longer in fynbos than in chaparral (Deacon 1986).

Due to a combination of higher fire frequencies and extensive coverage of restioid and ericoid growth forms, fire intensities are lower in fynbos (Van Wilgen et al. 1985).

Both fynbos and chaparral are resilient to fire and illustrate a remarkable degree of convergence in some aspects of regeneration, and marked differences in other aspects.

TEMPORARY POST-FIRE FLORA

The post-fire flora in fynbos is dominated by geophytes, whereas in chaparral it is dominated by annuals (Kruger 1983). Certainly part of the explanation is that bulbs and corms are a means of sequestering valuable nutrients (Le Maitre and Midgley this volume). Additionally, other factors could be involved. In chaparral, the longer intervals between fires may be important; for example, seed banks are a reliable mode of surviving a long interval between fires, and thus the annual habit may be more compatible with longer, unpredictable fire-free periods. In fynbos, geophytes can persist for many more years after fire due to the more open nature of the vegetation. As a result of the closed canopy in chaparral, geophytes that sprout between fires are less likely to find adequate light and are susceptible to animal predation under the chaparral.

Also, the greater summer water stress may make survival of perennials less likely in post-fire chaparral and this may have played a role in selecting for the annual habit. This is supported by the fact that in arid fynbos on the edge of karoo (in a climate more typical of chaparral e.g. Figure 15.1), annuals become more important (Kruger 1979).

Although annuals dominate the post-fire chaparral environment, geophytes are present and flowering is largely restricted to the first post-fire year, as in fynbos geophytes. One marked difference from fynbos is the depth of bulb or corm burial. Although comparative detailed data are largely lacking, my observation was that geophyte bulbs and corms were much more easily extracted from the soil than is the case for chaparral species. In general, the bulbs and corms of fynbos geophytes are buried between 5 and 10 cm (J Vlok personal communication; personal observation), whereas in chaparral they are nearly always greater than 20 cm in depth and often more than 30 cm (personal observation). During the dry summer months, this greater depth of burial, coupled with the finer textured chaparral soils, makes excavation nearly impossible. There are two reasons why Californian geophyte bulbs are buried so deeply: to reduce predation from animals and to reduce dessication during the summer. In sandy fynbos soils, burial may not be a viable means of escaping predation and thus we might expect more species to have evolved toxins that deter predation (see Johnson this volume). Also, the high predictability of measurable precipitation in fynbos during the summer may reduce the dessication of bulbs and corms near the soil surface.

SHRUB REGENERATION

Shrub regeneration in fynbos and chaparral is remarkably similar in the importance of lignotuberous resprouters and non-sprouting seeders (Le Maitre and Midgley this volume). One noteworthy difference, however, is in the preponderance of fynbos species that maintain a seed bank on the plant in serotinous fruits (Bond 1985) versus the preponderance of soil-stored seeds in chaparral. Several factors may be involved. Nutrient-deficient soils may have selected for larger seeds, and if, as argued above, seed predation pressure is greater in

fynbos, storing seeds on the plant may be safer. This strategy is apparently quite successful under the relatively frequent and predictable fire regime in the Cape. However, if the fire-free interval exceeds the lifespan of the plant, this could mean localized extinction since the seeds of serotinous species will not survive more than a year following dispersal (Midgley 1987) and successful seedling recruitment between fires is precarious (an important exception, deserving further study, is on semi-arid interior fynbos sites where some proteoid taxa have an uneven age structure suggesting continuous recruitment; W Bond personal communication; personal observation). Serotiny is a less viable mode in chaparral due to longer intervals between fire; the few serotinous species are often restricted to nutrient-

poor soils where growth rates are slower and plant longevities are significantly greater, than on more fertile soils.

