Original article

Variation in plant diversity in Mediterranean Climate Ecosystems: the role of climatic and topographical stability

Richard M. Cowling[1*] , Alastair J. Potts[1], Peter Bradshaw[1,2], Jonathan Colville[3], Margarita Arianoutsou[4], Simon Ferrier[5], Felix Forest[6], Nikolaos M. Fyllas[4], Stephen D. Hopper[6], Fernando Ojeda[7], Şerban Procheş[8], Rhian J. Smith[6], Philip W. Rundel[9], Emmanuel Vassilakis[10] and Brian R Zutta[11]

[1]*Department of Botany, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth 6032, South Africa, [2]South African National Parks, Nelson Mandela Metropolitan University, P.O. Box 76693, Port Elizabeth 6031, South Africa, [3]Applied Biodiversity Research Division' South African National Biodiversity Institute, Private Bag X7, Claremont 7735, South Africa, [4]Department Ecology and Systematics, Faculty of Biology, University of Athens, 15784 Greece, [5]CSIRO Ecosystem Sciences, GPO Box 1700, Canberra, ACT 2601, Australia, [6]Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS UK, [7]Centre of Excellence in Natural Resource Management and School of Plant Biology, The University of Western Australia , Foreshore House, Abany 6330, Australia, [7]Departamento de Biología, Universidad de Cádiz, Campus Río San Pedro, 11510-Puerto Real, Spain, [8]School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01 Scottsville 3209, South Africa, [9]Department of Ecology and Evolutionary Biology University of California (UCLA) Los Angeles CA 90095, USA, [10]Department of Dynamic, Tectonic, Applied Geology, Faculty of Geology and Geo-Environment, University of Athens, 15784 Greece, [11]Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Dr, Pasadena, CA 91109, USA.*

Running header: Plant diversity and stability in Mediterranean Climate Ecosystems

ABSTRACT

Aim Although all five of the major Mediterranean Climate Ecosystems (MCE) of the world are recognized as loci of high plant species diversity and endemism, there is considerable variation in regional-scale richness amongst them. 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 since these have had more time for species to accumulate than MCEs that are historically subject to greater topographic upheavals and fluctuating climates.

Location Southwestern Africa (Cape), southwestern Australia, California, central Chile and the eastern (Greece) and western (Spain) Mediterranean Basin.

Methods We estimate plant diversity for each MCE as the intercept of species area curves homogeneous in slope across all regions. We use two down-scaled Global

[*]Correspondence: Richard Cowling, Department of Botany, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth 6031, South Africa.
E-mail: richard.cowling@nmmu.ac.za

41 Circulation Models of Last Glacial Maximum (LGM) to quantify climate stability by
42 comparing the change in the location of MCE between the LGM and present. We
43 quantified Cenozoic topographic stability of each MCE by comparing contemporary
44 topographic profiles with those present in the late Oligocene and the early Pliocene.
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46 **Results** The most diverse MCEs - Cape and Australia – have the highest Cenozoic
47 environmental stability, and the least diverse ones – Chile and California – have the lowest
48 stability.
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50 **Main conclusions** Variation in plant diversity in MCEs is likely to be a consequence not
51 of differences in diversification rates, but rather the persistence of numerous pre-Pliocene
52 clades in the more stable MCEs. The extraordinary plant diversity of the Cape is a
53 consequence of the combined effects of both mature and recent radiations, the latter
54 associated with increased habitat heterogeneity produced by mild tectonic uplift in the
55 Neogene.
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61 Abstract: 279 words (300 max)
62 Text (abstract, text and references): 7 190 words (7 000 max)
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3   65   **INTRODUCTION**
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7   67   The five Mediterranean Climate Ecosystems (MCEs) of the world have attracted interest as
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9   68   loci for studying ecosystem and evolutionary convergence for almost 150 years (Grisebach,
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11   69   1872; Cody & Mooney, 1978; Specht & Moll, 1983; Keeley *et al.*, 2012; Cardillo & Pratt,
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13   70   2013). More recently, MCEs have been the focus of numerous molecular-level studies on
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15   71   the diversification of plants e.g. (Hopper *et al.*, 2009; Verboom *et al.*, 2009; Espindola *et*
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17   72   *al.*, 2010; Valente *et al.*, 2011; Buerki *et al.*, 2012; Lancaster & Kay, 2013). Interest in plant
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19   73   evolution in MCEs stems from their harboring the world's richest extratropical floras
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21   74   (Cowling *et al.*, 1996; Kreft & Jetz, 2007) and having high levels of endemism across all
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23   75   spatial scales (Cowling & Holmes, 1992; Hopper & Gioia, 2004; Georghiou & Delipetrou,
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25   76   2010; Kraft *et al.*, 2010). All five MCEs have been identified as biodiversity hotspots: areas
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27   77   which share large numbers of endemic taxa that are being increasingly threatened by
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29   78   human impacts (Myers *et al.*, 2000).
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35   81   While MCEs exhibit some of the best documented examples of ecological convergence
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37   82   (Mooney, 1977; Cowling & Witkowski, 1994), there are equally striking examples of
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39   83   divergence (Cody & Mooney, 1978; Cowling & Campbell, 1980). Researchers have resorted
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41   84   to categorizing MCEs in terms of their respective selective regimes in order to better
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43   85   explain convergences and divergences among them. Thus, MCEs have been differentiated
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45   86   in terms of climate (e.g. amount of summer rain, reliability of winter-rainfall) (Cowling *et*
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47   87   *al.*, 2005), soil nutrient status (Specht & Moll, 1983), fire regime (Keeley *et al.*, 2012),
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49   88   topography (Carmel & Flather, 2004) and the interactions between climate, fire and soil

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89   nutrient status (Keeley *et al.*, 2012).

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91   Contemporary ecological factors fail to explain comprehensively the variation in regional-

92   scale plant diversity of MCEs (Cowling *et al.,* 1996; Valente & Vargas, 2013). Energy

93   regimes, as measured by potential evapotranspiration, are highest in the South West

94   Australian Floristic Region and the California Floristic Province (Bradshaw & Cowling,

95   2014), which show contrasting diversity patterns. Moreover, topographical heterogeneity

96   – a surrogate for habitat diversity – is highest in the eastern Mediterranean Basin and

97   central Chile (relatively species-poor) and lowest in the South West Australian Floristic

98   Region (relatively species-rich), while the Cape Floristic Region, which is the most species-

99   rich area by far, has moderate heterogeneity (Bradshaw & Cowling, 2014). It appears that

100   variation in contemporary plant diversity patterns in MCEs is profoundly influenced by

101   their respective environmental histories and their impacts on patterns of diversification

102   (speciation minus extinction) (Cowling *et al.,* 1996; Jansson & Dynesius, 2002; Cowling *et*

103   *al.,* 2008; Linder, 2008; Hopper, 2009; Valente *et al.*, 2011; Valente & Vargas, 2013).

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105   In this regard, Hopper's (2009) categorization of MCEs in terms of environmental stability

106   is informative: he differentiated those associated with old, climatically buffered, infertile

107   landscapes (OCBILS), namely the South West Australian Floristic Region (hereafter

108   Australia) and the Cape Floristic Region of southwestern South Africa (hereafter the Cape),

109   and those dominated by young, often disturbed, fertile landscapes (YODFELS), namely the

110   Mediterranean Basin, the California Floristic Province (hereafter California) and central

111   Chile (hereafter Chile). Hopper (2009) predicted higher plant richness and endemism in

112   OCBIL than YODFEL MCEs, owing to higher rates of lineage persistence in the former. In

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113   other words, old, stable landscapes have had more time for species to accumulate than

114   those that are historically subject to greater topographic upheavals and fluctuating

115   climates. However, Hopper's (2009) categorization lacks a quantitative basis. This we

116   provide in this paper.

