

# Do Mediterranean-type ecosystems have a common history?—Insights from the Buckthorn family (Rhamnaceae)

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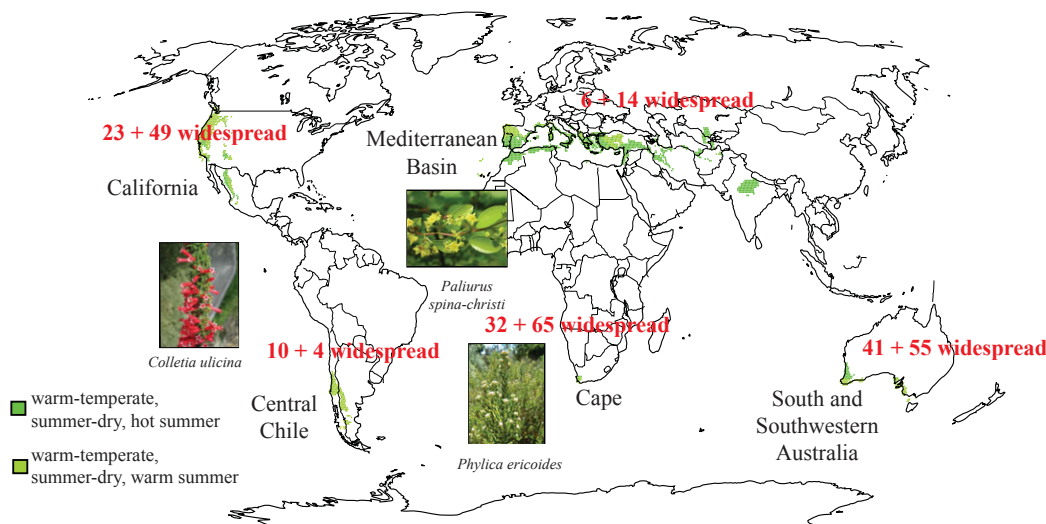
Mediterranean-type ecosystems (MTEs) are remarkable in their species richness and endemism, but the processes that have led to this diversity remain enigmatic. Here, we hypothesize that continent-dependent speciation and extinction rates have led to disparity in diversity between the five MTEs of the world: the Cape, California, Mediterranean Basin, Chile, and Western Australia. To test this hypothesis, we built a phylogenetic tree for 280 Rhamnaceae species, estimated divergence times using eight fossil calibrations, and used Bayesian methods and simulations to test for differences in diversification rates. Rhamnaceae lineages in MTEs generally show higher diversification rates than elsewhere, but speciation and extinction dynamics show a pattern of continent-dependence. We detected high speciation and extinction rates in California and significantly lower extinction rates in the Cape and Western Australia. The independent colonization of four of five MTEs may have occurred conterminously in the Oligocene/Early Miocene, but colonization of the Mediterranean Basin happened later, in the Late Miocene. This suggests that the in situ radiations of these clades were initiated before the onset of winter rainfall in these regions. These results indicate independent evolutionary histories of Rhamnaceae in MTEs, possibly related to the intensity of climate oscillations and the geological history of the regions.

**KEY WORDS:** Californian Floristic Province, Cape, diversification rate, extinction, speciation, Western Australia.

The five Mediterranean-type ecosystems (MTEs) of the world (the southern African Cape, California-Baja California, the Mediterranean Basin, central Chile, and South and Southwest Australia) are exceptional in their species richness and endemism, containing about 20% of the known vascular plant species, almost 50,000, in an area that covers less than 5% of the earth's surface (Cowling et al. 1996). Furthermore, more than 50% of the plant species occurring in MTEs are endemic to MTEs (Greuter 1994; Cowling et al. 1996), which may be due to the geographically and ecologically isolated position of MTEs, enclosed by oceans, deserts, and mountain ranges (Cowling et al. 1996; Kottek et al.

2006). The MTEs are geographically separated on different continents (Fig. 1) but are characterized by similar climatic conditions of generally dry, hot summers, and cool, wet winters (Aschmann 1973; Castri 1973; Kottek et al. 2006). The processes that resulted in the high in situ diversity are enigmatic (e.g., Linder 2003; Lancaster and Kay 2013). Three processes have been proposed: a higher diversification rate in MTEs than elsewhere, more time to accumulate diversity in these regions than elsewhere, or a high immigration rate into the MTEs (Sauquet et al. 2009; Valente et al. 2010b; Buerki et al. 2012, 2013; Lancaster and Kay 2013).





**Figure 1.** Mediterranean-type ecosystems (MTE) following the Köppen–Geiger climate classification. The number of Rhamnaceae species endemic to the MTE and the number of species widespread (occurring in the MTE as well as outside) are indicated for each region: California, central Chile, the Mediterranean Basin, the Cape, and South and Southwestern Australia.

Higher net diversification rates (speciation rate – extinction rate) in MTEs compared to other regions could result from increased speciation rates, reduced extinction rates, or a combination of both. Increased net diversification rates were shown for the Proteaceae in the Mediterranean hotspots of Africa (hereafter Cape) and Australia (hereafter Western Australia) compared to tropical environments (Sauquet et al. 2009). However, elevated diversification rates were not detected for the Western Australian *Banksia*'s and Cape *Protea*'s (both Proteaceae), which occur in the MTEs as well as in the upland regions of Africa and Eastern Australia, respectively, when analyzed separately (i.e., without being compared to the background rate of the Proteaceae as a whole) (Valente et al. 2010b; Cardillo and Pratt 2013). The Hyacinthaceae showed higher speciation and higher extinction rates in the Cape and Mediterranean Basin than elsewhere (Buerki et al. 2012). In comparison, the diversity in California was shown to result from generally low extinction rates as opposed to elevated speciation rates (Lancaster and Kay 2013). Longer time for speciation in MTEs compared to elsewhere was shown for more species-rich, but also older, Cape lineages compared to younger and species-poorer lineages in the same genus occurring in the Mediterranean Basin (Valente et al. 2011; Valente and Vargas 2013), but “time for speciation” did not affect diversity in the Mediterranean *Dianthus* compared to its African sister clade (Valente et al. 2010a). Finally, higher immigration rates into than out of MTEs may explain diversity in MTEs, but this hypothesis was rejected for most clades and regions (Valente et al. 2011; Cardillo and Pratt 2013; Lancaster and Kay 2013), but see Valente et al. (2010b) and Buerki et al. (2012) for dispersal of *Protea* and Hyacinthaceae, respectively, into the Cape.

The five MTEs have similarities as well as differences. The comparable climatic conditions in MTEs may have selected for plants with similar functional traits, resulting in analogous vegetation types (Schimper 1903; Specht 1979; Cowling et al. 1996). This “convergent” functional syndrome is fire-adapted, and includes traits such as a woody, shrubby growth form and often small, evergreen, sclerophyllous leaves (Schimper 1903; Specht and Moll 1983). The dominant vegetation type in all regions is dry shrub- or heathland (“fynbos” in the Cape, “chaparral” in California, “kwongan” in Western Australia, “maquis” in the Mediterranean Basin, and “matorral” in Chile), but extensive areas of sclerophyllous or drought deciduous forests or woodlands and semi-succulent shrublands can be found as well (Cowling et al. 1996). Although there are many similarities, there are also differences between the regions, such as the geological and geomorphological history, topography, heterogeneity and complexity of the ecosystem, fire frequency or absence (i.e., in Chile), soil nutrient status, biotic elements, and the timing of the onset of winter rainfall (Mediterranean climate) (Thrower and Bradbury 1973; Deacon 1983; Hobbs et al. 1995; Cowling et al. 2005). The Cape and Western Australia have been characterized as relatively stable landscapes compared to the other three MTEs (Cowling et al. 2014). This stability may have resulted from the almost absence of recent orogenic events, subduction or glaciation during the Cenozoic and both these regions have ancient basement complexes, dating back to at least the Paleozoic (Thrower and Bradbury 1973). The exception are two episodes of uplift in southern Africa during the Miocene and Pliocene, lifting the central plateau by ~900 m (Partridge and Maud 1987), these were more pronounced in the

