ORIGINAL ARTICLE

Variation in plant diversity in mediterranean-climate ecosystems: the role of climatic and topographical stability

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ABSTRACT

Aim Although all five of the major mediterranean-climate ecosystems (MCEs) of the world are recognized as loci of high plant species diversity and endemism, they show considerable variation in regional-scale richness. Here, we assess the role of stable Pleistocene climate and Cenozoic topography in explaining variation in regional richness of the globe's MCEs. We hypothesize that older, more climatically stable MCEs would support more species, because they have had more time for species to accumulate than MCEs that were historically subject to greater topographic upheavals and fluctuating climates.

Location South-western Africa (Cape), south-western Australia, California, central Chile and the eastern (Greece) and western (Spain) Mediterranean Basin.

Methods We estimated plant diversity for each MCE as the intercepts of species–area curves that are homogeneous in slope across all regions. We used two down-scaled global circulation models of the Last Glacial Maximum (LGM) to quantify climate stability by comparing the change in the location of MCEs between the LGM and present. We quantified the Cenozoic topographic stability of each MCE by comparing contemporary topographic profiles with those present in the late Oligocene and the early Pliocene.

Results The most diverse MCEs – Cape and Australia – had the highest Cenozoic environmental stability, and the least diverse – Chile and California – had the lowest stability.

Main conclusions Variation in plant diversity in MCEs is likely to be a consequence not of differences in diversification rates, but rather the persistence of numerous pre-Pliocene clades in the more stable MCEs. The extraordinary plant diversity of the Cape is a consequence of the combined effects of both mature and recent radiations, the latter associated with increased habitat heterogeneity produced by mild tectonic uplift in the Neogene.

Keywords
California, Cape Floristic Region, central Chile, diversification rate, mature radiation, Mediterranean Basin, OCBIL, recent radiation, south-western Australia, YODFEL.

INTRODUCTION

The world's five mediterranean-climate ecosystems (MCEs) have attracted interest as loci for studying ecosystem and

evolutionary convergence for almost 150 years (Grisebach, 1872; Cody & Mooney, 1978; Specht & Moll, 1983; Keeley *et al.*, 2012; Cardillo & Pratt, 2013). More recently, MCEs have been the focus of numerous molecular-level studies on

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the diversification of plants (e.g. Hopper *et al.*, 2009; Verboom *et al.*, 2009; Espíndola *et al.*, 2010; Valente *et al.*, 2011; Buerki *et al.*, 2012; Lancaster & Kay, 2013). Interest in plant evolution in MCEs stems from their harbouring the world's richest extratropical floras (Cowling *et al.*, 1996; Kreft & Jetz, 2007) and having high levels of endemism across all spatial scales (Cowling & Holmes, 1992; Hopper & Gioia, 2004; Georghiou & Delipetrou, 2010; Kraft *et al.*, 2010). All five MCEs have been identified as biodiversity hotspots: areas which share large numbers of endemic taxa that are being increasingly threatened by human impacts (Myers *et al.*, 2000).

Although MCEs exhibit some of the best-documented examples of ecological convergence (Mooney, 1977; Cowling & Witkowski, 1994), there are equally striking examples of divergence (Cody & Mooney, 1978; Cowling & Campbell, 1980). Researchers have resorted to categorizing MCEs in terms of their selective regimes in order to better explain convergences and divergences among them. Thus, MCEs have been differentiated in terms of climate (e.g. amount of summer rain, reliability of winter rainfall) (Cowling *et al.*, 2005), soil nutrient status (Specht & Moll, 1983), fire regime (Keeley *et al.*, 2012), topography (Carmel & Flather, 2004) and the interactions between climate, fire and soil nutrient status (Keeley *et al.*, 2012).

Contemporary ecological factors do not explain all the variation in regional-scale plant diversity of MCEs (Cowling *et al.*, 1996; Valente & Vargas, 2013). Energy regimes, as measured by potential evapotranspiration, are highest in the South West Australian Floristic Region and the California Floristic Province (Bradshaw & Cowling, 2014), which show contrasting diversity patterns. Moreover, topographical heterogeneity – a surrogate for habitat diversity – is highest in the (relatively species-poor) eastern Mediterranean Basin and central Chile and lowest in the (relatively species-rich) South West Australian Floristic Region, whereas the Cape Floristic Region, which is the most species-rich area by far, has moderate heterogeneity (Bradshaw & Cowling, 2014). It appears that variation in contemporary plant diversity patterns in MCEs is profoundly influenced by their respective environmental histories and their impacts on patterns of diversification (speciation minus extinction) (Cowling *et al.*, 1996, 2009; Jansson & Dynesius, 2002; Linder, 2008; Hopper, 2009; Valente *et al.*, 2011; Valente & Vargas, 2013).

In this regard, Hopper's (2009) categorization of MCEs in terms of environmental stability is informative: he differentiated those associated with old, climatically buffered, infertile landscapes (OCBILs), namely the South West Australian Floristic Region (hereafter Australia) and the Cape Floristic Region of south-western South Africa (hereafter, 'the Cape'), and those dominated by young, often-disturbed, fertile landscapes (YODFELs), namely the Mediterranean Basin, the California Floristic Province (hereafter, 'California') and central Chile (hereafter, 'Chile'). Hopper (2009) predicted higher plant richness and endemism in OCBIL than in YODFEL MCEs, owing to higher rates of lineage persistence in OCBILs. In other words, old, stable landscapes have had

more time for species to accumulate than landscapes that have been subject to greater topographic upheavals and fluctuating climates. Hopper (2009) did not define his categories quantitatively, however, which we hope to redress here.

