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Mediterranean Biomes: Evolution of Their Vegetation, Floras, and Climate

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Abstract

Mediterranean-type ecosystems (MTEs) are located today in southwestern Australia, the Cape Region of South Africa, the Mediterranean Basin, California, and central Chile. These MTEs possess the highest levels of plant species richness in the world outside of the wet tropics. These ecosystems include a variety of vegetation structures that range from the iconic mediterranean-type shrublands to deciduous and evergreen woodlands, evergreen forests, and herblands and grasslands. Sclerophyll vegetation similar to today's mediterranean-type shrublands was already present on oligotrophic soils in the wet and humid climate of the Cretaceous, with fire-adapted Paleogene lineages in southwestern Australia and the Cape Region. The novel mediterranean-type climate (MTC) seasonality present since the middle Miocene has allowed colonization of MTEs from a regional species pool with associated diversification. Fire persistence has been a primary driving

factor for speciation in four of the five regions. Understanding the regional patterns of plant species diversity among the MTEs involves complex interactions of geologic and climatic histories for each region as well as ecological factors that have promoted diversification in the Neogene and Quaternary. A critical element of species richness for many MTE lineages has been their ability to speciate and persist at fine spatial scales, with low rates of extinction.

1. INTRODUCTION

The world's mediterranean-type ecosystems (MTEs), with their characteristic and unique mediterranean-type climate (MTC) of mild wet winters and warm dry summers, have long attracted international interest for comparative studies on ecosystem and evolutionary dynamics. The MTEs occur in five regions of the world (**Figure 1**)—California, central Chile, the Mediterranean Basin (MB), the Cape Region of South Africa (the Cape), and southern Australia [most notably southwestern Australia (SWA)]. They are dominated by subtropical high-pressure cells in summer that produce dry descending air masses and clear skies, making summer rainfall rare and temperatures high. Winter conditions are influenced by the polar jet stream and associated prevailing westerlies that bring rain, with snow at higher elevations. Cold ocean currents off the west coast of these regions moderate temperatures, allowing plant growth in late winter and early spring. The degree of MTC strength, however, exhibits differing patterns of intra-annual and interannual variability in precipitation among regions (Cowling et al. 2005). California and Chile have the longest summer dry periods and greatest interannual variability, with the MB intermediate in these characteristics. The Cape and SWA experience small but significant amounts of summer rain and relatively low interannual variability.

The traditional boundaries of each MTE have been based not only on climatic regimes but also on vegetation structure, floristics, and historical precedent (**Table 1**). The comparable climatic conditions in MTEs have selected for plants with similar functional traits, resulting in analogous vegetation types (Cowling et al. 1996, Verdú et al. 2003, Valente & Vargas 2013, Vargas et al. 2014). MTC regions support a range of plant communities. Both winter-deciduous and evergreen woodlands and forests are present in all five MTE regions but are of limited extent in the Cape, and all regions except SWA have elements of montane and alpine vegetation, whereas winter-rainfall desert regions have traditionally been excluded from MTE boundaries. Despite this range of plant community structures, evergreen sclerophyll shrublands form the iconic mediterranean-type vegetation (MTV) and harbor the greatest diversity of plant species. These analogous shrublands are the primary focus of this review. They are termed kwongan in SWA, fynbos in the Cape, maquis in the MB, matorral in Chile, and chaparral in California.

Interest in plant evolution in MTEs stems from their harboring the world's richest extratropical floras (Cowling et al. 1996, Kreft & Jetz 2007, Cowling et al. 2015). This high level of species richness and associated endemism is present across all spatial scales (Cowling et al. 2015). Evergreen shrublands outside of MTEs are generally unexceptional in plant diversity. All five MTEs have been categorized as biodiversity hotspots—areas that share large numbers of species and are rich in endemic taxa yet are under threat from human activities. The origins of this diversity are complex and lead to a number of important questions relevant to understanding global patterns of species richness. What was the climatic and landscape history of today's MTEs before onset of the MTC, and when did this climate regime first develop? What traits of the MTEs have generated and maintained such high species richness and endemism?



Figure 1

Global occurrence of mediterranean-type ecosystems: southwestern Australia, the Cape Region of South Africa, Mediterranean Basin, California, and central Chile. Figure courtesy of the U.S. National Park Service.

To answer these questions we first look at the most recent evidence of the geologic and climatic history of the areas occupied today by MTEs to ask how and when the dominance of evergreen sclerophyll shrublands developed, how their floras evolved, and the relative significance of both time and climatic and geomorphic stability in assembling floras in the older landscapes of SWA and the Cape. Although acknowledging the significance of many ecological interactions promoting diversification, we show that the development of MTCs dates at least to the middle Miocene and, with their dry summers and associated fire regimes, created a novel landscape with opportunities for diversification associated with strategies of fire persistence in woody shrubs, annuals, and geophytes. This new biome was also open to colonization by fire-tolerant and drought-adapted species from other biomes. Finally, we address the complex patterns of species

Table 1 Biogeographic and plant diversity traits of the five mediterranean-type ecosystems of the world. Table adapted from Cowling et al. (1996)

Region	Area (10^6 km^2)	Native plant species	Endemism (%)	Modal natural fire frequency (years)	Topographic heterogeneity	Climate heterogeneity
Southwestern Australia	0.31	8,000	70	10–15	Low	Moderate
Cape Region	0.09	9,000	68	10–20	Moderate	High
Mediterranean Basin	2.30	25,000	50	30–100	High	Very high
California	0.32	5,000	60	30–100	Very high	Very high
Central Chile	0.16	2,900	30	Fire absent	Very high	Very high

richness by comparing and contrasting the individual MTEs to assess the evolutionary histories of their diverse floras. We compare and contrast the significance of diversification of early Cenozoic lineages in the ancient and stable landscapes of SWA and the Cape with the dynamic landscapes of the three younger MTC regions.

2. SUBTLE LANDSCAPE EVOLUTION OF SOUTHWESTERN AUSTRALIA AND THE CAPE

The Cretaceous was a time of globally warm and humid climate regimes and has been termed the “glasshouse world” (Beerling & Woodward 2001). Although this climate regime supported closed-canopy forests worldwide, certainly oligotrophic soils and other edaphic “ghettos” harbored shade-intolerant evergreen sclerophyll shrublands (Lamont & He 2012, Carpenter et al. 2015). Scleromorphic leaves would have evolved in the Cretaceous as a strategy for survival on oligotrophic soils and sites with seasonal aridity (Wright & Westoby 2003, Onstein & Linder 2016). The nutrient-impoverished substrates of the Cretaceous in SWA and the Cape where sclerophyll Proteaceae are dominant today would have supported MTV with highly flammable foliage particularly vulnerable to ignition by lightning long before the origin of MTCs (Cowling et al. 2005, Lamont & He 2012). Many of the traits allowing plants in these communities to survive oligotrophic soils and aridity would have been adaptive for persistence after fire (Bond & Scott 2010, Keeley et al. 2012, Bond 2015). While these fire-tolerant sclerophyll shrublands are largely invisible in the fossil record (but see Carpenter et al. 2015), this is not unexpected because of taphonomic biases against fossil formation in drier uplands where fires were most likely to burn (Keeley et al. 2012).

