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Baldwin, Bruce G

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Origins of Plant Diversity in the California Floristic Province

Bruce G. Baldwin

Jepson Herbarium and Department of Integrative Biology, University of California, Berkeley, California 94720-2465; email: bbaldwin@berkeley.edu

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Abstract

Recent biogeographic and evolutionary studies have led to improved understanding of the origins of exceptionally high plant diversity in the California Floristic Province (CA-FP). Spatial analyses of Californian plant diversity and endemism reinforce the importance of geographically isolated areas of high topographic and edaphic complexity as floristic hot spots, in which the relative influence of factors promoting evolutionary divergence and buffering of lineages against extinction has gained increased attention. Molecular phylogenetic studies spanning the flora indicate that immediate sources of CA-FP lineages bearing endemic species diversity have been mostly within North America—especially within the west and southwest—even for groups of north temperate affinity, and that most diversification of extant lineages in the CA-FP has occurred since the mid-Miocene, with the transition toward summer-drying. Process-focused studies continue to implicate environmental heterogeneity at local or broad geographic scales in evolutionary divergence within the CA-FP, often associated with reproductive or life-history shifts or sometimes hybridization.

1. INTRODUCTION

The California flora provides an outstanding system for exploring patterns of biodiversity and the contributions of dispersal and diversification to the assembly of a regional flora. California has over 6,500 native minimum-rank vascular plant taxa (species, subspecies, and varieties), >25% of which are endemic (Baldwin et al. 2012). The isolated and young Mediterranean-like climate of much of California coupled with its dynamic geological history and diversity in substrates, topography, and climates have been implicated in extensive evolutionary activity of the flora; at the same time, long-term environmental stability of some areas has been inferred to account for substantial paleoendemism (e.g., Stebbins & Major 1965, Raven & Axelrod 1978, Harrison 2013). California is also unusual in the close correspondence between a major biotic region (the California Floristic Province or CA-FP; Howell 1957) and a political unit, allowing pursuit of questions of basic evolutionary biology and immediate conservation importance in parallel (in the United States, only Hawaii has a closer alignment of biogeographic and political boundaries). Improved understanding of the evolutionary history of the flora and of areas of high diversity and endemism are critical for conservation planning in California, where urban/agricultural development, invasive organisms, and climate change pose increasing challenges to biodiversity protection (e.g., Loarie et al. 2008) and where protected areas do not encompass important floristic components (e.g., Kraft et al. 2010).

California contains a higher diversity of native and endemic vascular plant taxa than other states or provinces in North America north of Mexico (Kartesz 2013) and includes most (~88%) of the exceptionally diverse CA-FP (Howell 1957, Raven & Axelrod 1978). The CA-FP is recognized by Conservation International as the only North American area mostly north of Mexico that ranks among the top 35 global biodiversity hot spots. Those hot spots collectively have been estimated to contain >50% of Earth's vascular plant species but represent only about 2.3% of the Earth's surface, in reference to intact remaining habitat (Mittermeier et al. 2011). Areas of Mediterranean-like climate worldwide, including the CA-FP, central Chile, southern Australia, South Africa's Cape Floristic Province, and the Mediterranean Basin, are among those hot spots with unusually high plant diversity and endemism in comparison with most other temperate floras.

Major climatic and dispersal barriers have isolated the CA-FP for millions of years and required that colonizing plant lineages disperse there across unfavorable terrain, undergo climatic adaptation, or both (Ackerly 2009). The climatic isolation of the CA-FP is on a continental scale; the nearest other Mediterranean-like climatic area, in central Chile, is more than 8,000 km away. Limited long-distance dispersal between central Chile and the CA-FP within the time frame of Mediterranean-like climates in both areas has not made a sizable contribution to the assembly of the California flora (see Wen & Ickert-Bond 2009). The CA-FP is bounded by the Pacific Ocean to the west, an unbroken series of high mountain ranges (the Cascade, Sierra Nevada, Transverse, and Peninsular ranges) running from Oregon to Mexico to the east, the wetter and cooler Vancouverian Province to the north, and the dry Sonoran Desert to the south. The Mediterranean-like climate of wet, mild winters and dry, hot summers that dominates the CA-FP gives way, in eastern California, to cold desert conditions of the Great Basin and, further south, to the warmer Mojave and Sonoran desert environments. As noted above, California's complex geological and climatic history, and diverse topographic and edaphic conditions, has been implicated in *in situ* diversification and resultant neoendemism as well as persistence of ancient taxa or paleoendemics within environmentally stable or equable refugia (Raven & Axelrod 1978). Early attempts to understand the importance of such ecological and biogeographic factors in diversification of Californian plants led to major progress in plant evolutionary biology in general, through experimental studies at the interfaces of ecology, taxonomy, and genetics (e.g., Stebbins 1950, Clausen 1951, Kruckeberg

1954), and have made the flora a famous and continuing subject for studies of plant evolutionary processes and patterns (e.g., Carlquist et al. 2003, Patterson & Givnish 2003, Angert et al. 2008, Anacker & Harrison 2012, Yost et al. 2012, Anacker & Strauss 2014). Here, I review (a) regional patterns of native vascular plant diversity and endemism in California, with an emphasis on the CA-FP; (b) phylogenetic evidence on origins and assembly of the CA-FP flora in general; and (c) examples of evolutionary processes that have contributed to floristic richness in the CA-FP. The vast wealth of data and literature on these topics warrants a book-length treatment, as provided by Raven & Axelrod (1978), who inspired this relatively limited presentation of mostly recent findings.

2. SPATIAL PATTERNS AND ENVIRONMENTAL CORRELATES OF ENDEMISM AND DIVERSITY IN CALIFORNIA

2.1. Classic Syntheses

Stebbins & Major (1965) were among the first to take a flora-wide approach to understand evolution and assembly of California's vascular plant diversity by examining patterns of endemism at different geographic scales across the entire state. Their influential work resulted in recognition of floristic subdivisions within California that they delineated to conform roughly to regions of concentrated species-level endemism. The impact of their system is in part evident from the resemblance of those floristic areas to currently recognized subdivisions of California (see Baldwin et al. 2012). Stebbins & Major's (1965) analysis also resulted in conclusions about regions of high paleoendemism, and endemism in general, within the state. Based on their sampling of 70 large- to medium-sized genera and 64 putatively relict genera of Californian vascular plants, they found that endemic species were primarily concentrated in the three coastal subdivisions of California, with increasing endemic diversity progressing from north to south. Relicts (paleoendemics) were at highest frequency in northwestern California (Siskiyou-Trinity mountain area), where relatively mild Pleistocene conditions prevailed, and in far southern California along the western and northern margins of the Sonoran Desert. Lack of phylogenetic data at the time required the considerable but necessary assumption that relicts comprised mono- and ditypic genera that are largely or entirely confined to the state or isolated species with disjunct closest relatives elsewhere in North America or outside the continent. These patterns of endemism and others, including those involving neopolyploids (apoendemics), their presumed diploid relatives (patroendemics), and paleopolyploids, were explained biogeographically within the context of Tertiary Geoflora concepts, such as the Arcto-Tertiary and Madro-Tertiary geofloras, in the absence of an explicitly phylogenetic framework.

