Chapter 8

Drivers of Diversity in Evergreen Woody Plant Lineages Experiencing Canopy Fire Regimes in Mediterranean-Type Climate Regions

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Abstract

California has the most extreme Mediterranean-type climate (MTC) region on the planet. Between May and September there are almost no significant rain events. The topography of uplands tends to be rugged with many different soil types juxtaposed by tectonic activity into a complex landscape mosaic. Prolonged seasonal drought during warmer months favors shrubland over forest and sets the stage for relatively frequent, predictable, and intense canopy fires. Chaparral, a shrubland vegetation, is not only adapted to fire but many species are dependent upon fire regimes for recruitment of new generations. Geology, climate, and fire are intimately connected to the composition and distribution of chaparral. In this chapter, we hypothesize that it is the interactive nature of all three factors that drives chaparral ecology and, ultimately, the evolutionary processes that have shaped chaparral phylogenetic diversity as well. Ultimately, despite the extreme conditions that characterize MTC shrublands in California and elsewhere—or perhaps because of them—these MTC shrublands are renowned for their species diversity and, particularly, their abundance of local endemics. We use the genus *Arctostaphylos* (Ericaceae), a shrub lineage in California with the most taxa of all other shrubs (95) in this region, as an example to highlight this phenomenon. In particular, we focus on the relationship between *Arctostaphylos* and the summer marine layer along the California coast where almost half of its taxa (46) are narrow endemics (distribution < 1000 km^2) restricted to the narrow coastal zone. We further hypothesize that the more mild and moist climate regime along the coast, combined with greater rainfall on windward coastal uplands, sets the stage for a variety of interactions between geology, climate, and fire that ultimately drive the diversification of this genus. These interactions are enhanced by a number of circumstances in these specialized habitats. In the coastal region, chaparral

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occurs in archipelagos of nutrient poor, shallow, rocky soils that are situated in island-like stands in a forest matrix. These coastal sites are subject to long fire return intervals associated with higher fuel moisture levels. This environmental context has facilitated a number of biological responses, including selection for obligate seeder species, hybridization among species in these isolated stands, and episodes of selection for optimal genotypes following each fire event which, ultimately, leads to new species of probable hybrid origin. Finally, along with these neoendemics, we argue that the coast also harbors many paleoendemics that have found refuge in these more mild and mesic habitats. Consequently, the extraordinary endemism of *Arctostaphylos* along the coast reflects both production of new species and preservation of species arising from past ages.

INTRODUCTION

Mediterranean-type climate (MTC) ecosystems are among the most biologically diverse ecosystems on the planet (Cowling et al., 1996; Myers et al., 2000; Rundel, 2004). A Mediterranean-type climate is characterized by mild, wet winters and dry, hot summers. California has the driest summer periods with a tenth or less summer rain compared to other MTC regions (average for June-August: 3-6 mm vs. 40-125 mm in other MTC regions) and with almost no summer rain days (<1 summer rain day vs. 10-20 days for other MTC regions). Extremes of climate, soil, and fire conditions vary among the MTC areas as a consequence of different features. California, the Mediterranean Basin, and Chile all experience considerable tectonic and volcanic activity and have relatively young soils, but the latter two have some summer rainfall. Summer rainfall also occurs in SW Australia and the Cape Region of SW South Africa, but these sites have old and weathered landscapes containing nutrient-poor soils. Although all five MTC regions are dominated by sclerophyllous shrublands, a convergence first noted by Schimper (1903), we can expect variation among these regions because of their different selective contexts and these differences are well described elsewhere (Keeley et al., 2012). Here we concentrate on patterns of plant diversity in California chaparral, a sclerophyllous shrub-dominated vegetation inhabiting an environment with the most pronounced version of reduced summer rain among the five MTC regions (Cowling et al., 2005).

While climate and soils act as a principal influence on vegetation patterns, all terrestrial systems also experience some type of fire regime (Pausas & Keeley, 2009). Shrub dominated ecosystems in MTC regions exhibit high intensity canopy-type fire regimes. Other significant dimensions of fire regimes are spatial extent, temporal frequency, and intensity, among others. The two extremes of fire type, surface fire and canopy fire regimes, generally introduce quite different types of environmental change and have very different selective influences on plant traits. Surface fire ecosystems, such as is characteristic of many conifer forests, exhibit mortality in small plants or young age classes and biomass removal only near the ground. Consequently, dominant plants experience little mortality and minimal loss of canopy, resulting in slow change in the community's composition and demographic dynamic even though surface fires may differentially impact species. Canopy fire ecosystems such as chaparral, in contrast, experience considerable change in postfire environmental conditions. With the removal of the leaf canopy and most above ground biomass, light levels are drastically greater following a canopy fire and the potential for water deficit or temperature

extremes increases in more arid locations. While in both fire regime types newly establishing individuals are released from competition for light energy to some extent, seedlings of some species arising postfire in canopy fire vegetation experience a potentially harsher environment compared to seedlings in the understory prior to the fire due to this potential for temperature extremes and water deficit.

Fire acts as a peculiar type of disturbance regime because the spatial extent of fires is usually quite large, limiting long distance dispersal, and thus persisting organisms must survive all the different dimensions of the fire regime. In addition to opening space for recruitment dynamics at the local scale, fire interacts with aspects of plant longevity, persistence, or reproductive traits, and consequently plant composition. If the fire-return intervals and other dimensions of the fire regime are relatively predictable, fire leads to most plants exhibiting traits adaptive to fire. A particular fire regime will favor particular sets of fire-adaptive traits. The stronger the selection for fire-adaptive traits, often the less the vegetation seems to change postfire in composition within local communities. While there are arguments about whether traits have arisen *de novo* as a result of fire regimes (*e.g.*, Bradshaw et al., 2011; Keeley et al., 2011), fire-adaptive traits clearly characterize most dominant plants. Fire-adaptive traits may include dormant buds and underground storage organs that allow resprouting of surviving individuals. In many species other fire-adaptive traits mostly restrict seedling establishment to the first postfire growing season, for example, due to serotinous cones or fruits, or because seed dormancy is broken by the smoke or heat-pulse from a fire.