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118   There are many examples in the literature of the role of climatic and topographic stability

119   in influencing the processes that determine the number of species that particular regions

120   support e.g. (Qian & Ricklefs, 2000; Graham *et al.*, 2006; Araujo *et al.*, 2007; Mittelbach *et*

121   *al.,* 2007). No attempt has been made to comprehensively assess the role of historical

122   measures of climatic and topographical heterogeneity in explaining regional patterns of

123   plant diversity in MCEs. This is what we do in this paper by quantifying the climatic and

124   topographic stability of MCEs during the Pleistocene (climate) and the Neogene

125   (topography) in order to assess the OCBIL-YODFEL categorization of MCEs. We then test

126   whether OCBIL MCEs have more diverse floras than YODFEL ones, as predicted by Hopper

127   (2009).

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129   **METHODS**

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131   **Study area**

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133   Our study area comprises the five MCE biodiversity hotspots, namely California, the Cape,

134   Chile, Australia and the Mediterranean Basin. The Mediterranean Basin MCE occupies a

135   huge area (2.3 million km^2) and includes a wide array of subclimates (Blondel *et al.*, 2010).

136   Consequently, we chose two subregions for further analysis, one in the western Basin

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137   (Spain) and one in the eastern Basin (Greece). These regions differ substantially climatically

138   and biogeographically. The western Basin, west of the Sicily-Cap Bon line has less intense

139   summer aridity and higher autumn and spring rainfall relative to winter compared to the

140   eastern Basin (Blondel *et al.*, 2010). Furthermore, climate-driven isolation and vicariant

141   differentiation of many Mediterranean taxa seem to have occurred in the western and

142   eastern ends of the Mediterranean Basin during the Messinian Salinity Crisis (Migliore *et*

143   *al.*, 2012) and, particularly, the Pleistocene glaciations (Rodríguez-Sánchez & Arroyo,

144   2008). This, together with the west-east climatic differences, translates into different

145   biogeographical regions (Blondel *et al.*, 2010). Thus, we identified a total of six MCE

146   regions for analysis.

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148   **Delimitation of Mediterranean-climate ecosystems**

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150   There is no consensus regarding a global classification of MCEs, although the general

151   definition of cool, wet winters and warm, dry summers applies to all. To avoid using an

152   MCE delimitation that may bias our results, we used three models of MCE classification.

153   The first is the long-standing, expert-opinion classification proposed by Köppen (Geiger,

154   1961), and the remainder use algorithms widely applied in the field of distribution

155   modelling (Franklin, 2010), specifically maximum entropy and generalized additive models

156   (Hastie & Tibshirani, 1990; Phillips *et al.*, 2006). Both expert-opinion and statistical models

157   were used to establish the distribution of, and then changes between, Mediterranean

158   climate under current and past climate states.

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160   The Köppen climate classification system defines MCE areas (Csa and Csb classes) as warm

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161   temperate, with minimum monthly temperatures between -3°C and 18°C, and with at least

162   four months are above 10°C. Köppen (Geiger, 1961) applied three criteria to ensure that

163   winter precipitation predominates, namely 1) that the summer monthly minimum rainfall

164   amount is less than the minimum winter monthly rainfall amount; 2) that maximum winter

165   monthly rainfall amount is three times the minimum summer monthly rainfall amount; 3)

166   that the minimum summer monthly rainfall amount is less than 40 mm. To differentiate

167   between Mediterranean and more arid winter rainfall regions, Köppen (Geiger, 1961)

168   applied an aridity index, so that annual precipitation exceeds 20 times mean annual

169   temperature (where two-thirds of precipitation occurs in winter).

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171   The two statistical models were trained using the distribution of Mediterranean-type

172   vegetation and five bioclimatic variables (annual mean temperature, maximum

173   temperature of the warmest month, annual temperature range, precipitation of the

174   warmest quarter and precipitation of the wettest quarter) (Hijmans *et al.*, 2005). These

175   climate variables capture aspects of temperature, precipitation, seasonality and

176   continentality. However, there are two potential problems. Firstly, there is no standardized

177   global floristic or vegetation map of Mediterranean-type vegetation. Secondly,

178   Mediterranean climate and Mediterranean-type vegetation are not always strongly

179   associated (Keeley *et al.*, 2012); for example, the fynbos of the Cape Floristic Region

180   extends far into a non-seasonal rainfall regime. We identified the distribution of

181   Mediterranean-type vegetation from available floristic or vegetation maps, and where

182   these maps were misleading (e.g. the eastern Cape Floristic Region), we employed expert

183   opinion to refine the area further (see Appendix S1 for further details). From within each

184   regional vegetation map, we selected 500 localities at random. We used these, in

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185   conjunction with 10,000 background points sampled across the earth's terrestrial surface,

186   to train and test the distribution models. To avoid any bias that may have been introduced

187   by the non-standardized vegetation maps and any expert-opinion alteration thereof, for

188   any given MCE region we trained the statistical models using all the localities except those

189   from the region in question. This also avoids any potential circularity of including mapped

190   vegetation for a given MCE region that, in part, may have included climate as a delimiter.

191   These excluded locality points were then used to test the model (i.e. k-folding with each

192   fold representing an MCE) and to calculate the threshold to convert the continuous

193   probability of occurrence maps into binary presence/absence. The conversion to the binary

194   maps utilized the equal sensitivity plus specificity threshold criterion; the relative ranking

195   of the results were robust to the threshold criterion selected (e.g. maximum Kappa or

196   maximum sum of sensitivity plus specificity; results not shown).

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198   We constructed the expert opinion climate model and statistical models in R version 3.0.1

199   (Development Core Team, 2013), the latter using the dismo library (Hijmans *et al.*, 2013),

200   and using climate layers from the worldclim database (Hijmans *et al.*, 2005).

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202   **Plant diversity**

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204   We compiled regional richness data (native species only) for MCEs from Cowling *et al*.

205   (1996, 1997). Additional sources were as follows: Australia (NatureMap,

206   http://naturemap.dec.wa.gov.au/default.aspx), Cape (Cowling & Lombard, 2002), and

207   Spain (Ojeda *et al.*, 2000). Since there are no suitable data from mainland Greece, we had

208   to use data from the larger islands of the Aegean Sea (see Appendix S2 for data sources).

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209   With the exception of Thira (Santorini) which is an active volcanic caldera and Kos, the

210   southwest part of which is characterized by contemporary volcanic activity, the islands are

211   continental islands. Nonetheless, we would expect that the species-area relationship

212   would have a steeper curve and lower intercept than mainland samples (Rosenzweig,

213   1995). All sites were located within the strictly MCE area of each region. We fitted the

214   species-area data for each of the six regions to a double logarithmic regression model and

215   tested for homogeneity of slopes (z) and intercepts (c), following Rosenzweig (1995).

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217   **Climate stability**

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219   We assessed climate stability of MCEs as the difference in climate between the Last Glacial

220   Maximum (LGM) and present times, representing one of the largest fluctuations in climate

221   conditions experienced during the Quaternary. We used two down-scaled Global

222   Circulation Models (GCMs) of LGM climate that are currently available: the Community

223   Climate System Model (Collins *et al.*, 2004)and the Model for Interdisciplinary Research on

224   Climate (Hasumi & Emori, 2004). These LGM climate estimates have been statistically

225   down-scaled using the WorldClim data set (Hijmans *et al.*, 2005) and GCM data from the

226   Paleoclimate Modelling Intercomparison Project II (PMIP2) and are available at

227   http://www.worldclim.org. We performed analyses using both GCMs for each of the MCE

228   delimitations. We calculated climate stability by comparing the change in the location of

229   MCE between the LGM and present, i.e. the percentage of the MCE area under current

230   climate that persists under LGM conditions.

