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Inferring differential evolutionary processes of plant persistence traits in Northern Hemisphere Mediterranean fire-prone ecosystems

J. G. PAUSAS, J. E. KEELEY* and M. VERDÚ†

*Centro de Estudios Ambientales del Mediterráneo (CEAM), C/Charles R. Darwin 14, Parc Tecnològic, 46980 Paterna, València, Spain & Departament d'Ecologia, Universitat d'Alacant, Apartat Correus 99, E-03080, Alacant, Spain, *US Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, 47050 Generals Hwy, Three Rivers, CA 93271 & Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA, and †Centro de Investigaciones sobre Desertificación (CIDE, CSIC-UV), Camí de la Marjal s/n, Apartado Oficial, 46470 Albal, València, Spain*

Summary

1 Resprouting capacity (R) and propagule-persistence (P) are traits that are often considered to have evolved where there are predictable crown fires. Because several indicators suggest a stronger selective pressure for such traits in California than in the Mediterranean Basin, we hypothesize that plant species should have evolved to become R+ and P+ more frequently in California than in the Mediterranean Basin.

2 To test this hypothesis we studied the phylogenetic association between R and P states in both California and the Mediterranean Basin using published molecular phylogenies.

3 The results suggest that R and P evolved differently in the two regions. The occurrence of the states differs significantly between regions for trait P, but not for trait R. The different patterns (towards R+ and P+ in California and towards R+ and P– in the Mediterranean Basin) are reflected in the higher abundance and the wider taxonomic distribution of species with both persistence traits (R+P+ species) in California.

4 The differential acquisition of fire persistence mechanisms at the propagule level (P+) supports the idea that fire selective pressures has been higher in California than in the Mediterranean Basin.

5 Our comparative phylogenetic-informed analysis contributes to an understanding of the differential role of the Quaternary climate in determining fire persistence traits in different Mediterranean-type ecosystems and, thus, to the debate on the evolutionary convergence of traits.

Key-words: California, exaptation, fire ecology, fire and plant evolution, Mediterranean basin, persistence traits, resprouting, sprouting, seeding.

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Introduction

Mediterranean-type ecosystems are distributed worldwide in five disjunct regions (Di Castri *et al.* 1981). These areas share similar climates and their shrubland and woodland vegetation shares similar leaf traits (e.g. sclerophylly, evergreeness) and post-fire persistence traits (e.g. dormant seed banks and resprouting). These are commonly interpreted as convergent traits (Mooney 1977; Shmida & Whittaker 1979; Cowling & Campbell 1980). The floras of the Northern Hemisphere mediterranean ecosystems (i.e. the Mediterranean Basin and California) share many of the same families and some genera, and some portion of the apparent trait convergence between these two regions is therefore potentially due to parallel evolution from a common flora (Axelrod 1975; Verdú *et al.* 2003). For instance, although leaf traits have long been viewed as an adaptation to Mediterranean climates, recent phylogenetic studies indicate such traits predate development of this climate, and thus ancestry and community assembly

Correspondence: Juli G. Pausas (+34 96 1318227; +34 96 1318190; e-mail: pausas@gmail.com, juli@ceam.es).

processes are equally important in determining present leaf traits (Ackerly 2004).

Fire functional traits (post-fire resprouting and seeding) have traditionally been considered to be adaptations for persisting in fire-prone mediterranean environments although they are more closely aligned to stand-replacing crown fire regimes than to climate *per se* (Keeley & Zedler 1998; Pausas *et al*. 2004). Although there are few phylogenetic studies dealing with such traits, there is evidence that resprouting is a basal characteristic in some lineages (Wells 1969; Pausas & Verdú 2005) and a more labile or recently derived trait in others (van der Bank *et al*. 1999; Bond & Midgley 2003). Post-fire seed persistence (e.g. seed bank), which leads to increased post-fire recruitment, has also been considered an important plant trait in fire-prone ecosystems (Gill 1981; Keeley 1991; Keeley & Fotheringham 1998a,b; Pausas *et al*. 2004), and in serotinous pines this trait has coevolved with characteristics that enhance flammability (Schwilk & Ackerly 2001).