FIRE DEPENDENCE

Chaparral vegetation best responds to fires at 30-150+ year intervals, generally longer than occurs in most other MTC regions. Within those timeframes, chaparral returns quickly to pre-fire conditions dominated by sclerophyllous shrubs because of the low mortality of resprouting individuals and the rapid reestablishment of shrub seedlings from fire-dependent seed banks (Hanes, 1971). Critically, however, chaparral is adapted to a particular fire regime of a range of frequency, intensity, and seasonal timing so that excluding fire or increasing the frequency of fire reduces the sustainability of this ecosystem (Keeley et al., 2005; Parker, 1990; Parker & Pickett, 1998; Zedler et al., 1983). Chaparral dynamics correspond to the cycle of wildfire, postfire recovery, and stand maturation.

All woody plants in chaparral display fire-adaptive traits and can be grouped into three general postfire life history categories based on combinations of postfire resprouting and seed dormancy characteristics (Keeley, 1987; Keeley et al., 2012; Parker & Kelly, 1989). Most genera contain species that survive fire as adults and, even though their aboveground stems are killed, the plants resprout from stem or root crowns. This first group is termed obligate resprouters because they persist by vigorous resprouting and contain transient seed banks and have no postfire seedling recruitment. A second cluster of species considered facultative seeders are found principally in three genera in California that resprout following fire, but these genera also have soil seed banks that generally depend upon fire-stimulated recruitment. The third life history pattern is obligate seeding shrubs and trees, species that typically are killed by fire but that produce seeds that are dormant at maturity and remain as persistent soil

or aerial (canopy) seed banks until recruitment is stimulated after fire events. Similar to facultative seeders, their seeds are wholly or principally stimulated by wildfire and they typically germinate and establish in postfire stands. Populations of obligate seeders persist in chaparral exclusively because of the success of their seed banks and the flush of postfire seedling recruitment. Obligate seeders in California chaparral are generally found in *Arctostaphylos* and *Ceanothus* (Rhamnaceae) among shrubs and as serotinous lineages in *Pinus* (Pinaceae) and *Hesperocyparis* (Cupressaceae) among the trees.

Chaparral is a diverse ecosystem in the context of its woody species (Keeley & Keeley, 1988; Sawyer et al., 2009; Wells, 1962). The importance of fire in this system is clear when considering that species with fire-dependent reproduction represent about 80% of average stand dominance regardless of location (Vasey, 2012; Vasey et al., *In press*). Also, genera with a large number of chaparral species are either facultative or obligate seeders. While not considered in detail here, chaparral also contains a highly diverse component of annuals, herbaceous perennials, and suffrutescent shrubs that, with few exceptions, are found only in postfire stands of chaparral and are lacking in mature stands (Hanes, 1981; Sweeney, 1956). Dormant seed banks of these species are also fire-dependent and triggered by either intense heat shock or combustion products from smoke or charred wood (*e.g.*, Keeley, 1991; Keeley & Fotheringham, 2000). Composition of herbaceous species or suffrutescent shrubs varies among sites and their dominance depends on the rainfall and temperature pattern of the initial year following the fire event. Overall, chaparral typically has the highest plant compositional diversity in the first and second years after fire (Keeley et al., 2005; Sweeney, 1956) because of these herbaceous species in combination with the woody dominants.

DIVERSITY OF CHAPARRAL IN CALIFORNIA

The compositional diversity of chaparral communities must be distinguished from phylogenetic diversity of chaparral lineages, and particularly for sclerophyllous shrub genera. With regard to compositional diversity, Keeley et al. (2012) have argued that the interaction of multiple factors drives diversity rather more than any one particular factor (Figure 1). According to this conceptual framework, from a regional species pool (consisting of various lineages), an environmental template consisting primarily of climate factors, soil factors, and a fire regime filters the pool into different functional types (*e.g.*, fire-adapted sclerophyllous shrubs) that are then assembled into local communities. Observations of local community *alpha* diversity (number of species per plot) in California are generally not high in mature postfire chaparral which is characterized by closed canopies and stands dominated by relatively few species of mature shrubs with a sparse herbaceous understory (Vasey et al., *In press*). By contrast, low soil nutrient levels in mature fynbos and kwongan habitats are presumed to allow a more open canopy in these mature postfire shrublands and thus the coexistence of many more visible herbaceous and subshrub species situated in gaps between dominant shrubs (Keeley et al., 2012). Immediate postfire chaparral habitats often have about the same number of species per 0.1 h plot as immediate postfire fynbos and kwongan communities (Wisheu et al., 2000), but these higher levels of chaparral *alpha* diversity result from the expression of herbaceous species and subshrubs typically dormant within chaparral

seed banks and not visible in mature stands. Since fire-return intervals are long, estimating the true *alpha* diversity in a particular chaparral stand is a challenge.
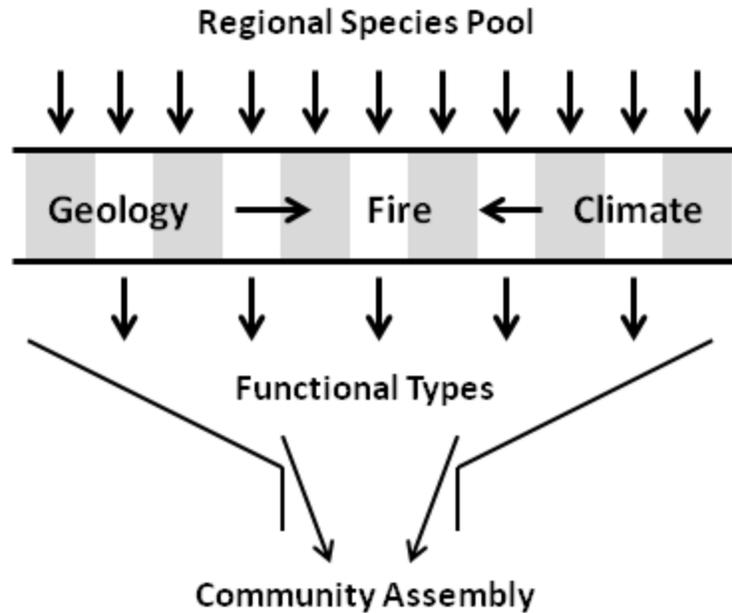

Figure 1. The "Geology-Fire-Climate" model of community assembly in chaparral modified with permission from Keeley et al. (2012).