Eastern Cape, thereby possibly enhancing summer aridity in the Western Cape (Tyson and Partridge 2000). The long coastline of the Cape and Western Australia, wedged between two oceans, could have enhanced long-term climatic stability, and even during the Pleistocene the climatic fluctuations in the Cape were minimal compared to the rest of the planet (Meadows and Sugden 1993). Typically, the ancient land surfaces and sandy soils have led to leached out, very nutrient poor soils in these MTEs—therefore called OCBILS (“old, climatically buffered, infertile landscapes,” Hopper 2009). This is dramatically different from the other three MTEs (Chile, California, Mediterranean Basin), which are more nutrient rich, and which have been physiographically much more turbulent (Thrower and Bradbury 1973; Hopper 2009). In contrast to the Cape and Western Australia, these areas are marked by relatively young (Late Miocene, Early Pliocene) orogenic events, with mountains rising close to the coast (Thrower and Bradbury 1973). Furthermore, temperature and moisture oscillations associated with Pleistocene glaciations were thought to be more severe in North America, South America, and Europe, compared to Australia and South Africa (Markgraf et al. 1995; Farmer and Cook 2013). These differences may therefore have affected the diversification dynamics (i.e., speciation and extinction rates) of the clades evolving in these areas.

First, we ask why MTEs are generally so diverse, and we hypothesize that overall higher net diversification rates of lineages in MTEs than elsewhere may explain this pattern, as opposed to longer time for speciation in MTEs than elsewhere or higher immigration rates into MTEs than vice versa. Second, we test if speciation and extinction dynamics differ between MTEs. We hypothesize that if the winter rainfall climate is the main factor driving speciation and/or extinction rates (and thus net diversification rates), we would detect similar diversification dynamics in MTEs on different continents, as climate is the consistent factor between the regions. However, if non-climatic factors, which vary between these regions, (additionally) influence speciation and/or extinction rates, we expect to find different, continent-dependent speciation and extinction patterns. To this end, we estimate speciation and extinction rates for each MTE separately, comparing rates of lineages restricted to the respective MTE to rates of lineages occurring elsewhere. Finally, we hypothesize that the timing of colonization of the five MTEs and the accumulation of lineage diversity through time in these areas may explain additional variation in species richness between the MTEs (i.e., due to time for speciation). To this end, we reconstruct the first occupation of each MTE to investigate if the colonization of the five MTEs happened in synchrony, and to evaluate how lineage diversity in the five MTEs has varied over time. Such variation could be related to the timing of the onset of winter rainfall: in the Pliocene (2–5 million years ago (Mya)) in the Mediterranean Basin and California (Axelrod 1973; Suc 1984; Suc and Popescu 2005), in the

Mid- to Late Miocene (10–15 Mya) in the Cape region (Cowling et al. 2009; Dupont et al. 2011) and similarly in Chile (8–15 Mya) (Armesto et al. 2007), and from the Early Miocene onwards (20 Mya) in Western Australia (Hopper and Gioia 2004; Martin 2006).

We test these hypotheses in Rhamnaceae Juss. (Rosales), which includes ~1055 species of predominantly warm temperate shrubs (Medan and Schirarend 2004, also see Table S1). This family is suitable to test these hypotheses for several reasons. First, it occurs in all five MTEs (Fig. 1)—Phylceae in the Cape, Pomaderreae in Western Australia, *Ceanothus* in California, Rhamneae and Paliureae in the Mediterranean Basin, and the Colletieae in Chile—as well as outside these regions. Second, it is phylogenetically well studied (Richardson et al. 2000b, 2004; Ladiges et al. 2005; Islam and Simmons 2006; Burge et al. 2011) and has a relatively good and well-studied fossil record (Reid and Reid 1915; Basinger and Dilcher 1984; Axelrod 1985; Manchester 2001; Calvillo-Canadell and Cevallos-Ferriz 2007; Burge and Manchester 2008). Finally, Rhamnaceae is often an ecologically important and dominant element in Mediterranean floras (Axelrod 1973; Linder 2003).

## Materials and Methods

### TAXON SAMPLING AND PHYLOGENETIC RECONSTRUCTION

Sequence data for species of Rhamnaceae and outgroup taxa were collected from GenBank ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov)) (513 accessions) or generated by ourselves (379 accessions; sequencing procedure and primers are provided in Supporting Information 1, GenBank accession numbers are provided in Table S2). We sampled species for six chloroplast markers (*matK* gene 1593 base pairs (bp), *trnL-F* genes and intergenic spacer 1232 bp, *rbcl* gene 1425 bp, *psbA* gene and *psbA-trnH* intergenic spacer 775 bp, *ndhF* gene 2163 bp, *rpl16* gene and intron 1344 bp) and one nuclear marker (ITS gene 952 bp). All sequences were aligned by Se-AL version 2.0a11 and manually adjusted in Geneious version 5.6 ([www.geneious.com](http://www.geneious.com)). The concatenated alignment contained 59% missing data, but this was not problematic for topological reconstruction or divergence-time estimation (Table S3) (Wiens and Morrill 2011). The final dataset consisted of 307 accessions representing 280 Rhamnaceae species, seven Rhamnaceae subspecies, and 13 outgroup species from related families: Elaeagnaceae, Dirachmaceae, and Barbeyaceae. Lineages from all three families were included because the sister family to Rhamnaceae has not been confidently placed yet. All 11 tribes and 50 of the 59 genera were represented by at least one species. At species level, 27% of the currently 1055 recognized species (Table S1) were included.

### PHYLOGENETIC RECONSTRUCTION AND DATING

Maximum likelihood (ML) analyses were conducted in RAxML version 7.0.4 (Stamatakis 2006) applying the GTR model of sequence evolution with across site rate variation modeled to a Gamma distribution. Gene trees for each marker were generated and manually assessed for incongruence (i.e., conflicting relationships between taxa with >80% bootstrap support), and in absence of incongruence a concatenated alignment was used in all subsequent analyses. Phylogenetically “unstable lineages (i.e., the monotypic *Schistocarpea* and *Lasiodiscus*), which may have caused the non-monophyly of the Pomaderreae and the low support for the relationships between the Gouanieae, Paliureae, and Phylliceae, respectively, were removed to investigate the change in relationship and node support. However, as the support for main clades decreased when removing these taxa, and as they are the only representatives of a genus, they were included in all subsequent analyses.

The best-fit model for the chloroplast and ITS markers were identified with the Bayesian information criterion implemented in PartitionFinder version 1.0.1 (Lanfear et al. 2012), as follows: GTR + G + I for the linked chloroplast markers, and SYM + G + I for the ITS marker. Chloroplast markers were linked to be able to reach convergence in substitution parameters in the dating analysis, which seemed otherwise problematic. The chloroplast and ITS partitions were unlinked for substitution and clock models, but we combined them when estimating the species tree. However, we regressed the median node ages obtained from the combined chloroplast and ITS analysis to the ages when using only chloroplast markers, and results indicate a very strong correlation ( $R^2 = 0.96$ , Fig. S1). Estimation of Rhamnaceae divergence times was conducted with an uncorrelated lognormal relaxed clock and a Yule tree prior available in BEAST version 1.7.5 (Drummond and Rambaut 2007). This was done in two steps. First, we calibrated seven nodes on this tree with fossil-derived mean ages (Supporting Information 2), using normally distributed priors with an SD of 0.01. The ML tree was used as an input tree. We ran a Markov chain Monte Carlo (MCMC) for 100 million steps, sampling one tree every 2000 steps. Second, we calibrated eight nodes on the tree with fossils (all seven from the previous run, plus one, Supporting Information 2), but using uniform priors, of which the minimum age was indicated by the minimum age of the fossil, and the maximum age by the maximum estimated crown age of Rosales (i.e., 103 Mya, Wang et al. 2009). Uniform priors were chosen to avoid making assumptions about the most probable node age without having additional fossil data (Sauquet et al. 2012). The chloroplast and ITS substitution rate and the Yule birth rate mean values as estimated by the previous run were set as initial prior values in this second run. The maximum clade credibility (MCC) tree from the previous run was used as an input tree. Eight independent MCMCs of two times 100

million and six times 30 million steps were conducted, sampling one tree every 2000 steps. Log- and tree-files of the eight chains were combined using LogCombiner version 1.7.5, after removing 20% generations as burn-in, and trees were randomly subsampled to obtain a set of 10,250 trees. Tracer version 1.5 (Rambaut and Drummond 2007) was used to evaluate the combined log-file and to obtain the effective sample size (ESS) for each parameter. An ESS of 200 or greater was considered adequate. TreeAnnotator version 1.7.5 was used to obtain the mean node heights, posterior distributions of estimated divergence dates, and the 95% highest posterior density (HPD), based on the 10,250 subsampled trees, which were mapped on the MCC tree.