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232   **Topographic stability**

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234   We located ca. 350 km transects in each MCE that are representative of each region's

235   topography. Using published sources (Table 1), we manually reconstructed topographic

236   profiles for each region during the late Oligocene (ca 20 million years ago (Mya)) and the

237   early Pliocene (ca. 5 Mya) (Fig. 1). We chose the late Oligocene as a starting point since it

238   preceded a period of prolonged relative aridity which, in conjunction with fire, would have

239   promoted the expansion of sclerophyllous vegetation allied to that in present-day MCEs

240   (Cowling *et al.*, 2009; Keeley *et al.*, 2012). The Oligocene also witnessed radiation of many

241   MCE lineages, especially in Australia and the Cape (Linder, 2005; Hopper *et al.*, 2009). In

242   order to quantify the topographic stability for the two geological periods (late Oligocene to

243   Late Miocene and Early Pliocene to present) we developed a stability index based on the

244   information in Figure 1 and Table 1. This stability index captures the altitudinal change

245   relative to the horizontal axis of the MCE region. It was calculate as:

246    $stability\ index = 1 - \frac{\Delta Alt}{Dist}$, where ΔAlt is the change in altitude over the horizontal

247   distance. A value of 1 is complete stability, whereas a value of 0 or less indicates equal or

248   greater vertical movement than the horizontal distance.

249   **Relationships between diversity and stability**

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251   We assessed relationships between an index of diversity (quantified as the intercept of the

252   respective species-area model) and measures of climatic and topographic stability

253   described above.

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255   **RESULTS**

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257   **Diversity patterns**

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259   Species-area relations for the six MCEs are shown in Fig. 2. While intercepts (c) of the

260   regressions were significantly different among the MCEs (F = 34.967, dfd = 5, dfn = 67, P <

261   0.0001), the slopes were homogeneous (F = 0.484, P = 0.787). Therefore, it was acceptable

262   to compute the c ratio for any two curves, namely the ratio of the values of the intercepts

263   in arithmetic space (Gould, 1979). This ratio provides a measure of relative species

264   densities (Rosenzweig, 1995). We computed c ratios for the Cape, the region with the

265   highest value, and all the other MCEs. This showed that for similar sized area, the Cape was

266   1.23 times richer than Australia, 1.62 times richer than Spain, 1.91 times richer than

267   California, 2.08 times richer than Greece and 2.63 times richer than Chile.

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269   **Climate stability**

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271   The stability estimates of the MCE area predicted to remain MCE at the LGM varied

272   between the Mediterranean climate models (i.e. Köppen, Maxent and GAM) and the global

273   climate model (MIROC and CCSM) used, resulting in high intra- and inter-region variance of

274   stability estimates (Fig. 3, Table S2). Nonetheless, general patterns were evident. The Cape

275   and Australia had consistently high stability with one exception for Australia (Table S2).

276   Chile had the lowest climate stability, followed by California. Spain and Greece had levels

277   of stability intermediate between California-Chile and Cape-Australia.

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279   **Topographic stability**

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281   While Chile, California and the Mediterranean Basin represent zones of tectonic plate

282   convergence, the Cape and Australia are located away from plate boundaries (Table 1).

283   Hence, the former three regions have experienced considerable, albeit varied topographic

284   instability during the Neogene. Within the Mediterranean Basin, Cenozoic topographic

285   instability has been almost twice as high in the east (Greece) than in the west (Spain),

286   which experienced the least stable conditions among all MCEs. In California and Chile,

287   overall instability was driven largely by the very high values recorded for the late Pliocene-

288   Present period. Paleogene landscapes in the two regions were much more stable than

289   Neogene ones. On the other hand, the Cape and Australia have remained largely

290   unchanged during the Cenozoic (Fig. 1). Even so, the Cape experienced some Neogene

291   uplift and this exposed clay-rich substrata on the coastal forelands, areas that had

292   previously been mantled with duricrusts and sandplains.

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Relationships between diversity and stability

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297   Generally, the highest plant diversity – quantified as the intercept (c-value) of the

298   respective MCE - was recorded for the most climatically and topographically stable MCEs,

299   namely Cape and Australia (Fig. 3). Spain, a MCE having the lowest topographic stability

300   but relatively high climatic stability, showed intermediate diversity scores. California and

301   Chile, MCEs having the lowest stability, including very low measures of topographic

302   stability since the late Pliocene, had the lowest diversity values. Greece was an anomaly,

303   having lower diversity that expected on the basis of its stability.

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305   **DISCUSSION**

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307   Our results are consistent with research for many different biomes and taxa: regions of

308   high environmental stability during the Cenozoic are associated with high species (and

309   genetic) diversity (e.g. Graham *et al.*, 2006; Araujo *et al.*, 2007; Carnaval *et al.*, 2009;

310   Werneck *et al.*, 2011; 2012). To our knowledge, no studies have attempted to quantify the

311   degree of both climatic and topographic stability within all examples of a particular biome

312   on Earth, and to link this to contemporary diversity of plant species. In this sense, our

313   results are novel and interesting. However, we acknowledge the limitations of this study.

314   Firstly, statistical inference is constrained by the low degrees of freedom associated with

315   our study system. However, in our favour is the global scale of the system. Secondly, there

316   is an unavoidable mismatch between the temporal scale we used for climate and

317   topographic stability. Unfortunately, it is not yet feasible to hind cast climates, at the scale

318   required for this study, much beyond the mid Pleistocene. Nonetheless, climate instability

319   during the Pleistocene has been more intense than any other time during the Cenozoic

320   (Zachos *et al.*, 2001) and this is likely to have had a profound effect on plant extinctions

321   (Jansson & Dynesius, 2002). Furthermore, hind casting topographic dynamics to the point

322   that accurate assessments of changes in landscape structure can be made, as well as

323   identifying threshold of topo-stability relevant to evolutionary processes, is not yet

324   feasible. Nevertheless, the results presented here provide new information on the

325   quantification of MCE's climatic and topographic stability in relation to OCBIL and YODFEL

326   categorization and address some fundamental issues about the evolution of plant diversity.

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328   Generally, more stable MCEs - both climatically and topographically (Cape and Australia) -

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329   had highest contemporary plant diversity, while the least stable (California and Chile) had

330   lowest diversity. Spain, an area of low topographic and high climatic stability, occupied an

331   intermediate position in terms of diversity. Greece had a lower diversity than expected

332   from its stability (see below). Differences in Neogene plant diversification rates are unlikely

333   to have produced these patterns: rates, albeit variable, are highest in the Mediterranean

334   Basin, similar in California and the Cape, and lowest in Australia (Linder, 2008; Madrinan *et

335   al.*, 2013). Studies on lineages shared amongst MCEs indicate that contrasting

336   diversification rates do not explain differences in extant species richness (Hopper, 2009;

337   Sauquet *et al.*, 2009; Valente *et al.*, 2011; Buerki *et al.*, 2012; Valente & Vargos, 2013).

338   Instead, we suggest that the persistence of older clades in the more stable MCEs of the

339   Cape and Australia is a more likely explanation for contemporary diversity patterns. These

340   regions include many extant, species-rich clades that began diversifying as early as the

341   Eocene but mostly from the early Oligocene to mid-Miocene (Linder, 2005; Hopper *et al.*,

342   2009; Sauquet *et al.*, 2009; Verboom *et al.*, 2009; Schnitzler *et al.*, 2011; Cardillo & Pratt,

343   2013; Valente & Vargos, 2013), a feature largely absent from other MCEs, where ancient

344   lineages are rare, and when extant, show little evidence of diversification, i.e. they are

345   relicts e.g. (Rodríguez-Sánchez & Arroyo, 2008; Sauquet *et al.*, 2009; Lancaster & Kay,

346   2013).

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348   There are, of course, factors other than environmental stability that could determine

349   differences in patterns of regional plant diversity among MCEs. Notable are differences in

350   disturbance regimes (history of human impacts, fire regimes) (Blondel *et al.,* 2010; Keeley

351   *et al.,* 2012) and soil fertility (Wisheu *et al.*, 2000; Lambers *et al.*, 2010). With regard to the

352   latter, it may be argued that the association between landscape stability and low soil

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353   fertility (Hopper, 2009) makes it impossible to untangle the independent effects of either

354   factor. However, young landscapes can have infertile soils (e.g. the pine barrens of eastern

355   North America and the mountain heathlands of south-western Spain) and old landscapes

356   can have fertile soils (e.g. exposures of mudstones in the Cape and dolerite outcrops in

357   Australia). The patterns of plant diversity in these regions is more consistent with OCBIL

358   theory than a theory based on soil fertility *per se* (Ojeda et al., 2001; RMC & SDH, pers.