Conversely, especially in coastal chaparral, the particular combination of shrub species can vary greatly among stands (also called species turnover)—a manifestation of *beta* diversity—or the distribution of species diversity at larger scales. To a significant degree, *beta* diversity in mature stands of chaparral intersects with the phylogenetic diversity of dominant sclerophyllous shrub lineages in linking patterns of compositional diversity and phylogenetic diversity together. This is because high species turnover among mature stands of chaparral is primarily associated with high levels of local endemism of sclerophyllous shrub species found within those stands. Further, at these larger spatial scales, discernable patterns of higher versus lower *beta* diversity, as well as higher *gamma diversity* (overall diversity at regional scales), are associated with climatic gradients and the distribution of different soil types. For example, where chaparral is found in highly infertile serpentine "islands" distributed as a mosaic embedded in more fertile sandstone soils, higher levels of *beta* diversity were found on the serpentine substrates due to the greater presence of local endemic species on those substrates (Chapter 6; Harrison & Inouye, 2002).

In the fynbos, Ojeda (1998) found that the highest concentration of obligate seeder endemism in *Erica* (Ericaceae) occurs in the southwestern region of the Cape in an area with reliable summer rains and more mild summer drought conditions. Another example of this phenomenon relates to an under-appreciated link between high *beta* diversity in coastal chaparral, extreme local endemism of *Arctostaphylos* in this region, and to a lesser extent in *Ceanothus*, and its linkage to the influence of a summer marine layer (coastal fog and low cloud cover) that is a persistent climatic phenomenon along the California coast.

INFLUENCE OF SUMMER MARINE LAYER ON SHRUB ENDEMISM IN COASTAL CHAPARRAL

The diversity of woody plants in California chaparral has long been recognized (Cooper, 1922), particularly in *Arctostaphylos* and *Ceanothus* (Wells, 1969); however, only during the last forty years has the exceptional diversity of *Arctostaphylos* been fully appreciated (Parker et al., 2009, 2012). Recent treatments of *Arctostaphylos* recognize 104 taxa (67 species and 37 subspecies), 95 of which occur in California and most of which occur in chaparral (Table 1). Diversity in *Ceanothus* (61 taxa in California) is also better known today. *Ceanothus* is also centered in California, and most species are found in chaparral as well (Wilken, 2012). In the early 1980s, interest emerged in conserving natural communities rather than species *per se*, and two natural communities that stood out as being both exceptionally rich in local endemics and at-risk due to human activities were Central Maritime Chaparral and Northern Maritime Chaparral (Holland, 1986). The conservation value of maritime chaparral was further bolstered by recognition of the high rate of species turnover along the coast in *Arctostaphylos* and *Ceanothus* (Cody, 1986). Later, Keeley (1992) recognized coastal chaparral as the closest approximation to the endemic-rich fynbos in California, and he recognized that the mildness of the climate in the endemic rich Pacific coastal chaparral was analogous to that of the endemic-rich fynbos in the southwestern Cape region.

Despite the recognition that coastal chaparral harbors the highest concentration of local endemics compared to other chaparral in California, few hypotheses have been offered to explain this phenomenon other than mountainous terrain near the sea (Cody, 1986) or higher levels of precipitation in coastal uplands (Loarie et al., 2008; Richerson & Lum, 1980; but see Keeley, 1992). These hypotheses did not, however, account for the fact that most local endemics are located in coastal lowlands below 400 m elevation rather than on coastal uplands. The summer marine layer generally occurs below the 400 m elevation (Johnstone & Dawson, 2010), and in the late 1990s, it became recognized as an important source of moisture for coastal vegetation, particularly lowland vegetation (Dawson, 1998; Corbin et al., 2005; Fischer et al., 2009). These earlier studies focused principally on conifer forests. Vasey and colleagues (Vasey, 2012; Vasey et al., 2012; Vasey et al., *In press*) hypothesized that the summer marine layer may create significant differences in water relations of chaparral shrubs along a coast-inland gradient and that chaparral diversity patterns might be correlated with more favorable (*i.e.*, less harsh) water availability conditions along the coast.

Table 1. Summary of *Arctostaphylos* taxa (67 species, 37 subspecies, total 104), with clade identity (1=small, 2=large), ploidy level (D=diploid, T=tetraploid), life history (seeder=obligate seeder, sprouter=facultative seeder), distribution (C=coast, < 50 km from coast, I=interior, > 50 km from coast), range classes (0=1-10 Km^2, 1=10-100 Km^2, 2=100-1000 km^2, 3=1000-10000 km^2, 4=10000-100000 km^2, 5=100000-1000000 km^2, 6=>1000000 km^2), and locations (Cal=California, W=Western North America, Pac NW= Pacific Northwest, AZ=Arizona, Mex=Mexico, N Hem=Northern Hemisphere). Source of taxonomy is Parker et al. (2009; 2012) or International Plant Names Index (http://www.ipni.org)

Taxon	Clade	Ploidy	Life History	Distribution	Range Class	Location
A. andersonii	2	D	seeder	C	3	Cal
A. auriculata	2	D	seeder	C	2	Cal
A. australis	2	D	seeder	C	2	Baja
A. bakeri	2	T	seeder	C	1	Cal
A. b. subsp. *sublaevis*	2	T	seeder	C	1	Cal
A. bolensis	2	D^2	seeder	C	0	Baja
A. canescens	2	D	seeder	I	4	Cal
A. c. subsp. *sonomensis*	2	D	seeder	I	4	Cal
A. catalinae	2	D^2	seeder	C	2	Cal
A. columbiana	2	D	seeder	C	3	Cal, Pac NW
A. confertiflora	2	D	seeder	C	1	Cal
A. cruzensis	2	D	seeder	C	0	Cal
A. crustacea	2	T	sprouter	C	4	Cal
A. c. subsp. *crinita*	2	T	sprouter	C	3	Cal