### HABITAT AND CLIMATE SAMPLING

We obtained distribution data at a  $1 \times 1$  degree resolution for 785 Rhamnaceae species (75% of total species) from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>) and our own collections and used these distribution data to assign each species to one or more of the 31 Köppen–Geiger climate zones (Fig. 1, Kottek et al. 2006). This classification is based on the mean annual temperature, monthly mean temperature of the warmest and coldest months, accumulated annual precipitation, and precipitation in the driest month. Species occurring in the climate zones with warm temperate climates with dry summers were coded as present in MTEs, the others coded as absent from MTEs. Occurrence records and species' presence or absence in MTEs were carefully examined for consistency with documented distributions of the species in floras and monographs (Table S1).

### DIVERSIFICATION RATE ANALYSES

Diversification rate analyses were performed on the Rhamnaceae MCC tree after pruning outgroups and subspecies. To investigate the effects of topological uncertainty and branch-length variation on the estimated rates, all analyses were also conducted on 100 equally spaced subsampled trees from the posterior distribution of the combined BEAST runs. We tested if our phylogenetic sampling of species was a good representation of the total sampling in terms of tribal coverage and presence/absence in MTEs (Fig. S2). To obtain a better proportional coverage of the tribes and their distribution in MTEs in the phylogeny, we randomly pruned lineages of overrepresented clades (i.e., *Phyllica* and *Ceanothus*). Analyses were run on the full (i.e., nonpruned, 280 species) as well as the reduced (i.e., pruned, 114 species) phylogeny (hereafter referred to as “full dataset” and “reduced dataset”). Finally, to assess the effect of nonfully sampled trees and therefore missing character states on type I and II errors, we estimated known speciation and extinction rates on simulated trees after pruning lineages with states proportionally to obtain our observed character state proportions.



We tested the effect of MTEs on speciation, extinction, and “dispersal” (immigration) rates with the Geographic State Speciation and Extinction (GeoSSE) algorithm (Goldberg et al. 2011) implemented in the R package “diversitree” (FitzJohn et al. 2009; FitzJohn 2012). This algorithm can be used to estimate region-dependant rates of speciation, extinction, and range evolution based on a fully resolved dated phylogenetic tree and geographical regions assigned to the tips of the tree. Importantly, this algorithm can incorporate species not sampled in the phylogeny and their character states. The sampling proportion for each character state was calculated as the proportion of phylogenetically sampled species for this state divided by the total number of species in the family having this state (Table 1).

First, we asked whether speciation, extinction, and dispersal rates vary significantly between lineages occurring in or outside MTEs. We estimated the sampling proportion of species in MTEs, non-MTEs, and both regions from 785 Rhamnaceae species, based on their occurrence in the Köppen–Geiger climate zones (Fig. 1). The 280-species phylogeny contained 62% of species that occur in both MTEs and non-MTEs (117 of 188), 44% of only MTE species (50 of 113), and 16% of non-MTE species (96 of 532).

Second, we ask if speciation and extinction rates differ between MTEs. To this end, we ran five separate GeoSSE models contrasting each MTE against the rest (i.e., “the rest” includes the other regions with MTEs as well as non-MTE; for sampling proportions, see Table 1). The Multiple State Speciation and Extinction (MuSSE) algorithm is able to estimate speciation and extinction rates for a trait with multiple states, and could therefore be used to analyze the MTEs as separate states in a combined analysis. We did not use this approach because, first, this model does not consider geographical regions and it is not possible to assign species to more than one state (62% of the Rhamnaceae species occur in MTEs as well as outside). Consequently, it may overestimate extinction rates (in the GeoSSE model lineages can only go extinct after being restricted to one of the geographical areas). Second, the MuSSE model with six states (five for the MTEs plus one for non-MTE) would estimate 54 parameters (compared to seven GeoSSE parameters): six speciation and six extinction rate parameters, and 42 transition rates. Simultaneously estimating so many parameters with a relatively small dataset may lead to a significant loss of power (Davis et al. 2013). Third, comparing the speciation and extinction rates of lineages occurring in one specific MTE to the remaining Rhamnaceae using the GeoSSE algorithm is unlikely to artifactually produce an apparent pattern of different diversification rates between states; rather, we may fail to reject the null hypothesis of equal rates of diversification, due to the noise caused by the speciation and extinction rate dynamics occurring in the remaining Rhamnaceae lineages.

**Table 1.** Number of species for each state in the GeoSSE model: “both” refers to species occurring in the MTE as well as outside, “MTE” refers to species restricted in their distribution to the MTE, and “non-MTE” refers to species not occurring in the respective MTE.

Trait	States	Total species	Species present in phylogeny		Sampling proportion	
			full dataset	reduced dataset	full dataset	reduced dataset
All	Both/MTE/non-MTE	188/113/532	117/50/96	80/37/85	0.622/0.442/0.18	0.426/0.327/0.16
California	Both/Californian MTEs/ non-Californian MTEs	49/23/870	32/13/231	22/9/179	0.653/0.565/0.266	0.449/0.391/0.206
Chile	Both/Chilean MTEs/non-Chilean MTEs	4/10/927	3/2/271	3/2/205	0.75/0.2/0.292	0.75/0.2/0.221
Mediterranean Basin	Both/Mediterranean Basin MTEs/non-Mediterranean Basin MTEs	14/6/857	11/3/255	11/3/189	0.786/0.5/0.298	0.786/0.5/0.221
Cape	Both/Cape MTEs/non-Cape MTEs	65/32/851	51/16/203	24/7/178	0.784/0.5/0.239	0.369/0.219/0.209
Australia	Both/Australian MTEs/non-Australian MTEs	55/41/862	20/15/240	20/15/174	0.364/0.366/0.278	0.364/0.366/0.202

GeoSSE sampling proportions for the full 280 taxa dataset and the reduced 114 taxa dataset are indicated.

For all analyses, ML parameter estimation and model comparison were conducted followed by Bayesian parameter estimation through MCMC on the MCC trees of the full and reduced datasets. We tested a series of eight models that allowed speciation, extinction, and dispersal rates to vary between MTE-lineages and non-MTE-lineages (Supporting Information 3) and selected the best-fitted model considering the least number of parameters (assessed by a likelihood ratio test, Supporting Information 3). This model was then used in the Bayesian MCMC, which we ran for 5000 or 10,000 steps (depending on the ESS of the parameters), using ML rate estimates as starting points and an exponential prior whose distribution was in relation to the general diversification rate, estimated using the Kendall–Moran estimate for net diversification rate (Kendall 1949; Moran 1951). We evaluated independence of the samples for each parameter in Tracer 1.5 (Rambaut and Drummond 2007). To assess the effect of topological uncertainty on the results, we also ran an MCMC over 100 randomly sampled postburnin trees of the BEAST analysis for 5000 steps per tree, for the full dataset. If the 5–95 percentiles of the posterior densities of the two rates are nonoverlapping, this is strong support for different diversification rates between them (FitzJohn et al. 2009).