359   obs.).

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361   Within the overall pattern we document, there are some interesting anomalies. Why does

362   Australia have lower diversity than the Cape, given their similar environmental histories?

363   We can think of at least two reasons. The lower topographic heterogeneity of Australia

364   both now (Bradshaw & Cowling, 2014) and during the Tertiary, may have constrained

365   opportunities for radiation owing to shallower environmental gradients than the Cape,

366   with its impressive and ancient topography (Tinker *et al.*, 2008). Secondly, mild Neogene

367   uplift in the Cape eroded duricrusts and sandplains to create large tracts of novel,

368   moderately fertile habitats associated with shale bedrock (Cowling *et al.*, 2009), which

369   initiated a flurry of recent diversification (Verboom *et al.*, 2009). Moreover, the now

370   submerged Agulhas Bank comprised a relatively fertile landscape, covering an area more

371   than half the size of the present-day Cape, that was exposed for much of the Pleistocene

372   (Fisher *et al.*, 2010); this YODFEL supported a largely extinct fauna of grazing mammals

373   (Marean *et al.*, 2014) associated with – in the context of the present-day Cape – novel

374   habitats that were likely the locus of Pleistocene plant radiations. Products of these

375   radiations likely persist on the present-day Cape littoral and adjacent lime-rich hinterland

376   (Cowling & Holmes, 1992). In Australia, more recent, YODFEL-like landscapes are mainly

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377   restricted to the Swan Coastal Plain and south coast and associated offshore shelf, a much

378   smaller zone than in the Cape. However, like the Cape, this region is associated with recent

379   diversification, albeit on a much smaller scale than in the Cape, and with evident

380   persistence of old lineages as well (Coates *et al.*, 2003; Nevill *et al.*, 2014). Overall, as

381   shown by Linder (2008), the poorer Australian flora may be dominated by mature (pre-

382   Pliocene) radiations, while the richer Cape flora includes an abundance of both recent

383   (Plio-Pleistocene) radiations – associated with the younger, lowland landscapes - and

384   mature radiations associated with the ancient Cape mountains (Verboom *et al.*, 2009;

385   Slingsby *et al.*, in press)

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387   Why does Greece have lower plant diversity than expected on the basis of its

388   environmental history? An obvious reason is our use of island data to assess regional

389   richness patterns in Greece. In particular, as predicted by island biogeographic theory, the

390   depauperate floras of the smaller islands elevated the slope, albeit not significantly, and

391   depressed the c-value for the Greek data; the larger islands had comparable diversity to

392   similar-sized regions in nearby Spain. Moreover, the MCE part of mainland Greece, which

393   comprises an area similar to the CFR, supports half the number of species (Valente &

394   Vargos, 2013); this is consistent with our reported Cape-Greece c-ratio of 2.08. Thus, there

395   may be a longitudinal (west-east) gradient of declining plant diversity in the Mediterranean

396   Basin, as has been demonstrated for the Cape (Cowling & Lombard, 2002) and Australia

397   (Sniderman *et al.* 2013).

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400   Our results are consistent with the notion that given sufficient stability, plant

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401   hyperdiversity can develop outside of the humid tropics (Cowling *et al.*, 1996; Cowling *et*

402   *al.*, 2009; Hopper *et al.*, 2009; Sniderman *et al.*, 2013) implying that water-energy variables

403   are not consistent predictors of high regional-scale plant richness (Davies *et al.*, 2004;

404   Davies *et al.*, 2005; Kreft & Jetz, 2007; Cowling *et al.,* 2008; Hopper, 2009). The

405   concentration of plant species in the humid tropics of the world is likely a consequence of

406   Cenozoic environmental stability at these latitudes (Ricklefs, 2004). Moreover, rich floras

407   can be the product of mature radiations (Australia and the Cape mountains) or recent

408   radiations, such as the succulent karoo and the Cape lowlands (Linder, 2008; Verboom *et*

409   *al.*, 2009) and alpine habitats in the tropics (Hughes & Eastwood, 2006; Madrinan *et al.*,

410   2013). The extraordinary plant diversity of the Cape is a consequence of the combined

411   effects of both mature and recent radiations (Linder, 2008). This raises the issue of the

412   importance of relative stability, or how much stability is necessary for the evolution of

413   hyperdiversity? Too much stability, especially topographic stability, leads to a drop in

414   diversification rates, as may be the case in Australia (Linder, 2008) and on the Cape

415   mountains (Slingsby *et al.,* in press). Too much instability, as witnessed by California and

416   Chile during the Pleistocene, results in high extinction rates and the depression of species

417   numbers. The Cape appears to have had – at least for many of its component lineages –

418   just the right amount of environmental heterogeneity for the preservation of old clades

419   and the radiation of younger ones.

420

421   The hypothesis presented here – that environmentally stable MCEs have higher diversity

422   owing to greater persistence of lineages over time – yields predictions that can be tested

423   using dated molecular phylogenies. For example, lineage-through time plots would differ

424   systematically among the five MCEs. The environmentally stable MCEs

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425   – Cape and Australia – would show a greater spread of lineages across time slices of the

426   Cenozoic (i.e. a relatively constant rate of diversification), whereas the less stable MCEs

427   would show patterns skewed in favour of younger lineages (i.e. increased diversifications

428   rates towards the present). Limited available data are largely consistent with this

429   hypothesis (Hopper *et al.*, 2009; Sauquet *et al.*, 2009; Valente *et al.*, 2011; Buerki *et al.*,

430   2012; Valente & Vargos, 2013).

431

432   In conclusion, the patterns we have shown and the processes invoked to explain them are

433   largely consistent with the predictions of Hopper's (2009) OCBIL theory: old, climatically

434   buffered landscapes are associated with high contemporary diversity, owing to the

435   persistence of old lineages. However, the hyperdiversity of the Cape may well be a

436   consequence of the juxtaposition of an ancient and topographically heterogeneous

437   landscape (the Cape Fold Belt) and a relatively young lowland landscape. The former has

438   provided a pool of lineages for colonizing and diversifying recently and rapidly on these

439   lowlands.

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441   **Acknowledgements**

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687 **SUPPORTING INFORMATION**
688 Additional Supporting Information may be found in the online version of this article:
689

690 **Appendix S1**. The vegetation layers used to build the maximum entropy and generalized
691 additive model
692

693 **Appendix S2**. Data sources for plant species richness of Greek islands.
694
695
696

697 **Biosketch**

698 Richard Cowling has a keen interest in the comparative ecology and evolution of the
699 world's Mediterranean Climate Ecosystems. He has collaborated on this and other topics
700 with many of the coauthors of this paper. R.M.C., P.B., J.C., S.F., F.F., S.D.H., S.P. and P.W.R.
701 conceived the project, contributed data and edited the manuscript. R.M.C. led the writing.
702 M.A., N.K.M., F.O., R.J.S. and E.V. and B.R.Z. contributed data and edited the manuscript.
703 R.M.C and A.J.P. performed the analyses.
704

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Caption for figures

Figure 1. Topographic profiles in the six Mediterranean Climate Ecosystems (MCEs) in the late Oligocene (dotted), early Pliocene (dashed) and present day (solid lines). Vertical arrows refer to historical coastlines at the corresponding times. Shaded horizontal bars delimit the extent of MCE along the profiles. Note that owing to the low topographic change in Australia, differences in the profiles for each period have been exaggerated.

Figure 2. Plant species-area relationships for the six Mediterranean Climate Ecosystems (MCEs) with regression models.