Predictable crown fire regimes in mediterranean-type ecosystems, have led to resprouting capacity (R) and propagule-persistence (P) being recognized as particularly important (Gill 1981; Keeley 1998; Pausas *et al*. 2004). Even though all four possible fire functional groups (R+P– (obligate resprouters), R–P+ (obligate seeders), R+P+ (facultative species) and R–P–; Pausas 1999; Pausas *et al*. 2004) can occur in a given region, some are more frequent than others, and these frequencies vary for the different ecosystems. This suggests that the correlation between R and P may differ between regions (Pausas *et al*. 2004) and prediction of changes in fire-response patterns may be possible locally but not globally. Local differences in fire functional traits between different regions would indicate different selective pressures. For instance, it has been suggested that strong serotiny (Givnish 1981; Lamont *et al*. 1991; Enright *et al*. 1996), fire-induced flowering (Lamont & Downes 1979), smoke or charred wood-induced germination (Brown 1993; Keeley & Fotheringham 1998a,b; Read *et al*. 2000; Enright & Kintrup 2001) and resprouting lignotubers (Keeley 1981; James 1984; Canadell & López-Soria 1998) are more common in mediterranean-type ecosystems with a longer fire history or with higher fire frequency or intensity (Barbour & Minnich 1990; Cowling *et al*. 1996).

At a global scale, the frequency of Quaternary climatic cycles was probably similar for all mediterranean type ecosystems, but glacial conditions were more severe in the northern than in the southern hemisphere (Deacon 1983; Cowling *et al*. 1996). Thus, the strong historical and biogeographical differences between the two hemispheres might have led to different abiotic conditions (Di Castri *et al*. 1981), which could be confounded with the selective pressure by fire. In the present paper, we focus on the two northern hemisphere regions because they have similar biogeographical histories (Axelrod 1975).

There are several indicators that there has been stronger selective pressure for fire persistence traits in California than in the Mediterranean Basin, such as higher frequency of lignotubers, serotiny and fire-induced germination by smoke or charred wood (Keeley 1981, 1995; Keeley & Keeley 1999). Although heat-induced germination is common in both regions (Thanos *et al*. 1992; Keeley & Fotheringham 2000), there is evidence that germination in response to smoke or charred wood is poorly developed in the Mediterranean Basin (Keeley & Keeley 1999; Pérez-Fernández & Rodríguez-Echeverría 2003), in contrast to its wide distribution in California (Keeley & Fotheringham 2000). However, there may be alternative explanations for the commonalities and differences between the two regions. For example, *Arbutus*, *Cupressus*, *Lonicera*, *Pinus*, *Prunus*, *Quercus* and *Rhamnus* are typical of fire-prone environments in both regions, and thus these ancestral connections could have placed these regions on a parallel course of evolution. Also, traits such as lignotubers (as a normal ontogenetic stage and not just a developmental response to coppicing) or heat stimulated germination could be responses to climate or other disturbance factors rather than to fire *per se* (Keeley 1981; Mesléard & Lepart 1989; Vesk & Westoby 2004). The most striking difference in fire responses between the two regions is annual plant specialization on fire. In California several dozen species from different genera are fire endemics that persist as dormant seed banks for many decades between fires and establish for only 1–2 years after fire, whereas such specialization is unknown in the Mediterranean floras (Keeley 1995), despite similarity in the proportion of annuals (Keeley & Fotheringham 2003).

The apparent differences in fire persistence traits lead us to hypothesize that Californian plant species should have evolved towards the states of R and P that enhance fire persistence (R+ and P+) more frequently than Mediterranean Basin plants. We used published plant molecular phylogenies to test this hypothesis and to infer differential evolutionary processes of the two main fire persistence traits between the two regions.

Methods

DATA

The EIBER data set for the eastern Iberian Peninsula (Mediterranean Basin) and the CALIF data set for California were first compiled by Pausas *et al*. (2004) and include information on the resprouting capacity (R) and the propagule persistence capacity (P) of woody species living in ecosystems characterized by stand-replacing (crown) fires. Resprouting ability was considered a binary character with levels codified as R+ (presence of traits that allow resprouting of individuals after 100% scorch by fire) and R– (absence). Similarly, propagule persistence (P) was codified as a binary character with P+ (presence of traits that allow the persistence of populations in propagule form, i.e. seed or fruit,

Table 1 Number of species and families in each data set (EIBER: in the Mediterranean basin; CALIF: California; EICA: the two data sets together), and the number of species in each of the fire response functional groups as defined in Pausas *et al*. (2004)