SEED GERMINATION

A remarkable degree of convergence is evident in the seed germination patterns in chaparral and fynbos (e.g. Table 15.3). Particularly striking is the presence of charred wood-stimulated species in both fire-prone regions. These species arise after fire from a dormant seed bank that persists between fires. Other species in both regions, which accumulate a persistent seed bank between fires, have seeds that are stimulated to germinate by heat shock (Table 15.3). Additionally, in both regions geophytes have similar life histories; they resprout immediately after fire from bulbs or corms but not from seed. Due to substantial carbon reserves, these sprouts are capable of flowering in profusion in the first post-fire year. Consequently, seedling recruitment in such species is likely restricted to the second or third post-fire year and thus is not cued directly to any fire-related stimulus. In both regions such

species have seeds that germinate readily under adequate temperature and moisture conditions (Table 15.3).

CONCLUSIONS

The convergence of many aspects of fynbos and chaparral supports the hypothesis that similar climates select for similar plant structures and functions. The lack of convergence focused on in this chapter may be explained by regional differences in climate, soil characteristics, and disturbance regimes. Thus, it may be more appropriate to consider the hypothesis that similar *environments* will select for similar structures and functions. Since the environment consists of an n-dimensional hypervolume, it may not be possible to test this hypothesis, and attempts to do so invariably lead to equivocal conclusions (e.g. Barbour and Minnich 1990). In many respects testing the notion of ecosystem convergence is like early attempts to test Gause's theorem that no two species could occupy the same niche. Numerous papers purportedly falsified this hypothesis until Hutchinson's seminal paper (1957) defined niche in such a way as to make it no longer possible to test the competitive exclusion principle. Today it is taken as axiomatic that no two species occupy the same niche and ecologists follow a more productive line of enquiry and focus on the question: 'How dissimilar do species have to be in order to coexist in stable equilibrium?' Likewise, I suggest it be taken as axiomatic that 'similar environments will select for similar characteristics' (within phylogenetic constraints e.g. Peet 1978). Thus, a productive line of enquiry for mediterranean ecologists would be to address the question: 'How dissimilar do environments have to be in order to generate differences in structure and function between mediterranean regions?'

TABLE 15.3 A comparison of seed germination response between species from fynbos and chaparral (Keeley 1991a; J Keeley and W J Bond unpublished data). Methods are as described in the publication; heating treatments were slightly different between fynbos and chaparral experiments and are indicated; $n = 3$ dishes of 50 seeds each; percentages within the same row with the same superscript are not significantly different at $P > 0.05$. F = fynbos; C = chaparral.

Species	Family	Life form	Control	Percentage germination		
				Heated F: 80°C/30 min C: 80°C/120 min	Heated 115°C/5 min 120°C/5 min	Charred wood added
Fynbos species						
Non-refractory seeds:						
<i>Wachendorfia paniculata</i> (Haemodoridae)		Geo-	80 ^a	72 ^a	0	80 ^a
<i>Geissorhiza</i> sp. (Iridaceae)		Geo-	74 ^a	77 ^a	0	60 ^a
Heat shock-stimulated seeds:						
<i>Phyllica ericoides</i> (Rhamnaceae)		Phano-	9 ^a	44	84	11 ^a
<i>Hermannia alnifolia</i> (Sterculiaceae)		Chamae-	0 ^a	17	67	1 ^a
Charred wood-stimulated seeds:						
<i>Pharaceum elongatum</i> (Aizoaceae)		Chamae-	0 ^a	4 ^a	1 ^a	47
<i>Nemesia cf lucida</i> (Scrophulariaceae)		Thero-	7 ^a	9 ^a	2 ^a	84
Chaparral species						
Non-refractory seeds:						
<i>Marah macrocarpus</i> (Cucurbitaceae)		Geo-	73 ^a	19	25	89 ^a
<i>Zigadenus fremontii</i> (Liliaceae)		Geo-	84 ^a	71 ^a	9	83 ^a
Heat shock-stimulated seeds:						
<i>Ceanothus leucodermis</i> (Rhamnaceae)		Phano-	3 ^a	29	64	7 ^a
<i>Camissonia hirtella</i> (Onagraceae)		Chamae-	30 ^a	49	66	26 ^a
Charred wood-stimulated seeds:						
<i>Eriophyllum confertiflorum</i> (Asteraceae)		Chamae-	4 ^a	6 ^a	4 ^a	52
<i>Emmenanthe penduliflora</i> (Hydrophyllaceae)		Thero-	5 ^a	6 ^a	1 ^a	67

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