## SIMULATIONS

Disentangling speciation and extinction parameters using molecular phylogenies is problematic as they covary along a ridge of optimal diversification rates, especially for extinction rates (Rabosky 2010). Estimated extinction rates often approach zero, possibly because cladogenetic (speciation) events can be directly inferred from molecular phylogenies, but extinction events cannot (Paradis 2005). Simulations show that the Binary State Speciation and Extinction (BiSSE) algorithm (similar to the GeoSSE algorithm) and the GeoSSE algorithm can accurately estimate rate parameters, including extinction, associated with character states given sufficient sampling of species (Goldberg et al. 2011; Davis et al. 2013). However, phylogenetic trees with too few tips (i.e., less than 300) or with a biased character state ratio (i.e., less than 10% of the species in one state) may give unreliable results (Davis et al. 2013). Rhamnaceae are represented by relatively few lineages in the Mediterranean Basin and Chile, suggesting that our dataset may not have enough statistical power to detect different diversification rates comparing these regions to Rhamnaceae occurring elsewhere, if they exist.

We tested for the possible biased outcome of our dataset by performing two simulation studies, to test for type I and II errors (FitzJohn et al. 2009; Verdú and Pausas 2013), and results were consistent with the expectations (R scripts are available on request). First, we simulated 100 completely sampled Rhamnaceae trees (1055 species) in which character states evolved following estimated speciation and extinction rates, and then we tested the accuracy by inferring those rates from the trees after pruning

70% of the species, with a proportion to obtain the known character state ratio (i.e., as used in our initial analysis) (FitzJohn et al. 2009). Thereby we test if we fail to reject the false null hypothesis of equal diversification rates between the states (type II error). We used the estimated median speciation and extinction rates for the lineages occurring in MTEs, non-MTEs, and both obtained from the MCMC on the MCC tree, and dispersal rates were chosen to obtain the observed tip (character-) state ratio as known from the literature (i.e., 22% of species occur in MTEs and non-MTEs, 14% is restricted to MTEs, and 64% occur outside MTEs). These rates were  $s_A$  (speciation rate in MTE) = 0.148,  $s_B$  (speciation rate in non-MTE) = 0.079,  $s_{AB}$  (speciation rate in MTE + non-MTE) = 0.06,  $x_A = x_B$  (extinction rate in MTE and non-MTE) = 0.033,  $d_A$  (dispersal rate from MTE to non-MTE) = 0.4, and  $d_B$  (dispersal rate from non-MTE to MTE) = 0.004. We then randomly dropped 66% of the lineages with state MTE, 86% of the lineages with state non-MTE, and 51% of the lineages with state MTE + non-MTE, resulting in sampling proportions of 0.336, 0.144, and 0.488 for these states, respectively (similar to the known sampling fractions).

In the second experiment, we again simulated 100 completely sampled Rhamnaceae trees (1055 species), but this time we simulated them using the same speciation and extinction rates for both character states, to evaluate if we may incorrectly reject the true null hypothesis of equal diversification rates (type I error). Dispersal rates were chosen to obtain the tip state ratio as known from the literature (see above), and again we pruned 70% of the species, with a proportion to obtain the character state ratio as we used in the initial analysis. The rates we used were  $s_A = s_B = s_{AB} = 0.148$ ,  $x_A = x_B = 0.033$ ,  $d_A = 0.5$ , and  $d_B = 0.05$ , and we randomly dropped 66% of the lineages with state MTE, 85% of the lineages with state non-MTE, and 53% of the lineages with state MTE + non-MTE, resulting in sampling proportions of 0.336, 0.146, and 0.47 for these states, respectively (similar to the known sampling fractions). For both simulations studies, we then compared the simulated posterior distributions of the diversification rates to the known ones (i.e., our observed posterior distributions).

## TIME

Finally, we ask if the colonization of the five MTEs happened in synchrony, and how the lineage diversity in the five MTEs varied over time. To this end, we performed an ML ancestral state reconstruction on the Rhamnaceae MCC tree under an equal rate model for the transition between the discrete states (i.e., non-MTE, California, Chile, Mediterranean Basin, Cape, and Western Australia), implemented by the “ace” function in the “ape” package in R (Pagel 1994; Paradis et al. 2004). Speciation and extinction may bias ancestral state reconstructions, consequently we compared the results to reconstructions using the speciation, extinction, and dispersal rates as estimated by GeoSSE. We used the marginal

probabilities of ancestral nodes occupying non-MTE or specific MTEs to estimate the lineage diversity present in that MTE at the time of occurrence of that particular node, using the “asr” method in the *estDiversity* function in the “phytools” package in R (for more details, see Mahler et al. 2010; Revell 2012).

## Results

### PHYLOGENETIC RELATIONSHIPS

The MCC tree resulting from the dating analyses (Figs. 2A, S3) is topologically mostly congruent with previously published phylogenetic trees of Rhamnaceae (Richardson et al. 2000b, 2004; Ladiges et al. 2005; Islam and Simmons 2006; Burge et al. 2011), and includes the most extensive sampling of Rhamnaceae to date. The 11 tribes (Richardson et al. 2000a) were found to be monophyletic with high posterior probabilities ( $p.p. > 0.9$ ), with the exception of the paraphyletic Pomaderreae and Paliureae (for more details, see Supporting Information 4). For discussion on inferred divergence times, see Discussion.

### DIVERSIFICATION RATES IN MTEs

For all diversification analyses, the results between the full dataset and reduced dataset were similar (compare Fig. 3 to Figs. S4, S5), therefore only results using the full dataset are shown here. Results on the MCC trees were similar to results obtained on a set of trees (Figs. 3, S4, S5), except for Western Australia, where the signal detected on the MCC tree was not retrieved on a set of trees.

We detected higher speciation rates in lineages occurring inside than outside MTEs, resulting in higher net diversification rates for MTE-restricted lineages than non-MTE lineages (Fig. 3A–C, Table 2). The best-fit GeoSSE model was a model where the extinction rate of MTE lineages and non-MTE lineages were equal (Supporting Information 3). This model estimated a speciation and diversification rate for lineages occurring in MTEs that is 1.9 times higher than that of non-MTE lineages. The speciation rate for MTE-lineages was estimated to be 2.5 times higher than that of species occurring in MTEs as well as outside of these systems. Relative extinction fractions (extinction rate/speciation rate) are 0.22 in MTEs and 0.42 in non-MTEs. Finally, dispersal rates from MTEs to non-MTEs are significantly higher than dispersal into MTEs. Dispersal into MTEs can therefore not explain the high species diversity in the relatively small areas covered by MTEs (Fig. S4).