			Groups			
Data sets	Number of species	Number of families	R+P+	R+P–	R– P+	R– P–
EIBER	37	16	7	22	7	1
CALIF	86	30	30	44	10	2
EICA	123	34	37	66	17	3

after 100% scorch by fire) and P– (absent) (for details see Pausas *et al*. 2004). The numbers of species used were 37 for the Mediterranean Basin and 86 for California (Table 1; Appendix S1 in Supplementary Material); 12 families were common to the two regions. We used the EIBER phylogenetic tree developed in Pausas & Verdú (2005), and we developed a phylogenetic tree for CALIF using a similar methodology. Both trees were constructed by pruning the Soltis *et al*. (2000) tree to the family level and subsequently grafting on the necessary species. Phylogenetic information below the family level was obtained from Doyle *et al*. (1997), Manos *et al*. (1999), Wallander & Albert (2000), Hileman *et al*. (2001), Hardig *et al*. (2000), Ackerly (2004) and Liston *et al*. (2003). The two phylogenetic trees were then merged to form a new supertree (EICA; Fig. 1). The EIBER phylogenetic tree was fully resolved (Pausas & Verdú 2005) but the CALIF tree, and consequently the EICA tree, presented several polytomies. In all cases, unit branch length was assumed because it could not be realistically estimated on the basis of the available information. Although we repeated all phylogenetic tests with an arbitrary (Grafen 1989) branch length transformation (for similar procedure see Nosil 2002; Nosil & Mooers 2005) and obtained very similar results (not shown), care should be taken in interpreting the results given the possible bias introduced by the uncertain branch lengths (Huelsenbeck & Rannala 2003, Donoghue & Ackerly 1996).

COMPARATIVE ANALYSIS

Comparative tests that focus on particular communities or geographical areas, as does the present study, are prone to taxon sampling bias because of the filters imposed by community assembly processes (Ackerly 2000). This means that the character association shown by the species inhabiting these communities reflects not only the evolutionary history of the traits but also the sorting and assembly processes acting in such local areas. The effect of taxon sampling bias on correlated evolution has only been evaluated using parsimony methods. For continuous characters, non-random sampling strongly influences the correlation estimate (Ackerly 2000). For discrete characters, the susceptibility of the Concentrated Changes Test (CTT) to type-I errors is not increased by including a large proportion of white branches (i.e. branches reconstructed to have the ancestral state of two characters), although it may be sensitive to type-II errors. In other words, the CTT test is unlikely to detect a significant correlation when no such correlation exists, but under certain circumstances, it may fail to detect true correlations (Lorch & Eadie 1999). It is not known whether the performance of Maximum Likelihood tests of correlated evolution is likely be affected by the presence of taxon sampling bias, although Ree & Donoghue (1999) have shown that such an effect may have been present when the rates of evolution from zygomorphic to actinomorphic flowers were studied. In spite of this lack of information, we used Maximum Likelihood methods (DISCRETE software, Pagel 1994, 1997) because they allow hypothesis tests that are not available to parsimony methods (Pagel 1999). Furthermore, Maximum Likelihood methods estimate the evolution rate parameters over all possible ancestral state reconstructions and are thus not dependent on any one particular reconstruction (Lutzoni & Pagel 1997). Taxon sampling bias is difficult to assess, not only because of our lack of knowledge about the overall number of species and their character states, but also because differential extinction may alter the estimations of evolution rates (Oakley 2003; Vamosi *et al*. 2003). It is therefore important to recognize that taxon sampling bias due to Mediterranean community assembly processes represents a historical legacy and that our results will need to be interpreted not only in terms of adaptation to fire but also as the spatial and temporal sorting of existing lineages across California and Mediterranean Basin communities (see Webb *et al*. 2002; Chazdon *et al*. 2003).

CORRELATED EVOLUTION

First, non-phylogenetic association between R and P was determined using the standard χ^2 test. Then correlated evolution between R and P on the CALIF phylogenetic tree was studied using the DISCRETE software (as for EIBER, Pausas & Verdú 2005). The correlated evolution was tested by comparing the likelihood of a model in which R and P are allowed to evolve independently against another model in which R and P evolve in a dependent fashion (Omnibus test; Pagel 1994). The significance of the likelihood ratio statistic (LR) was tested by assuming a χ^2 distribution with four degrees of freedom.