There are many examples in the literature of climatic and topographic stability influencing processes that determine the number of species supported by particular regions (e.g. Qian & Ricklefs, 2000; Graham *et al.*, 2006; Araújo *et al.*, 2007; Mittelbach *et al.*, 2007). No attempt has yet been made to comprehensively assess the role of measures of historical climatic and topographical heterogeneity in explaining regional patterns of plant diversity in MCEs. We attempt to do this here, by quantifying the climatic and topographic stability of MCEs during the Pleistocene (climate) and the Neogene (topography) in order to assess the OCBIL–YODFEL categorization of MCEs. We then test whether OCBIL MCEs have more diverse floras than YODFEL ones, as Hopper (2009) predicted.

MATERIALS AND METHODS

Study area

We examined the five MCE biodiversity hotspots, namely California, the Cape, Chile, Australia and the Mediterranean Basin. Because the Mediterranean Basin MCE occupies a huge area (2.3 million km^2) and includes a wide array of subclimates (Blondel *et al.*, 2010), we chose two subregions for further analysis, one in the western basin (Spain) and one in the eastern basin (Greece). These regions differ substantially in climate and biogeography. The western basin, west of the Sicily–Cap Bon line, has less intense summer aridity than the eastern basin and a higher ratio of autumn and spring rainfall to winter rainfall (Blondel *et al.*, 2010). Furthermore, climate-driven isolation and vicariant differentiation of many Mediterranean taxa seems to have occurred in the western and eastern ends of the Mediterranean Basin during the Messinian Salinity Crisis (Migliore *et al.*, 2012) and, particularly, the Pleistocene glaciations (Rodríguez-Sánchez & Arroyo, 2008). This, together with the west–east climatic differences, translates into different biogeographical regions (Blondel *et al.*, 2010). Thus, we identified a total of six MCE regions for analysis.

Delimitation of mediterranean-climate ecosystems

There is no consensus regarding a global classification of MCEs, although the general definition of cool, wet winters and warm, dry summers applies to all. To avoid using an MCE delimitation that may bias our results, we used three models of MCE classification. The first is the long-standing, expert-opinion classification proposed by Köppen (Geiger, 1961), and the remainder use algorithms widely applied in the field of distribution modelling (Franklin, 2010): maximum entropy (Maxent; Phillips *et al.*, 2006) and generalized additive models (GAM; Hastie & Tibshirani, 1990). Both expert opinion and statistical models were used to establish

the distribution of, and then changes in distribution of, mediterranean climate under current and past climate states.

The Köppen climate classification system defines MCE areas (Csa and Csb classes) as warm temperate, with minimum monthly temperatures between −3 °C and 18 °C, and with at least four months above 10 °C. Köppen (Geiger, 1961) applied three criteria to ensure that winter precipitation predominates: (1) that the minimum summer monthly rainfall is less than the minimum winter monthly rainfall; (2) that maximum winter monthly rainfall is three times the minimum summer monthly rainfall; and (3) that the minimum summer monthly rainfall is less than 40 mm. To differentiate between mediterranean and more arid winter-rainfall regions, Köppen (Geiger, 1961) applied an aridity index, so that annual precipitation (mm) exceeds 20 times mean annual temperature (°C) (where two-thirds of precipitation occurs in winter).

The two statistical models were trained using the distribution of mediterranean-type vegetation and five bioclimatic variables (annual mean temperature, maximum temperature of the warmest month, annual temperature range, precipitation of the warmest quarter and precipitation of the wettest quarter; Hijmans *et al.*, 2005). These climate variables capture aspects of temperature, precipitation, seasonality and continentality. There are, however, two potential problems. First, there is no standardized global floristic or vegetation map of mediterranean-type vegetation. Second, mediterranean climate and mediterranean-type vegetation are not always strongly associated (Keeley *et al.*, 2012); the fynbos of the Cape Floristic Region, for example, extends far into a non-seasonal rainfall regime. We identified the distribution of mediterranean-type vegetation from available floristic or vegetation maps, and where these maps were misleading (e.g. the eastern Cape Floristic Region) (Keeley *et al.*, 2012), we employed expert opinion to refine the area further (see Appendix S1 in Supporting Information for further details). We selected 500 localities at random from within each regional vegetation map. We used these in conjunction with 10,000 background points sampled across the Earth's terrestrial surface to train and test the distribution models. To avoid any bias that may have been introduced by the non-standardized vegetation maps and any expert-opinion alteration thereof, we trained the statistical models for any given MCE region using all localities except those from the region in question. This also avoids any potential circularity of including mapped vegetation for a given MCE region that may, in part, have included climate as a delimiter. These excluded locality points were then used to test the model (i.e. *k*-folding with each fold representing an MCE) and to calculate the threshold to convert the continuous probability of occurrence maps into binary presence/absence. The conversion to the binary maps utilized the 'equal sensitivity plus specificity' threshold criterion, although the relative ranking of the results were robust to the threshold criterion selected (e.g. maximum kappa or maximum sensitivity plus specificity; results not shown).

We constructed the expert-opinion climate model and statistical models in R 3.0.1 (R Core Team, 2013) and using climate layers from the WorldClim database (Hijmans *et al.*, 2005). The distribution models were constructed in R using Maxent 3.3.3e called from the DISMO library 0.9-3 (Hijmans *et al.*, 2013), while GAMs were conducted using the MGCV library 1.7-29 (Wood, 2014).