Raven & Axelrod (1978) extended Stebbins & Major's work greatly by expanding the scope of discussion to encompass the entire vascular flora, rather than a subset of groups, and by giving more attention to edaphic endemism (restriction to particular substrates) and especially serpentine exposures, where ~10% of Californian endemic plant taxa are restricted (Kruckeberg 1984). They also addressed modes of evolution, drawing on the wealth of biosystematic data for California plants available by then, with detailed accounts of exceptionally diverse genera and families.

2.2. Insights from Recent Floristic Analyses

More recent analyses of floristic endemism or diversity in California have attempted to refine Stebbins & Major's (1965) and Raven & Axelrod's (1978) findings by examining patterns at finer geographic and ecological scales. Richerson & Lum (1980), for example, used multiple regression

analysis to assess the importance of particular climatic or topographic variables on vascular plant species diversity (not just endemics) throughout the state. In general, they found that climatic factors were the strongest predictors of elevated diversity, especially mean precipitation. Using the same subcounty regions, Qi & Yang (1999) examined correlation coefficients between native species richness (not just endemics), on a per genus or per family basis, and elevational means or standard deviations to conclude that elevational or habitat heterogeneity was the most important determinant of plant diversity in Californian environments. Thorne et al. (2009) used a finer-scale geographic system of 228 units to examine patterns of endemism and native diversity of species, subspecies, and varieties across the entire Californian vascular flora. Their results indicated that the Sierra Nevada is a native plant diversity hot spot within the state and that Californian endemics are most concentrated in the central Coast Ranges; Stebbins & Major's (1965) southern Californian endemic hot spot was mostly accounted for by the Transverse Ranges. Concentrations of narrow endemics were greatest in the Channel Islands and in general were associated with coastal or montane situations on the Californian mainland or with other mainland environmental islands, including some that roughly corresponded with local hot spots identified by Stebbins & Major (1965). Thorne et al. (2009) concluded that topographic complexity, edaphic diversity, and isolation were likely more important than areal extent of habitat in explaining richness of plant endemism and diversity in California. Kraft et al. (2010) incorporated terminal taxon age, from phylogenetic branch lengths of ~15% of Californian endemic taxa, in analyses of patterns of Californian vascular plant neoendemism. Using a system of geographic areas totaling 800 nonoverlapping regions, they found that the central coast, Sierra Nevada, and San Bernardino Mountains (one of the Transverse Ranges) had the highest concentrations of narrow endemics within the state. They also found that the deserts (outside the CA-FP), including the Great Basin, had the youngest and narrowest endemics on average and that a large proportion of Californian areas with high neoendemic diversity were outside of protected lands.

3. ORIGINS AND RELATIONSHIPS OF CALIFORNIAN VASCULAR PLANTS

Resolving the ages, biogeographic origins, and phylogenetic relationships of native CA-FP vascular plant lineages is important for understanding the extent of diversification and duration of lineages, the evolution of ecological adaptations (or exaptations) to the Californian environment, and historical factors that may help to explain patterns of diversity in the flora (Ackerly 2009). Raven & Axelrod's (1978) monumental synthesis on this topic, based on analysis of modern and fossil floras, considered past and present ecological contexts of different taxa in the framework of Tertiary Geoflora concepts to show that CA-FP plant groups represent a wide diversity of biogeographic sources, including north temperate (Arcto-Tertiary), subhumid southwestern North American (Madro-Tertiary), warm temperate or desert, and cosmopolitan elements, in addition to some immigrants from other Mediterranean-like areas (in central Chile and the Mediterranean Basin) and taxa mainly associated with the CA-FP and of uncertain relationships to plants elsewhere.

The rise of molecular phylogenetic data since the 1980s has provided refined evidence for relationships of CA-FP plants and biogeographic sources of the modern flora. At an intercontinental level, major floristic interchange accounting for plant disjunctions between Eurasia and North America evidently has occurred mostly since the Oligocene (<30 Ma), when a North Atlantic corridor for overland migration between Europe and North America was likely no longer in place and a far northern, Beringian route between east Asia and North America, as well as long-distance dispersal, were potential means of exchange (e.g., Donoghue & Smith 2004, Wen

et al. 2010, Kadereit & Baldwin 2012). At a similar scale within the New World, phylogenetic studies have reinforced earlier conclusions by Raven (1963, 1973) that amphitropical plant disjunctions between the CA-FP and central Chile generally reflect late Cenozoic long-distance, bird-mediated dispersal within the general time frame of development of a Mediterranean-like climate in both regions (see Wen & Ickert-Bond 2009).

3.1. Lack of Immigration to the CA-FP from Other Mediterranean-Like Climatic Regions

An important implication of recent phylogenetic and biogeographic analyses is that the CA-FP has received even fewer natural immigrants from other Mediterranean-like climatic areas than was previously apparent. Strong asymmetry of dispersal directionality from north to south between the CA-FP and central Chile has been long recognized (Raven 1963, 1973) and has gained support from more recent studies (reviewed by Wen & Ickert-Bond 2009). That pattern contrasts with the more extensive south-to-north dispersals reflected by amphitropical disjunctions of desert taxa outside the CA-FP (Wen & Ickert-Bond 2009). Unusual examples of northward dispersal from southern South America to the CA-FP likely include *Eryngium* (Umbelliferae; Calviño et al. 2010) and some lineages of Montiaceae (e.g., *Calandrinia*, *Cistanthe*; Hershkovitz 2006).

Previously noted disjunctions between the Mediterranean Basin and the CA-FP (putative Madrean-Tethyan elements) were revisited by Kadereit & Baldwin (2012), who concluded from phylogenetic considerations that most of these examples were probably best explained by parallel evolution to dry environments rather than by descent from a dry-adapted common ancestor (also see Wen & Ickert-Bond 2009). Those lineages that were best explained by long-distance dispersal within the time frame of aridification in the two regions (Jiménez-Moreno et al. 2010, Millar 2012) were each represented by only one or two CA-FP endemic taxa at most, e.g., *California* (Geraniaceae) and *Polycarpon* (Caryophyllaceae), with possible rare exceptions, such as the diverse, mostly Californian clade of *Antirrhinum* sensu lato (Plantaginaceae; also see Vargas et al. 2014) and the New World endemic clade of subtribe Filaginae (Compositae). Migration to North America via the North Atlantic or Bering land bridges is consistent with estimated divergence times for some Mediterranean-Californian disjuncts from mesic or cool settings, such as *Datisca* (Datiscaceae), *Cicendia* (Gentianaceae), and *Zeltnera* and relatives (Gentianaceae).