Figure 3. Relationships between diversity indices (c-value of species-area regression; see Fig.2) and mean values of topographic and climate stability in the six Mediterranean Climate Ecosystems (MCEs). A topographic stability index of 1 indicates complete stability. The down-facing triangle is the index for the late Oligocene- to late Miocene period; up-facing triangles for the early Pliocene to Present period. Mean climate stability values for Mediterranean climate models (Köppen, Maxent, GAM) and downscaled global clime simulations (MIROC and CCSM) are shown with black dots, whereas individual combinations are shown in grey. All values are given in Appendix S2.

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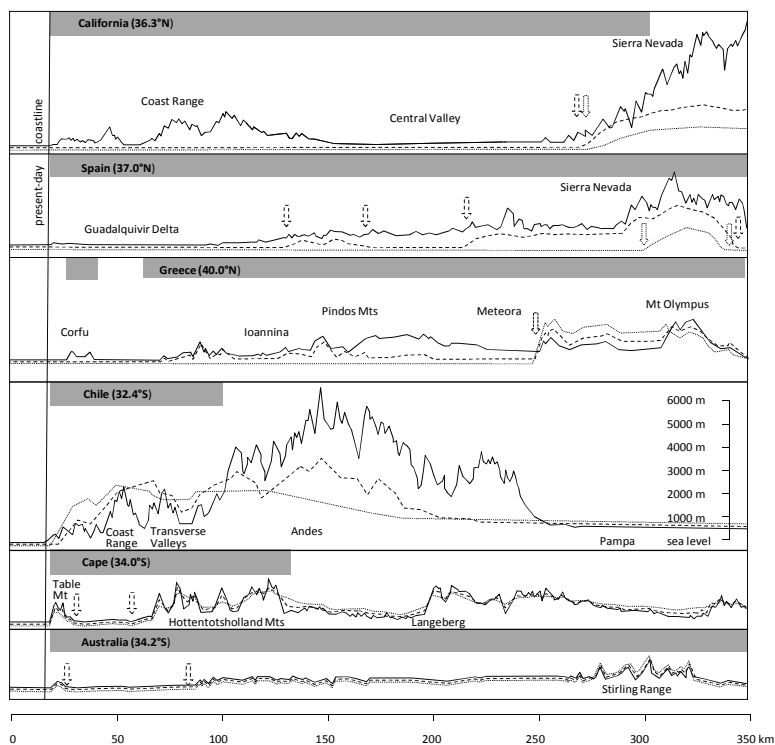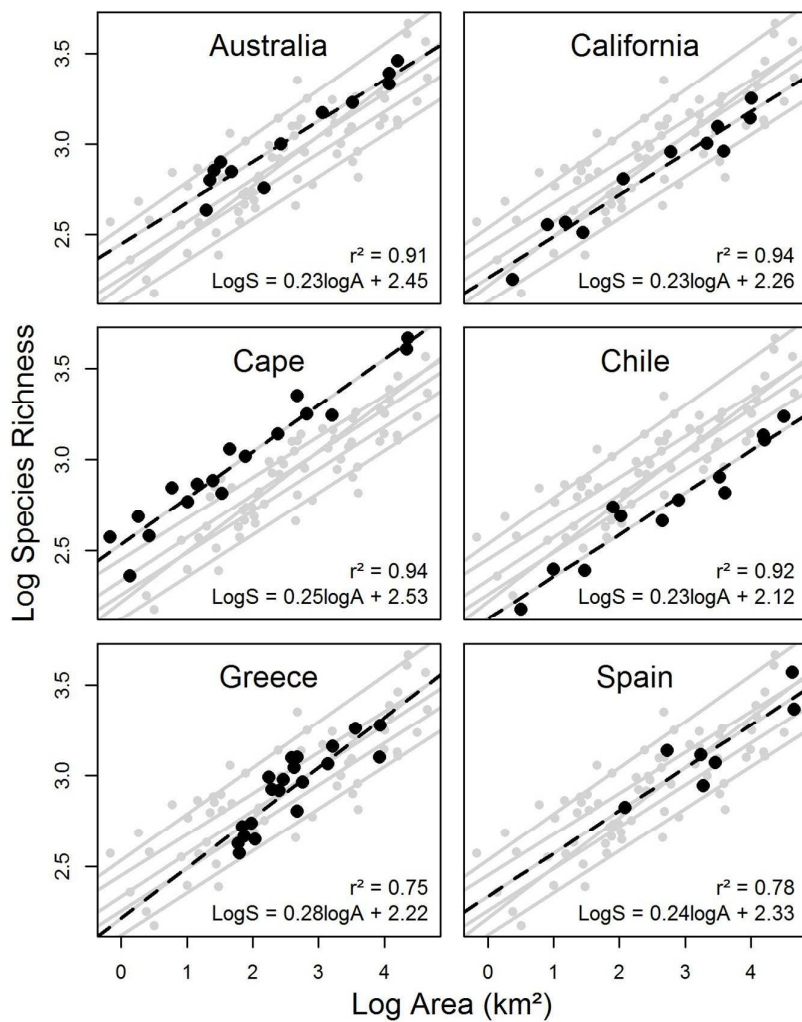
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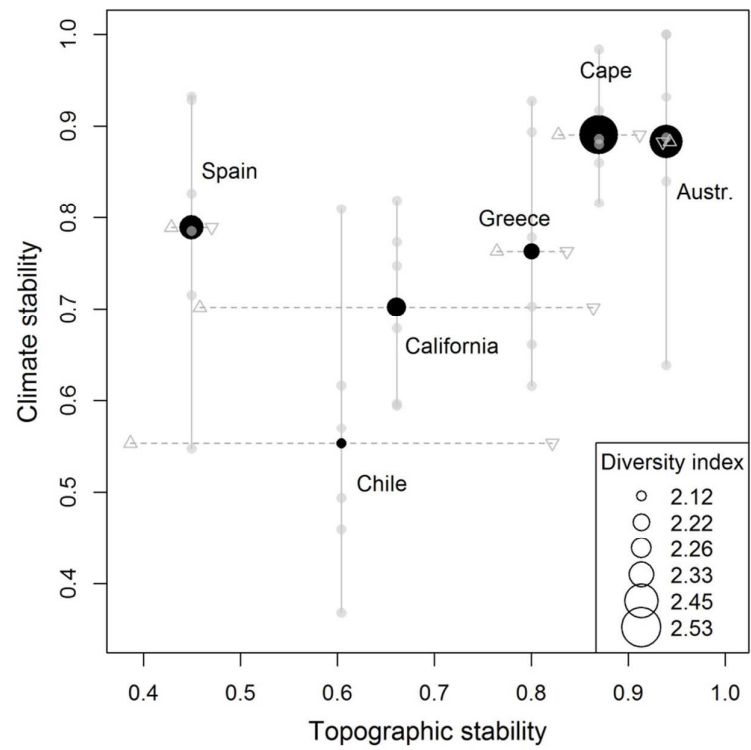
Table 1. Major geomorphic processes affecting topographic dynamics since the late Cenozoic in six Mediterranean Climate Ecosystems (MCEs).			
MCE	Late Oligocene to late Miocene	Early Pliocene to Pleistocene	References
California	Multiple orogenies, dating back to the middle Mesozoic and resulting from subduction associated with the Farallon and Pacific Plates, have uplifted the proto Sierra Nevada, but to a much lesser extent than the contemporary mountains. The current area of the Coast Ranges remains beneath the Pacific Ocean. The Central Valley, which began as a trough associated with tectonic forces of subduction in the Mesozoic, forms a large marine embayment for most of the Cenozoic	Although until recently it was thought that fault-block tilting during the past 10-5 Ma 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 Paleogene and remained high through subsequent millennia. However, the form, topography, and elevation of the modern Sierra Nevada were strongly influenced by extensional and faulting processes over the past 3 million years which added major uplift to the southern Sierra Nevada. This orogeny has left a legacy of volcanic geomorphology in the northern portion of the range. All but the lowest peaks are severely glaciated during the Pleistocene glacials. Significant uplift of the Coast Ranges begins in the Pliocene about 3.5 Ma and is still ongoing. 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 blocks 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 form a freshwater lake of glacial meltwater.	(Montgomery, 1993; Small & Anderson, 1995; Wolfe *et al.*, 1998; Kellogg & Minor, 2005; Mix *et al.*, 2011)
Spain	The Betic Cordillera at the southern end of the Iberian Peninsula has achieved moderate uplift resulting from collision between the Alborán Terrane and the Iberian microplate. However, only the proto Sierra Nevada, the westernmost mountain range of the European Alpine belt, is emergent from the sea at this time.	Ongoing orogeny results in the uplift of mountains in the western Betic by the middle Miocene. By the Late Messinian (ca 5 Ma), the Betic Cordillera approximates 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 Mt Olympus, the region is submerged. Considerable topography, trending along and east-west axis, exists in this zone and	Shortly after the Late Miocene, mainland Greece - a more-or-less rigid slab - is rotated clockwise, a consequence of the westward movement of the Anatolian Plate towards the Aegean Sea. This produces the contemporary NNW-trending direction of the Hellenides and results the uplift of the Pindos mountain chain at the western mainland as well as the emergence of numerous basins and	(Kahle *et al.*, 1998; Royden & Husson, 2006; Papanikolaou & Royden, 2007; Reilinger *et al.*, 2010; Vassilakis *et al.*, 2011; Pearce *et al.*, 2012)