Warm temperate forests with a broad representation of Gondwanan elements were widespread across SWA and the Cape in the Cretaceous and continued their dominance into the early Cenozoic (Scholtz 1985). For SWA, the rifting of Antarctica and southern Australia from the middle Cretaceous to middle Eocene and uplift of the Stirling and Barren Ranges along the south Australian coast were the last major tectonic events for the region, setting the baseline for a long period of geologic stability that continues today (McLoughlin & MacNamara 2001). Despite humid forest dominance, there were clearly examples of sclerophyll woodland and shrubland communities with the early evolution of fire-adapted lineages within the Proteaceae and Myrtaceae (Mack & Milne 2015). Also indicative of ancient evolutionary lineages is the survival today of monotypic clades, such as the Cephalotaceae, Emblingiaceae, and *Nuytsia* (Loranthaceae), as well as the diversity of Dasypogonaceae centered in SWA.

For the Cape, the origins of sclerophyll shrublands in southern Africa are also ancient and, like those in SWA, are closely associated with the geologic presence of infertile soils. Some fynbos lineages originated and began radiating in the late Cretaceous, possibly concomitant with the exhumation of the Cape Fold Belt as Africa separated from South America (Tinker et al. 2008). Within the matrix of the temperate forests, oligotrophic quartzitic soils of the uplands provided an important foothold for the emerging protofynbos flora (Linder 2003).

The global climate moderated from the hot and humid conditions of the Cretaceous and began a gradual cooling trend through the Paleocene and Eocene, although periodically disrupted by warm periods. Despite limited seasonality, evidence for the continued importance of fire throughout the epoch has been found (Crisp et al. 2011). A major cooling occurred in the Oligocene 33 Ma associated with the return of glacial conditions in Antarctica (Liu et al. 2009, Byrne et al. 2011). This increasing degree of aridity and seasonality is consistent with the widespread formation of laterites, silcretes, and calcretes in SWA at this time, as well as sharp restrictions in the distribution of wet forest elements and an expansion of sclerophyll shrublands and woodlands (Frakes 1999,

Hopper & Gioia 2004). Mild tectonic activity led to the uplift of the Darling and Ravensthorpe Ranges, rejuvenating coastal rivers and providing a range of new habitats for the development of woodlands and shrublands (Macphail 2007).

In the Cape, forest–thicket communities dominated the lowland sand plains, with fynbos dominating on the skeletal soils of the upper mountain reaches. Many modern fynbos lineages existed in the Oligocene as pockets of MTV on resource-poor substrates or more broadly in the interior of southern Africa. Lightning-ignited fires in these flammable pockets of vegetation would have carried fire sufficiently to restrict the spread of more mesic thicket and forest vegetation to fertile sands, thus creating new habitats (Cowling et al. 2009, Verboom et al. 2009, Bond & Scott 2010).

The Miocene brought increased aridity and intensification of seasonality in SWA with further expansion of sclerophyll shrublands and woodlands, while the formation of the arid calcareous Nullabor Plain isolated SWA from the rest of the continent. Small pockets of subtropical species were still present in favorable microhabitats at the end of the Miocene, but most remaining elements of subtropical rainforest had disappeared by 2.6 Ma (Dodson & Macphail 2004).

Apart from a modest uplift of the Cape landscapes in the Neogene, the Cape has similarly been tectonically stable through the later Pliocene and Pleistocene. However, erosion across the lowlands exposed large tracts of moderately fertile soils, while sea level fluctuations during this period exposed large areas of coastal forelands with calcareous substrates (Cowling et al. 2009). Thus, the Cape uplands have changed little since the Paleocene, while geomorphic changes in the lowlands have created novel habitats for diversification (Verboom et al. 2015).

3. DYNAMIC LANDSCAPE EVOLUTION OF THE MEDITERRANEAN BASIN, CALIFORNIA, AND CHILE

The modern geography of the MB was shaped by global plate dynamics in the Cenozoic as the African-Arabian Plate collided with the stable Eurasian Plate, closing the proto-Mediterranean (Tethys) Sea. The former Tethys Sea was restricted in the east and west by folding and subduction extending from the Pyrenees to the Zagros Mountains in Iran (Meulenkamp & Sissingh 2003). Many paleotropical forest species were lost with cooling that began in the Oligocene. Sclerophyll shrublands and woodlands were widely present in the Oligocene but restricted to local areas of oligotrophic and arid soils (Palamarev 1989, Postigo-Mijarra et al. 2009).

The Miocene fossil record indicates the presence of high plant richness in the Iberian Peninsula (Postigo-Mijarra et al. 2009, Jiménez-Moreno et al. 2010), due in part to the diversity of landscapes present. These landscapes included tropical and subtropical forests that co-occurred with warm-temperate, cold-temperate, and xeric open woodlands. Cooling and drying with increasing seasonality in the middle Miocene brought about expansion of sclerophyll shrublands and extirpation of many tropical elements (Palamarev 1989, Kovar-Eder et al. 2008).

Tectonic activity in the late Miocene 6 Ma closed the western end of the Mediterranean Sea and brought about dramatic cycles of sea withdrawal and flooding known as the Messinian Salinity Crisis (Duggen et al. 2003, Jiménez-Moreno et al. 2013). These cycles had a profound effect on plant distributions and speciation patterns during a period of more than 500 ka. Broad-leaved evergreen laurel forests retreated at this time, persisting on the Macaronesian islands, while sclerophyll shrublands and steppe communities expanded (Kovar-Eder et al. 2006).

For California, Cretaceous landscapes included low-diversity coastal wetlands along the western margin and conifers dominating in the mountains to the east (Millar 2012). The early Cenozoic saw a lowland dominance of subtropical forests much like that of southeastern Asia today. The high plateau of the Nevadaplano drained from its crest in central Nevada westward to the

Pacific Ocean and provided a source of temperate forest conifer and hardwood forest communities to colonize lowland areas as the major global cooling event in the Oligocene 33 Ma forced the subtropical forest to retreat. Much of the diversification of pines and oaks in California likely resulted from new ecological opportunities opened up by this change in climate. In interior sites to the west of present day Nevada, sclerophyll chaparral was present on rocky slopes, with many modern chaparral genera present (Wing 1987), forming a mosaic with more mesic woodlands (Keeley et al. 2012). Open woodlands expanded, promoting diversification of herbaceous plants and leading to marked evolutionary radiation of many groups, most notably Asteraceae (Baldwin 2014).

By the beginning of the Miocene the lowlands of California supported a diverse mosaic of woodlands, forests, and sclerophyll shrublands, with indications of moderate levels of rainfall throughout the year (Axelrod 1975). By 15 Ma, however, there was an intensification of seasonality with gradients of aridity and temperature extremes from mild at the coast to more extreme inland. One driver of these changes was the development of the cold California Current that brought a coastal belt moderated by fog and sharp temperature gradients from coast to inland. Proto-chaparral shrublands and woodlands were increasing in dominance in the lowlands, and it appears that many of these elements derived from earlier Cenozoic assemblages in the interior southwest (Ackerly 2009, Keeley et al. 2012, Baldwin 2014). Much of the Coast Ranges, Central Valley Basin, and Southern California Basin remained underwater until well into the Pliocene.

From the Cretaceous through the Eocene, South America remained connected to Antarctica, with dominant humid aseasonal conditions and tropical forests (Pross et al. 2012). A change to cooler conditions came with the opening of the Drake Passage in the Eocene (Scher & Martin 2006), followed by global Oligocene cooling linked with glaciation in Antarctica (Liu et al. 2009).

Sclerophyll woodland genera were already present in Chile in the Miocene (Hinojosa et al. 2006). Early Miocene floras indicate woodlands extended across southern South America under a summer rainfall regime, with a mixture of neotropical and Gondwanan elements (Hinojosa & Villagrán 2005). With the uplift of the Andes, beginning approximately 15 Ma (Gregory-Wodzicki 2000), and the cold Humboldt Current in place, an increasing barrier to the entrance of moist summer storms from the east developed, gradually changing the climate regime to summer drought but virtually eliminating fire. Importantly, the Andean uplift and associated active volcanism produced a highly dissected landscape of geographically isolated valleys, strong slope-aspect contrasts, and steep altitudinal gradients.