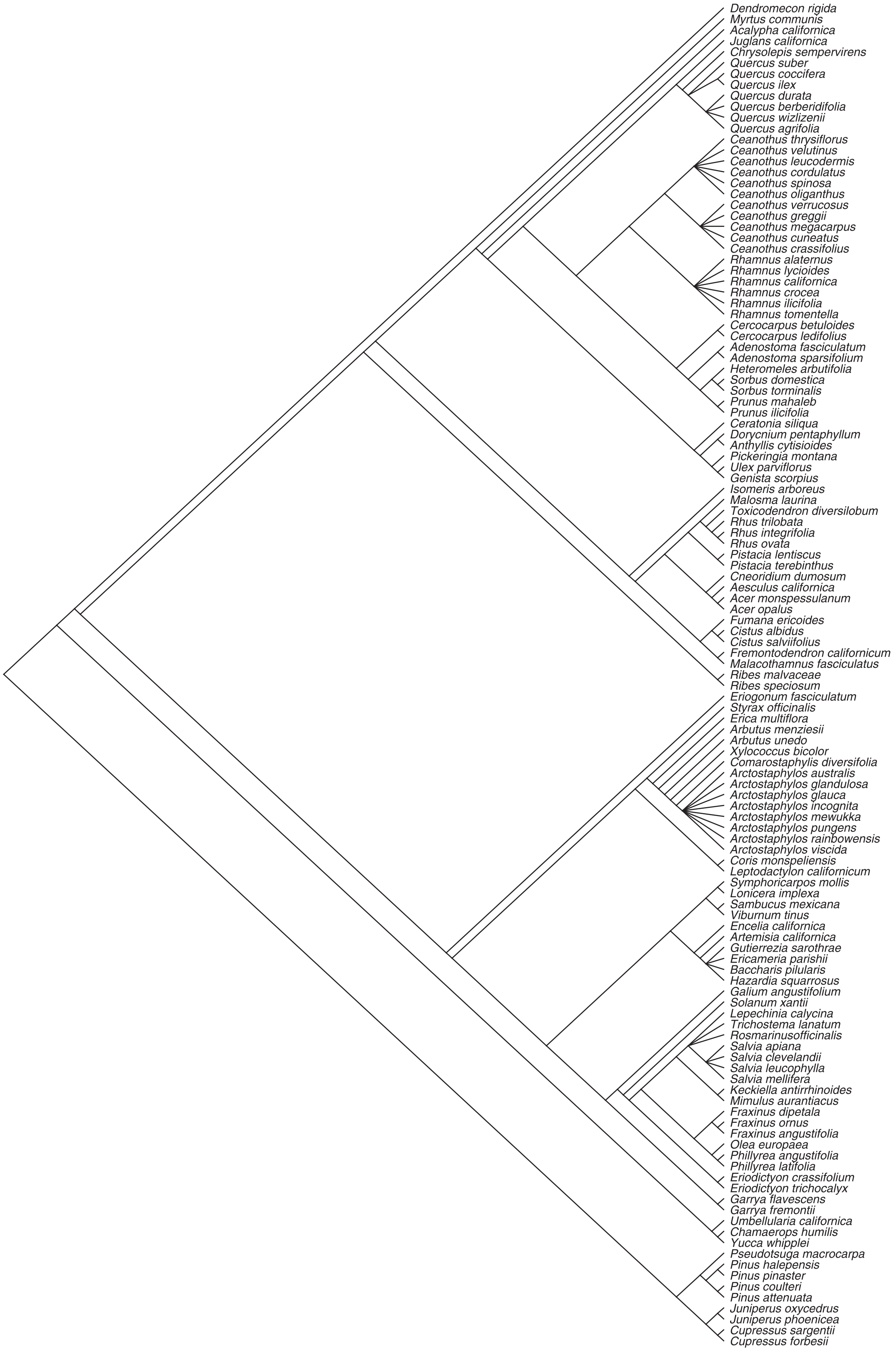

Fig. 1 EICA phylogenetic tree.

REGIONAL DIFFERENCES

If Californian plant species have evolved towards the states of R+ and P+ more frequently than Mediterranean Basin plants, we would expect these states to be distributed differently in the two regions. This is analysed by testing the association between R and Region and P and Region, where Region is a binary variable with two categories, California and Mediterranean Basin. First, a non-phylogenetic analysis is performed using the standard χ^2 test. Then phylogenetic association is tested for the EICA tree using the DISCRETE software (see Vamosi *et al*. 2003 for a similar approach). We further analysed which state of each trait (R and P) is preferentially acquired within the phylogeny for each region by comparing the gains and losses of each state. If the states enhancing fire persistence (R+ or P+) are preferentially acquired, then we would expect a bias on gains vs. losses, that is, higher forward (from R– to R+ or P– to P+) than backward transitions *sensu* Pagel (1994). Thus, the comparison of forward and backward rates between regions allows us to infer different sorting processes, regardless of whether the evolution of R and P was correlated or not. The test is performed for the EIBER and CALIF phylogenies by using a likelihood ratio test (with one degree of freedom) to compare the model in which forward and backward rates were fixed to be equal against the model without this constriction.

To account for the phylogenetic uncertainty derived from CALIF and EICA polytomies, all the phylogenetically informed analyses were tested on 100 trees with randomly resolved polytomies (Donoghue & Ackerly 1996).