A. c. subsp. *eastwoodiana*	2	T	sprouter	C	1	Cal
A. c. subsp. *insulicola*	2	T	sprouter	C	2	Cal
A. c. subsp. *rosei*	2	T	sprouter	C	2	Cal
A. c. subsp. *subcordata*	2	T	sprouter	C	2	Cal
A. densiflora	1	D	seeder	C	0	Cal
A. edmundsii	2	D	seeder	C	1	Cal
A. franciscana	21	D	seeder	C	0	Cal
A. gabilanensis	2	D	seeder	C	2	Cal
A. glandulosa	2	T	sprouter	I	4	Cal, Baja
A. g. subsp. *adamsii*	2	T	sprouter	I	3	Cal, Baja
A. g. subsp. *atumescens*	2	T	seeder	C	0	Baja
A. g. subsp. *crassifolia*	2	T	sprouter	C	3	Cal
A. g. subsp. *cushingiana*	2	T	sprouter	I	4	Cal
A. g. subsp. *erecta*	2	T	sprouter	I	1	Baja
A. g. subsp. *gabrielensis*	2	T	sprouter	I	2	Cal
A. g. subsp. *howellii*	2	T	sprouter	I	2	Cal
A. g. subsp. *leucophylla*	2	T	sprouter	I	3	Cal, Baja
A. g. subsp. *mollis*	2	T	sprouter	I	4	Cal
A. glauca	2	D	seeder	I	4	Cal, Baja
A. glutinosa	2	D	seeder	C	1	Cal

A. hispidula	2	D^2	seeder	I	4	Cal
A. hookeri	1	D	seeder	C	2	Cal
A. h. subsp. *hearstiorum*	1	D	seeder	C	0	Cal
A. hooveri	2	D	seeder	C	3	Cal
A. imbricata	2	D	seeder	C	0	Cal
A. incognita	2	D	sprouter	I	1	Baja
A. insularis	2	D	seeder	C	1	Cal
A. klamathensis	2	D^2	seeder	I	2	Cal
A. luciana	2	D	seeder	C	1	Cal
A. manzanita	2	T	seeder	I	5	Cal
A. m. subsp. *elegans*	2	T	seeder	I	3	Cal
A. m. subsp. *glaucescens*	2	T	seeder	I	3	Cal
A. m. subsp. *laevigata*	2	T	seeder	C	1	Cal
A. m. subsp. *roofii*	2	D^2	sprouter	I	3	Cal
A. m. subsp. *wieslanderi*	2	D^2	seeder	I	3	Cal
A. malloryi	2	D^2	seeder	I	3	Cal
A. mewukka	2	T	sprouter	I	3	Cal
A. m. subsp. *truei*	2	T	seeder	I	2	Cal
A. montana	2	T	seeder	C	1	Cal
A. m. subsp. *ravenii*	2	T	seeder	C	0	Cal
A. montaraensis	2	D	seeder	C	2	Cal

A. montereyensis	2	D	seeder	C	2	Cal
A. moranii	2	T	sprouter	I	1	Baja
A. morroensis	2	D	seeder	C	0	Cal
A. myrtifolia	2	D	seeder	I	1	Cal
A. nevadensis	2	T	seeder	I	5	Cal
A. n. subsp. *knightii*	2	T	sprouter	I	2	Cal
A. nissenana	2	D	seeder	I	3	Cal
A. nortensis	2	D	seeder	I	2	Cal
A. nummularia	1	D	seeder	C	2	Cal
A. n. subsp. *mendocinoensis*	1	D	seeder	C	1	Cal
A. obispoensis	2	D	seeder	C	3	Cal
A. ohloneana	1	D	seeder	C	0	Cal
A. osoensis	2	D^2	seeder	C	0	Cal
A. otayensis	2	D	seeder	C	0	Cal
A. pacifica	1	T^2	seeder	C	0	Cal
A. pajaroensis	2	D	seeder	C	2	Cal
A. pallida	2	D	seeder	C	1	Cal
A. parryana	12	T	seeder	I	3	Cal
A. p. subsp. *deserticum*	12	T	sprouter	I	2	Cal
A. p. subsp. *tumescens*	12	T	sprouter	I	0	Cal
A. patula	1	D	sprouter[1]	I	5	Cal, Baja,W

A. pechoensis	2	D	seeder	C	1	Cal
A. peninsularis	2	D	sprouter	I	3	Baja
A. p. subsp. *juarezensis*	2	D	seeder	I	1	Baja
A. pilosula	2	D	seeder	C	3	Cal
A. pringlei	2	D	seeder	I	4	Cal, Baja, AZ
A. p. subsp. *drupacea*	2	D	seeder	I	4	Cal
A. pumila	2	D	seeder	C	2	Cal
A. pungens	21	D	seeder	I	5	Cal,SW, Mex
A. purissima	2	D	seeder	C	3	Cal
A. rainbowensis	2	D	seeder	C	2	Cal
A. refugioensis	2	D	seeder	C	1	Cal
A. regismontana	2	D	seeder	C	2	Cal
A. rudis	1	D	seeder	C	3	Cal
A. sensitiva	1	D	seeder	C	3	Cal
A. silvicola	2	D^2	seeder	C	1	Cal
A. stanfordiana	1	D	seeder	I	3	Cal
A. s. subsp. *decumbens*	1	D	seeder	I	0	Cal
A. s. subsp. *raichei*	1	D	seeder	I	1	Cal
A. tomentosa	2	T	sprouter	C	2	Cal
A. t. subsp. *bracteosa*	2	T	sprouter	C	1	Cal
A. t. subsp. *daciticola*	2	T	sprouter	C	0	Cal

A. t. subsp. *hebeclada*	2	T	sprouter	C		1	Cal
A. uva-ursi	11	T	sprouter[1]	I		6	Cal, N Hem
A. virgata	2	D	seeder	C		1	Cal
A. viridissima	2	D	seeder	C		0	Cal
A. viscida	2	D	seeder	I		5	Cal
A. v. subsp. *mariposa*	2	D	seeder	I		4	Cal

[1]Both conditions are known to occur.
[2]Trait has been predicted, but not confirmed.