### DIVERSIFICATION RATE DYNAMICS IN THE FIVE MTEs

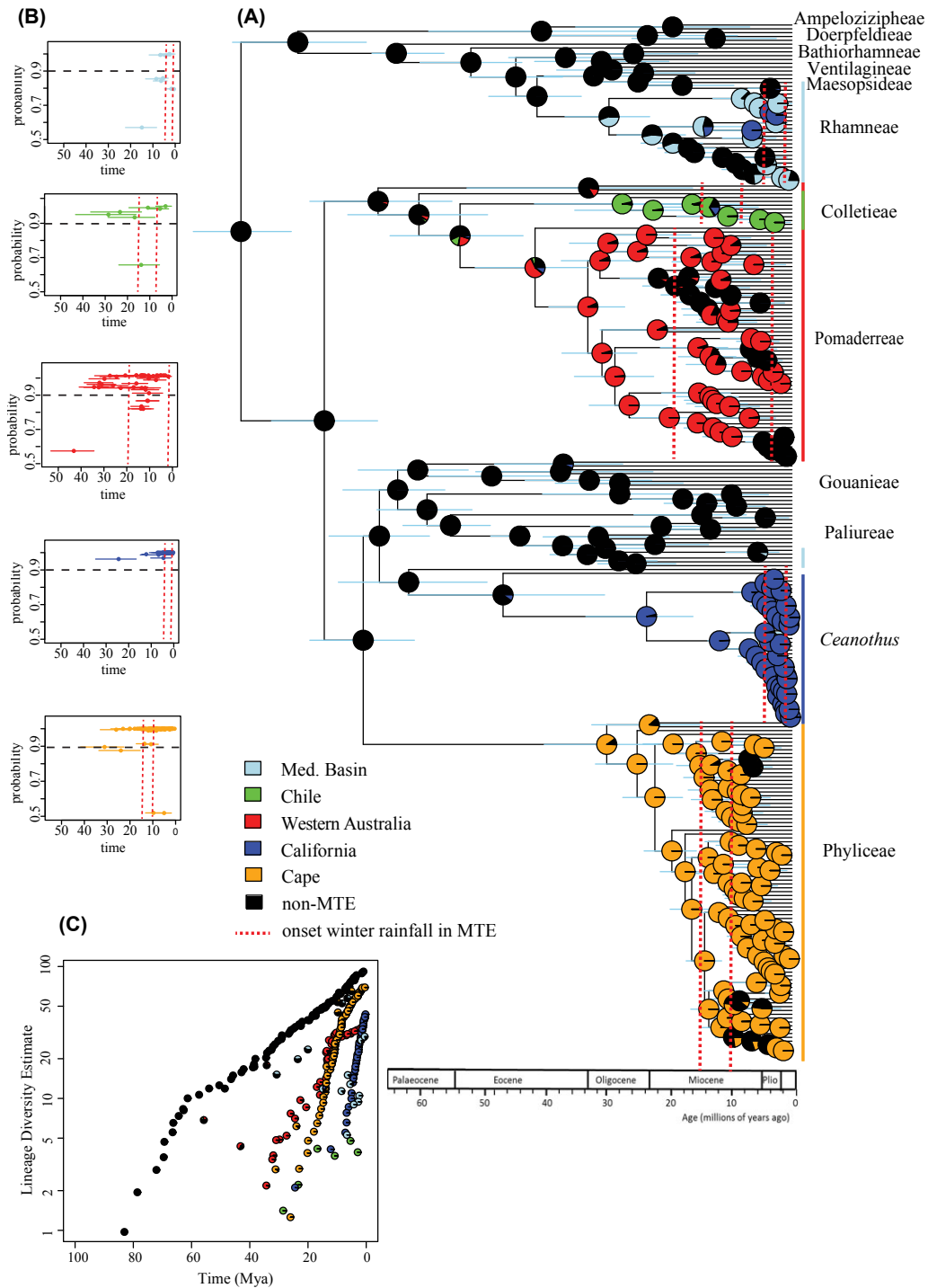
Diversification dynamics (speciation and extinction rates) differ between the five MTEs (Fig. 3D–O, Table 2), but dispersal rates showed a similar pattern for all five MTEs: dispersal from that

particular MTE to elsewhere was significantly higher than vice versa, consistent with the generally very low dispersal rate into MTEs (Fig. S5). The best-fit GeoSSE models for each region (Supporting Information 3) included all seven parameters (speciation, extinction, and dispersal rates for that particular MTE, for regions elsewhere, and widespread lineages occurring in the MTE as well as elsewhere). The exception was the Chilean model, where speciation and extinction rates for the MTE and non-Chilean areas were similar, and consequently net diversification rates did not differ significantly between Chilean and non-Chilean lineages.

For California, the optimal model specifies a speciation rate for lineages occurring in MTEs that is 3.6 times higher than that of non-Californian lineages and five times higher than that of species occurring in California as well as outside (Fig. 3D–F). Remarkably, extinction rates are also much higher (5.4 times) in California than outside, resulting in relative extinction fractions of 0.95 in California compared to 0.64 outside. Net diversification rates in California are therefore not significantly different from those outside the region, but these results suggest high turnover of species in California. For the Mediterranean Basin (Fig. 3G–I), estimated speciation, extinction, and consequently net diversification rates were not different from non-Mediterranean Basin areas. However, due to the small number of lineages present in this MTE, and thus relatively low power of the dataset, these results may not reflect true diversification rates in this region. The Cape and Western Australia gave very similar results (Fig. 3J–O). Speciation rates of lineages restricted to the MTEs were 1.5 times (Cape) and 2.5 times (Western Australia) lower than speciation rates of lineages occurring elsewhere, but were 9.2 times (Cape) and 5.3 times (Western Australia) higher than widespread lineages occurring in the MTEs as well as outside these regions. Extinction rates of lineages restricted to the MTEs were 40 times (Cape) and 42 times (Western Australia) lower than those of lineages occurring elsewhere, resulting in net diversification rates that were 2.5 times (Cape) and 1.9 times (Western Australia) higher within than outside these MTEs. However, the Western Australian signal disappeared when using a set of trees, and this result should therefore be taken with caution (Fig. S5).