Relatively little is known of the late Cenozoic conditions that promoted the spread of sclerophyll vegetation in central Chile, but increasing aridity and intensification of summer drought were important (Hinojosa 2005). During the last glacial maximum, as southern temperate forest migrated northward and vegetation belts descended altitudinally, sclerophyll woodlands became restricted to coastal areas of central Chile, expanding to their current extent in postglacial times (Villagrán 1995).

4. WHEN DID MEDITERRANEAN-TYPE CLIMATES APPEAR?

Although our understanding of the geologic and climatic history of the MTC regions is incomplete, emerging evidence places the onset of a proto-MTC back to at least the middle Miocene. Older literature has generally hypothesized a much younger age of 4–3 Ma in the Pliocene (e.g., Suc 1984, Axelrod 1989). A key event in the onset of a proto-MTC may have been the Middle Miocene Climate Optimum 17–14 Ma, followed by growth of the East Antarctic ice sheet and a global cooling (Zachos et al. 2008). Atmospheric and oceanic circumpolar circulation intensified during this period, resulting in increased latitudinal gradients in temperature and stronger zonal winds

(Heinrich et al. 2011). These changes would have impacted the development and/or strength of Hadley cell circulation and seasonal movement of the subtropical high-pressure center, promoting conditions favorable for MTC formation. Less certainly, periods of MTC formation may have been associated even earlier with Antarctic glaciation in the Oligocene. Although the global patterns of atmospheric circulation that determine MTCs are clear, the seasonal intensity of MTCs may have varied through time. Changing offshore ocean currents can also influence the nature of MTC regimes, with cold currents intensifying summer drought and warm currents increasing summer rainfall.

Middle Miocene conditions, with a strong pole-equator temperature gradient promoting the equatorial movement and intensification of ocean currents and subtropical high-pressure centers, suggest that a proto-MTC was present in SWA as early as 20–15 Ma (Hopper & Gioia 2004, Byrne et al. 2011). It is worth noting that Australia's position during the Miocene was approximately 4° farther south, suggesting that MTC conditions may have first formed in northwestern Australia (Beard 1977). The Hammersley Range in northwestern Australia supported a fire-prone landscape dominated by Casuarinaceae and Myrtaceae in the late Oligocene and early Miocene (Macphail & Stone 2004), suggesting the existence of a proto-MTC regime even at that time. Evidence for a Miocene MTC in SWA can be seen in the phylogeny of *Hakea* (Proteaceae), a drought-tolerant genus that evolved in SWA 18 Ma from rainforest ancestors and gave rise to a needle-leaved clade adapted to summer drought conditions 14 Ma (Lamont et al. 2016).

The onset of a proto-MTC in the Cape Region is not entirely clear, but it has been hypothesized that summer drought conditions were in place in the early Miocene (Schnitzler et al. 2011) and characterized the region by 15 Ma (Linder 2003, Bytebier et al. 2011). The intensification of seasonality favored fynbos communities over those of forest and thicket, a process that would have accelerated as a consequence of the development of larger tracts of fire-prone vegetation. The Benguela Current was well established as early as 10 Ma (Rommerskirchen et al. 2011), intensifying summer drought and strengthening aridity at the drier margins of the region.

The modern California flora developed rapidly with the appearance of a novel proto-MTC and associated fire regime in the middle Miocene approximately 15 Ma, contemporaneously with the development of the cold California Current along the Pacific Coast (Jacobs et al. 2004). This onset can be seen in an abrupt floristic change in western Nevada at this time associated with a sharp decrease in summer precipitation (Axelrod & Schorn 1994). A similar date for the gradual appearance of a proto-MTC with summer drought in Chile was influenced by the uplift of the Andes (Gregory-Wodzicki 2000), although key floristics elements appeared earlier as seen in Rhamnaceae (28.5 Ma) (Onstein et al. 2015). The modern seasonal patterns and marked east-west climatic differentiation within central Chile were fully established by approximately 8 Ma (Armesto et al. 2007).

A sharp intensification of summer drought in the MB occurred in the middle Pliocene, and this change was associated with the disappearance of many forest elements and the stimulation of diversification in other lineages (Suc 1984, Barrón et al. 2010). However, there are several lines of evidence for an MTC even earlier. For the period 11–9 Ma, temperate C₃ grasses were abundant in contrast to summer-rainfall C₄ grasses (Edwards et al. 2010). In the Mediterranean Sea, maximum photosynthetic activity of *Porites* coral was equated with clear summer skies, while seasonal binding of sediments from local rocks by *Porites* signified strong freshwater influx during winter (Mertz-Krauss et al. 2009). Finally, there is a strong indication that the ancestral MB pines at 10 Ma were serotinous (Grivet et al. 2013), a trait linked to mediterranean climates (Lamont et al. 2013, Causley et al. 2016). All these findings suggest an MTC may have existed, perhaps temporally, by the middle to late Miocene, especially in the eastern half of the MB.

5. DRIVERS OF DIVERSIFICATION IN THE MEDITERRANEAN BIOMES

Hypotheses to explain the remarkable species diversity of the five MTEs have centered on adaptive radiation associated with heterogeneity in topography, climate, and soils. Evolution across habitat islands is evident in examples of speciation in all MTEs. This pattern of diversification can be seen in narrow habitat endemism in the MB (Medail & Diadema 2009) and in the granite outcrops of SWA (Hopper & Gioia 2004, Byrne & Hopper 2008). In California, serpentine substrates, vernal pools, and island archipelagos are examples of such habitat islands, but these examples alone cannot explain the hyperdiversity of the California flora.

To understand MTE species diversity, it is important to ask if there are ecological factors unique to MTEs that could explain their high plant species diversities. In addition, any hypothesis to explain the globally significant species diversity of the five MTEs must take into account the differing levels of species richness among the regions across a wide range of spatial scales (Cowling et al. 2015). The Cape is consistently the most diverse of the five regions relative to area at any spatial scale, followed closely by SWA (Figure 2). Both the western and eastern MB show an intermediate pattern of contemporary plant diversity when scaled against area, followed by California and finally Chile. This correlation between local and regional patterns of diversity cannot be easily explained by a purely ecological theory of species diversity (Cornell & Lawton 1992).

Controversies in resolving questions of species diversity have led many ecologists to discount the significance of ecological interactions and niche specialization in favor of a historical and geographic approach in which diversity is a function of the areal extent of suitable habitat and the rate of diversification (Latham & Ricklefs 1993, Ricklefs 2006). This geohistorical approach articulated in Hubbell's (2001) neutral theory posits that species extinction is a stochastic process