Plant diversity

We compiled regional richness data (native species only) for MCEs from Cowling *et al.* (1996, 1997). Additional sources were: Australia, NatureMap (http://naturemap.dec.wa.gov.au/default.aspx); Cape, Cowling & Lombard (2002); and Spain, Ojeda *et al.* (2000). Because there are no suitable data from mainland Greece, we had to use data from the larger islands of the Aegean Sea (see Appendix S2 for data sources). With the exception of Thira (Santorini), which is an active volcanic caldera, and Kos, the south-western part of which is characterized by contemporary volcanic activity, the islands are all continental islands. We would nonetheless expect that their species–area relationship would have a steeper curve and lower intercept than mainland samples (Rosenzweig, 1995). All sites were located within the strictly MCE area of each region. We fitted the species–area data for each of the six regions to a double-logarithmic regression model and tested for homogeneity of slopes (z) and intercepts (c), following Rosenzweig (1995).

We assessed the relationships between an index of diversity (quantified as the intercept of the respective species–area model) and measures of climatic and topographic stability described below.

Climate stability

We assessed the climate stability of MCEs as the difference in climate between the Last Glacial Maximum (LGM) and the present day, representing one of the largest fluctuations in climate conditions experienced during the Quaternary. We used two down-scaled global circulation models (GCMs) of LGM climate: the Community Climate System Model (CCSM; Collins *et al.*, 2004) and the Model for Interdisciplinary Research on Climate (MIROC; Hasumi & Emori, 2004). These LGM climate estimates have been statistically down-scaled using the WorldClim data set (Hijmans *et al.*, 2005) and GCM data from the Paleoclimate Modelling Intercomparison Project II (PMIP2) and are available at http://www.worldclim.org/. We performed analyses using both GCMs for each of the MCE delimitations. We calculated climate stability by comparing the change in the location of MCE between the LGM and the present, i.e. the percentage of the current MCE area that also existed under LGM conditions.

Topographic stability

Within each MCE, we located *c.* 350-km transects that are representative of each region's topography. Using published

sources (Table 1), we manually reconstructed topographic profiles for each region during the late Oligocene (*c.* 20 Ma) and the early Pliocene (*c.* 5 Ma) (Fig. 1). We chose the late Oligocene as a starting point because it preceded a period of prolonged relative aridity which, in conjunction with fire, would have promoted the expansion of sclerophyllous vegetation allied to that in present-day MCEs (Cowling *et al.*, 2009; Keeley *et al.*, 2012). The Oligocene also witnessed radiation of many MCE lineages, especially in Australia and the Cape (Linder, 2005; Hopper *et al.*, 2009). In order to quantify the topographic stability for the two geological periods (late Oligocene to late Miocene and early Pliocene to present), we developed a stability index based on the information on topographical change generated from the geological descriptions (Table 1, Fig. 1). This stability index captures the elevational change relative to the horizontal axis of the MCE region. It was calculate as $1 - \frac{\Delta Elev}{Dist}$, where $\Delta Elev$ is the change in elevation over the horizontal distance. A value of 1 indicates complete stability, whereas a value of 0 or less indicates equal or greater vertical movement than the horizontal distance.

RESULTS

Diversity patterns

Although the intercepts (*c*) of the species–area regressions for the six MCEs (Fig. 2) were significantly different among the MCEs ($F = 34.967$, $\text{d.f.}_1 = 5$, $\text{d.f.}_2 = 67$, $P < 0.0001$), the slopes were homogeneous ($F = 0.484$, $\text{d.f.}_1 = 5$, $\text{d.f.}_2 = 72$, $P = 0.787$). It was thus acceptable to compute the *c*-ratio for any two curves (Gould, 1979). This value – the ratio of the values of the intercepts in arithmetical space – provides a measure of relative species densities (Rosenzweig, 1995). We computed *c*-ratios comparing the Cape, the region with the highest value, with each of the other MCEs. This showed that for similar-sized areas, the Cape was 1.23 times richer than Australia, 1.62 times richer than Spain, 1.91 times richer than California, 2.08 times richer than Greece and 2.63 times richer than Chile.

Climate stability

Estimates of the area of MCE predicted to have also been MCE at the LGM varied depending on the model (Köppen, Maxent and GAM) and global climate model (MIROC and CCSM) used, resulting in high intra- and inter-region variance of stability estimates (Fig. 3, Appendix S3). Some general patterns were nonetheless evident. The Cape and Australia had consistently high stability, with one exception for Australia (Appendix S3). Chile had the lowest climatic stability, followed by California. Spain and Greece had intermediate levels of stability.

Topographic stability

Chile, California and the Mediterranean Basin represent zones of tectonic plate convergence, whereas the Cape and

Australia are located away from plate boundaries (Table 1). Hence, the former three regions have experienced considerable, albeit varied topographic instability during the Neogene. Within the Mediterranean Basin, Cenozoic topographic stability has been almost twice as high in the east (Greece) as in the west (Spain), the west having experienced the least stable conditions of all the MCEs. In California and Chile, overall instability was driven largely by the very high values between the late Pliocene and the present. Palaeogene landscapes in the two regions were much more stable than Neogene ones. On the other hand, the Cape and Australia have remained largely unchanged during the Cenozoic (Fig. 1). Even so, the Cape experienced some Neogene uplift and this has exposed clay-rich substrata on the coastal forelands, areas that had previously been mantled with duricrusts and sandplains.