	molassic sediments are being deposited on its western margin (Meteora), building a thick conglomerate cover derived from continental material. This topography is a consequence of the subduction of the African Plate beneath Eurasia.	ranges (the Hellenides) between this chain and the Olympus massif, which remains active to this day.	
Chile	Proto-Andean orogeny, dating from the late Protoerozoic to the breakup of Pangea at the end of the Permian, has produced considerable relief, albeit much less than at present. The region is still exposed to the incursion of moist air from the Atlantic Ocean to the east.	The uplift of the Andean Cordillera is 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, result in the uplifting, faulting and folding of ancient sedimentary and metamorphic cratons to the east. By 15 Ma the Andes has uplifted sufficiently to develop the hyperarid conditions of the Atacama Desert. South of 33°S the dip angle of the subducting plate is relatively steep, producing active volcanism. North of this at 28-33°S the dip angle is gentle and volcanism over this latitude ended 9-10 Ma. The Cordillera de la Costa (Coast range) in central Chile separates from the Andes in the Neogene as the result of subsidence which formed the Central Valley. This range is dominated by granites of Carboniferous to Permian age, which represent part 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 Mya), is subject to erosion that decreases 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 are 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 – results 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 remains largely unchanged although some incision of softer (shale) intermontane valleys probably occurred. The entire region is tectonically stable during the mid Pliocene although regression during Pleistocen glacials exposes 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 is a gently-dissected and slowly eroding palaeo-surface on basement granitoid rock. The Darling Scarp and its southcoast equivalent (the Ravensthorpe Ramp) are	Very slow erosion and weathering is associated with accentuated aridity and the onset of Mediterranean climate. Among 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)

	elevated – starting in the mid Cenozoic - by minor marginal up-warping. On the Darling Plateau a phase of hematite formation occurs at 10Ma. The Stirling Range is an old intrusion of quartzite, offering the highest peaks (to 1100 m) on the otherwise subdued paleoland surface.		

Appendix S1. The vegetation layers used to build the maximum entropy and generalized additive model,
Distribution models of Mediterranean climate ecosystems.

MTE	Comments	Reference
Austalia	Entire South West Australian Floristic Region	Hopper and Gioia, 2004
California	California chaparral and woodlands, including California coastal sage and chaparral, California interior chaparral and woodlands and California montane chaparral and woodlands, but excluding Pacific Temperate Rainforests	Olson & Dinerstein, 1998, 2002
Cape	The following bioregions (Mucina and Rutherford, 2006) were selected as representative of MTV, Southwest Fynbos (but excluding Potberg Sandstone Fynbos and Potberg Ferricrete Fynbos which were too far east and thus in the more aseasonal rainfall area), Northwest Fynbos (but excluding the coastal too arid Namaqualand Sand Fynbos), West Coast Renosterveld, West Strandveld and Namaqualand Cape Shrublands (but excluding the northerly very arid Stinkfonteinberge Quartzite Fynbos).	Mucina and Rutherford, 2006
Chile	The Central Chilean Province	Luebert & Pliscoff, 2006 Pliscoff & Luebert, 2011
Greece	Aegean & West Turkey sclerophyllous and mixed forest and Crete Mediterranean forests	Pahino & Augusto, 2005 DMEER, 2012
Spain	From the Region Mediterránea, in the Super-province Mediterraneo-Iberoatlántica, the Luso-Extremadurense, Gaditano-Onubo-Algarviense and Bética Provinces (but excluding the Carpetano-Ibérico-Leonesa Province)	Rivas-Martinez, 1987

DMEER (2012) Digital map of European Ecological Regions (DMEER): Version 2012. European Environmental Agency, available from at: http://www.eea.europa.eu/data-and-maps/data/digital-map-of-european-ecological-regions (accessed 2012-12-15).

Hopper, S.D. & Gioia P. (2004) The Southwest Australian Floristic Region: evolution and conservation of a global hotspot of biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **35**, 623–650.

Mucina, L. & Rutherford, M. C. (2006) *Vegetation Map of South Africa, Lesotho, and Swaziland*. Strelitzia 19. South African National Botanical Institute. Pretoria.

Olson, D.M. & Dinerstein, E. (2002) The Global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden*, **89**, 199–224.

Pahino, M. & Augusto, G. (2005) A digital map of European ecological regions (DMEER): Application and analysis of the map of the natural vegetation of Europe. *BfN-Skripten*, **156**, 446.

Pliscoff, P.Y. & Luebert, F. (2006) *Ecosistemas terrestres. En: Biodiversidad de Chile: Patrimonio y desafíos*. Comisión Nacional del Medio Ambiente, Santiago.

Pliscoff, P. & Luebert, F. (2011) *Pisos de Vegetación de Chile (Terrestrial Ecosystems of Chile)*. National Environmental Commission, available at the Data Basin Database: http://databasin.org/datasets/46a0ca242b174b09aaa24e34e613023e (accessed 2013-07-15).

Rivas-Martinez, S. (1987) *Memoria Del Mapa De Series De Vegetacion De Españia*. Catedrático de Botánica de la Universidad Complutense. Madrid.

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

Island	Source
Symi	Carlstrøm, A. (1987). A survey of the Flora and Phytogeography of Rodhos, Simi, Tilos and the Marmaris Peninsula (SE Greece, SW Turkey). PhD Thesis. University of Lund, Sweden.
Tilos	Carlstrøm, A. (1987). A survey of the Flora and Phytogeography of Rodhos, Simi, Tilos and the Marmaris Peninsula (SE Greece, SW Turkey). PhD Thesis. University of Lund, Sweden.
Kalimnos	Hansen, A. (1980). Eine Listeder Flora der Inseln Kos, Kalimnos, Pserimos, Telendos und Nachbar-Inselchen (Ostagais, Griechenland). Biologia Gallo-Hellenenica 9, 3 -105.
Thira	Hansen, A. (1971). Flora der Inselgruppe Santorin. Candollea 26, 109-163. Raus, Th. (1988). Vascular plant colonization and vegetation development on sea-born volcanic islands in the Aegean (Greece). Vegetatio 77(1-3),139-147. Raus, Th. (1991). Die Flora (Farne und Blütenpflanzen) des Santorin-Archipels. In Schmalfuss, H. (ed.): Santorin - Leben auf Schutt und Asche. Ein naturkundlicher Reiseführer, Weikersheim: Verlag Josef Markgraf, pp. 109-124.
Skopelos	Economidou, E. (1973). Contribution ϋ l ιtude de la flore et de la phytogeographie de l' Ile de Skopelos. Phytogeographie des Sporades du Nord, II. Biologia Gallo-Hellenica 5, 78-121.
Kasos	Greuter, W., Pleger, R. & Raus, Th. (1983). The vascular flora of the Karpathos island group (Dodecanesos, Greece). A preliminary checklist. Willdenowia 13, 43-78. Raus T, 1989. Die Flora von Armathia und der Kleininseln um Kasos (Dodekanes, Griechenland). Botanika Chronika, 9, 19-39.
Samothraki	Strid, A. & Tzanoudakis, D. (1999). Contribution to the Greek insular flora: The flora and the phytogeographical connections of Samothraki. In: E.P. Eleftheriou (ed). Proceedings of the 7th Panhellenic Scientific Conference, Thessaloniki, pp. 332-335.
Paros	Raus, Th. (1996). Flora von Paros und Antiparos (Kykladen, Griechenland). Ann. Naturhistorischen Museum Wien 98 B Suppl., 237-278.
Ikaria	Christodoulakis, D. (1996).The flora of Ikaria (Greece, E. Aegean islands). Phyton (Horn, Austria) 36, 63-91.
Kos	Hansen, A. (1980). Eine Liste der Flora der Inseln Kos, Kalimnos, Pserimos, Telendos und Nachbar-Inselchen (Ostagais,Griechenland). Biologia Gallo-Hellenica 9, 3-105.
Thasos	Strid, A. & Tan, K. (1998). Flora and Vegetation of North East Greece Icluding Thasos and Samothraki: Report of a Student Excursion from the University of Copenhagen. Botanical Institute,