Direct floristic ties between the CA-FP and other Mediterranean-like climatic regions (i.e., in southern Australia and South Africa) that reflect dispersal within the time frame of development of those climates are generally lacking. Probable evidence of long-distance dispersal from the CA-FP or elsewhere on the Pacific Coast of North America to Australasia has emerged from phylogenetic studies of *Microseris* (Compositae; Vijverberg et al. 2000) and *Lepidium* (Cruciferae; Dierschke et al. 2009), with subsequent evolutionary radiation after arrival of both groups in Australia and New Zealand, which is reminiscent of the more extensive radiations of tarweeds, sanicles, mints, violets, and other angiosperms in the high Hawaiian Islands from western North American ancestors (see Baldwin & Wagner 2010). Other potential examples of CA-FP to Australasia dispersal, e.g., in *Plagiobothrys* (Boraginaceae) and the *Crocidium-Blennosperma-Ischnea* clade (Compositae; Pelsner et al. 2010) await more detailed analysis. Dispersal in the other direction, toward the CA-FP, has been suggested as a possible explanation for phylogenetic data uniting South Australian *Malva preissiana* (= *Lavatera plebeia*; Malvaceae)—reportedly with strongly saltwater-buoyant fruits (and seeds that remain viable under those conditions)—with native mallows of the California Islands, where the taxa have fruits that lack persistent buoyancy, putatively because of secondary loss of dispersibility in the island environment (Ray 1995; also see Escobar Garcia et al. 2009).

Beyond the scope of this review is consideration of the vast, nonnative component of the CA-FP, which includes a wide diversity of naturalized taxa, especially from other Mediterranean-like climatic areas, and which provide some evidence of evolutionary change since introduction, including origin of distinctive new lineages, e.g., in *Raphanus* (Cruciferae; Hegde et al. 2006).

In summary, the ecological fit of native plants to the Mediterranean-like climate in the CA-FP rarely can be explained by earlier adaptation to Mediterranean-like climates elsewhere (i.e., by synclimatic shift sensu Ackerly 2009), as earlier concluded by Raven & Axelrod (1978). In contrast, California has been an important source of herb lineages to central Chile (especially to vernal pools), as long understood, and a more important source area than earlier believed for other regions, such as the Hawaiian Islands (Baldwin & Wagner 2010), as well as adjacent regions of North America (e.g., see Lancaster & Kay 2013). An understanding of climatic adaptation or exaptation to CA-FP conditions requires a closer look at the primary source areas of most native plant lineages there. A review of recent phylogenetic studies that included CA-FP taxa in more broadly focused analyses indicates that achieving that understanding for most of the diverse CA-FP clades warrants even closer attention to nearby relatives.

3.2. North American Angiosperm Diversification

Available molecular phylogenetic evidence indicates that North America has been a site for more extensive angiosperm radiations than earlier recognized and an even more important source of CA-FP lineages than was previously evident. North American ancestry is evident not only for most CA-FP-occurring clades associated by Axelrod (1958) with the Madro-Tertiary Geoflora but also for most CA-FP clades of putative warm temperate/desert or even north temperate origin (Raven & Axelrod 1978) that include at least one endemic CA-FP species (B. Baldwin, unpublished data). The great diversity of mainly CA-FP taxa not assignable to a source area at the time of Raven & Axelrod's (1978) study also evidently belong to larger North American clades—usually from the west or southwest—with few well-resolved exceptions (B. Baldwin, unpublished data), most discussed below. Relevant North American or New World clades often descend from common ancestors that can be inferred to have arrived in the Western Hemisphere by immigration from Eurasia, but most show evidence of having undergone diversification in North America before establishment and evolutionary divergence in the CA-FP.


Examples of such diverse, principally North American clades for the sunflower family (Compositae) alone include the New World true thistles (*Cirsium*, tribe Cardueae; Kelch & Baldwin 2003); a clade encompassing the vast majority of North American taxa of the aster tribe, Astereae (Noyes & Rieseberg 1999); the New World subtribe Filaginae clade (tribe Gnaphalieae; Galbany-Casals et al. 2010); the clade of primarily North American genera of the chicory tribe, Cichorieae (Lee et al. 2003); the expanded, mostly Californian tarweed tribe, Madieae (Baldwin et al. 2002); and the clade containing most primarily western North American genera of the ragwort tribe, Senecioneae (Pelser et al. 2010). Highly diverse New World (primarily North American) clades also have been resolved in different groups of legumes, as in the lotus tribe, Loteae (Allan & Porter 2000); the milk-vetches (*Astragalus*; Wojciechowski et al. 1999, Scherson et al. 2008); tribe Psoraleae (Egan & Crandall 2008); the clover genus *Trifolium* (tribe Trifolieae; Ellison et al. 2006); the sweet-pea genus *Lathyrus* (tribe Fabeae; Schaefer et al. 2012); and the lupines (*Lupinus*; tribe Genisteae), with a major western North American clade (Drummond 2008). In Umbelliferae, the perennial endemic western North American genera of subfamily Apioideae constitute a highly diverse, previously unrecognized clade (Sun & Downie 2010, George et al. 2014). In the mint family (Labiatae), the Californian sages (*Salvia* subg. *Audibertia*, including sect. *Echinosphece*) represent a diverse western North American clade (Walker et al. 2004), as does a set of three mainly CA-FP

genera, *Acanthomintha* (thorn mints), *Pogogyne* (mesa mints), and *Monardella* (coyote mints), that belong to a recently resolved clade encompassing New World taxa of subtribe Menthinae (Bräuchler et al. 2010). The bellflower family, Campanulaceae, also contains a novel North American clade (cam02) that encompasses a primarily CA-FP subclade of annual and perennial taxa spanning multiple genera: *Campanula* (in part), *Githopsis*, and *Heterocodon* (Mansion et al. 2012).

These and other recently resolved examples are consistent with the conclusions from studies of Eurasian–North American disjunct angiosperms that western North American taxa (including those of the CA-FP) are usually more closely related to their eastern North American counterparts than to those in East Asia or Europe regardless of the direction of migration or dispersal between the two hemispheres that originally established the intra- and intercontinental distributional patterns (Xiang et al. 1998, Donoghue & Smith 2004, Wen et al. 2010, Harris et al. 2013). As widely noted, such disjunctions may have occurred at different times and thus have different historical explanations; such considerations are also important for establishing the basis for CA-FP vascular plant diversity.