Relationships between diversity and stability

The highest plant diversities – quantified as the intercept (*c*-value) of the respective MCE – were generally recorded for the most climatically and topographically stable MCEs, namely Cape and Australia (Fig. 3). Spain, an MCE having the lowest topographic stability but relatively high climatic stability, showed intermediate diversity. California and Chile, the MCEs with the lowest stability, including very low measures of topographic stability since the late Pliocene, had the lowest diversity values. Greece was an anomaly, having lower diversity that expected on the basis of its stability.

DISCUSSION

Our results are consistent with research for many different biomes and taxa: regions of high environmental stability during the Cenozoic are associated with high species (and genetic) diversity (e.g. Graham *et al.*, 2006; Araújo *et al.*, 2007; Carnaval *et al.*, 2009; Werneck *et al.*, 2011, 2012). To our knowledge, no studies have attempted to quantify the degree of both climatic and topographic stability within all examples of a particular biome on Earth, and to link this to contemporary diversity of plant species. In this sense, our results are novel and interesting. However, we acknowledge the limitations of this study. First, our statistical inference is constrained by the few degrees of freedom associated with our study system, although the global scale of the system is in our favour. Second, there is an unavoidable mismatch between the temporal scales we used for climate and topographic stability. Unfortunately, it is not yet feasible to hindcast climates much beyond the mid-Pleistocene at the scale required for this study. Climatic instability during the Pleistocene was nonetheless more intense than any other time during the Cenozoic (Zachos *et al.*, 2001) and this is likely to have had a profound effect on plant extinctions (Jansson & Dynesius, 2002). Furthermore, it is not yet feasible to hindcast topographic dynamics to the point that accurate

Table 1 Major geomorphic processes affecting topographic dynamics since the late Cenozoic in six mediterranean-climate ecosystems (MCEs).

MCE	Late Oligocene to late Miocene	Early Pliocene to Pleistocene	References
California	Multiple orogenies, dating back to the middle Mesozoic and resulting from subduction associated with the Farallon and Pacific plates, lifted up the proto-Sierra Nevada, but to a much lesser extent than the contemporary mountains. The current area of the Coast Ranges remained beneath the Pacific Ocean. The Central Valley, which began as a trough associated with tectonic forces of subduction in the Mesozoic, formed a large marine embayment for most of the Cenozoic.	Although it was thought until recently that fault-block tilting during the past 10–5 Myr was largely responsible for the uplift of the high elevation of the modern Sierra Nevada, new data from analyses of tectonics suggest that the range achieved heights > 3000 m in the Palaeogene and remained high through subsequent millennia. The form, topography and elevation of the modern Sierra Nevada were, however, strongly influenced by extensional and faulting processes over the past 3 Myr, which added major uplift to the southern Sierra Nevada. This orogeny left a legacy of volcanic geomorphology in the northern portion of the range. All but the lowest peaks were severely glaciated during the Pleistocene glacials. Significant uplift of the Coast Ranges began in the Pliocene, about 3.5 Ma, and is still ongoing. The uplift is a response to compressional deformation associated with strike-slip movement of the Pacific and North American plates along the San Andreas Fault. These ranges have a complex geological history with granitic basement rock lying west of the fault and deep-ocean metamorphic and sedimentary rocks, including serpentines, east of the fault. Scattered volcanic activity exists all along the ranges. Rotational movements of microplates along a bend in the fault produce the east–west orientation of the Transverse Ranges of contemporary southern California. The onset of uplift of the Coast Ranges blocked the connection of the Central Valley to the Pacific Ocean, and the basin is filled with continental sediments derived from the growing Sierra Nevada. As late as the late Pleistocene, however, large areas of the valley formed a freshwater lake of glacial meltwater.	Montgomery (1993); Small & Anderson (1995); Wolfe *et al.* (1998); Kellogg & Minor (2005); Mix *et al.* (2011)
Spain	The Baetic Cordillera at the southern end of the Iberian Peninsula achieved moderate uplift resulting from a collision between the Alborán Terrane and the Iberian microplate, but only the proto-Sierra Nevada, the westernmost mountain range of the European Alpine belt, is emergent from the sea at the time.	The ongoing orogeny resulted in the uplift of mountains in the western Baetic Cordillera by the middle Miocene. By the late Messinian (*c.* 5 Ma), the Baetic Cordillera approximated its present topography.	Michard *et al.* (2002); Braga *et al.* (2003); Iribarren *et al.* (2009); Martín *et al.* (2009)
Greece	Except for the easternmost range, including present-day Mount Olympus, the region was submerged. Considerable topography, trending along an east–west axis, existed in this zone and molassic sediments were being deposited on its western margin (Meteora), building a thick conglomerate cover derived from continental material. This topography was a consequence of the subduction of the African Plate beneath Eurasia.	Shortly after the late Miocene, mainland Greece – a more-or-less rigid slab – was rotated clockwise, a consequence of the westward movement of the Anatolian Plate towards the Aegean Sea. This produced the contemporary NNW-trending direction of the Hellenides and resulted in the uplift of the Pindos mountain chain in the western mainland as well as the emergence of numerous basins and ranges (the Hellenides) between this chain and the Olympus massif, which remains active to this day.	Kahle *et al.* (1998); Royden & Husson (2006); Papanikolaou & Royden (2007); Reilinger *et al.* (2010); Vassilakis *et al.* (2011); Pearce *et al.* (2012)