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	University of Copenhagen, 98 pages.
Naxos	Böhling, N.B. (1994). Studien zur landschaftsokologischen Raumgliederung auf der mediterranen Insel Naxos (Griechenland); unter besonderer Berócksichtigung von Zeigerpflanzen. Dissertationes Botanicae, J Cramer Verlag, Berlin, Stuttgart, 230 p. Böhling, N.B. (1995). Zeigerwerte der Phanerogamen-Flora von Naxos(Griechenland). Ein Beitrag zur ökologischen Kennzeichnung der mediterranen Pflanzenwelt. Stuttgarter Beitr. Naturk., A 533, 1-75.
Limnos	Panitsa, M., Snogerup, B., Songerup, S. & Tzanoudakis, D. (2003). Floristic Investigation of Lemnos Island (NE Aegean Area, Greece). Willdenowia, 33(1), 79-105.
Samos	Christodoulakis D (1986) The Flora and Vegetation of the Island of Samos, Greece. Ph.D Thesis, University of Patras (In Greek with German summary). Snogerup, S. & Snogerup. B. (1993). Additions to the flora of Samos, Greece. Flora Mediterranea, 3, 211-222. Burton R. M. (1999). Yet more new plants from the East Aegean island of Samos. – Annals Museum Goulandris 10, 45–51.
Karpathos	Greuter, W., Pleger, R. & Raus, T. (1983). The vascular flora of the Karpathos island group (Dodecanesos, Greece). A preliminary checklist. Willdenowia, 13, 43-78. Raus, T. (1996). Additions and amendments to the flora of the Karpathos island group (Dodekanesos, Greece). Botanika Chronika, 12, 21-53. Jahn, R. & Schonfelder, P. (1995). *Exkursionsflora fór Kreta.* Eugen Ulmer, Stuttgart.
Rodos	Carlstrφm, A. (1987). A survey of the Flora and Phytogeography of Rodhos, Simi, Tilos and the Marmaris Peninsula (SE Greece, SW Turkey). PhD Thesis. University of Lund, Sweden.
Lesvos	Bazos, I. (2005). Study of the Flora and Vegetation of Lesvos. Ph D Thesis. University of Athens. In Greek with an English summary
Evvoia	Rechinger, K.H. (1961). Die Flora von Euboea. Bot. Jahrb. Syst. 80, 294-465. Trigas P. & Iatrou, G. (2000). The local endemic flora of Evvia (W Aegean, Greece). Willdenowia 36, 257-270.
Chios	Meikle, R.D. (1954). A survey of the Flora of Chios. Kew Bulletin 9(1), 85-199.
Kriti	Jahn, R. & Schonfelder, P. (1995). Exkursionsflora fór Kreta. Eugen

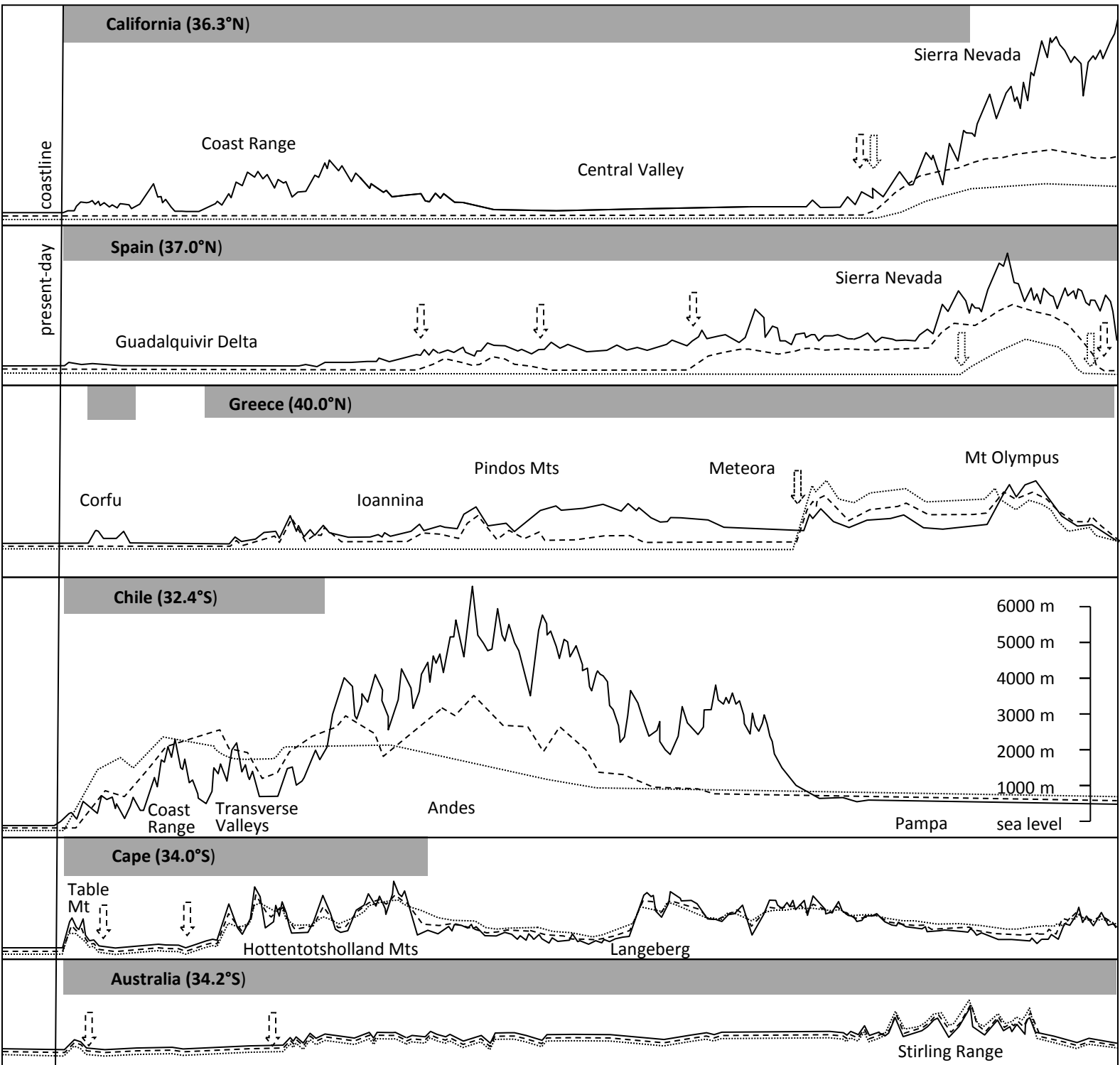|	Ulmer, Stuttgart.