Results

Non-phylogenetic analysis suggests a significant association between R and P in the CALIF data set ($\chi^2_1 = 8.53$, $P < 0.01$); however, this relationship cannot be supported when phylogenetic relatedness is taken into account (Omnibus test with four degrees of freedom.; LR statistic ranged from 1.09 to 10.5 with a median of 3.9; 79% of the trees with randomly resolved polytomies had *P*-values > 0.05). This result suggests that correlated evolution is very unlikely in California, in contrast to the Mediterranean Basin (for the EIBER data set, Pausas & Verdú 2005).

To examine these differences further, we looked at the association between fire traits and region for the EICA data set. The non-phylogenetic analysis suggests that proportions of neither R+ vs. R– nor of P+ vs. P– differ between CALIF and EIBER ('non-phylo' in Table 2). However, when phylogenetic relatedness is taken into account, the occurrence of the states of trait P differs significantly between the two regions (in 100% of trees; Table 2), while the occurrence of the states of trait R remains non-significant. That is, P is phylogenetically distributed in a different way in each region.

Table 2 Summary of the non-phylogenetic association (χ^2 test) and the phylogenetic association (LR, Likelihood Ratio statistic with 4 degrees of freedom, obtained from DISCRETE omnibus test) between Region (California, Mediterranean Basin) and R or P for the EICA data set. The range of likelihood ratios and *P*-values are obtained from 100 trees with randomly resolved polytomies. The table shows that California has a different representation of P+ and P– species than the Mediterranean Basin once phylogenetic relatedness is accounted for

	Non-phylo		Phylo	
Association	χ^2	*P*	LR	*P*
R – Region	0.625	0.429	2.00–4.45	0.35–0.73
P – Region	0.477	0.490	11.13–21.14	0.0003–0.025

For both CALIF and EIBER, there is a significant bias towards the acquisition of R+ (Table 3). However, there is a regional difference in the trend for P: in EIBER the bias is towards P– while in CALIF it is towards P+ (Table 3). This difference is reflected in the higher abundance of R+P+ (35% in CALIF vs. 19% in EIBER) and its wider taxonomic distribution in CALIF than EIBER (Fig. 2).

Discussion

Our results indicate that in California, the resprouting (R) and the propagule persistence (P) capacity have evolved independently (non-correlated evolution). This contrasts with the Mediterranean Basin, where R and P show a negatively correlated evolution (Pausas & Verdú 2005). In the Mediterranean Basin, species able to resprout almost never evolved persistent propagules while species unable to resprout had a great probability of evolving persistent propagules. In contrast, the acquisition of propagule persistence is independent of the resprouting capacity for Californian species.

These different evolutionary processes arise mainly from the differential acquisition of the fire persistence mechanism at the propagule level (P+, Table 2), with Californian species acquiring this trait more often than Mediterranean Basin species. In contrast, this regional

Table 3 Forward (from – to +) and backward (from + to –) transition rates for the two studied traits (R and P). The difference between forward and backward is tested by using the likelihood ratio statistic and assuming a χ^2 distribution with one degree of freedom; the last column indicates whether the trait is biased towards the + or – state of the trait. Due to the presence of polytomies in CALIF, the values are the range obtained from 100 trees with randomly resolved polytomies. The results show that Californian species tend to acquire R+ and P+ whereas Mediterranean Basin species tend to acquire R+ and P–

		Forward (α)	Backward (β)	Likelihood ratio	*P*		
CALIF	R	0.15–0.21	0.017–0.025	3.35–5.90	0.015–0.055	$\alpha > \beta$	R+
EIBER	R	0.31	0.07	11.24	0.0007	$\alpha > \beta$	R+
CALIF	P	0.13–0.14	0	3.77–6.19	0.012–0.052	$\alpha > \beta$	P+
EIBER	P	0.13	0.24	10.08	0.0015	$\alpha < \beta$	P–

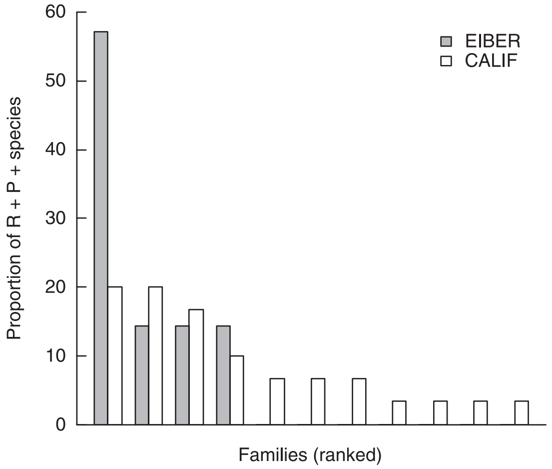

Fig. 2 Proportion of R+P+ species in the different families in each data set (EIBER for the Mediterranean Basin and CALIF for California). Families are ranked for each data set from those richest in R+P+ species (left). Families without R+P+ species are not included.