Table 1 Continued

MCE	Late Oligocene to late Miocene	Early Pliocene to Pleistocene	References
Chile	Proto-Andean orogeny, dating from the late Proterozoic to the breakup of Pangaea at the end of the Permian, produced considerable relief, albeit much less than at present. The region was still exposed to the incursion of moist air from the Atlantic Ocean to the east.	The uplift of the Andean Cordillera was initiated in the early Miocene, a consequence of the subduction of the Nazca Plate beneath the continental South American Plate. The compressional forces along the western margin of the South American Plate, resulted in the uplift, faulting and folding of ancient sedimentary and metamorphic cratons to the east. By 15 Ma, the Andes had been lifted enough to develop the hyperarid conditions of the Atacama Desert. South of 33° S, the dip angle of the subducting plate was relatively steep, producing active volcanism. North of this, at 28–33° S, the dip angle was gentle and volcanism over this latitude ended 9–10 Ma. The Cordillera de la Costa (coastal range) in central Chile separated from the Andes in the Neogene as the result of the subsidence that formed the Central Valley. This range is dominated by granites of Carboniferous to Permian age, which represent part of a proto-Andean orogeny.	Alpers & Brimhall (1988); Gregory-Wodzicki (2000); Charrier et al. (2002); Hartley (2003)
Cape	The quartzitic sandstone core of the Cape Folded Belt, exhumed by the break-up of Gondwana in the Cretaceous (140–65 Ma), was subject to erosion that decreased markedly in the Cenozoic. Essential features of Cretaceous erosion persist in the complex topography of the mountains, with topography similar to present. Lowlands and intermontane valleys were capped with silcretes and ferricretes that were deposited in the early Palaeocene.	Mild tectonic uplift during the Miocene and early Pliocene, and the consequent denudation of the lowlands – underlain by shales – resulted in the erosion of sil-ferricretes and the exposure of clay-rich substrata. Owing to slow denudation rates associated with the dominant quartzitic sandstones, mountain topography remained largely unchanged, although some incision of softer (shale) intermontane valleys probably occurred. The entire region was tectonically stable during the mid-Pliocene, although regression during Pleistocene glacials exposed a large area (up to 200 km offshore from the present day) of the Agulhas Bank in the south east and 60–80 km offshore along the west coast.	Partridge & Maud (1987); Tinker et al. (2008); Cowling et al. (2009); Fisher et al. (2010); Erlanger et al. (2012); Scharf et al. (2013)
Australia	Tectonically stable since the mid-Proterozoic, the landscape was a gently-dissected and slowly eroding palaeosurface on basement granitoid rock. The Darling Scarp and its south coast equivalent (the Ravensthorpe Ramp) are elevated – starting in the mid Cenozoic – by minor marginal up-warping. On the Darling Plateau, a phase of haematite formation occurred 10 Ma. The Stirling Range is an old intrusion of quartzite, offering the highest peaks (to 1100 m) on the otherwise subdued palaeoland surface.	Very slow erosion and weathering was associated with accentuated aridity and the onset of mediterranean climate. Some of the oldest persistent landscapes on Earth survived this period with relatively little change. Shorelines oscillated with sea-level change during the Pleistocene, up to 100 km offshore from present day at the Last Glacial Maximum.	Finkl & Fairbridge (1979); Kendrick et al. (1991); Anand & Paine (2002); Anand (2005); Pillans (2007); Jakica et al. (2011)

assessments of changes in landscape structure can be made or to identify thresholds of topostability relevant to evolutionary processes. Nevertheless, the results presented here provide new information on the quantification of MCEs' climatic and topographic stability in relation to OCBIL and YODFEL categorization, and address some fundamental issues about the evolution of plant diversity.