3.3. A Predominant Pattern of CA-FP Diversification Since the Mid-Miocene

Published divergence time estimates for CA-FP vascular plant clades with at least one endemic species indicate that most sampled lineages shared a common ancestor with a non-CA-FP clade since the mid-Miocene, <15 Ma (**Supplemental Table 1**; follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>), when Cenozoic cooling and drying intensified and summer rainfall decreased markedly, in association with onset of development of a marine upwelling regime along the Pacific Coast (Jacobs et al. 2004). Those trends ultimately led to a fully developed Mediterranean-like climate in the CA-FP by the late Neogene, when uplift of the Coast Ranges, inundation and changes in drainage of the Great Central Valley, and other geological change implicated in ecogeographic divergence were underway (Millar 2012). The onset of this climatic shift also is reflected by broader-scale biogeographic patterns. For example, estimated divergence times for most temperate Northern Hemisphere disjuncts involving eastern Asia and western and eastern North America reviewed by Wen et al. (2010) date from the Miocene or Pliocene (25 to 3 Ma), and the interval from ~15 Ma onward was noted by Harris et al. (2013) for disruption of floristic connections by episodes of global cooling, aridification of western North America, and renewed uplift of the Rocky Mountains. Diversification that predates the mid-Miocene has been estimated for some clades associated primarily with the CA-FP and may reflect evolutionary response to earlier episodes of Cenozoic cooling and aridification in western North America (Millar 2012), although such ancient crown-group ages for diverse CA-FP clades are rare and often in conflict with younger estimates from other studies of the same groups.

 Supplemental Material

3.4. Paleoendemics and Other CA-FP Lineages that Predate the Mid-Miocene

CA-FP lineages that evidently predate the mid-Miocene include conspicuous paleoendemics, such as the well-known coast redwood (*Sequoia*) and giant sequoia (*Sequoiadendron*), whose precise relationships to one another and the other living member of the redwood clade, *Metasequoia* (an Asian relict), remain uncertain but which all have extensive fossil records in the Northern Hemisphere that date to the Mesozoic (Yang et al. 2012). Ancient divergence of other paleoendemic conifers is reinforced by molecular phylogenetic data, as well. Bristlecone fir (*Abies bracteata*; Pinaceae), restricted to California's Santa Lucia Range but similar to Neogene fossils in Nevada, was resolved as sister to all other sampled taxa of *Abies* worldwide, based on nuclear rDNA (nrDNA) (Xiang et al. 2009), or as sister to one of the two major clades of the genus, based on chloroplast

DNA (cpDNA), with an estimated Eocene divergence time (Aguirre-Planter et al. 2012). Brewer spruce (*Picea breweriana*; Pinaceae), endemic to the Klamath Ranges and long regarded as a paleo-endemic with closest relatives in Asia, was resolved as sister to all other sampled spruces, based on cpDNA, or as sister to northern Asian *Picea obovata*, outside the North American clade, based on mitochondrial DNA (mtDNA), also in keeping with relict status (Bouillé et al. 2011). Incense cedar (*Calocedrus decurrens*; Cupressaceae), which ranges to central western Oregon but is otherwise within the CA-FP, is known from fossils outside its current range in the Pacific Northwest and was estimated from an nrDNA phylogeny to have diverged from a common ancestor with all other living, Asian taxa of *Calocedrus* at ~25.2 Ma, putatively because of vicariance; fossils of the genus also occur in Alaska, Asia, and Europe from as early as the lower Eocene (Chen et al. 2009).

Available molecular phylogenetic data also advance understanding of particularly ancient CA-FP angiosperm lineages, including paleoendemics, which often are evergreen or drought-deciduous trees or shrubs long regarded as having adapted initially to xeric conditions during Paleogene cooling and drying episodes that predated the mid-Miocene onset of summer-drying in western North America (Raven & Axelrod 1978). Those woody lineages sometimes include modest contemporary diversity that probably reflects limited diversification under later, Mediterranean-like conditions. For example, Catalina ironwood, *Lyonothamnus* (Rosaceae), an evergreen tree endemic to the Channel Islands but known from mainland fossils in California, Oregon, and Nevada from as early as the Miocene, was resolved as sister to all other genera of subfamily Spiraeoideae (Potter et al. 2007) and is now treated as the sole genus of tribe Lyonothamneae (Brouillet 2008). Reinterpretation of fossil and modern *Lyonothamnus* (Irwin & Schorn 2000) and consideration of minimal molecular divergence between representatives of the two extant taxa (Bushakra et al. 1999) indicate that the modern Channel Island representatives are probably best interpreted as CA-FP neoendemics of a paleoendemic genus. Chaparral pea, *Pickeringia* (Leguminosae), an evergreen shrub usually interpreted as a CA-FP paleoendemic of tribe Thermopsidae, was estimated to have diverged at ~31 Ma within the “Cladrastis clade” of tribe Sophoreae, which includes two other genera (*Cladrastis*, *Styphnolobium*) that each represent eastern North American/east Asian disjuncts and are known from fossils in western, central, and southern North America (Wojciechowski 2013). Although interpreted as having diverged under ancient subtropical or tropical conditions initially (Wojciechowski 2013), *Pickeringia* includes two intergrading taxa that abut geographically in southwestern California and likely reflect recent evolutionary divergence in the CA-FP.

Carpenteria (Hydrangeaceae), an evergreen shrub from the Sierra Nevada, is an example of a monotypic, putatively paleoendemic genus evidently nested phylogenetically within another genus, a pattern usually associated with young taxa (e.g., Sytsma & Gottlieb 1986) and warranting taxonomic attention. *Carpenteria* was resolved as having diverged from within the mock oranges (*Philadelphus*) in the late Oligocene, after the divergence of southwestern North American taxa of *Philadelphus* subg. *Deutzoides*, which are sister to both *Carpenteria* and other New and Old World taxa of *Philadelphus* based on cpDNA and nrDNA data (Guo et al. 2013). The authors concluded that *Carpenteria*–*Philadelphus* represents an example of “out of western North America” migration to Eurasia via Beringia; that pattern contrasts with the “out of Asia” pattern of migration that is more commonly resolved for Eurasian–North American clades (Wen et al. 2010) but is consistent with evidence for other ancient American clades, such as *Ribes* (Grossulariaceae) and *Fraxinus* (Oleaceae), that Axelrod (1958) considered part of the Madro-Tertiary Geoflora and that also show evidence of North American to Old World migration (Schultheis & Donoghue 2004, Wallander 2008).

Other xeric-adapted woody taxa primarily associated with the CA-FP that molecular data indicate as having diverged from their nearest relatives in the Paleogene include *Adenostoma* (Rosaceae;

Töpel et al. 2012), *Cneoridium* (sister to Old World *Haplophyllum*, Rutaceae; Salvo et al. 2010), *Malosma* (Anacardiaceae; Yi et al. 2004), and *Aesculus californica* (Sapindaceae; Harris et al. 2009). Molecular evidence for mesic-adapted, woody CA-FP endemic angiosperms of similar antiquity is relatively limited, e.g., *Cornus sessilis* (Cornaceae; Xiang et al. 2008).