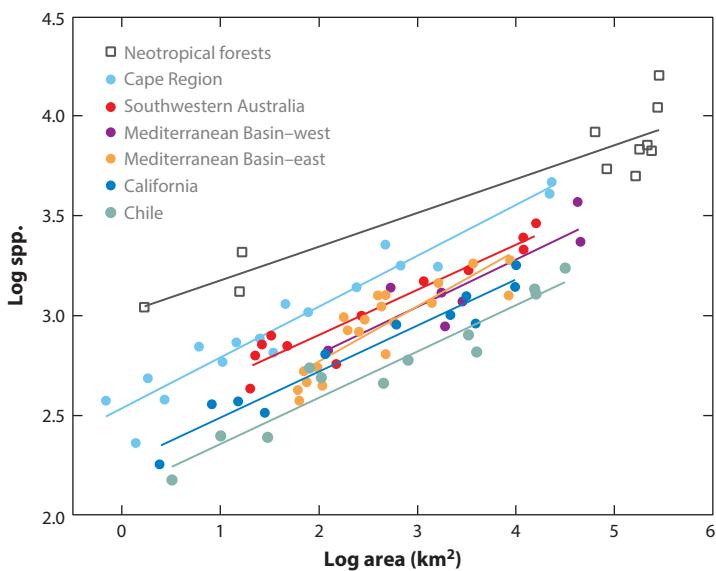


Figure 2

Plant species-area relationships for six mediterranean-type ecosystems (MTEs) and neotropical forests. Note the Mediterranean Basin is divided into western (Iberia) and eastern (Greece) sectors. Slopes of regression curves are homogeneous among MTEs, but the slope for neotropical rainforests is significantly shallower than those for MTEs, suggesting that at larger areas there is convergence in richness between the richest MTEs (Cape and southwestern Australia) and neotropical forests. Data from Cowling et al. (2015).

and a function of population size, although biotic interactions remain relevant. More realistic in understanding patterns of species richness in MTEs is a theory that combines elements of both local determinism and neutral theory in hypothesizing that net diversification rate combined with historical and geographic influences determines both local and regional diversity (Wiens & Donoghue 2004, Groeneweld et al. 2013).

Time-to-adapt and environmental stability are clearly significant factors in promoting the relative species richness among the MTC regions. SWA and the Cape have relatively stable and ancient landscapes compared with the other three MTEs (Hopper 2009, Cowling et al. 2015). This stability has resulted from the almost complete absence of major orogenic events, subduction, or glaciation during the Cenozoic (Hopper 2009). The landscapes of SWA and the Cape with their nutrient-poor soils differ dramatically from the more nutrient-rich soils of Chile, California, and the MB. These younger regions were exposed to major orogenic events in the Late Neogene and Quaternary. Moreover, climatic oscillations in temperature and precipitation associated with Pleistocene glaciation were strong compared with the more muted cycles in SWA and the Cape. Taken together, these regional differences suggest that much of the variation in plant diversity is a consequence of the diversification and persistence of numerous ancient Cenozoic lineages in SWA and the Cape rather than just differences in diversification rates (Cowling et al. 2015), although high rates of diversification are shown by some lineages in the MB (Valente & Vargas 2013) and indeed in all five regions. The key to diversity for many MTE lineages lies in the ability of their ancestors to survive agents of directional selection, such as poor soils, fire, drought, and novel herbivores and pollinators, then speciate and persist via stabilizing selection at fine spatial scales, with low rates of extinction (Valente et al. 2012, Ellis et al. 2014, Lamont et al. 2016). Although some old paleoendemic lineages are also present in the younger MTEs, and in some cases form ecological dominants, these lineages have not diversified in any significant manner and contribute little to overall species richness.

Beyond the impact of time and environmental stability, it is important to ask if rates of diversification today and in the past are unusually high in the MTC regions. Using a global perspective, rates of net species diversification for most lineages in these regions are generally not remarkably high despite the overall species richness of these areas. Based on existing phylogenies, the rates of diversification are lower than that present in the páramo ecosystem of the northern Andes, which has experienced rapid speciation in the Pliocene and Quaternary (Madriñán et al. 2013). Although individual MTE lineages have exhibited high rates of Neogene diversification [e.g., *Dianthus* in the MB (Valente et al. 2010a,b) and core Ruschioideae (Aizoaceae) in the Cape (Klak et al. 2004)], the regional patterns of species richness cannot be explained by high diversification rates alone. These rates, although variable, tend to be highest in the MB, intermediate in California and the Cape, and lowest in Chile and SWA (Linder 2008, Madriñán et al. 2013). Overall, species diversity is less a function of elevated rates of speciation than of low rates of extinction (Valente et al. 2010a,b; Lancaster & Kay 2013; Onstein & Linder 2016). Differences in net diversification rates in different clades may arise in many ways (Verdú & Pausas 2013). The relevant variable is not diversification rate per se but a net diversification rate that integrates the results of all factors impinging on diversification and persistence into one metric.

6. FIRE REGIME AS A STIMULUS TO DIVERSIFICATION

Patterns of life history and morphology related to fire persistence challenge the long-held belief that diversity patterns can be explained by climate, geography, and soils alone. The role of selection for fire persistence as a stimulus for diversification has received little attention, owing in part to the complexity of evolutionary mechanisms for fire-driven speciation (Mucina &

Wardell-Johnson 2011, Schnitzler et al. 2011, Keeley et al. 2012), and its significance has often been underrated (Axelrod 1980, 1989; Hopper et al. 2015). The two basic modes of adaptation to fire in MTEs, resprouting and obligate postfire seedling recruitment, allow for a complex array of life history traits that are influenced by aridity, landscape structure, and fire regime. The high-intensity crown fires characteristic of sclerophyll shrublands have selected for traits contributing to diversification in many lineages (Crisp et al. 2011, Keeley et al. 2012, Crisp & Cook 2013). Fire-adaptive traits such as seed release by fire (serotiny), resprouting, thick bark, postfire seedling recruitment, smoke-stimulated seed germination, and fire-stimulated flowering can be traced back to the late Cretaceous to early Cenozoic in a number of MTE lineages (Pausas & Keeley 2009, Lamont & Downes 2011, Lamont & He 2012).

Distinctive morphological structures associated with epicormic resprouting after fire appeared in eucalypts in the Paleocene 60 Ma (Crisp et al. 2011), and fire-adapted clades of other Australian Myrtaceae were already well differentiated by the middle Eocene (50 Ma). *Banksia*, an iconic genus of Australian Proteaceae, had serotinous cones when it first appeared approximately 60 Ma, and modern *Banksia* lineages of SWA and eastern Australia were largely separated by the Oligocene, approximately 30 Ma (He et al. 2011). In the Cape, fire-adapted lineages of *Protea* (Lamont et al. 2013) and *Leucadendron* (Proteaceae) appeared in the Oligocene (30 Ma), and divergence continued in the Miocene with the appearance of new genera with fire-stimulated germination, such as *Leucospermum* and *Mimetes*. With broad expanses of fire-prone sclerophyll shrublands dating from the Paleogene (Mack & Milne 2015), the evolution of fire-killed reseeders also had a major impact on diversification in the species-rich Cape and SWA with their high levels of obligate reseeding shrubs. Consistent with the significance of summer drought in the evolution of fire-persistence strategies is the lower frequency of obligate seeding taxa in the eastern Cape, with biseasonal patterns of precipitation, compared with the western Cape, with more typical MTC conditions (Le Maitre & Midgley 1992, Ojeda 1998).

Unlike SWA and the Cape, where several early Cenozoic lineages were present in sclerophyll shrublands, the younger landscapes and richer soils of the other three MTC regions had a limited early Cenozoic history of shrublands, with these scattered in arid patches within a mosaic of more mesic-adapted woodlands and forests (Keeley et al. 2012). Although many of the modern chaparral shrub genera were present in the Eocene, the evolution of fire-dependent pulse recruitment of seedlings is thought to be tied to an MTC that greatly increased fire spread and thus the predictability of fire in the environment (Pausas & Keeley 2014). The increasing aridity and development of an MTC in the Miocene expanded the coverage of these shrublands and contributed to the expansion of fire-prone landscapes with unique combinations of climate, soils, and fire regimes. It is notable that obligate reseeding strategies in California are largely concentrated in just two genera, *Arctostaphylos* (Ericaceae) and *Ceanothus* (Rhamnaceae), each of which has undergone extensive speciation. In the MB, obligate reseeding is rare, with the subshrub genus *Cistus* as the best known example (Guzmán et al. 2009, Pausas & Keeley 2014). This life history strategy of fire persistence is absent in Chilean shrublands, associated with the lack of fire as an evolutionary force following the Miocene uplift of the Andes (Armesto et al. 2007, Keeley et al. 2012).