difference was not found for resprouting capacity, and in both regions the bias towards the acquisition of R+ may be partly due to the widespread presence of resprouting in angiosperms. Thus, Californian species have acquired the combination of both fire persistence traits (R+ and P+) more frequently than Mediterranean Basin plants. This is also reflected in the wider taxonomic distribution of R+P+ in California (20% of the species in Ericaceae, 20% in Rhamnaceae, 17% in Lamiaceae, with the remaining 43% in a further eight families) than in the Mediterranean basin (57% in Fabaceae and the rest in three families) (Fig. 2). Thus, we can rule out the possibility that regional differences in R and P are explained by different contributions of lineages with conserved traits to both floras, and conclude that evolutionary processes have differed between regions (Harvey & Pagel 1991).

In addition to evolutionary adaptation, sorting processes involving taxon-specific and site-specific components are relevant for explaining present-day regional species assemblages (Herrera 1992). Sorting processes imply that species possessing a particular trait encounter and then occupy a new environment to which they were exadapted (*sensu* Gould & Vrba 1982), and thus it is not necessary to invoke directional selection to explain the observed match between organisms and their environment (Ackerly 2004). In this framework, fire may act both as a selective pressure for adaptation and as a filter sorting out the species already possessing fire persistent traits.

The present day species pool in both California and the Mediterranean Basin is an assemblage of species whose origins are tied to the Tertiary Madrean-Tethyan sclerophyllous vegetation that was broadly distributed in North America and Eurasia (Axelrod 1975; Herrera 1992; Verdú *et al.* 2003). In both California and the Mediterranean Basin some fire persistence traits clearly predate the Mediterranean climate, which is thought to be relatively recent, occurring at intermittent intervals since the beginning of the Quaternary (Axelrod 1975). Parallel evolution of resprouting is apparent in the origin of R+P– species that occur in old genera shared by both regions, such as *Prunus*, *Quercus*, *Rhamnus* and *Arbutus*. Furthermore, there is evidence that resprouting ability is a basal character in most angiosperm lineages, and is so widespread in fire- and non-fire-prone ecosystems (e.g. Wells 1969; Bellingham *et al.* 1994; Lloret *et al.* 1999) that it cannot be clearly identified as adaptation, and in some lineages it is very likely an exaptation to fire. This process could also contribute to explaining the bias towards the acquisition of R+ in both regions (Table 3). However, fire was an important phenomenon in seasonal climates by the late Tertiary (Keeley & Rundel 2005), and one season providing conditions suitable for high biomass production followed by a season where this biomass dried to become fuel is typical of earlier climates as well as the current mediterranean one. Fire traits need not therefore necessarily be exaptations.

In contrast, propagule-persistence traits show different patterns among the two regions. In the Mediterranean Basin, P+ species are considered to be recent in origin, coinciding with the modern Mediterranean climate (Verdú 2000; Pausas & Verdú 2005), and thus suggesting fire as an adaptive force in Quaternary species evolving under Mediterranean conditions. However, this may not be true for many Californian lineages, where the acquisition of the P+ trait predates the current Mediterranean climate. The western North American genus *Ceanothus* is an interesting example which originated before the Mediterranean climate appeared (Jeong *et al.* 1997) and has radiated widely, becoming a current element of both mesic forests in the Pacific Northwest, as well as arid chaparral under both summer drought and summer rain climates in the south-west. Despite the range of climates and vegetation types, these are all fire-prone ecosystems, albeit with quite different fire regimes, and all *Ceanothus* produce seeds that are deeply dormant and persist in the soil for decades to centuries until stimulated by fire. Thus, the higher proportion of P+ in California can be explained because some pre-Mediterranean lineages were already P+ in California, while there is no evidence of this pattern in the Mediterranean Basin. In fact, if we fix the age of each node of the phylogenies as pre-Pliocene (i.e. pre-Mediterranean) or post-Pliocene (i.e. Mediterranean) based on fossil and biogeographical evidence (Verdú *et al.* 2003) and assume that tips (current species) are post-Pliocene, and then test the association with R and with P using DISCRETE, we find that P+ is significantly associated to post-Pliocene lineages in EIBER ($P = 0.08$) but not in CALIF ($P > 0.15$). This suggests that mediterranean conditions may have had some influence on the occurrence of P + in the Mediterranean Basin but not in California. For R, we found no relationship with the age of fossil records either in EIBER ($P = 0.15$) or in CALIF ($P > 0.80$), supporting the independence of evolution of the resprouting character with respect to the appearance of the Mediterranean climate.