Woody taxa endemic or nearly restricted to the CA-FP that phylogenetic data have shown to be geographically isolated from relatives in Mesoamerica include two taxa regarded by Axelrod (1958) as part of the Madro-Tertiary Geoflora but of then-uncertain relationships: California bay (*Umbellularia*; Lauraceae) and flannelbush (*Fremontodendron*; Malvaceae). *Umbellularia* was long thought to belong to tribe Laureae but instead was resolved as part of tribe Cinnamomeae, nested among Central American members of the *Ocotea* complex, which in turn were part of a larger primarily South American clade (Chanderbali et al. 2001). *Fremontodendron* was resolved sister to the southern Mexican/Guatemalan devil's hand tree (*Chiranthodendron*), both once placed in Sterculiaceae. Those two, genetically similar and crossable taxa, constituting tribe Fremontodendreae, were resolved as part of a basal grade of southern, tropical, or subtropical clades of Malvoideae (Alverson et al. 1999).

CA-FP herbs previously regarded as paleoendemics that phylogenetic evidence indicates as having diverged from closest relatives elsewhere before the mid-Miocene include taxa generally associated with ecological settings or characteristics that may have allowed them to persist with limited interference by other plants (Stebbins 1942). Monotypic *Odontostomum* (Tecophilaeaceae), a cormose monocot from northern California, is the only North American taxon of a primarily Southern Hemisphere family and was resolved as diverging in late Cretaceous from its diverse African sister group, possibly arriving in North America via a South American route (Buerki et al. 2013). *Odontostomum* often occurs on serpentine soils, which can pose major challenges to plant growth (e.g., low calcium/magnesium ratios, high concentrations of heavy metals, low concentrations of macronutrients) and are widely associated with plant endemism in the CA-FP and elsewhere (Kruckeberg 1984). Serpentine paleoendemism has been widely discussed for CA-FP plants (Raven & Axelrod 1978), but molecular evidence for great antiquity of serpentine lineages was lacking until recently. California pitcher-plant (*Darlingtonia*; Sarraceniaceae) evidently diverged from a common ancestor with the two other genera of New World insectivorous pitcher-plants, *Sarracenia* (eastern North America) and *Heliamphora* (northern South America), in the Paleogene, putatively because of vicariance stemming from late Eocene cooling and aridification (Ellison et al. 2012). *Darlingtonia* occurs in wet or boggy sites, often on serpentine, as does CA-FP endemic *Pseudotrillium* (Melanthiaceae), a rhizomatous herb that is sister to *Trillium* (Eurasia–North America) plus the Eurasian genera *Daiswa*, *Kinugasa*, and *Paris* (Farmer & Schilling 2002).

4. EVOLUTIONARY PROCESSES IN THE CA-FP

4.1. Diversification in CA-FP Vascular Plants

Clade- or taxon-focused studies of plant diversification within the CA-FP have revealed some general evolutionary patterns and raised questions about the importance of different factors in explaining how the flora became so diverse. Endemic diversity is greatest among eudicots in clades representing more than 30 families (Harrison 2013), such as Boraginaceae, Compositae, Cruciferae, Labiatae, Leguminosae, Onagraceae, Polemoniaceae, and Polygonaceae, with Ericaceae and Rhamnaceae containing the two most diverse radiations of woody taxa, *Arctostaphylos* (Boykin et al. 2005) and *Ceanothus* (Burge et al. 2011), respectively. Endemic succulent diversity is highest in Crassulaceae, primarily from the largely CA-FP diversification of *Dudleya* (Yost et al. 2013). Hemiparasite and holoparasite diversification is strongly evident in Orobanchaceae

(especially subtribe Castillejinae; Tank & Olmstead 2008) and Convolvulaceae (*Cuscuta*; Costea & Stefanovic 2009). Monocot diversity and endemism is much lower, particularly in annuals as noted earlier (Raven & Axelrod 1978), with diversification most evident in Agavaceae, Alliaceae (*Allium*), Cyperaceae (e.g., *Carex* sect. *Ovales*), Gramineae (e.g., tribe Orcuttieae), Iridaceae, Liliaceae, Melanthiaceae, and Themidaceae. Conifer diversification has been most extensive in *Hesperocyparis* (Cupressaceae), which now appears to be a north temperate (Asian) rather than Mediterranean or Madro-Tethyan element (Terry et al. 2012), and in the big-cone pines (*Pinus coulteri*, *P. sabiniana*, *P. torreyana*; Gernandt et al. 2009) and closed-cone pines (*P. attenuata*, *P. muricata*, *P. radiata*; Eckert & Hall 2006). Fern and lycophyte diversifications are best represented by families with desiccation-tolerant taxa, particularly Pteridaceae (e.g., *Pentagramma*) and Selaginellaceae (*Selaginella* subg. *Tetragonostachys*; Arrigo et al. 2013).

Researchers have recently reevaluated the question of whether high diversity in Californian plant clades is the result of elevated evolutionary activity compared with that of source areas. As noted above, environmental and historical factors that have been widely discussed as important in explaining plant diversification in the CA-FP include the shift to a Mediterranean-like climate in isolation from climatically similar source areas, a high degree of temporal and spatial environmental heterogeneity (e.g., in climatic and edaphic factors), and physical barriers to dispersal between similar habitats, including a diversity of island-like conditions (Raven & Axelrod 1978). A phylogenetic meta-analysis of 16 angiosperm clades did not find significantly elevated diversification rates in general following a shift to the Californian environment or to its Mediterranean-like climate using a 5-Ma climatic threshold (Lancaster & Kay 2013). Based on estimates of the speciation and extinction components of diversification rates, the authors noted low extinction in general for Californian lineages and the possibility that high diversity in the California flora may have more to do with factors that limit loss of lineages (e.g., climate-change buffering by dispersal along steep topographic gradients and the moderating effects of montane areas on precipitation patterns) rather than conditions that promote speciation. Although this hypothesis warrants further testing, e.g., with a larger sample of clades, exploration of different climatic thresholds, and normalization of geographic scale for diversification-rate comparisons, the proposal that both paleoendemics and neoendemics have been sheltered from extinction is an important stimulus to reexamine assumptions about Californian plant evolution.

4.2. Effects of Life History

The high diversity of annuals in the CA-FP, amounting to about a quarter of native species, is unusual worldwide (especially for the New World) and accounts for more than half of the CA-FP endemic eudicot species (Raven & Axelrod 1978). The ability of annuals to opportunistically escape harsh conditions by remaining in the seed bank or confining their activity to relatively brief, environmentally favorable periods might be expected to limit their vulnerability to extinction. Based on a molecular phylogeny for Saxifragales worldwide, speciation rates were estimated to be lower for annuals than for herbaceous or woody perennials, but estimated extinction rates were so much lower for annuals than for either type of perennial that net diversification rates were highest for annuals in general (Soltis et al. 2013).