7. ASSEMBLING THE FLORAS OF MEDITERRANEAN-TYPE ECOSYSTEMS

No single theory can explain the overall and regional patterns of plant species diversity in the five MTEs. It is necessary to consider the complexity of both geologic and climatic histories for each region as well as ecological factors that have promoted diversification of herbaceous lineages in the

Neogene and Quaternary. Sclerophylly is related to convergent traits across MTEs already shaped before current MTC conditions appeared. Historical processes (phylogenetic inertia) rather than evolutionary convergence driven by mediterranean climates have been postulated to account for much of the phenotypic similarities among MTEs (Verdú et al. 2003).

7.1. Southwestern Australia

Some of the major extant families, such as the Myrtaceae, Proteaceae, and Haemodoraceae, had their SWA origins in the middle to late Cretaceous, with tropical rainforests dominated by conifers, ferns, and dicot trees still clothing much of Australia (**Figure 3**). This trend continued into the Paleogene with the emerging sclerophyll element retreating to the drier west side of the continent during the Middle Eocene Climatic Optimum (Lamont & He 2012). By the late Eocene,

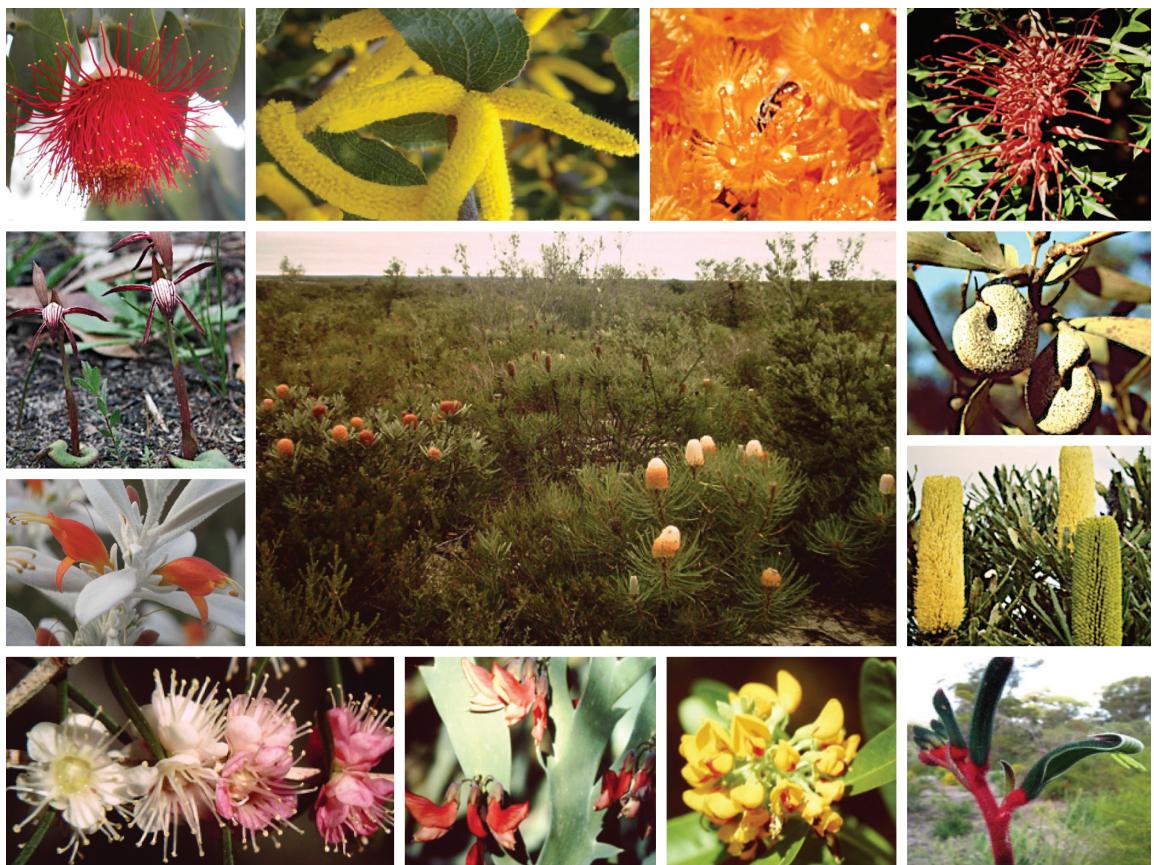


Figure 3

Southwestern Australia. Centerpiece, scrub-heath in the northern sandplains with *Banksia menziesii* (left) and *Banksia hookeriana* (right) in flower (113 evergreen species in a 40 × 40 m plot at this site). From upper left clockwise: *Eucalyptus rhodantha* (Myrtaceae); *Acacia denticulosa* (Fabaceae); *Verticordia nitens* (Myrtaceae), with a *Euryglossa morrisoni* bee; *Grevillea bipinnatifida* (Proteaceae); fruits of *Hakea cyclocarpa* (Proteaceae); *Banksia attenuata* (Proteaceae); *Anigozanthos manglesii* (Haemodoraceae); *Gastrolobium celsianum* (Fabaceae), which contains poisonous fluoroacetate; *Daviesia epiphyllum* (Fabaceae) with phylloclades; *Hypocalymma angustifolium* (Myrtaceae) with flower color change; *Eremophila subfloscosa* (Scrophulariaceae); and postfire flowering of *Pyrorchis nigricans* (Orchidaceae).

temperate rainforest, dominated by *Nothofagus* and scattered conifers, including *Araucaria* and *Podocarpus*, occurred on wetter, upland sites, and fire-prone sclerophyll forests, woodlands, and scrub-heath occurred on the drier sands and laterites. In the Oligocene, many lineages that remained species poor in the rainforest began to speciate in sclerophyll communities. Examples include Proteaceae (Banksiinae, Persoonioideae, and Hakeinae) (Sauquet et al. 2009); Casuarinaceae (Crisp et al. 2004); *Callitris* (Cupressaceae) (Pye et al. 2003); Elaeocarpaceae sensu lato (Craven et al. 2006); and *Eucalyptus* (Myrtaceae) (Crisp et al. 2004). Both rainforest and (especially) sclerophyllous Proteaceae were abundant in the Paleogene, reaching levels almost 10 times those in equivalent vegetation types elsewhere in Australia (Itzstein-Davey 2004, Mack & Milne 2015). By the end of the Neogene, the dry-fruited Myrtaceae possessed 39 clades (at the high diversification rate of 0.894 lineages per initial lineage per My), which are still extant in SWA, with the nonrainforest Proteaceae (mainly Proteoideae), Restionaceae, and Haemodoraceae well represented (see **Supplemental Table 1**; follow the **Supplemental Material** link from the Annual Reviews home page at <http://www.annualreviews.org>).