These studies revealed that significant differences were found in late dry season water potentials among *Arctostaphylos* shrubs along the lowland coast (maritime), upland coast (transition), and interior gradient (Figure 2). Further, chaparral composition sampling revealed that in 0.1 h plots, coastal lowlands and coastal uplands had significantly higher levels of *beta* diversity than interior plots, as might have been predicted based on Cody (1986) (Figure 3). Correlations with dry season and wet season climate data showed that lowland coastal chaparral had a more favorable climate regime primarily due to the summer marine layer whereas upland coastal chaparral had a similarly favorable climate regime primarily due to significantly greater rainfall than the lowland coast or the interior (Vasey et al., *In press*). In summary, the hypothesis is supported that more favorable climatic conditions exist in coastal chaparral and that these conditions are positively correlated with high *beta* diversity in coastal chaparral. This higher level of *beta* diversity is a function of greater levels of local endemism in coastal chaparral, particularly in *Arctostaphylos, Ceanothus, Pinus,* and *Hesperocyparis*. Yet, this observation does not explain why more favorable climatic conditions along the coast might translate into a higher concentration of local chaparral endemics. Based on our studies of *Arctostaphylos*, we suggest a framework for future testing that ties together the ecological model suggested by Keeley et al. (2012) with an evolutionary process over time that might account for the hyperaccumulation of local *Arctostaphylos* endemics along the California coast. Potentially, this framework could apply to other analogous situations for other genera in California chaparral as well as shrublands in other MTC regions.
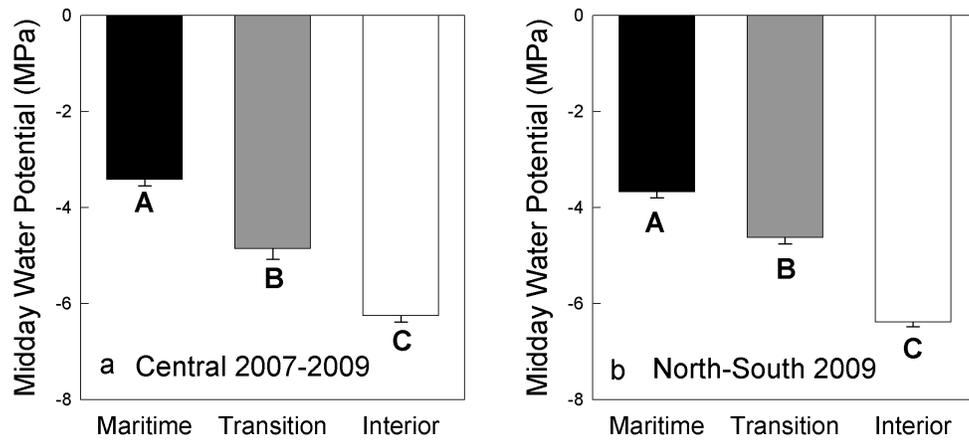
Figure 2. Water potential values from *Arctostaphylos* populations at the end of the dry season in maritime (lowland coast), transition (upland coast), and interior chaparral habitats (Vasey et al., 2012). Figure 2a shows three years of data from a transect in the Monterey Bay region; Figure 2b shows values from north, central, and south transects (San Francisco Bay region to Morro Bay, San Luis Obispo) that experience pronounced summer marine layer effects. Water potential gradient is thus consistent over time and space. Capital letters indicate significant differences at $p < 0.0001$ based on linear mixed model and Tukey HSD test, error bars represent standard error.
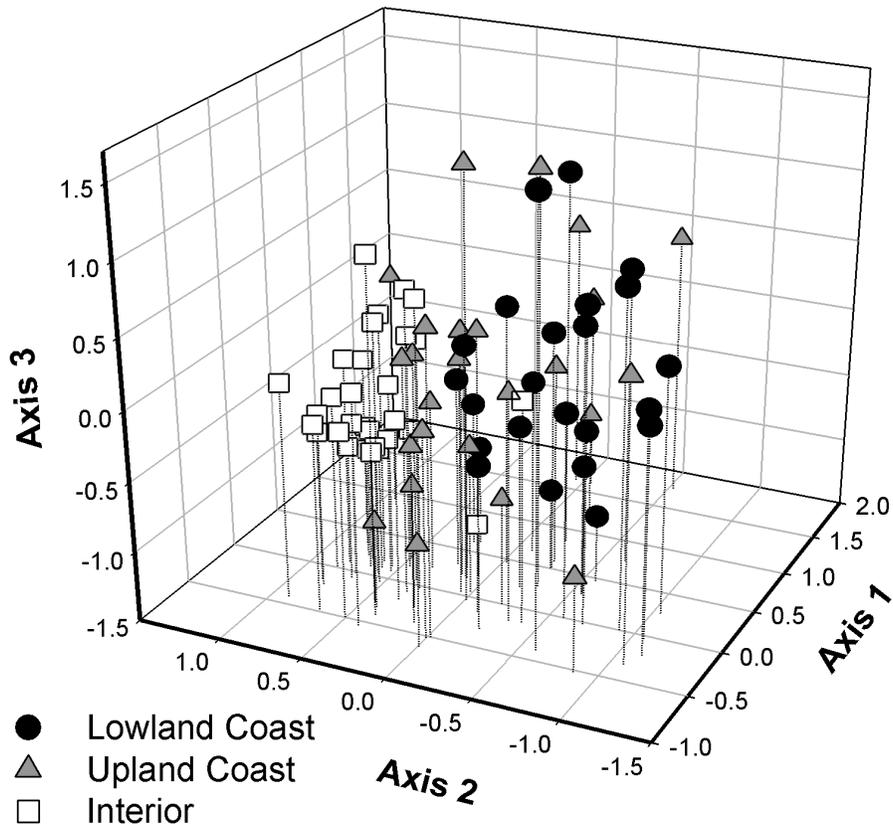
Figure 3. Non-metric multidimensional scaling analysis of maritime (lowland coast), transition (upland coast) and interior 0.1 h chaparral plots (n=87 for all) sampled at a regional scale from the San Francisco Bay region to northern Santa Barbara County (Vasey et al., *In press*). Dissimilarity among maritime and transition plots compared to interior plots suggests greater *beta* diversity for coastal chaparral. A multivariate analysis of dispersion (Anderson, 2006) confirmed that the maritime and transition plots were significantly different ($p < 0.0001$) than interior but not significantly different from each other.