Phylogenetic analyses of CA-FP clades with life-history diversity indicate that shifts from annual to perennial habit have occurred repeatedly, in Compositae [e.g., *Chaenactis* (Baldwin et al. 2002), *Deinandra* (Baldwin 2007)], the *Eriophyllum-Pseudobabia-Syntrichopappus* clade (Baldwin et al. 2002), *Helianthus* (Moyers & Rieseberg 2013), *Lasthenia* (Chan et al. 2001), *Malacothrix* (Lee et al. 2003)], Leguminosae (*Lupinus*; Drummond 2008), Orobanchaceae (*Castilleja*; Tank & Olmstead

2008), Phrymaceae (*Diplacus*; Beardsley & Olmstead 2002), Plantaginaceae (*Antirrhinum* sensu lato; Oyama & Baum 2004), Polemoniaceae (*Linanthus*; Bell & Patterson 2000), and Polygonaceae (*Eriogonum*; Kostikova et al. 2013). Until recently, evolutionary transitions from perennial to annual were widely regarded as irreversible (see Tank & Olmstead 2008) despite compelling evidence to the contrary from anatomical studies (e.g., Carlquist 1962). Annual to perennial shifts instead appear to be relatively common compared with perennial to annual shifts for CA-FP taxa based on available phylogenetic data, in keeping with findings for Saxifragales worldwide (Soltis et al. 2013).

The transition from annual to perennial in primarily CA-FP-based clades has been repeatedly associated with ecological shifts to maritime conditions along the immediate mainland coast or on the California Islands (e.g., *Deinandra*, *Lasthenia*, *Malacothrix*), where an equable climate may select for persistence (Carlquist 1965, 1974), or to montane environments (e.g., *Lupinus*, *Eriogonum*), where selection for persistence may be associated with high juvenile mortality compared with adult mortality (Drummond 2008) or low growth rates in cold climates or on poorly developed soils. In *Lupinus*, the shift from annual to perennial habit was accompanied by accelerated diversification, as well, and was suggested to reflect a key innovation for occupying newly available high montane habitat following Pliocene uplift, in light of synchrony with estimated divergence times and a significant phylogenetic correlation between perennial habit and highest elevation (Drummond 2008). In *Eriogonum* and related eriogonoids, perennial species were found to have broader climatic tolerance than annuals and more rapidly increasing niche breadth with increasing mean elevational range (Kostikova et al. 2013). These contrasts were reflected by estimates of climatic niche evolution, with niche breadth evolving much faster in perennials than in annuals and niche optimum evolving more rapidly in annuals. In *Delphinium* (Ranunculaceae), wide elevational occurrence in the diverse CA-FP clade was noted in the context of a transition from annual to perennial in Eurasian ancestors that was associated with higher elevational occurrence and accelerated diversification in the Eurasian/North American clade (Jabbour & Renner 2012).

4.3. Divergence in Ecology

As noted above, ecological gradients and spatial environmental heterogeneity in general in the CA-FP have been invoked in elevating speciation rates and/or reducing extinction rates of plants. Evolutionary change along climatic/habitat gradients in the CA-FP was made famous by Clausen, Keck and Hiesey's pioneering reciprocal transplant studies along the Carnegie transect from the San Francisco Bay Area to the Sierra Nevada (see Clausen 1951). More recent studies have built on their methods to examine the relative evolutionary influence of different extrinsic and intrinsic factors in some of the same systems studied by members of Clausen's team, especially in monkeyflowers (*Mimulus* sensu lato; Phrymaceae) and yarrow (*Achillea*; Compositae). In general, these studies have reinforced the importance of ecological differences between sister taxa or cryptic sister lineages as components of reproductive isolation and as determinants of range limits (e.g., Angert & Schemske 2005). In the Sierra Nevada, ecogeographic factors and pollinator preference were estimated to account for ~99% of reproductive isolation between sister species *Mimulus lewisii* (bee pollinated) and *M. cardinalis* (hummingbird pollinated), with the highest contribution to total isolation from ecogeographic (climate/habitat) differences, except in an area of sympatry (Ramsey et al. 2003).

Clausen, Keck and Hiesey's evidence for evolutionary importance of steep ecological gradients in coastal CA-FP from the shoreline to the interior (see Clausen 1951) has been extended by studies of semicryptic lineages that replace one another along such transects. In *Mimulus*

sensu lato, experimental studies involving reciprocal transplants demonstrated that (derived) perennial *M. guttatus* in the salt-spray, moist environment along the immediate coast and annual *M. guttatus* outside the salt-spray zone in drier inland sites are genetically differentiated and almost completely isolated reproductively by habitat-mediated selection and differences in flowering phenology but not by postzygotic barriers (Lowry et al. 2008). In *Achillea*, differences in ploidy between populations of the *A. borealis* (= *A. millefolium*) autopolyploid complex on coastal dunes versus coastal grasslands were found to correlate with differential performance in the two environments, with the derived hexaploid condition associated with much higher fitness (home-site advantage) compared with tetraploid (grassland) plants in the dune setting, even when tested with synthetic neo-hexaploids (Ramsey 2011). In *Layia* (Compositae), Clausen's (1951) evidence from common garden studies of putative ecotypic differentiation of *L. gaillardoides* along a coast-to-interior transect was found to reflect deep clade structure corresponding to three semicryptic lineages that replace one another across that transect (Baldwin 2006).

Edaphic or substrate heterogeneity has been widely implicated in evolutionary divergence within the CA-FP, especially in serpentine environments (Kruckeberg 1984, Kay et al. 2011). Transitions from nonserpentine to serpentine ecology have been well documented in the CA-FP between plant taxa or populations that retain high interfertility, as in *Layia* (Baldwin 2005), or are intersterile, as in *Collinsia sparsiflora* (Plantaginaceae; Moyle et al. 2012). Strength of natural selection that can be imposed by distinct edaphic settings may be in part reflected by lack of evidence for gene flow in parapatric, fully interfertile taxa, as between *Ceanothus cuneatus*, on relatively nutrient-rich soils, and putative descendant species *C. roderickii*, on adjacent soils derived from gabbro, another (mafic) rock associated with plant endemism (Burge et al. 2013). In *Mimulus guttatus*, tight linkage between genes associated with recent adaptation to copper-mine soil and genetic factors associated with hybrid inviability provide a different type of evidence for reproductive isolation as a by-product of evolutionary divergence on different substrates (Wright et al. 2013). A general pattern of range asymmetry and regional-scale sympatry between young sister species of CA-FP angiosperms may be explained in large part by evolutionary divergence involving soil and habitat heterogeneity (Anacker & Strauss 2014).

A phylogenetic meta-analysis of 23 genera with serpentine-endemic taxa suggested that transitions between edaphic states were biased in the direction of serpentine endemism and that diversification rates in serpentine endemics were in general much lower than those of serpentine nontolerators, possibly in part because of habitat limitation (Anacker et al. 2010). A more recent study of jewelflowers (*Streptanthus* and relatives; Cruciferae) found evidence of multiple (four) transitions to serpentine endemism and only one loss of endemism (Cacho et al. 2014); in core Chlorogaloideae (*Camassia*, *Chlorogalum*, *Hastingsia*; Agavaceae) estimated losses of serpentine tolerance outnumbered gains (Halpin & Fishbein 2013).