Generally, more stable MCEs – both climatically and topographically (Cape and Australia) – have the highest contemporary plant diversity, whereas the least stable (California and Chile) have the lowest diversity. Spain, an area of low topographic stability and high climatic stability, occupied an intermediate position in terms of diversity. Greece had a lower diversity than expected from its stability (see
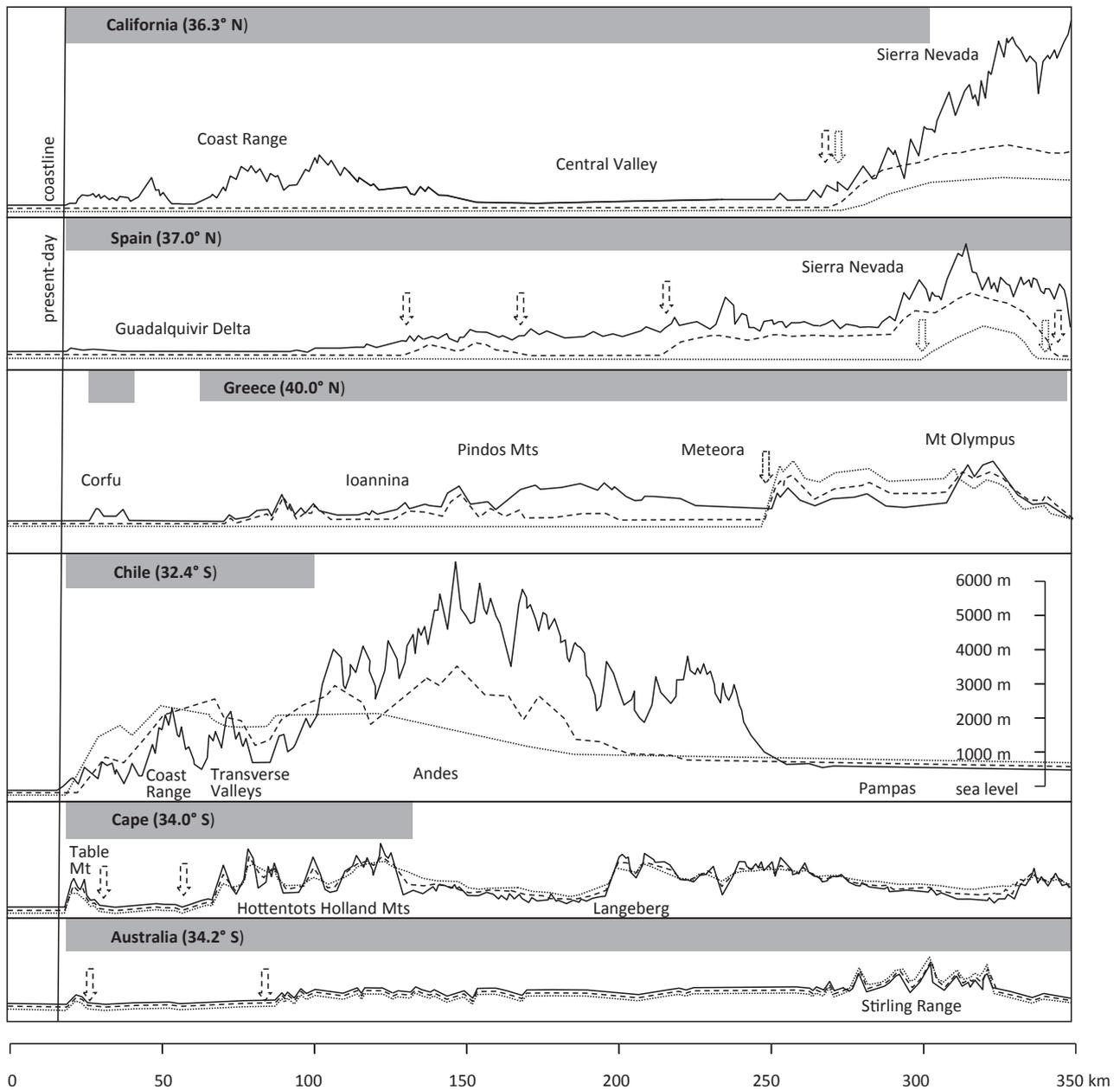
Figure 1 Topographic profiles of the six mediterranean-climate ecosystems (MCEs) in the late Oligocene (dotted), early Pliocene (dashed) and present day (solid lines). Vertical arrows mark the historical coastlines at the corresponding times. Shaded horizontal bars delimit the extent of the MCE along the profiles. Because of the low topographic change in Australia, differences in the profiles for each period have been exaggerated.

below). Differences in Neogene plant diversification rates are unlikely to have produced these patterns: these rates, although variable, are highest in the Mediterranean Basin, intermediate in California and the Cape, and lowest in Australia (Linder, 2008; Madriñán *et al.*, 2013). Studies on lineages shared between MCEs indicate that contrasting diversification rates do not explain differences in extant species richness (Hopper, 2009; Sauquet *et al.*, 2009; Valente *et al.*, 2011; Buerki *et al.*, 2012; Valente & Vargas, 2013). Instead, we suggest that the persistence of older clades in the more stable MCEs of the Cape and Australia is a more

likely explanation for contemporary diversity patterns. These regions include many extant species-rich clades that began to diversify as early as the Eocene but mostly diversified from the early Oligocene to the mid-Miocene (Linder, 2005; Hopper *et al.*, 2009; Sauquet *et al.*, 2009; Verboom *et al.*, 2009; Schnitzler *et al.*, 2011; Cardillo & Pratt, 2013; Valente & Vargas, 2013), a feature largely absent from other MCEs, where ancient lineages are rare and, when extant, show little evidence of diversification, i.e. they are relicts (e.g. Rodríguez-Sánchez & Arroyo, 2008; Sauquet *et al.*, 2009; Lancaster & Kay, 2013).
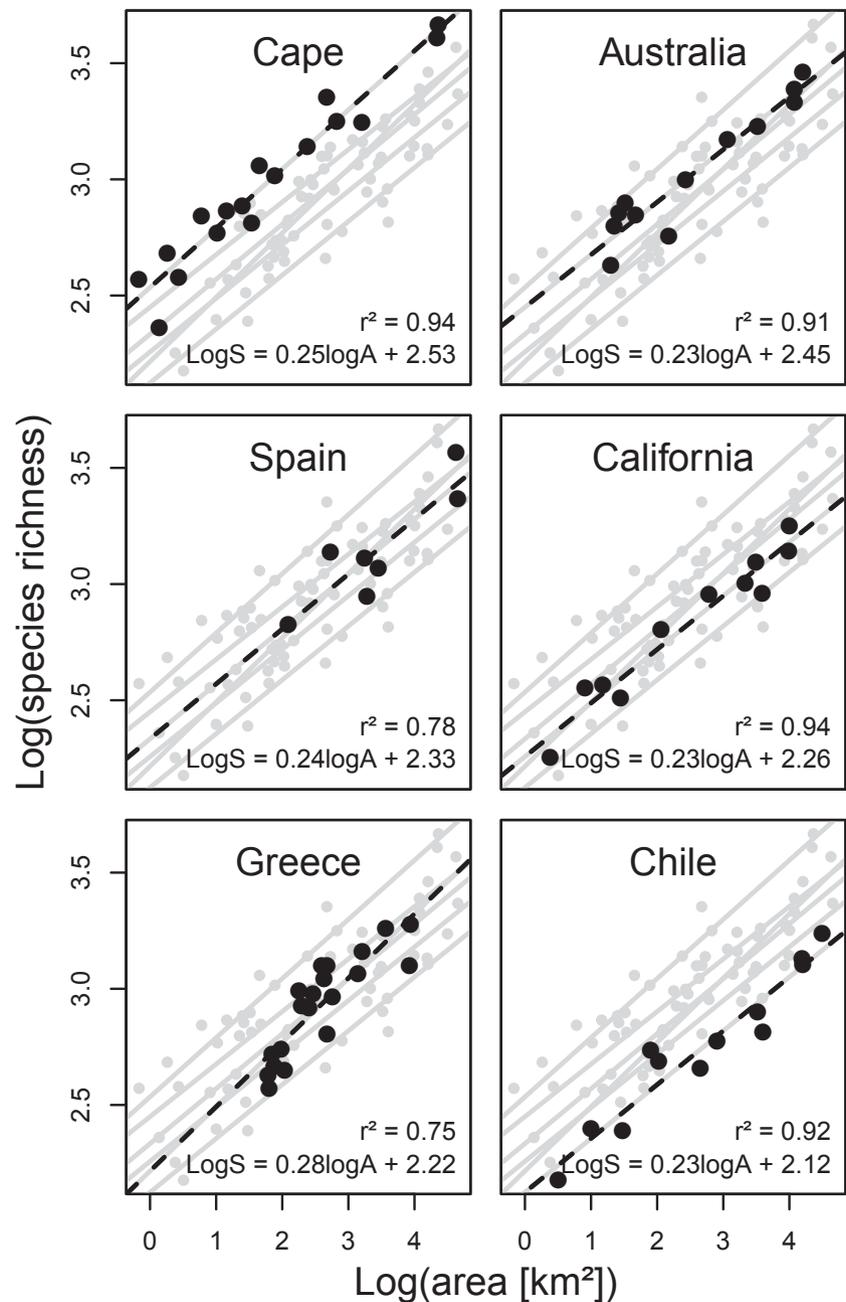
Figure 2 Plant species–area relationships for six mediterranean-climate ecosystems (MCEs) with regression models.