LOCAL ENDEMISM IN ARCTOSTAPHYLOS ALONG THE CALIFORNIA COAST: AN EVOLUTIONARY PERSPECTIVE

Of the 95 taxa of *Arctostaphylos* recognized in California (Parker et al., 2012), over half (54%) are restricted to ranges within 50 km of the coast. Of these 57 species, 46 (81%) are local endemics, occupying distributions of less than 1000 km^2 (*i.e.*, an area approximately 30 km x 30 km) (Figure 4). Conversely, *Arctostaphylos* species and subspecies that primarily or exclusively occur in the interior constitute little more than a third of the taxa (36%) and only 10 of these taxa (26%) have a range of less than 1000 km^2; almost three quarters of the interior species (74%) are relatively widespread (Vasey & Parker, unpublished data). Local endemics along the coast are primarily concentrated in lowland gaps in otherwise relatively continuous Coast Range mountains (*e.g.*, Monterey Bay, San Francisco Bay, Morro Bay, and the Santa Maria plains).
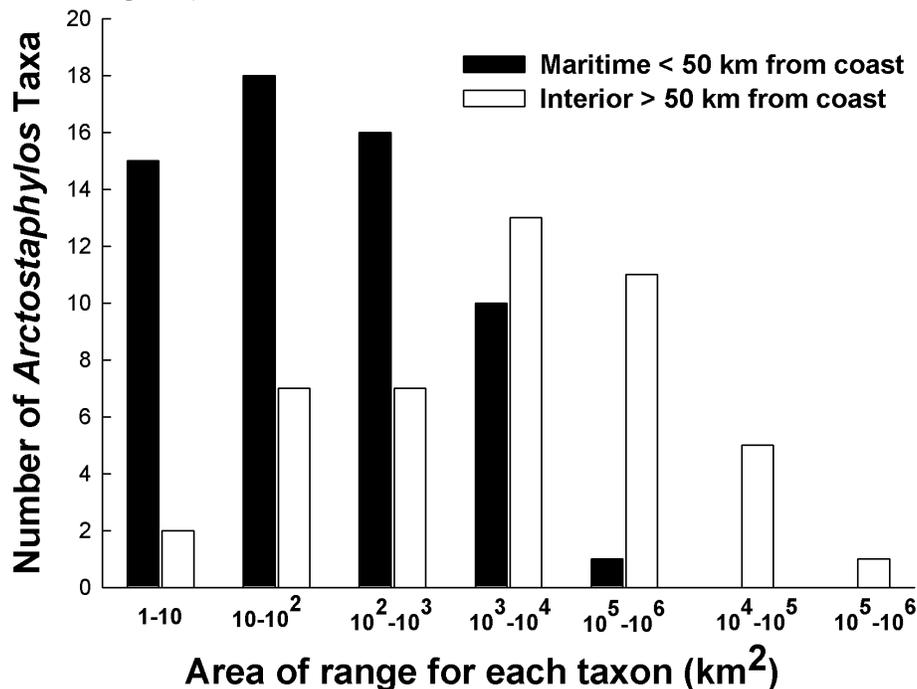

Figure 4. Comparison of range distributions for 104 *Arctostaphylos* taxa (species and subspecies) restricted to maritime habitats (< 50 km from the coast) or mostly distributed in the interior (> 50 km from the coast). Note that the great majority of coastal taxa are local endemics (ranges < 1000 km^2). Based upon Vasey & Parker (unpublished data).

Monterey Bay provides a good example. Within a 1000 km^2 area centered on Monterey Bay, a total of twelve species and subspecies of *Arctostaphylos* can be found in stands of coastal chaparral on a variety of different substrates from deep sand to granite to Monterey shale to Aromas sandstone. Of these twelve taxa, four species and two subspecies are local endemics restricted to this area while a seventh, *A. gabilanensis*, is a local endemic restricted to the Gabilan Range with one small population located slightly to the south of this artificial boundary. This pattern of local endemism first drew the attention of ecologists such as Griffin (1978) who coined the term "maritime chaparral", and later Holland (1986) and state agencies that implemented policies to protect lowland maritime chaparral (Sawyer et al., 2009).

Given the intrinsically harsh conditions associated with MTC regions, and particularly California (Cowling et al., 2005), it is somewhat of a conundrum that MTC regions in general are renowned for their high levels of biodiversity and, in particular, species richness (*alpha* diversity) and species turnover (*beta* diversity) associated with local endemism. The compelling question that arises from this observation is intrinsically both ecological *and* evolutionary; *i.e.*, what ecological factors over time would give rise to so many recognizably different, closely related lineages occupying such relatively small ranges within such close proximity and what biological factors would enhance such diversification? This question is all the more vexing given that *Arctostaphylos* and other dominants of MTC shrublands are relatively long-lived, woody plants. Below is a conceptual framework for considering how to address this question, specifically with regard to *Arctostaphylos* and also in the context of its pattern of local endemism along the California coast.