Distinctions between grades of serpentine conditions and biotic influences associated with transition to serpentine environments (e.g., disease, herbivores) are of increasing interest in studies of serpentine and other edaphic adaptation. Reciprocal transplant and other experimental studies of two recently recognized cryptic taxa of common goldfields (*Lasthenia californica*, *L. gracilis*) that co-occur in the San Francisco Bay Area demonstrated that they have differential fitness (home-site advantage) in their respective habitats along a serpentine gradient (Yost et al. 2012). In dwarf flaxes (*Hesperolinon*; Linaceae), evolutionary transitions from soils with less serpentine influence to extreme (lower calcium/magnesium) serpentine exposures evidently have occurred repeatedly, with the extreme serpentine habitat associated with less fungal rust infection and potentially serving as a refuge from such pathogens (Springer 2009). In *Streptanthus* sensu lato, cryptic leaf pigmentation and lack of apparency to herbivores are characteristic of endemics of serpentine barrens, where plants susceptible to herbivory have been shown to be more subject to such activity

than when growing with neighbors or when contrasting with substrate in color (Strauss & Cacho 2013).

4.4. Evolution Across Habitat Islands

As in other areas of the world, oceanic islands and island-like habitats in the CA-FP provide some evidence of insular diversification. In the California Islands (Channel Islands, and Pacific islands of Baja California, Mexico), where ~20% of species are endemic, endemism often has been attributed to survival of lineages that once occurred on the mainland but became extinct there with late Cenozoic climate change (e.g., Axelrod 1967). Distinguishing such relictual endemism from in situ divergence in lineages with minimal insular diversity is difficult, especially when the opposing mainland coast is so close and so climatically and floristically similar (Thorne 1969).

Carlquist's (1965) hypothesis that the shrubby tarweeds (*Deinandra*) of the California Islands provide a likely example of insular adaptive radiation was upheld by molecular and cytological evidence for the taxa on Guadalupe Island, the most remote and second largest of the California Islands (Baldwin 2007). Other lineages with insular diversity, including *Dudleya* (Yost et al. 2013), *Malacothrix* (Davis 1997), and *Malva* (Ray 1995), warrant more study for possible examples of island diversification. Comparisons between closely related insular and mainland populations or taxa also have been productive for studying island biogeographic and evolutionary phenomena, such as colonization filters (Schueller 2004), loss of defense traits (Bowen & Van Vuren 1997), and potential loss of genetic diversity with increasing insular isolation, which was not evident for *Acmispon* (Leguminosae) in the Channel Islands (McGlaughlin et al. 2014).

Studies of some plant lineages that span archipelago-like distributions of serpentine exposures or vernal pools have provided evidence of diversification across those habitats. Phylogenetic data indicate that some angiosperm clades have undergone considerable diversification on CA-FP serpentines, which is in contrast to the more general pattern of low diversification rates noted above. *Streptanthus* sensu lato (Cruciferae; Cacho et al. 2014), *Harmonia* (Compositae; Baldwin 2001), *Hesperolinon* (Springer 2009), and *Allium* sect. *Lophioprason* (Alliaceae; Nguyen et al. 2008) include clades comprised largely or entirely of serpentine endemics that are often scattered across discontinuous serpentine exposures of the Bay Area, Coast Ranges, Klamath Ranges, and/or Sierra Nevada. Among the recent discoveries of new serpentine endemics that continue to be made in the CA-FP are *Navarretia paradoxiclara* and *N. paradoxinota*, semicryptic sister species that represent divergence across serpentine islands in the North Coast Ranges and Sierra Nevada, which are separated by the Sacramento Valley (Johnson et al. 2013).

Vernal pools (ephemeral pool systems that fill during winter rains and dry slowly by evaporation as rains end in spring) also have island-like qualities, such as a highly endemic flora and widely scattered geographic distribution, primarily in and around the Great Central Valley in the CA-FP. Vertical zonation of individual pools is often evident from concentric bands of different herbaceous taxa associated with distinct soil conditions that have been shown to represent distinct niche space (e.g., Emery et al. 2009). Phylogenetic analysis of different niche components in *Lasthenia* indicated that the vernal pool depth niche was more evolutionarily conservative than the climate niche; that is, dispersal between pool systems in different climatic regions was more commonly associated with diversification than ecological shifts in pool zonation (Emery et al. 2012). Diversification in vernal pools has been associated with increasing specialization to an amphibious life history and associated evolutionary change in photosynthetic pathway in the C₄ grass tribe Orcuttieae, with the most ancestral condition retained in *Neostaffia*, the sister group to the other two vernal pool genera, *Orcuttia* and *Tuctoria* (Boykin et al. 2010), and with loss of Kranz anatomy in submerged juvenile foliage of the more highly amphibious *Orcuttia* (Keeley 1998).

4.5. Evolution of Reproductive Systems

Evolution of mating and pollination systems has long been of interest in studies of angiosperm diversification in the CA-FP (e.g., Grant & Grant 1964). Although such shifts may be made possible by initial ecogeographic or habitat divergence, or in some cases driven by reproductive interference from distantly related plants, the involvement of floral and other reproductive changes in the evolution of biodiversity and ecological interactions is widely evident (Armbruster & Muchhala 2009, Kay & Sargent 2009). Relatively intimate, long-term coevolutionary relationships between pollinators and plants include associations involving pollinating floral parasites, which in the CA-FP (and Pacific Northwest) are especially well documented in *Lithophragma* (Saxifragaceae) and *Greya* moths, with repeated innovations during diversification in floral ovary position and moth oviposition (Thompson et al. 2013). Repeated pollinator shifts may be implicated in evolutionary convergence or parallelism in floral morphology responsible for major taxonomic confusion in *Calochortus* (Liliaceae; Patterson & Givnish 2003) and CA-FP Themidaceae (Pires & Sytsma 2002). In *Calochortus*, such shifts were suggested to be in response to evolutionary transitions in habitat and resultant changes in availability of different potential pollinators (Patterson & Givnish 2003). Studies including CA-FP clades corroborate earlier evidence that transitions to hummingbird pollination have occurred repeatedly, but these may be unidirectional or only rarely reversible (Barrett 2013), as in the highly diverse *Penstemon* and *Keckiella* (Plantaginaceae), possibly because of high efficiency of hummingbirds as pollinators (Wilson et al. 2007) or mutational disruption of the anthocyanin biosynthetic pathway with the shift to red corollas (Rausher 2008).