By 15 Ma, SWA had been carried sufficiently north to be in the path of the prevailing westerlies during winter; thus, seasonality intensified and switched to a wet winter/dry summer regime. Fire frequency increased and evolution of genera with fire-adapted traits peaked at 15–10 Ma (B.B. Lamont, unpublished data; see **Supplemental Figure 1**). Intense summer droughts became a regular feature, and periods of overall aridity interspersed with the MTC by the Pliocene had drastic effects on the flora and vegetation (Dodson & Macphail 2004). Drifting sands, exposed parent rock and laterite, and saline/calcareous soils became causes of spatial exclusion and extinction or new substrates to be adapted to and colonized. Gradually, the rainforest element was eliminated (unlike eastern Australia). Both fire and drought were potent agents of selection at this time, as well as the advent of granivorous cockatoos (Cacatuidae), herbivorous marsupials and emus, and nectar-seeking birds (Meliphagidae) (Groom & Lamont 2015). By the end of the Neogene, extant lineages of major shrub and herbaceous clades such as *Banksia*, *Hakea*, Haemodoraceae, and *Daviesia* (Fabaceae) were already well represented, and 12 clades exceeded their Paleogene numbers by a mean of 13 times. Differentiation at the generic level had almost ceased in Proteaceae but was maintained at the species level in Restionaceae, *Hakea*, and *Daviesia*, at a mean of 0.041 lineages per initial lineage per My for 12 clades examined, 2.7 times the rate for matched clades in eastern Australia (**Supplemental Table 1**).

The SWA flora showed remarkable resilience to increasing climatic fluctuations in the Quaternary. Many species retreated to moister refugial uplands and coastal dune habitats. Other taxa invaded the new substrates as they stabilized owing to their phenotypic plasticity. These bouts of extinction, contraction, and expansion of populations were accompanied by genetic changes at the subspecific (Byrne & Hopper 2008, Byrne et al. 2011) and species (Lamont et al. 2016) levels. No new genera of Proteaceae or Myrtaceae appeared, but speciation remained substantial in some clades. For 12 clades, the mean increase in number of lineages was 13% for the Paleogene, 63% for the Neogene, and 24% for the Quaternary (**Supplemental Table 1**). The mean speciation rate for these clades in the Quaternary was 0.123, 3 times the rate in the Neogene, but only 60% of the Paleogene rate, and 3 times that for matched clades in eastern Australia.

7.2. Cape Region

The fynbos flora today is not the primary result of recent and rapid radiations triggered by climate change; rather, it is a product of gradual diversification associated with low rates of extinction (**Figure 4**). The upland fynbos flora today is associated with early Cenozoic lineages



Figure 4

Cape Floristic Region. Centerpiece, sandstone fynbos on the eastern Tsitsikamma Mountains with *Protea cynaroides* in flower. From upper left clockwise: *Pelargonium cordifolium* (Geraniaceae), *Conicosia pugioniformis* (Aizoaceae), *Chasmanthe aethiopica* (Iridaceae), *Searsia glauca* (Anacardiaceae), *Agathosma stenopetala* (Rutaceae), *Cyclopia subternata* (Fabaceae), *Satyrium princeps* (Orchidaceae), *Leucospermum praecox* (Proteaceae), *Syncarpha eximia* (Asteraceae), and *Erica diaphana* (Ericaceae).

linked to an aseasonal and relatively mesic climate (Verboom et al. 2015). Examples of these lineages include small and isolated families of heathland shrubs like the Bruniaceae, Penaeaceae, Geissolomataceae, and Grubbiaceae. In contrast, the lowland fynbos flora is characterized by younger lineages with more rapid evolutionary radiation beginning in the late Miocene 8–7 Ma (Lamont & He 2012, Hoffmann et al. 2015).

Uplift and erosion of the Cape landscapes in the Miocene and Pliocene exposed richer underlying substrates, providing opportunities for the diversification of renosterveld and succulent karoo floras (Cowling et al. 2009, Hoffmann et al. 2015, Verboom et al. 2015). These two floras contribute significantly to total plant species richness of the Greater Cape Floristic Region (Bergh et al. 2014). New opportunities for speciation also came in the Late Pliocene and Pleistocene as lowered sea levels exposed extensive calcareous substrates along the South African coastline (Fisher et al. 2010) and provided novel opportunities for the radiation of fynbos lineages. Several Cape genera experienced rapid speciation in the Neogene. Examples include shrubs such as *Phyllica* (Rhamnaceae) (Onstein et al. 2015) and herbaceous perennials such as *Moraea* (Iridaceae) (Goldblatt et al. 2002).

Diversification of the Cape flora is strongly associated with shrubs, geophytes, and evergreen graminoid life-forms (Ellis et al. 2014). The key cues for this development were increasing seasonality of precipitation and exposure of new soil environments through geomorphic weathering and sea level fluctuations (Cowling et al. 2009, Schnitzler et al. 2011). Under these conditions, flammable shrublands would have spread from upland areas, replacing fire-sensitive lowland thicket and forest (Bond 2015). Beyond the fynbos, the ancient pan-African forest and thicket have had low diversification rates. These diversification patterns and processes associated with both old and young landscapes (Hopper 2009), together with relative climate stability, are key to explaining the region's exceptionally high species diversity (Linder 2003, 2008; Cowling et al. 2009; Verboom et al. 2009).

7.3. Mediterranean Basin

The MB harbors a rich flora of approximately 25,000 species distributed across 75% of the global MTE land area, combining numerous floristic clades of Pliocene and Quaternary origin coupled with a few ancient lineages from pre-mediterranean epochs (**Figure 5**). Three waves of extinction during the Cenozoic and Quaternary took a toll on many lineages: tropical elements by emergence of strong seasonality in the middle Miocene (16–14 Ma); tropical and subtropical elements by aridification during the Messinian Salinity Crisis (6–5 Ma); and mesic elements by cool temperatures and drying during Quaternary glaciations (<2.5 Ma) (Postigo-Mijarra et al. 2009, 2010; Barrón et al. 2010). Thus, descendant lineages of the Cenozoic paleoflora that once occupied wide areas of warm temperate rainforests and swamp forests of the Northern Hemisphere compose only a small part of the modern flora. The lack of angiosperm families endemic to the MB, with the exception of the monotypic carnivorous Drosophyllaceae, supports failure of long-term isolation and relatively recent immigration for many lineages. Annual herbs (50% in some local floras) in the Asteraceae, Caryophyllaceae, Lamiaceae, and Poaceae are well represented as are shrubs in the Fabaceae, Lamiaceae, and Cistaceae that dominate postfire forest succession. The diversity of tree species, however, is low in comparison with other biomes at similar latitudes (Thompson 2005).

Intensification of seasonality and the onset of a full MTC in the Pliocene and Pleistocene were associated with the disappearance of many paleotropical and mesic temperate forest taxa and gave way to the MTV that exists today (Suc 1984). This, together with extinctions during Quaternary glaciations, gave lineages new environment opportunities to differentiate. Fluctuating climate at the northern and southern margins of the MB provided multiple events of species isolation, as did mosaics of vegetation due to the east–west orientation of mountain ranges that hindered north–south migrations during glaciation. Additionally, the Mediterranean Sea itself has been a significant geographical barrier for plant dispersal between North Africa and Europe, with exceptions seen in dispersal bridges across the sea, such as the Strait of Gibraltar and the Tunisia–Sicily link, that buffered the effects of glaciations and permitted persistence of old pre-mediterranean lineages (Rodríguez-Sánchez et al. 2008, Rodríguez-Sánchez & Arroyo 2011). As a result of migration barriers, common patterns of subspecific (phylogeographic) (Vargas 2003) and specific (phylogenetic) differentiation are associated with geographic isolation (Vargas et al. 2009, Fiz-Palacios & Valcárcel 2013). Nevertheless, several paleotropical lineages—for example, *Myrtus* (Myrtaceae), *Phillyrea* (Rhamnaceae), and *Pistacia* (Anacardiaceae)—overcame the environmental and climatic challenges of the late Cenozoic and remained as widespread components of the modern flora in the region (Barrón et al. 2010).