It appears that the mediterranean climate has played a limited role in the present distribution of resprouting and propagule-persistence traits in the Californian woody flora, while it has played a more important role in the distribution of propagule-persistence strategy in the woody floras of the Mediterranean Basin. This is not to say that the mediterranean climate has had no impact on fire traits in California; coupling drought with warm summer conditions appears to have greatly expanded the available habitat for chaparral and this alone may have contributed to the rapid evolution of *Ceanothus* and *Arctostaphylos* obligate seeders (Raven & Axelrod 1978).

Other evidence of greater specialization to fire in California includes the highly specialized 'fire-endemic' life histories of the annual plant flora with deeply dormant seed banks that are triggered to germinate by fire and essentially disappear after the first or second year (Keeley & Fotheringham 2000). Despite a much richer annual flora in the Mediterranean Basin (Keeley & Fotheringham 2003), no such life-history specialization has been reported in the literature. It remains unknown whether the absence of a post-fire specialization by annual plants is due to different disturbance regimes, to different adaptive strategies or to different sorting processes. The Mediterranean Basin has had a substantially longer history of human disturbance from increased fire frequency, grazing (livestock) and cultivation. This is made more significant by the fact that such anthropogenic disturbances in California often result in the displacement of fire endemics by weeds from the Mediterranean Basin (Keeley 2001). The possibility exists that the much longer human history in the Mediterranean Basin could have affected the flora persisting to the present day. In addition, the work here focuses only on woody dominants, and a rich story on fire adaptation could be covered by a community-wide study of all life forms.

The increased frequency of R+P+ as a consequence of the selective pressure imposed by fire (Mediterranean Basin vs. California) could be extrapolated to other areas. The higher selective pressure by fire in Australian and South African Mediterranean-type ecosystems could explain the observed dominance of R+P+ species in comparison to the Mediterranean Basin and California (Pausas *et al*. 2004). This trend may also occur within a region, and could explain the increased abundance of R+P+ species along a fire frequency gradient in Australian heathlands (Pausas *et al*. 2004). However, further phylogenetic analyses are needed for an accurate testing of these predictions.

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com:

Appendix S1 List of the species considered for the two regions (California and Mediterranean Basin) with the states of the two traits (resprouting capacity and propagule-persistence capacity).

Supplementary material

Appendix S1. Species considered in the two regions (CA: California and MB: Mediterranean Basin) and the states of the two trait (R: resprouting capacity and P: propagule persistence capacity; Pausas *et al.* 2004). Phylogenetic relatedness is provided in Figure 1. Names for Californian species are according to Hickman (1993), except for Keeley and Massihi (1994) and Keeley et al. (1997). Names for species in the Mediterranean Basin are according to Mateo and Crespo (2001).

Species	Region	R	P
Acalypha californica	CA	R+	P-
Acer monspessulanus	MB	R+	P-
Acer opalus ssp. granatense	MB	R+	P-
Adenostoma fasciculatum	CA	R+	P+
Adenostoma sparsifolium	CA	R+	P-
Aesculus californica	CA	R+	P-
Anthyllis cytisioides	MB	R+	P+
Arbutus menziesii	CA	R+	P-
Arbutus unedo	MB	R+	P-
Arctostaphylos australis	CA	R-	P+
Arctostaphylos glandulosa	CA	R+	P+
Arctostaphylos glauca	CA	R-	P+
Arctostaphylos incognita	CA	R+	P+
Arctostaphylos mewukka	CA	R+	P+
Arctostaphylos pungens	CA	R-	P+
Arctostaphylos rainbowensis	CA	R+	P+
Arctostaphylos viscida	CA	R-	P+
Artemisia californica	CA	R+	P+
Baccharis pilularis	CA	R+	P-
Ceanothus cordulatus	CA	R+	P+
Ceanothus crassifolius	CA	R-	P+
Ceanothus cuneatus	CA	R-	P+
Ceanothus greggii	CA	R-	P+
Ceanothus leucodermis	CA	R+	P+
Ceanothus megacarpus	CA	R-	P+
Ceanothus oliganthus	CA	R+	P+
Ceanothus spinosa	CA	R+	P+
Ceanothus thrysiflorus	CA	R+	P+
Ceanothus velutinus	CA	R+	P+
Ceanothus verrucosus	CA	R-	P+
Ceratonia siliqua	MB	R+	P+
Cercocarpus betuloides	CA	R+	P-
Cercocarpus ledifolius	CA	R+	P-
Chamaerops humilis	MB	R+	P+
Chrysolepis sempervirens	CA	R+	P-
Cistus albidus	MB	R-	P+
Cistus salviifolius	MB	R-	P+
Cneoridium dumosum	CA	R+	P-
Comarostaphylis diversifolia	CA	R+	P-
Coris monspeliensis	MB	R+	P-
Cupressus forbesii	CA	R-	P+
Cupressus sargentii	CA	R-	P+
Dendromecon rigida	CA	R+	P+
Dorycnium pentaphyllum	MB	R+	P+