A 'GEOLOGY-FIRE-CLIMATE' MODEL FOR DIVERSIFICATION IN *ARCTOSTAPHYLOS*

We propose that the "geology-fire-climate" model of Keeley et al. (2012) as a process shaping compositional diversity in MTC shrublands is also a good framework from which to build a phylogenetic diversity model. Variation in soils, climate, and fire regimes provide a context for examining long-term patterns of diversification in *Arctostaphylos* and particularly the concentration of local endemic *Arctostaphylos* taxa along the California coast. As a relatively "young" coast, California's coastal margin has a high level of topographic heterogeneity and tectonic activity along a transform fault system that has been present during the past thirty million years. Consequently, many different rock formations, and hence soil types, have been juxtaposed into a rich landscape mosaic characterized by archipelagos of different-sized "edaphic islands" (Kruckeberg, 2002). Although these soils are not as nutrient deficient as those in southwest South Africa or southwest Australia, they are relatively inhospitable compared to surrounding soils due to shallow, rocky conditions, deep sand, or challenging nutrient compositions (*e.g.*, serpentines). As previously discussed, coastal lowlands are cooler and more humid due to the summer marine layer whereas winter rainfall on coastal uplands is almost double that of coastal lowlands or interior mountains (Vasey et al., *In press*). These relatively moist and equable conditions consequently favor a penetration of conifer forest and mixed evergreen forest far down the coast while more fine-grained and deep clay soils favor coastal prairie and coastal scrub. Chaparral typically is restricted to isolated edaphic islands within these topographically heterogeneous landscapes in a mosaic with forest, grassland, or coastal scrub (Wells, 1962). Finally, chaparral along the coast has been found to have much longer fire return intervals than interior chaparral (Odion & Tyler,

2002). This could well be due, in part, to higher fuel moisture levels, especially through the summer dry season due to the marine layer (Figure 5), but also less frequent lightning strikes (Keeley, 1982). Cooler, moist conditions during the dry season and longer fire intervals allow more flammable biomass to accumulate in coastal chaparral stands and thus when canopy fires occur they tend to be high intensity. This constellation of environmental conditions characterizing the California coastal template is distinctive compared to conditions in chaparral around the rest of the state (Parisien & Moritz, 2009).

Within this environmental context, we begin the discussion of *Arctostaphylos* diversification by considering a classic paper by Stebbins & Major (1965) that identifies several centers of endemism in California. Most of these endemic areas were concentrated along the California coast. Subsequent work by Richerson & Lum (1980) and Loarie et al. (2008) have been consistent with this pioneering work in terms of recognizing the California coast as a hot spot for plant species diversity. Stebbins & Major (1965) focused on two alternative routes to local endemism: 1) the case of "paleoendemics" which evolved in the distant past under different climatic regimes, were once widespread, and have now become restricted to local refugia within their present range (*e.g.*, the Catalina ironwood, *Lyonothamnus floribundus* [Rosaceae]; Raven & Axelrod, 1978); and 2) the case of "neoendemics" which evolved in the recent past under climatic regimes similar to the present but are restricted to particular substrates or habitat conditions that inherently limit widespread dispersal and establishment (*e.g.*, *Stephanomeria malheurensis* [Asteraceae]; Gottlieb, 1978).
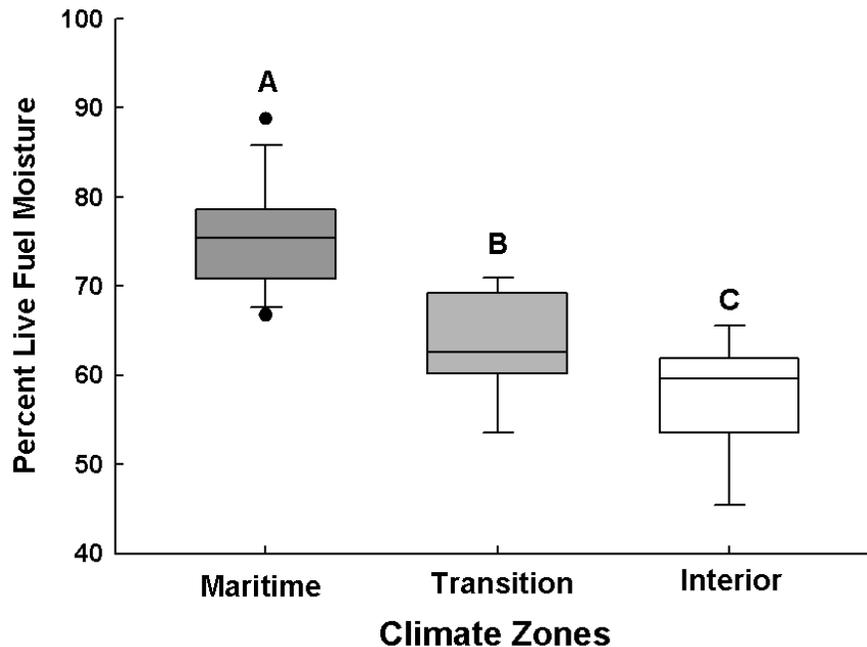
Figure 5. Live Fuel Moisture (LFM) percent calculated from leaves obtained from individual *Arctostaphylos* shrubs (n=10 per species) during sampling for water potentials and stable isotope analyses from maritime (n=100), transition (n=69), and interior (n=71) localities during the end of the dry season, 2009 (based on data collected in Vasey et al., 2012). Live Fuel Moisture is defined as the water content of live vegetation expressed as a percentage of the dry mass of vegetation (*md*) where LFM = *mw* – *md* / *md* and *mw* = is the mass of undried vegetation (Dennison et al., 2008). Box plots

present the results of ANOVA analysis with Tukey HSD test for differences among means. Capital letters indicate significant differences at $p < 0.0001$, error bars represent 95% confidence intervals and "periods" represent outliers.