Differences between sister lineages in floral size consistent with mating system shifts are widespread in CA-FP angiosperms and have been traditionally considered to reflect highly outcrossing versus highly selfing conditions, with the shift to selfing regarded as irreversible (Stebbins 1957). Although convincing examples of shifts from selfing to outcrossing strategies are lacking, the dichotomy between those conditions may be simplistic (Barrett 2013); mixed mating systems are increasingly identified from genetic estimates of outcrossing rates (Goodwillie et al. 2005), even in instances in which late floral development indicates early self-pollination, as in some small-flowered taxa of *Collinsia* (Armbruster et al. 2002, Kalisz et al. 2012). In any case, shifts between large-flowered and small-flowered states are common in CA-FP angiosperms, e.g., *Collinsia* (Armbruster et al. 2002, Baldwin et al. 2011), *Mimulus* sensu lato (Grossenbacher & Whittall 2011), and *Leptosiphon* (Goodwillie 1999), and sympatry between sister taxa with distinct floral sizes is often evident. In *Leptosiphon*, phylogenetic studies indicated such highly convergent evolution of small flowered, self-fertilizing taxa that some had been mistakenly treated as conspecific (Goodwillie 1999). Some degree of phenological or elevational displacement between closely related taxa differing in mating system, with the more strongly selfing taxon active earlier in the season, or under cooler, wetter conditions at higher elevation, may indicate that drought avoidance can be an important driver of mating system divergence, as suggested for *Mimulus* sensu lato (Ivey & Carr 2012).

4.6. Hybridization

The importance of hybridization in plant evolution has been long appreciated by evolutionists working in the CA-FP (e.g., Anderson & Stebbins 1954). Evidence of retained interfertility between taxa and natural hybridization in many young CA-FP clades has contributed to hypotheses of hybrid origins and introgression that are increasingly being tested with molecular evidence. Molecular data are consistent with hypotheses of homoploid hybrid origin of the annual wire-lettuce *Stephanomeria diegensis* (Compositae; Sherman & Burke 2009) and some annual sunflowers (*Helianthus bolanderi*, *H. exilis*; Rieseberg 1991), which include other, well-characterized examples

of such evolution outside the CA-FP (Rieseberg 2006). Comparisons of cytogenetic and molecular phylogenetic data support a homoploid hybrid origin of *Collinsia tinctoria* associated with convergent evolution of a chromosomal arrangement and expanded elevational range (Baldwin et al. 2011). Hybrid origin of the vernal-pool endemic spurge *Euphorbia hooveri* (Euphorbiaceae) from upland taxa *E. albomarginata* and *E. serpens* inferred from nuclear phylogenies (Yang & Berry 2011) may represent a major transgressive habitat shift associated with hybrid ancestry. Strong incongruence between plastid trees versus nuclear trees and morphology have been interpreted as evidence of introgressive chloroplast capture in various CA-FP lineages, including rockcresses (*Boebera*, Cruciferae), possibly involving unreduced sperm and nuclear replacement (Alexander et al. 2013), and oaks (*Quercus*, Fagaceae), including an apparent example of wide hybridization between taxa of sect. *Protobalanus* and sect. *Quercus* (Manos et al. 1999).

Extensive polyploidization across vascular plants (Wood et al. 2009) frequently has involved hybridization (allopolyploidization; see Ramsey & Schemske 1998), as inferred from molecular and cytogenetic data in a wide diversity of CA-FP lineages. For example, diversification of CA-FP blazing stars of *Mentzelia* sect. *Trachyphytum* (Loasaceae) involved an extensive and complex history of allopolyploid (and autopolyploid) origins (Brokaw & Hufford 2010). Tetraploidy in Pacific Coast polypody ferns (*Polypodium*, Polypodiaceae) was shown to represent separate allopolyploidizations based on different diploid hybrid combinations and reciprocal parentage of the same combination (Haufler et al. 1995). Molecular and cytogenetic data often indicate that modern allopolyploids reflect hybridization between lineages that no longer occur in proximity or that have undergone divergence or extinction. For example, *Clarkia gracilis* (Onagraceae) was inferred to have an extinct diploid parent probably closely related to *C. lassenensis* (Ford & Gottlieb 1999). One of the putative genomic contributors to perennial *Helianthus californicus* is evidently represented by a southeastern North American clade (Timme et al. 2007). Lack of potential diploid genome contributors has complicated understanding of the basis of polyploidy across the largely North American (including CA-FP) champions of *Silene* sect. *Physolychnis* sensu lato, although hexaploid *S. hookeri* (Caryophyllaceae) was resolved to represent an allopolyploid from wide hybridization between sect. *Trachyphytum* and the *S. menziesii* group (Popp & Oxelman 2007). Discovery of cryptic allopolyploidy of some populations long treated as belonging to the otherwise diploid *Lithophragma bolanderi* underscores the importance of genetic data for diagnosing and corroborating the allopolyploid condition (Kuzoff et al. 1999).

5. FUTURE DIRECTIONS

The potential for evolutionary studies to resolve the origins and evolutionary histories of CA-FP plants is far from realized, and too few clades are well-enough sampled phylogenetically to provide a detailed estimate of relationships within those groups, although advances over the past decade have been dramatic. The frequent discovery of undescribed CA-FP lineages worthy of taxonomic recognition from phylogenetic studies that involved sampling across the ecological, morphological, and geographic axes of variation within taxonomic species or infraspecific taxa indicates that baseline estimates of diversity should be questioned even within those plant groups that were subjects of experimental biosystematic studies (see Baldwin 2000). Some of the most interesting clades of CA-FP plants are those that appear to have diversified so rapidly and recently that available molecular data so far have been inadequate to gain a robust understanding of their evolutionary histories [e.g., *Grindelia* (Compositae; Moore et al. 2012) and *Monardella* (K. Andreasen & B.G. Baldwin, unpublished information)]. Genomic tools may provide a means of understanding their complexity and resolving important processes operating during early stages of divergence in such groups.

In the short term, targeted expansion of molecular phylogenetic coverage for plant clades is underway to improve resolution and interpretation of spatial patterns of biodiversity and endemism at various levels of geographic resolution across California (B. Mishler, D. Ackerly, and B. Baldwin, in preparation). In part, that effort is geared toward locating areas of high evolutionary activity and ancient refugia of importance to evolutionary studies and conservation planning, as well as considering diversity and endemism in light of the entire phylogeny as opposed to just terminal taxa.

Growing appreciation for the importance of ecology in understanding evolutionary change and recent evidence indicating evolutionary decoupling of niche parameters warrants more attention to resolving the history of ecological factors in a phylogenetic context as well (e.g., Emery et al. 2012, Töpel et al. 2012, Arrigo et al. 2013, Anacker & Strauss 2014), in part to characterize likely future responses of lineages to environmental change. Field-based descriptive and experimental work is invaluable to these goals and, although often difficult and unavoidably slow, continues to be the source of some of the most important contributions to evolutionary understanding of the California flora (e.g., Ramsey et al. 2003, Angert & Schemske 2005, Lowry et al. 2008).

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