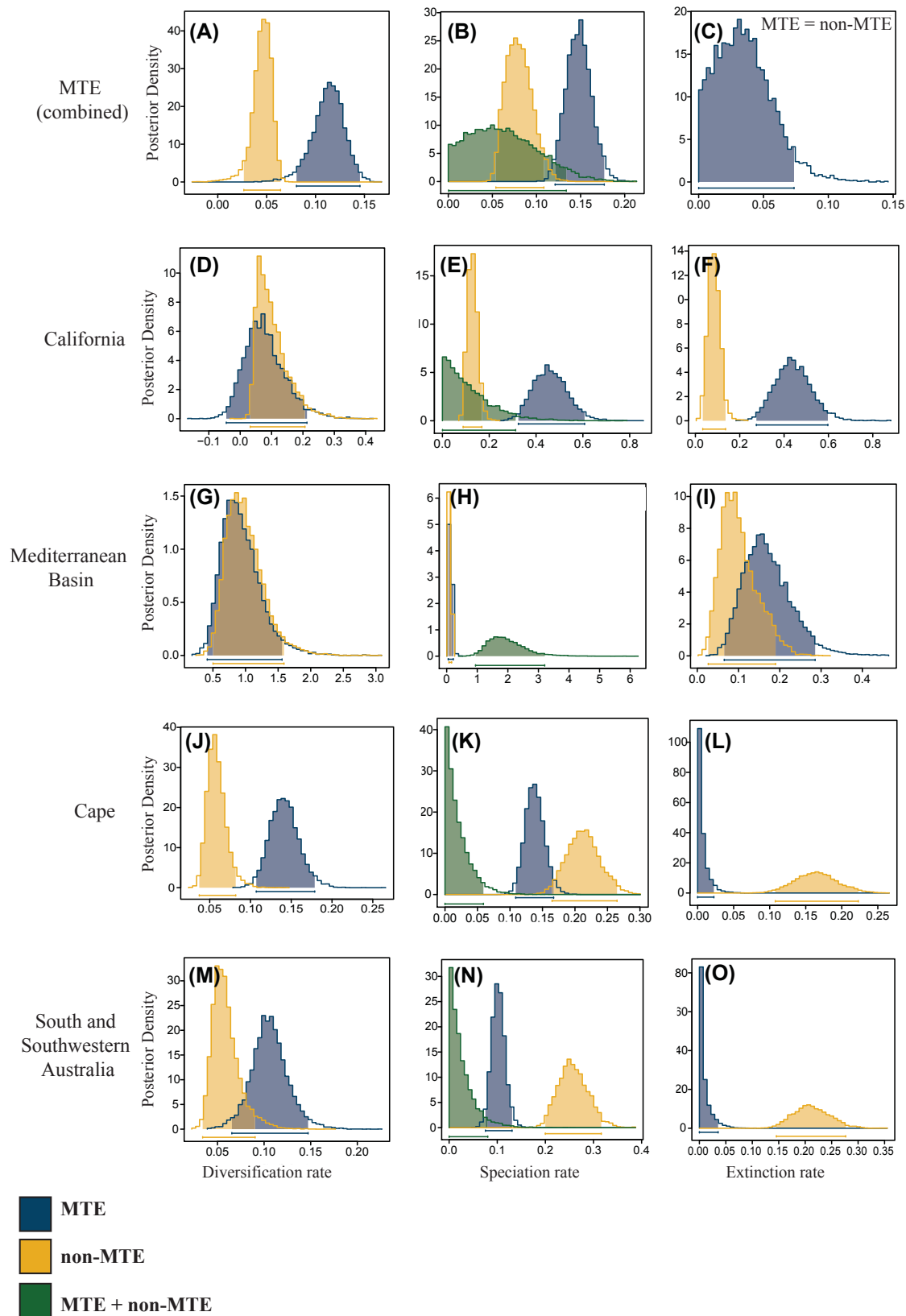
### SIMULATIONS

Our first simulation study indicated that our dataset had enough power to reject the false null hypothesis of equal diversification rates between the MTE versus non-MTE states and in the second simulation study we were correctly unable to reject the true null hypothesis of equal diversification rates (Fig. S6). This shows that speciation and extinction rates of the character states can be well predicted when all five MTEs are combined into one state, even after pruning 70% of the lineages from the tree.



**Figure 2.** (A) Maximum likelihood ancestral area reconstruction under an equal transition rate model (states: California/Chile/Cape/Mediterranean Basin/Western Australia/ non-MTE) on the Rhamnaceae MCC tree resulting from the BEAST analysis. Blue bars indicate 95% HPDs of estimated node ages. (B) Probability > 0.9 of colonization of each MTE based on the maximum likelihood ancestral area reconstructions in (A) for each node over time. (C) Comparison of historical lineage diversity estimates over time for each node in the Rhamnaceae MCC tree for each MTE. Fifty-five percent of the extant species occurring in MTEs was sampled, so recent diversity estimates in MTEs (as well as outside MTEs) is underestimated. The colonization of Western Australia, Chile, the Cape, and California happened more or less in synchrony (35–20 Mya), but colonization of the Mediterranean Basin happened much later (~8 Mya). Accumulation of lineages was gradual in the Cape and Western Australia, with a slowdown in Western Australia from 10 Mya onwards. Increase in lineage diversity in California happened around 6–8 Mya.





**Figure 3.** Posterior densities (A–O) resulting from the Bayesian MCMC using the GeoSSE model on the Rhamnaceae MCC tree. Net diversification, speciation, and extinction rates for lineages that occur in the Mediterranean-type ecosystems (MTEs) of the world (blue) and outside (yellow), or widespread lineages occurring both in the MTE as well as outside (green) are shown. If only one probability density in a plot is shown, it means that the model selected indicated equal rates between MTE/non-MTE for this parameter.

**Table 2.** Median (95% HPD) estimates of speciation, extinction, and dispersal rates resulting from the MCMC analyses of the Geosse algorithm on the MCC trees of the full dataset, for the analyses combining all MTEs and for each MTE separately.

Analysis	Selected model	s		s MTE + Non-MTE		x		r		d		d Non-MTE to MTE
		s MTE	Non-MTE	s MTE	Non-MTE	x MTE	Non-MTE	MTE	Non-MTE	d MTE to Non-MTE	Non-MTE	
All	Different speciation rates	0.1478	0.0791	0.0595	0.033	0.033	0.033	0.1437	0.0761	0.3741	0.004	
		(0.1217–0.1772)	(0.0544–0.1084)	(0.0003–0.134)	10 <sup>-6</sup> –0.0732	10 <sup>-6</sup> –0.0732	0.201	(0.2692–0.5117)	(0.0325–0.1249)	(0.2692–0.5117)	(0.002–0.0065)	
California	Different speciation and extinction rates	0.4558	0.1268	0.0911	0.0807	0.4345	0.0807	0.0735	0.0923	0.9975	0.0041	
		(0.3242–0.6088)	(0.0893–0.1676)	(0–0.3154)	(0.0321–0.1314)	(0.2825–0.604)	0.2128	(0.5428–1.6105)	(–0.0543–0.2128)	(0.0309–0.2068)	(0.0017–0.0075)	
Chile	Same speciation and extinction rates	0.2492	0.2492	-	0.1982	0.1982	0.1982	0.0515	0.0515	0.0754	0.0003	
		(0.1939–0.309)	(0.1939–0.309)		(0.1308–0.2675)	(0.1308–0.2675)	(0.0345–0.0701)	(0.0345–0.0701)	(0.0085–0.3038)	(0.0085–0.3038)	10 <sup>-8</sup> –0.0011	
Mediterranean Basin	Different speciation and extinction rates	0.1182	0.1148	1.877	0.0944	0.1642	0.0944	0.8905	0.9546	2.5763	0.0036	
		(0.0483–0.2141)	(0.0756–0.1607)	(0.9345–3.1891)	(0.0265–0.1898)	(0.0684–0.2895)	(0.4108–1.551)	(1.2991–4.8652)	(0.4999–1.5809)	(1.2991–4.8652)	(0.0014–0.0067)	
Cape	Different speciation and extinction rates	0.1375	0.2131	0.0149	0.1651	0.0041	0.1651	0.1409	0.0571	0.4301	0.0002	
		(0.1092–0.1675)	(0.1657–0.2647)	(2.12 × 10 <sup>-7</sup> –0.059)	(0.1099–0.2241)	10 <sup>-7</sup> –0.0221	(0.11071–0.1786)	(0.252–0.6879)	(0.0375–0.0819)	(0.252–0.6879)	10 <sup>-5</sup> –0.0004	
Western Australia	Different speciation and extinction rates	0.1018	0.2571	0.0191	0.2118	0.005	0.2118	0.1052	0.0564	0.2376	0.0003	
		(0.0754–0.1309)	(0.1989–0.3162)	(3.38 × 10 <sup>-6</sup> –0.0803)	(0.1439–0.2764)	10 <sup>-7</sup> –0.0358	(0.0621–0.1438)	(0.1262–0.398)	(0.0341–0.0908)	(0.1262–0.398)	10 <sup>-7</sup> –0.0007	

“s” refers to speciation rate, “x” to extinction rate, “r” to net diversification rate, and “d” to dispersal rate. Net diversification rates for MTE lineages were calculated as follows: s MTE + ½ x s both – x MTE, and for non-MTE lineages: s non-MTE + ½ x s both – x non-MTE, where “both” refers to lineages with state “MTE + non-MTE.”

**Table 3.** Timing of colonization of the area currently covered by MTEs by Rhamnaceae lineages based on the ancestral state reconstructions (ASR) for the respective nodes, and the timing of onset of winter rainfall and the corresponding references for this.

MTE	Timing of colonization in Mya (95% HPD) when probability ASR > 0.5		Timing of colonization in Mya (95% HPD) when probability ASR > 0.9		Timing of onset of winter rainfall regime in Mya	Reference
	p.p.		p.p.			
Mediterranean Basin	15.0 (8.3–22.3)	0.97	8.5 (4.6–13.3)	1	2–5	Suc (1984); Suc and Popescu (2005)
California	24.4 (16.6–34.7)	1	24.4 (16.6–34.7)	1	2–5	Axelrod (1973)
Chile	28.5 (16.2–43.3)	1	28.5 (16.2–43.3)	1	8–15	Armesto et al. (2007)
Cape	31.1 (22.7–41.7)	1	31.1 (22.7–41.7)	1	10–15	Cowling et al. (2009); Dupont et al. (2011)
Western Australia	43.2 (34.3–53.3)	0.99	34.3 (28.1–40.9)	1	3–20	Hopper and Gioia (2004); Martin (2006)

The median (95% HPD) estimates of the node age and the posterior probability (p.p.) of the node are indicated.