In contrast to SWA and the Cape, phylogenetic studies suggest that diversification rates have been high (>1 species Myr⁻¹) in herbaceous and subshrub clades (Verdú & Pausas 2013),

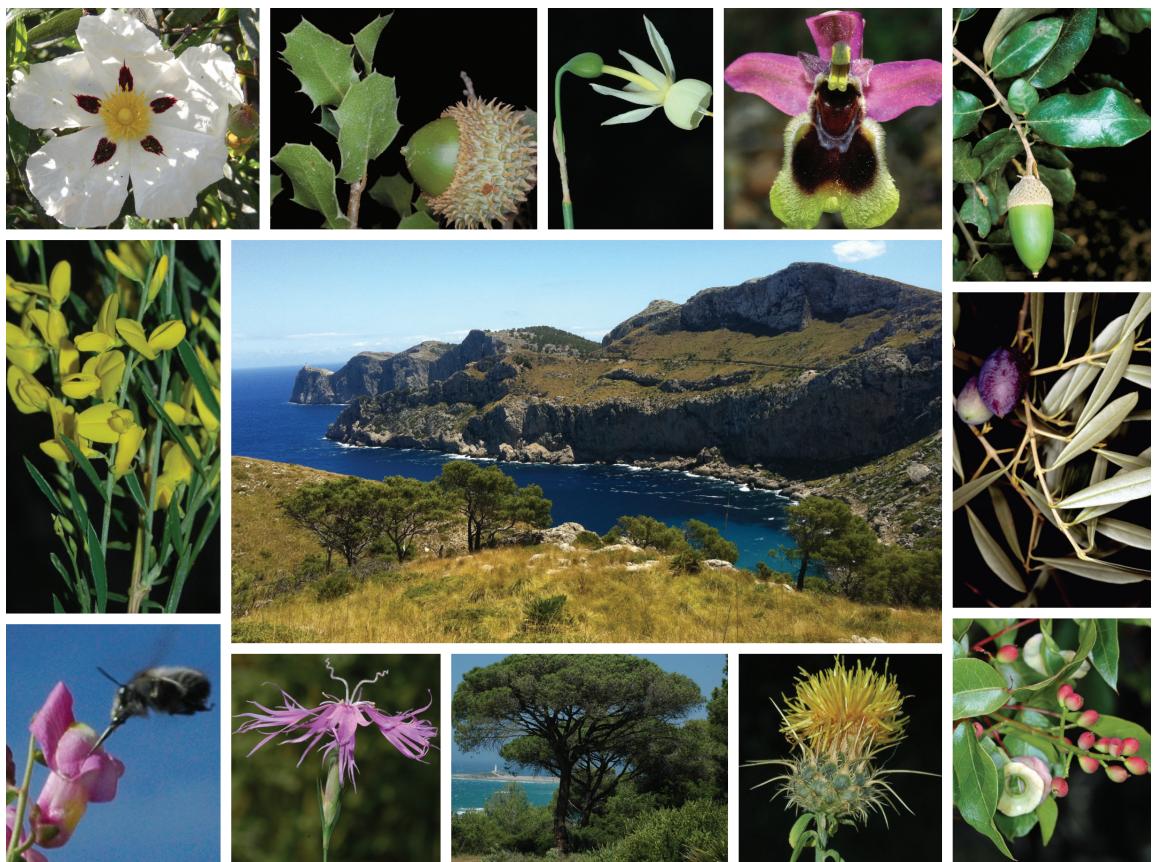


Figure 5

Mediterranean Basin. Centerpiece, rugged geography of the coastline of Majorca Island, Spain, where degraded *Pinus halepensis* woodlands give way to maquis vegetation. From upper left clockwise: *Cistus ladanifer* (Cistaceae); *Quercus coccifera* (Fagaceae); *Narcissus pallidulus* (Amaryllidaceae); *Ophrys tenthredinifera* (Orchidaceae); *Quercus ilex* (Fagaceae); *Olea europaea* (Oleaceae); *Pistacia terebinthus* (Anacardiaceae); *Centaurea toletana* (Asteraceae); *Pinus pinaster* (Pinaceae); *Dianthus hyssopifolius* (Caryophyllaceae); *Antirrhinum charidemi* (Plantaginaceae), pollinated by *Anthophora dispar*; and *Genista florida* (Fabaceae).

rivaling or exceeding the fastest known global plant radiations [e.g., *Centaurea* and *Tragopogon* (Asteraceae), *Cistus* (Cistaceae), and particularly *Dianthus* (Caryophyllaceae)] (Valente et al. 2010a,b). The influence of geographic restriction on diversification rates over differential clade ages and spatio-ecological isolation appears to have primarily been responsible for the high levels of plant diversity (Valente & Vargas 2013). Abundant opportunities for species isolation were provided by numerous islands, peninsulas, and high mountains since the Paleogene (Rosenbaum et al. 2002). Speciation of mediterranean plants is also clearly linked to soil type. Narrow endemics occur both on Cenozoic deposits of calcareous sediments that resulted in extensive plains and coastal mountains and on acid soils derived from granites, shales, and sandstones primarily of inland mountains (Thompson 2005). Thus, vegetation across the MB is primarily determined by base-rich and acidic soils that filter species chemically (Arroyo & Marañón 1990). Given that plant isolation is related to both edaphic adaptation and geographic confinement, the question remains as to whether geography or soils has been the more significant driver of

speciation (Molina-Venegas et al. 2013). In addition, the flora observed today has been shaped by long-term human activity, more than in any other MTE region, by more than 10,000 years of domestication, plant cultivation, livestock spread, and fire.

7.4. California

The origin of a flora high in plant diversity in California can be traced to the novel proto-mediterranean climate and fire regime of the middle Miocene approximately 15 Ma (Keeley et al. 2012) and associated with the development of the cold California Current along the Pacific Coast (Jacobs et al. 2004). Most diverse clades have diverged since this time from a broad set of North American lineages (**Figure 6**). Endemic diversity is most prominent in radiations of herbaceous and subshrub lineages in the Asteraceae, Boraginaceae (including Hydrophyllaceae), Brassicaceae, Fabaceae, Lamiaceae, Onagraceae, Polemoniaceae, and Polygonaceae. Although annual plant



Figure 6

California. Centerpiece, chaparral in the San Gabriel Mountains of southern California. From upper left clockwise: *Ceanothus megacarpus* (Rhamnaceae), *Heteromeles arbutifolia* (Rosaceae), *Malosma laurina* (Anardiaceae), *Adenostoma fasciculatum* (Rosaceae), *Hesperoyucca whipplei* (Asparagaceae), *Ribes speciosum* (Grossulariaceae), *Eriogonum fasciculatum* (Polygonaceae), *Quercus berberidifolia* (Fagaceae), *Encelia californica* (Asteraceae), *Salvia mellifera* (Lamiaceae), and *Arctostaphylos hookeri* (Ericaceae).

diversity is quite high, accounting for approximately one quarter of the flora, diversification in these families and others has often been associated with ecological shifts in life history to perennial growth forms (see Baldwin 2014 for a more detailed discussion). Despite high diversification in clades of annuals and herbaceous perennials, shrub diversification has been limited with the exception of the two genera mentioned previously.

Several lineages have undergone significant patterns of speciation across what are functionally island archipelagos of serpentine or other ultramafic substrates (Harrison et al. 2006, Anacker et al. 2011). Approximately 10% of endemic species in California are serpentine specialists. Vernal pools, which fill with winter rains and dry under summer drought, also exhibit a scattered geographic distribution and a highly endemic flora. The California Islands present a case of true geographic isolation, with approximately 20% of their species endemic. Many of these, however, are relicts of a former mainland distribution rather than examples of island diversification. The sum total of these various edaphic and habitat islands has played a role in the evolution of species richness but cannot alone explain the hyperdiversity of the California flora.