Encelia californica	CA	R+	P-
Erica multiflora	MB	R+	P+
Ericameria parishii	CA	R+	P-
Eriodictyon crassifolium	CA	R+	P+
Eriodictyon trichocalyx	CA	R+	P+
Eriogonum fasciculatum	CA	R+	P-
Fraxinus angustifolia	MB	R+	P-
Fraxinus dipetala	CA	R+	P-
Fraxinus ornus	MB	R+	P-
Fremontodendron californicum	CA	R+	P+
Fumana ericoides	MB	R-	P+
Galium angustifolium	CA	R+	P-
Garrya flavescens	CA	R+	P+
Garrya fremontii	CA	R+	P+
Genista scorpius	MB	R+	P+
Gutierrezia sarothrae	CA	R+	P-
Hazardia squarrosus	CA	R+	P-
Heteromeles arbutifolia	CA	R+	P-
Isomeris arboreus	CA	R+	P-
Juglans californica	CA	R+	P-
Juniperus oxycedrus	MB	R+	P-
Juniperus phoenicea	MB	R-	P-
Keckiella antirrhinoides	CA	R+	P-
Lepechinia calycina	CA	R+	P-
Leptodactylon californicum	CA	R+	P-
Lonicera etrusca	MB	R+	P-
Malacothamnus fasciculatus	CA	R+	P+
Malosma laurina	CA	R+	P+
Mimulus aurantiacus	CA	R+	P+
Myrtus communis	MB	R+	P-
Olea europaea	MB	R+	P-
Phillyrea angustifolia	MB	R+	P-
Phillyrea latifolia	MB	R+	P+
Pickeringia montana	CA	R+	P-
Pinus attenuata	CA	R-	P+
Pinus coulteri	CA	R-	P-
Pinus halepensis	MB	R-	P+
Pinus pinaster	MB	R-	P+
Pistacia lentiscus	MB	R+	P-
Pistacia terebinthus	MB	R+	P-
Prunus ilicifolia	CA	R+	P-
Prunus mahaleb	MB	R+	P-
Pseudotsuga macrocarpa	CA	R+	P-
Quercus agrifolia	CA	R+	P-
Quercus berberidifolia	CA	R+	P-
Quercus coccifera	MB	R+	P-
Quercus durata	CA	R+	P-
Quercus ilex	MB	R+	P-
Quercus suber	MB	R+	P-
Quercus wizlizenii	CA	R+	P-
Rhamnus alaternus	MB	R+	P-
Rhamnus californica	CA	R+	P-
Rhamnus crocea	CA	R+	P-
Rhamnus ilicifolia	CA	R+	P-
Rhamnus lycioides	MB	R+	P-

Rhamnus tomentella	CA	R+	P-
Rhus integrifolia	CA	R+	P+
Rhus ovata	CA	R+	P+
Rhus trilobata	CA	R+	P-
Ribes malvaceae	CA	R+	P-
Ribes speciosum	CA	R+	P-
Rosmarinus officinalis	MB	R-	P+
Salvia apiana	CA	R+	P+
Salvia clevelandii	CA	R+	P+
Salvia leucophylla	CA	R+	P+
Salvia mellifera	CA	R+	P+
Sambucus mexicana	CA	R+	P-
Solanum xantii	CA	R+	P-
Sorbus domestica	MB	R+	P-
Sorbus torminal	MB	R+	P-
Styrax officinalis	CA	R+	P-
Symphoricarpos mollis	CA	R+	P-
Toxicodendron diversilobum	CA	R+	P-
Trichostema lanatum	CA	R+	P+
Ulex parviflorus	MB	R-	P+
Umbellularia californica	CA	R+	P-
Viburnum tinus	MB	R+	P-
Xylococcus bicolor	CA	R+	P-
Yucca whipplei	CA	R-	P-

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