## TIME

Ancestral state reconstructions using the GeoSSE parameters agreed with the ML ancestral state reconstructions using an equal rate between states model (Figs. 2A, B, S7). As the reconstructions based on the equal rate model distinguished between the five MTEs (the GeoSSE parameters were only estimated for MTE vs. non-MTE), we will present the results from this method. The dispersal to the areas currently covered by MTEs (Fig. 1) happened more or less in synchrony in Western Australia, Chile, the Cape, and California, but could have happened any time between the Middle Eocene and Middle Miocene based on 95% HPD values of nodes reconstructed as MTE with a probability >0.9 (Fig. 2A, B, Table 3). Colonization of the Mediterranean Basin happened later, in the Late Miocene. Accumulation of lineages in MTEs in the Cape and Western Australia was steady initially, but a slowdown in Western Australia from 10 Mya onwards was detected. The main increase in lineage diversity in California happened much later, around 6–8 Mya in the Late Miocene–Pliocene. No clear pattern of increase in lineage diversity over time was detected in Chile or the Mediterranean Basin (Fig. 2C).

## Discussion

We demonstrate here that the extraordinary species richness of MTEs (California, the Cape, Western Australia, central Chile, and the Mediterranean Basin) may be, in Rhamnaceae, partly explained by higher diversification rates compared to elsewhere. However, this apparently global signal is mainly driven by high diversification rates in the Cape and possibly Western Australia (Table 2, Fig. 3). Time for speciation and dispersal direction unlikely affected Rhamnaceae species richness in MTEs, as MTE lineages generally derived from non-MTE ancestors (Fig. 2A), and dispersal rates into MTEs were significantly lower than

dispersal rates out of MTEs (Fig. S4). However, different evolutionary histories underlie diversification of Rhamnaceae lineages in the five MTEs of the world, as speciation and extinction rate dynamics of MTE-lineages differ between the MTEs (Fig. 3). No significant increase or decrease in speciation or extinction rates could be detected in the Mediterranean Basin and central Chile compared to the outside regions. Lineages occurring in California show higher speciation and extinction rates, suggesting high turnover of species (“ephemeral” species, Rosenblum et al. 2012), compared to lineages occurring outside California, but no difference in net diversification rates was detected between Californian and non-Californian Rhamnaceae. Western Australia and the Cape show a very similar pattern of lower speciation rates, but extremely low extinction rates, resulting in higher net diversification rates, compared to lineages occurring elsewhere, but this pattern is not retrieved for Australia when topological uncertainty and branch length variation is taken into account. Time to accumulate species in these systems seems not to have affected the species richness differences between the Cape, Western Australia, Chile, and California, as the colonization of these MTEs (or their ancient equivalent) happened approximately at the same time (Table 3, Fig. 2B). However, colonization of the Mediterranean Basin happened later, and time for speciation may therefore additionally explain the relatively low Rhamnaceae diversity in this MTE.

## FRAMEWORK FOR FUTURE STUDIES

We presented a methodological framework to assess the impact of limited and biased taxon sampling on estimates of diversification rates in biodiversity hotspots when using molecular phylogenies. Specifically, (1) the use of geo-referenced data to assess taxon distributions, cross-checked with observation from local floras, allows for the objective assignment of taxa to geographical areas. Furthermore, (2) if all taxa in the clade are sampled for a certain

area (also those for which sequence data are unavailable), this allows for sampling proportions to be included in the model (FitzJohn et al. 2009) (Table 1), and for evaluation of sampling biases (Fig. S2). The effects of these on model outcome may be tested (i.e., the full and reduced datasets). And finally, (3) a simulation study could be used to test for type I and II errors on model outcome. We suggest that this framework may be generally useful in diversification rate assessments in species-rich areas where complete species sampling is problematic.

### AREA AS A DIVERSIFICATION DRIVER

Area has been suggested to be an important variable impacting diversification rates, and in explaining differences in species richness between regions (Kisel et al. 2011). The five MTEs differ in area (Fig. 1), and in the ratio between species number and area (Mediterranean Basin with 22,500 species in 2,085,292 km<sup>2</sup> = 0.01 species/km<sup>2</sup>; Western Australia with 5500 species in 356,717 km<sup>2</sup> = 0.015 species/km<sup>2</sup>; California with 8000 species in 293,804 km<sup>2</sup> = 0.027 species/km<sup>2</sup>; and the Cape with 9000 species in 78,555 km<sup>2</sup> = 0.196 species/km<sup>2</sup>) (Madriñán et al. 2013). Clearly, as the area available for non-MTE lineages is much larger than the area covered by MTEs, this seems not a factor explaining the high species richness of Rhamnaceae in MTEs compared to elsewhere. In addition, available area seems not to affect species richness differences between the five MTEs, where the Cape is exceptional in its high diversity in a relatively small area, compared to the other MTEs. Consequently, we find that area availability does not explain the differences in diversification rates or the standing diversity differences among the MTEs.

### DIVERGENCE TIME ESTIMATES

Here we estimated crown node ages of 84.1–100.6 Mya (95% HPD, hereafter consistently used for age intervals) for Rhamnaceae. These are substantially older than previous estimates based on molecular data. Bell et al. (2010) used lognormal and exponential prior distributions to estimate crown Rhamnaceae to be 46–73 Myr old, and Richardson et al. (2004) estimated it to be even younger: 43.6–49.5 Myr old. However, these estimates are in conflict with recently described Rhamnaceae fossils: fossil flowers from Mexico from the Late Campanian (~73 Mya) (Calvillo-Canadell and Cevallos-Ferriz 2007) and fossil fruits and leaves from Colombia from the Cretaceous-Maastrichtian (~68 Mya) onwards (Correa et al. 2010), which all show affinities with Rhamnaceae and Paliureae, tribes within the Rhamnaceae. This suggests that crown Rhamnaceae should at least be 73 Myr old, but probably even older. Furthermore, our Rhamnaceae crown age is in agreement with the Rose Creek fossil flower from the Cretaceous-Cenomanian, ~94 Mya, which shows affinities with Rhamnales as well as with Saxifragales (Basinger and Dilcher 1984; Crepet

et al. 2004), and was here used as a minimum age calibration on the root node of Rhamnaceae.

Of central interest in this article is the dating of the MTE lineages, and here we find agreement with previous studies. There are three recent estimates for the age of the crown Phylloceae, which radiated in the Cape: our study provides the oldest (22.7–41.7 Mya), but shows overlap with previous estimates (19.8–26.7 Mya, Richardson et al. 2004; 10.3–36.5 Mya, Onstein et al. 2014). A similar wide range is available for *Ceanothus* in California: our estimate is the oldest (16.6–34.7 Mya), but overlaps with that of Burge et al. 2011 (0.3–26.0 Mya).

Our use of uniform prior distributions, and setting the maximum age to the presumed age of the Rosales (Wang et al. 2009), may overestimate the node ages and so underestimate diversification rates of the more recently diversifying MTE clades. However, as we compare diversification rates across the Rhamnaceae, relative rather than absolute estimates of divergence times are most relevant. The only absolute estimates we use are the colonization times of the MTEs, in comparison to the hypothesized onset of winter rainfall (Table 3). However, uniform priors, as opposed to exponential or lognormal priors, are known to result in the widest 95% HPDs, and are therefore most conservative (Sauquet et al. 2012). It may be better to consider the whole range of possible posterior outcomes, that is, the 95% HPD, than using the absolute median estimates.