Analyses of existing phylogenies have indicated that diversification rates in California lineages during the past 5 Ma are not higher than those in source areas and suggest that low extinction rates are the key to species diversity (Lancaster & Kay 2013). Consistent with this hypothesis is the presence of numerous paleoendemic lineages of woody plants that have not undergone significant diversification. These include not only the iconic conifers *Sequoia* and *Sequoiadendron* but also a number of isolated chaparral lineages that date back to at least the Oligocene (Baldwin 2014). Examples include *Pickeringia* (Fabaceae), *Adenostoma* (Rosaceae), *Cneoridium* (Rutaceae), *Malosma* (Anacardiaceae), *Carpenteria* (Hydrangeaceae), and *Lymanothamnus* (Rosaceae).

The onset of the Pleistocene brought not only cycles of glacial advances and retreats with consequent effects on upland plant distributions but also major impacts on the strength of the California Current. Although this ocean current remained strong during interglacial periods, it weakened during glacial intervals, reducing fog and increasing temperatures along the coast. Much of the modern coastal disjunction in conifer species (*Pinus*, *Hesperocyparis*) in California can be attributed to these cyclical changes in coastal climate, and those patterns have persisted to the present (Axelrod 1980, Millar 2012).

7.5. Central Chile

Compared with the other MTC floras, overall plant species diversity in central Chile is less spectacular as seen in its relatively small flora of 2,900 species (Arroyo et al. 2002) and comparatively low species and generic richness on an equal area basis (Cowling et al. 1996) (Figure 7). Two factors limit species richness in Chile compared with other MTC regions. First is the strong biogeographic isolation produced by the hyperarid Atacama Desert and the high Andes. Numerous herbaceous lineages present east of the Andes and north of Atacama Desert have failed to reach Chile. Second, fire as a stimulus for diversification has been virtually absent since the Miocene uplift of the Andes. Novel life history traits of fire-dependent seed germination and canopy seed storage are absent (Keeley et al. 2012).

Many woody clades predate the establishment of the MTC in the middle Miocene. Gondwanan lineages with Australasian linkages that split very early can be seen in *Lomatia* and the monotypic *Gevuina* (Proteaceae) (Barker et al. 2007) and the monotypic *Peumus* (Monimiaceae) (Renner et al. 2010). Other groups of Gondwanan origin include *Caldchuvia* (Cunoniaceae) (Bradford & Barnes 2001), *Eucryphia* (Eucryphiaceae) (Taylor & Hill 1996), *Fuscopora* (Nothofagaceae) (Sauquet et al. 2012), and the monotypic Gomortegaceae and Aextoxicaceae.



Figure 7

Central Chile. Centerpiece, matorral vegetation near Alicahue, V Region, Chile. From upper left, clockwise: *Oxalis arenaria* (Oxalidaceae), *Montiopsis potentilloides* (Montiaceae), *Alstroemeria pelegrina* (Alstroemeriaceae), *Lomatia hirsuta* (Proteaceae), *Escallonia pulvifera* (Escalloniaceae), *Trevoa quinquenervia* (Rhamnaceae), *Chaetanthera elegans* (Asteraceae), *Quinchamalium chilense* (Schoepfiaceae), *Leucocoryne ixioides* (Amaryllidaceae), *Gavilea venosa* (Orchidaceae), and *Chloraea gavilu* (Orchidaceae).

The moderate oceanic climate of Chile has allowed the persistence of many woody lineages, contributing to a woody flora proportionately larger than that of California (Arroyo et al. 1995) with many genera represented by a single or few species, as with the neotropical *Quillaja* (Quillajaceae) and *Lithraea* (Anacardiaceae). Legacies of more woody lineages in the past are evident in generic disjunctions to wetter ecosystems in southeastern Brazil (Arroyo et al. 1995, Murillo et al. 2012). Radiations in herbaceous clades dating to the Miocene are seen in *Alstroemeria* (Alstroemeriaceae) (Chacón et al. 2012), *Chaetanthera* (Asteraceae) (Hershkovitz et al. 2006), and *Leucocoryne* (Amaryllidaceae) (Jara-Arancio et al. 2014). In contrast, *Montiopsis* (Montiaceae) (Hershkovitz 2006) and *Puya* (Bromeliaceae) (Jabaily & Sytsma 2010) are examples of younger clades. The annual life-form is important in central Chile but less so than in California with fewer genera evolving annuals (Arroyo et al. 1995). Several ecological factors bode against the evolution of annuals in Chile, including the absence of natural fire as stimulus for germination and more

closed shrubland cover, signifying fewer habitats available for light-demanding annuals. Annuals are most abundant and diverse in lower elevation foothills in California, whereas the Chilean landscape exhibits more mountainous terrain with higher average elevations.

8. CONCLUSIONS

The five MTE biomes of the world are linked by a novel climate regime of winter rainfall and summer drought that first appeared in the middle Miocene and perhaps intermittently as early as the Oligocene. However, many lineages of the modern floras of SWA and the Cape have earlier origins in evergreen sclerophyll shrublands on oligotrophic soils of these regions dating back to the late Cretaceous–early Cenozoic (Lamont & He 2012). These old, climatically buffered, fire-prone, nutrient-poor landscapes owe much of their contemporary diversity to the persistence of these old lineages (Hopper 2009). Supplementing the diversity of the Cape has been the juxtaposition of an ancient and topographically heterogeneous landscape associated with the Cape Fold Belt and a relatively young lowland landscape that has provided novel habitats for the diversification of geophytes and leaf succulents, most notably in the Iridaceae and Aizoaceae.

Although paleoendemic taxa that predate an MTC regime are also present in the younger and more dynamic landscapes of the MB, California, and Chile, these have contributed only a small part to the modern species diversity despite a widespread ecological distribution and dominance of many species. More recent immigration and diversification account for a large portion of modern species richness in their floras. For these regions, and to a lesser extent SWA and the Cape, the novel climate seasonality and predictable crown fire regimes (with Chile as an exception) present since the Miocene have allowed colonization from a large regional species pool with associated diversification. Consistent with this hypothesis is the breadth of independent lineages in disparate plant families that developed key life history strategies to cope with fire. Chile is a clear exception to this pattern (Keeley et al. 2012). The MB provides an interesting case study deserving of more research given that despite a long fire history much of its species richness lies in diversification of herbaceous lineages unrelated to obvious fire adaptation.

Thus, diversification in the three younger MTE regions, in contrast to that present in the early Cenozoic lineages of SWA and the Cape, suggests a relative absence of phylogenetic niche conservatism (Donoghue 2008), with a permeable habitat boundary open to recruitment of many growth forms from other biomes. This permeable habitat boundary and the absence of a strong pattern of niche conservatism are parallel to those hypothesized for the diversification of the flora of the Brazilian cerrado in response to savanna expansion and an intensifying fire regime (Simon et al. 2009).

Many other ecological factors not unique to MTEs have promoted speciation in these five regions. These include pollination ecology, adaptations to oligotrophic soils in SWA and the Cape, and diverse spatial patterns of climatic, topographic, and edaphic heterogeneity during the Pliocene and Quaternary in all five regions but most notably in the three younger MTEs. Despite differing tectonic and climatic histories, the relatively moderate climates of the five MTEs have rendered these regions rich in relict paleoendemic lineages. In the same manner, the key to diversity for many MTE lineages has been their ability to speciate and persist at fine spatial scales, with low rates of extinction of the adapted lineages. Nevertheless, much is still unknown about patterns and rates of diversification in MTE lineages. Existing phylogenetic information is limited and unequally available across the five MTE regions. There remains a strong need for further research.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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