Table S3. The stability of Mediterranean climate between current and Last Glacial Maximum conditions (as % of current) using one expert-opinion (Köppen) and two statistical models (GAM and Maxent).

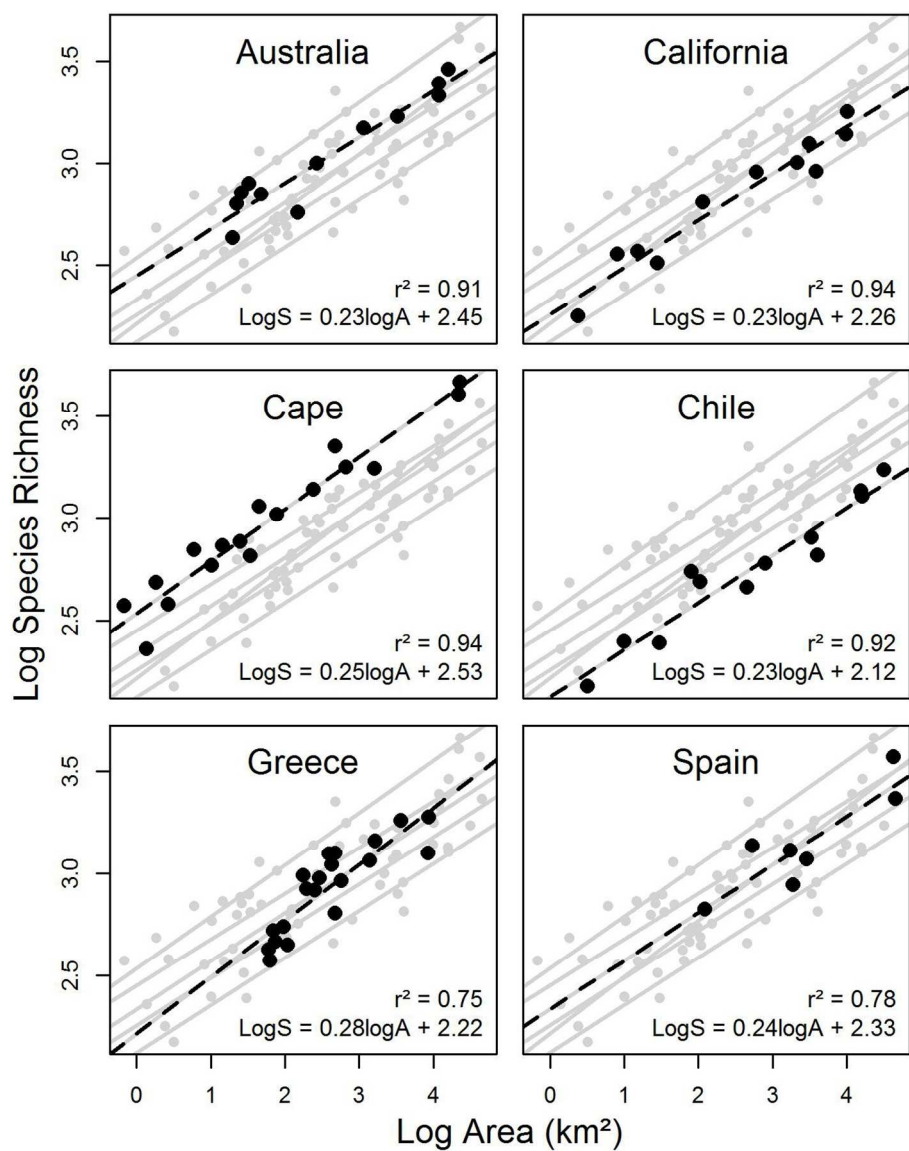| MTE model	Climate simulation model	Australia	California	Cape	Chile	Greece	Spain
Köppen	CCSM	84.0	59.7	98.4	81	89.3	92.8
	MIROC	100.0	59.4	91.6	61.6	92.7	93.3
GAM	CCSM	99.9	58.9	86.4	42.3	58.1	74.7
	MIROC	85.2	63.8	82.7	41.3	54.9	55.8
Maxent	CCSM	94.3	76.0	88.3	41.0	84.8	83.7
	MIROC	66.4	83.4	88.3	53.0	73.3	70.0

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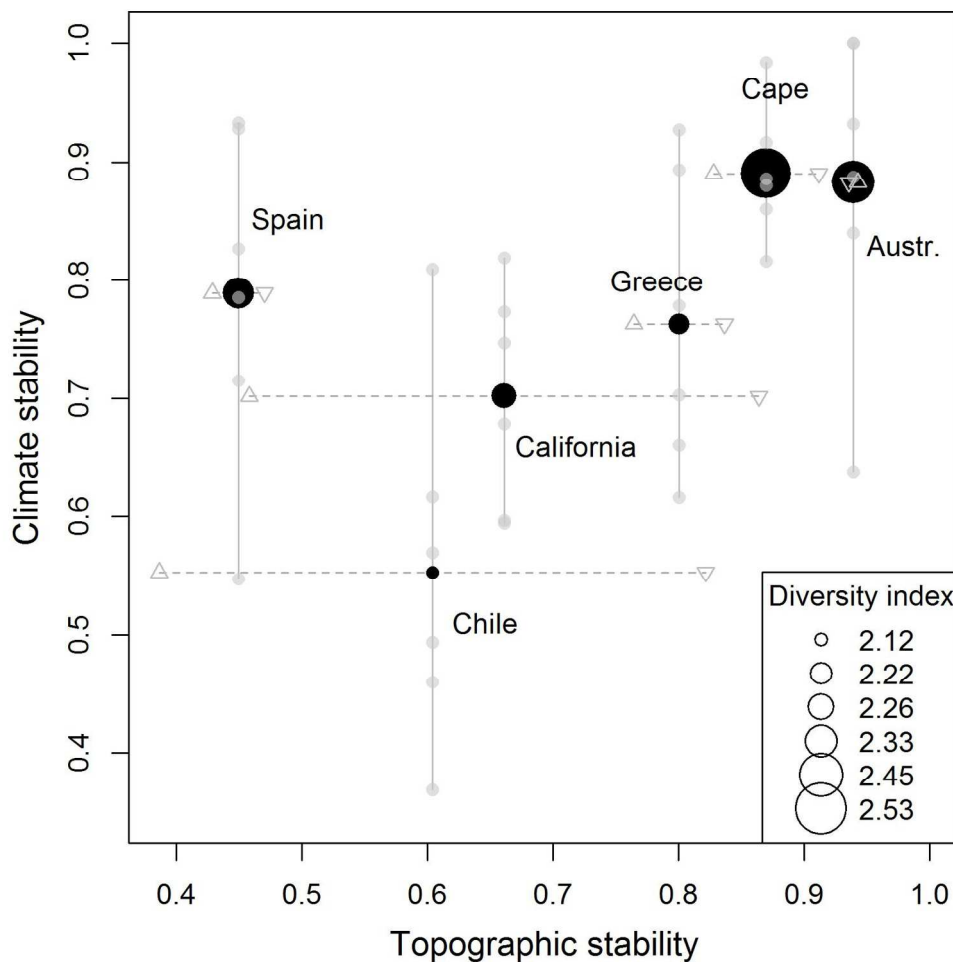48
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Australia
$r^2 = 0.91$
LogS = 0.23logA + 2.45

California
$r^2 = 0.94$
LogS = 0.23logA + 2.26

Cape
$r^2 = 0.94$
LogS = 0.25logA + 2.53

Chile
$r^2 = 0.92$
LogS = 0.23logA + 2.12

Greece
$r^2 = 0.75$
LogS = 0.28logA + 2.22

Spain
$r^2 = 0.78$
LogS = 0.24logA + 2.33

Log Species Richness

Log Area (km²)

119x149mm (300 x 300 DPI)

149x149mm (300 x 300 DPI)