### DIVERSIFICATION UNDER A WINTER RAINFALL CLIMATE

The timing of the onset of winter rainfall was different in the several MTEs, and may have affected the time to accumulate lineages in the systems (time for speciation). However, our reconstructions indicate that Rhamnaceae lineages colonized the MTEs before the probable onset of winter rainfall, even when considering the lower bound of the 95% HPD of the node age of the node on which the presence in the MTE was reconstructed with a probability of >0.9 (Fig. 2B, Table 3). There is a consensus among Richardson et al. (2004), Onstein et al. (2014), and Burge et al. (2011) that diversification of Phylloceae and *Ceanothus* started prior to the onset of winter rainfall in the Cape and California, respectively, but possibly during periods of progressive aridification in the regions. The dating of crown groups in the Cape flora prior to the onset of winter rainfall has been found for several lineages (Verboom et al. 2009, and references therein), with only few radiations postdating the winter rainfall, most markedly that of Ruschioideae from the semiarid Namaqualand (Klak et al. 2004) and *Heliophila* (Mummenhoff et al. 2005) also in part from Namaqualand. The ancestral state reconstructions (Fig. 2A) therefore unlikely reflect the climatic adaptation to winter rainfall, but rather the colonization of the respective areas.



Nevertheless, it is possible that the generation of the modern diversity was driven by the onset of winter rainfall, as was demonstrated, for example, in the Mediterranean Basin for *Dianthus* (Valente et al. 2010a) and *Tragopogon* (Bell et al. 2012) among other clades (Fiz-Palacios and Valcárcel 2013), in California for *Linanthus* (Polemoniaceae) (Bell and Patterson 2000), and in Australia and the Cape for Haemodoraceae (Hopper et al. 2009). However, the accumulation of Rhamnaceae lineages in the MTEs is constant (linear increase of lineage diversity on a logarithmic scale) and thus seems unaffected by the onset of winter rainfall (Fig. 2C). Similarly, the hypothesized drying of California in the Pliocene did not seem to affect rates of diversification in most of the 16 Californian angiosperm clades (Lancaster and Kay 2013). However, few lineages have to date been tested for a diversification rate change in response to the establishment of winter rainfall (but see Verdú and Pausas 2013).

The slowdown in diversification during the Plio-Pleistocene in Western Australia is puzzling (Fig. 2C), but a similar slowdown was detected in the Australian danthonioids (Linder et al. 2014), which the authors explained by Pleistocene extinctions due to difficulties to move to suitable habitats during periods of climate change, in the topographically subdued Australian landscapes. Alternatively, this pattern may suggest an upper bound to diversity in Western Australia due to diversity-dependent regulatory mechanisms (Etienne et al. 2011), but this is speculative as clades were undersampled.

### DIVERSIFICATION IN THE CAPE AND WESTERN AUSTRALIA

We show that the high diversification rate of Rhamnaceae in both the Cape and Western Australia is the result of a very low extinction rate (Fig. 3J–O), which has been suggested for the Cape flora (Cowling and Holmes 1992; Cowling and Lombard 2002; Goldblatt and Manning 2002; Cowling et al. 2004) and for the Western Australian flora (Sniderman et al. 2013; Cowling et al. 2014). The low extinction rate in these OCBILS is proposed to be the result of long-term stable conditions in orogeny and physiography (but see Cowling et al. 2009). The hypothesized long-term climatic stability and gradual aridification in these MTEs, even during the Pleistocene (Meadows and Sugden 1993), could have facilitated diversity (Dynesius and Jansson 2000; Jansson and Dynesius 2002). Cowling et al. (2014) quantified climatic and topographic stability in the five MTEs during the Cenozoic, and showed that the more environmentally stable MTEs (Cape and Australia) have the highest contemporary plant diversity, whereas the least stable (California and Chile) have the lowest diversity. Long-term stability may have led to the evolution of large numbers of highly range restricted species, with low extinction and low turnover rates. These differences in orogeny

and physiography between the Cape/Western Australia and the other three MTEs (Chile, California, Mediterranean Basin) are corroborated by our results, indicating continent-dependent speciation and extinction dynamics.

### EXTANT DIVERSITY IN MTEs

Whether this pattern of speciation and extinction applies to other clades, and may therefore be a general feature of MTEs, remains to be seen. However, there does not seem to be a consensus based on previous studies (see Introduction). The Cape flora is thought to have resulted from both recent (Plio-Pleistocene) and mature radiations, potentially characterized by high speciation rates and low extinction rates, respectively, whereas the Western Australian flora is mainly characterized by mature radiations (Linder 2008; Verboom et al. 2009), which seems to apply to the Pomaderreae (Fig. 3M–O). The high speciation and extinction rates detected for *Ceanothus* in California (Fig. 3E, F) are different from the general low extinction rates found in Californian clades (Lancaster and Kay 2013), however, these are comparable to high turnover rates in Californian lineages nonendemic to serpentine soils, compared to their serpentine endemic sister clades (Anacker et al. 2011). Furthermore, *Ceanothus* lineages in chaparral vegetation were shown to have higher speciation rates than their Mediterranean forest members (Goldberg et al. 2011), similarly as fynbos *Phyllica* to their Cape forest sister *Noltea* (Onstein et al. 2014). This suggests that lineage-specific speciation and extinction rates may be dependent on local factors other than (environmental) stability, variable within MTEs (Goldberg et al. 2011; Onstein et al. 2014).

### Conclusions

Here, we show that the extraordinary Rhamnaceae diversity in MTEs has resulted from high net diversification rates rather than from time for speciation or from high immigration rates into this biome. However, we show, in contrast to previous ideas (Cox 2001), that the processes leading to this diversity are continent dependent. The variation in speciation and extinction rates may be the result of intercontinental differences in the orogeny, physiography, and climatic fluctuations, and so predated the onset of the common winter rainfall climate in these regions.

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## DATA ARCHIVING

Our data are archived in GenBank (GenBank accession numbers are provided in Table S2) and in Table S1, in which species numbers per genus and species traits (climate zones) and references for these can be found.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Supporting Information 1.** Procedures for DNA isolation, amplification and primers.

**Supporting Information 2.** Fossil selection and BEAST settings.

**Supporting Information 3.** Model testing GeosSE.

**Supporting Information 4.** Rhamnaceae phylogenetic reconstruction.

**Figure S1.** Rhamnaceae median node ages and the minimum and maximum bound of the 95% highest posterior density of the estimated age of the combined dataset (ITS + chloroplast) against the chloroplast only dataset.

**Figure S2.** Sampling proportions of Rhamnaceae tribes and MTEs in the full dataset (phylogeny with 280 species) and the reduced dataset (phylogeny with 214 species) compared to the total (1055 species).

**Figure S3.** Rhamnaceae MCC tree resulting from the BEAST analysis including all taxa; posterior probabilities (p.p.) are shown on the nodes.

**Figure S4.** Posterior distributions of the GeoSSE analysis estimating speciation and extinction rates for Rhamnaceae MTE-lineages (all MTEs combined) against non-MTE lineages over 100 trees, and for the reduced datasets (I, extinction rate constrained; II, speciation rate constrained).

**Figure S5.** Posterior distributions of the GeoSSE analysis estimating net diversification, speciation, extinction, and dispersal rates for MTEs of California, the Mediterranean Basin, the Cape, Western Australia, and Chile against the remaining Rhamnaceae over 100 trees, and for the reduced datasets (following model selection, see Supporting Information 3).

**Figure S6.** Posterior distributions of the net diversification rate resulting from 100 simulated trees with known speciation and extinction rates (unequal between states in A (left), equal in B (right)), after pruning the tree with states proportionally to obtain our observed proportion of MTE and non-MTE lineages.

**Figure S7.** GeoSSE ancestral area reconstruction (states: MTE/non-MTE/both) on the Rhamnaceae MCC tree resulting from the BEAST analysis.

**Table S1.** Rhamnaceae species numbers, habitats and climate zones.

**Table S1.** References.

**Table S2.** GenBank accession numbers.

**Table S3.** Comparison of median node ages for Rhamnaceae clades under different scenarios of missing data in the alignment, resulting from BEAST (all same settings, see main text).