There are, of course, factors other than environmental stability that could determine differences in patterns of regional plant diversity among MCEs, notably differences in disturbance regimes (history of human impacts; fire regimes) (Blondel *et al.*, 2010; Keeley *et al.*, 2012) and soil fertility (Wisheu *et al.*, 2000; Lambers *et al.*, 2010). It may be argued that the association between landscape stability and low soil fertility (Hopper, 2009) makes it impossible to untangle the independent effects of either factor. Young landscapes can, however, have infertile soils (e.g. the pine barrens of eastern North America and the mountain heathlands of south-western Spain) and old landscapes can have fertile soils (e.g. exposures of mudstones in the Cape and dolerite outcrops in Australia). The patterns of plant diversity in these regions are more

consistent with OCBIL theory than a theory based on soil fertility *per se* (Ojeda *et al.*, 2001; R.M.C. & S.D.H., pers. obs.).

Within the overall pattern we document, there are some interesting anomalies. Why does Australia have lower diversity than the Cape, given their similar environmental histories? We can think of at least two reasons. The lower topographic heterogeneity of Australia both now (Bradshaw & Cowling, 2014) and during the Tertiary, may have constrained opportunities for radiation owing to the shallower environmental gradients there than in the Cape, with its impressive and ancient topography (Tinker *et al.*, 2008). Second, mild Neogene uplift in the Cape eroded duricrusts and sandplains to create large tracts of novel, moderately fertile habitats associated with shale bedrock (Cowling *et al.*, 2009),
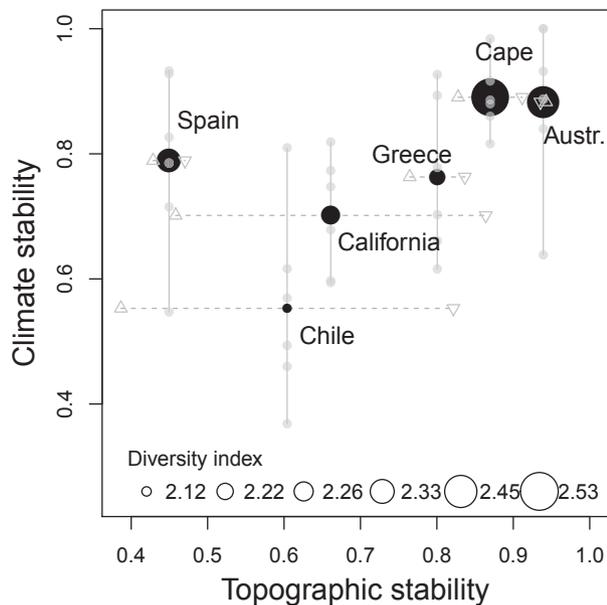
Figure 3 Relationships between diversity indices (*c*-value of species–area regression; see Fig. 2) and mean values of topographic and climate stability in six mediterranean-climate ecosystems (MCEs); a topographic stability index of 1 indicates complete stability. The downward-pointing triangles are the index for the period from the late Oligocene to the late Miocene; upward-pointing triangles are for the period from the early Pliocene to the present-day. Mean climate stability values for mediterranean climate models (Köppen, Maxent, GAM) and down-scaled global climate simulations (MIROC and CCSM) are shown as black dots, and individual combinations are shown in grey. (See Appendix S2 for values).