Since recognizable *Arctostaphylos* fossils are known from western Nevada as far back as 13.7 mya in the middle Miocene (Edwards, 2004), when climatic conditions were presumably more mesic (Axelrod, 1973), possibly several locally endemic *Arctostaphylos* species represent "paleoendemics" (*i.e.*, relict lineages) now restricted to relatively favorable refugial habitats. In fact, molecular genetic studies in *Arctostaphylos* have demonstrated strong evidence that there are two "deep" lineages within the genus (Boykin et al., 2005; Markos et al., 1998; Wahlert et al., 2009) that are likely to be a legacy of this long evolutionary history. *Arctostaphylos* species have retained a limited ability to hybridize between these two deep lineages but empirical observation has shown that hybridization between diploids from these two clades is minimal (typically <4 % in the field) (Parker & Vasey, unpublished). Tetraploid species in *Arctostaphylos* in some cases may represent stabilized allopolyploid hybrids between the two deep clades (Scheirenbeck et al., 1992). Particularly because coastal chaparral is relatively more mesic, contains edaphic islands that resist colonization by surrounding forest, and tends to have longer fire intervals, several locally endemic *Arctostaphylos* species may be examples of paleoendemics. Yet, this is probably not the only answer to our question of *why so many local coastal endemics in Arctostaphylos* because a large number of these species have essentially the same ITS molecular sequence despite presenting widely divergent morphologies (Boykin et al., 2005, Wahlert et al., 2009). This pattern is consistent with a more recent diversification of these *Arctostaphylos* taxa, similar to the pattern of more recent diversification of several Cape *Erica* clades (Pirie et al., 2011). Therefore, we turn to possible mechanisms that may have driven the production of these more "neoendemic" species.

Of the 46 local *Arctostaphylos* endemics along the California coast, 33 are diploid species that belong to the larger clade (Wahlert et al., 2009). These 33 species represent over half of the 62 species found in the state (Table 1). Further, most of these species are in the group that is morphologically distinct but possess virtually identical ribosomal ITS sequences. Allopatric speciation or founder effects would provide a prominent mechanism for ecological selection to promote the diversification of species among the different soil types. Additionally, diploid species within each clade appear to be able to freely hybridize, so it is possible—if not probable—that many of these species arose via homoploid hybridization followed by ecological selection. Some of these species clearly contain traits that link them to two morphologically different species (*e.g.*, Parker & Vasey, 2004; Wahlert et al., 2009).

Another biological trait that all the endemic species have in common is persistent soil seed banks (Parker & Kelly, 1989). Seedlings generally occur only in postfire habitats and are subjected to strong ecological selection pressures at that stage. Most of the endemic species are obligate seeders. Due to a higher turnover rate of generations, obligate seeding may permit a higher rate of speciation over time (Wells, 1969; Wisheu et al., 2000). Obligate seeding species not only depend upon fire to stimulate germination, but pre-existing adults in the population are killed by intense canopy fires. Thus, new individuals that establish from the postfire seed bank are influenced by current, rather than past, climatic and edaphic conditions. New gene combinations of individuals within the population are relatively free from the swamping effects of a large population of pre-existing adults. Further, virtually all of

the obligate seeding species occur on distinctive soil types, suggesting that this life history trait is effective at fine-tuning surviving genotypes to their particular *in situ* conditions over multiple fire events. Fewer coastal endemics are facultative seeders (resprouters), and while ecological selection would act on their seedlings as well, surviving adults may be expected to slow the genetic transformation of those populations through gene flow. Overall, these dynamics indicate some of the biological dimensions to the "geology-fire-climate" evolutionary model that may help to account for this relatively recent proliferation of local endemics along the California coast.

The key to this model is the *interaction* of all three factors—geology, fire, and climate—facilitated by biological features like persistent soil seed banks and obligate seeding that are critical to overcoming the harsh environmental conditions that characterize the California MTC region and that lead to the exceptional pattern of local endemism described herein along the California coast. Anacker et al. (2011) demonstrated that an evolutionary trait, specific leaf area, is linked to the interaction of soil fertility, a coast-interior climate gradient, and fire history. They cautioned that it might be impossible to tease apart any one of these factors in explaining specific leaf area differences among chaparral shrubs. This may well be because of the interactive nature of this relationship. Another key factor may be the coastal mosaic of vegetation restricting maritime chaparral to separate "islands". The isolation of chaparral patches by forest or coastal scrub would limit gene flow among populations and permit localized ecological specialization as described above. Coastal forests invade chaparral only slowly because soils are shallow or nutrient poor (Dunne & Parker, 1999; Horton et al., 1999). Adjacent chaparral communities persist at the site because their persistence is reinforced by more intense fires than the invading forest can tolerate (Odion et al., 2010).

To summarize, the geological template is a "slow variable" that provides a relatively fixed environmental setting in which different plant species move over the landscape in response to different climate regimes that characterize a given region on millennial time scales. As in all MTC regions, fires are both predictable and important disturbance events that operate on different lineages over time to select for different fire adaptive traits and, in extreme conditions (such as chaparral), fire dependent recruitment in postfire environments. Among obligate seeders, these fire events create lottery-style filters for surviving genotypes and set the stage for natural selection to shift populations in one direction or another over relatively long time scales after multiple fire events. In the coastal region, relaxation of the extremes of the summer dry period allow the establishment of multiple vegetation types, isolating most chaparral stands. Allopatric speciation, founder effects, and hybridization all contribute to the diversification seen along the coast of California.

CONCLUSION

California is the most extreme of all MTC regions in terms of its summer dry period (Cowling et al., 2005) yet it makes an important contribution along with other MTC regions to approximately 15-20% of the world's total vascular plant diversity (Cowling et al., 1996). In California chaparral, the greater diversity of shrub lineages in coastal regions is associated with higher moisture availability due to different combinations of the summer marine layer, more rainfall at higher elevations, and more mild summer temperatures and reduced

evapotranspiration near the coast. The relaxation of California's otherwise harsh MTC environment permits other vegetation, such as forests, to coexist and restrict coastal chaparral to isolated areas characterized by azonal soil conditions. This diversity of soil types, isolation of chaparral stands, and prolonged but intense fire regimes drives the dynamics of fire dependent lineages such as *Arctostaphylos* in this coastal region, and it also is most likely responsible for the preservation of paleoendemic species isolated in coastal refugia. Obligate seeders contribute to chaparral diversity by their faster generation times, permitting relatively rapid speciation and ecological specialization. In the context of an intrinsically harsh climate regime like the extreme MTC summer drought characterizing California, the relaxed end of the gradient of this harsh environment seems to express the greatest species diversity.

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