which initiated a flurry of recent diversification (Verboom *et al.*, 2009). Moreover, the now-submerged Agulhas Bank was a relatively fertile landscape, covering an area more than half the size of the present-day Cape, which was exposed for much of the Pleistocene (Fisher *et al.*, 2010); this YODFEL supported a largely extinct fauna of grazing mammals (Marean *et al.*, 2014) associated in the context of the present-day Cape with novel habitats that are likely to have been loci of Pleistocene plant radiations. Products of these radiations are likely to persist on the present-day Cape littoral and adjacent lime-rich hinterland (Cowling & Holmes, 1992). In Australia, more recent YODFEL-like landscapes are mainly restricted to the Swan Coastal Plain and south coast and associated off-shore shelf, a much smaller area than in the Cape. Like the Cape, however, this region is associated with recent diversification, albeit on a much smaller scale than in the Cape, and with evident persistence of old lineages as well (Coates *et al.*, 2003; Nevill *et al.*, 2014). Overall, as shown by Linder (2008), the poorer Australian flora may be dominated by mature (pre-Pliocene) radiations, whereas the richer Cape flora includes an abundance of both recent (Plio-Pleistocene) radiations associated with the younger, lowland landscapes and mature radiations associated with the ancient Cape mountains (Verboom *et al.*, 2009; Slingsby *et al.*, 2014).

Why does Greece have lower plant diversity than expected on the basis of its environmental history? An obvious reason is our use of island data to assess regional richness patterns in Greece. In particular, as predicted by island biogeographical theory, the depauperate floras of the smaller islands elevated the slope, albeit not significantly, and depressed the *c*-value for the Greek data; the larger islands had comparable diversity to similar-sized regions in nearby Spain. Moreover, the MCE part of mainland Greece, which comprises an area similar to the Cape Floristic Region, supports half the number of species (Valente & Vargas, 2013); this is consistent with our reported Cape–Greece *c*-ratio of 2.08. Thus, there may be a longitudinal (west–east) gradient of declining plant diversity in the Mediterranean Basin, as has been demonstrated for the Cape (Cowling & Lombard, 2002) and Australia (Sniderman *et al.*, 2013).

Our results are consistent with the notion that given sufficient stability, plant hyperdiversity can develop outside the humid tropics (Cowling *et al.*, 1996, 2009; Hopper *et al.*, 2009; Sniderman *et al.*, 2013) implying that water and energy variables are not consistent predictors of high regional-scale plant richness (Davies *et al.*, 2004, 2005; Kreft & Jetz, 2007; Cowling *et al.*, 2009; Hopper, 2009). The concentration of plant species in the humid tropics of the world is likely to be a consequence of Cenozoic environmental stability at these latitudes (Ricklefs, 2004). Moreover, rich floras can be the product of mature radiations (Australia and the Cape mountains) or recent radiations, such as the succulent karoo and the Cape lowlands (Linder, 2008; Verboom *et al.*, 2009) and alpine habitats in the tropics (Hughes & Eastwood, 2006; Madriñán *et al.*, 2013). The extraordinary plant diversity of the Cape is a consequence of the combined effects of both mature and recent radiations (Linder, 2008). This raises the issue of the importance of relative stability, or how much stability is necessary for the evolution of hyperdiversity. Too much stability, especially topographic stability, leads to a drop in diversification rates, as may be the case in Australia (Linder, 2008) and on the Cape mountains (Slingsby *et al.*, 2014). Too much instability, as occurred in California and Chile during the Pleistocene, results in high extinction rates and a reduction in species numbers. The Cape appears to have had – at least for many of its component lineages – just the right amount of environmental heterogeneity for the preservation of old clades and the radiation of younger ones.

The hypothesis presented here – that environmentally stable MCEs have higher diversity owing to a greater persistence of lineages over time – yields predictions that can be tested using dated molecular phylogenies. For example, lineages-through-time plots would differ systematically among the five MCEs. The environmentally stable MCEs – Cape and Australia – would show a greater spread of lineages across time-slices of the Cenozoic (i.e. a relatively constant rate of diversification), whereas the less stable MCEs would show patterns skewed in favour of younger lineages (i.e. increased diversification rates towards the present). The limited available data are largely consistent with this hypothesis (Hopper

et al., 2009; Sauquet et al., 2009; Valente et al., 2011; Buerki et al., 2012; Valente & Vargas, 2013).

In conclusion, the patterns we have shown and the processes invoked to explain them are largely consistent with the predictions of Hopper's (2009) OCBIL theory: old, climatically buffered landscapes are associated with high contemporary diversity, owing to the persistence of old lineages. However, the hyperdiversity of the Cape may well be a consequence of the juxtaposition of an ancient and topographically heterogeneous landscape (the Cape Fold Belt) and a relatively young lowland landscape. The former provided a pool of lineages for colonizing and diversifying recently and rapidly on these lowlands.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Vegetation layers used to build the Maxent and GAM distribution models of mediterranean climate ecosystems.

Appendix S2 Data sources for plant species richness of Greek islands.

Appendix S3 The stability of the mediterranean climate between current and Last Glacial Maximum conditions.

BIOSKETCH

Richard Cowling has a keen interest in the comparative ecology and evolution of the world's mediterranean-climate ecosystems. He has collaborated on this and other topics with many of the coauthors of this paper.

Author contributions: R.M.C., P.B., J.C., S.F., F.F., S.D.H., S.P. and P.W.R. conceived the project, contributed data and edited the manuscript; R.M.C. led the writing; M.A., N.K.M., F.O., R.J.S. and E.V. and B.R.Z. contributed data and edited the manuscript; R.M.C and A.J.P. performed the analyses.

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