

1 **Title Page**

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3 **Title:** Plant richness, turnover and evolutionary diversity track gradients of stability and ecological
4 opportunity in a megadiversity centre

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34 models.

35

36 **Abstract:**

37 Research on global patterns of diversity has been dominated by studies seeking explanations for the
38 equator-to-poles decline in richness of most groups of organisms, namely the latitudinal diversity
39 gradient. A problem with this gradient is that it conflates two key explanations, namely biome
40 stability (age and area) and productivity (ecological opportunity). Investigating longitudinal gradients
41 in diversity can overcome this problem. Here we investigate a longitudinal gradient in plant diversity
42 in the megadiverse Cape Floristic Region (CFR). We test predictions of the age and area and
43 ecological opportunity hypotheses using metrics for both taxonomic and phylogenetic diversity and
44 turnover. Our plant data set includes modelled occurrences for 4,813 species and dated molecular
45 phylogenies for 21 clades endemic to the CFR. Climate and biome stability were quantified over the
46 past 140 000 years for testing the age and area hypothesis, and measures of topographic diversity,
47 rainfall seasonality and productivity were used to test the ecological opportunity hypothesis. Results
48 from our spatial regression models showed biome stability, rainfall seasonality and topographic
49 heterogeneity were the strongest predictors of taxonomic diversity. Biome stability alone was the
50 strongest predictor of all diversity metrics, and productivity played only a marginal role. We argue
51 that age and area in conjunction with non-productivity-based measures of ecological opportunity
52 provide a robust explanation of the CFR's longitudinal diversity gradient. We suggest that this model
53 may also be a general explanation for global diversity patterns, unconstrained as it is by the
54 collinearities underpinning the latitudinal diversity gradient.

55 **Significance Statement:**

56 What explains global patterns of diversity – environmental history or ecology? Most studies have
57 focussed on latitudinal gradients – the decline of diversity from the tropics to the poles. A problem
58 with this gradient is that it conflates predictions of historical and ecological hypotheses: The
59 productive tropics have also experienced high Cenozoic biome stability. Longitudinal diversity
60 gradients can overcome this constraint. We use a longitudinal plant diversity gradient in the
61 megadiverse Cape Floristic Region to model species and evolutionary diversity in terms of
62 Pleistocene climate stability and ecological heterogeneity. We find that biome stability is the strongest

63 predictor for all diversity measures, and argue that stability, in conjunction with measures of
64 ecological opportunity – other than productivity – provide a general explanation for global diversity
65 patterns.

66 **Author contributions:** R.M.C., J.F.C., and F.F. designed research; R.M.C., J.F.C., C.B., and F.F.
67 performed research; C.B., J.F.C., F.F., R.A. and B.H. analyzed data; R.M.C., J.F.C., F.F, and C.B.
68 wrote the paper; and R.A., and B.H. revised the paper.

69

70 **Text**

71 **Introduction**

72 The roles of contemporary ecological factors vs. Cenozoic environmental stability in determining
73 large-scale biodiversity patterns continues to generate lively debate (1–7). Research on this topic has
74 been dominated by studies of the latitudinal decline in richness towards the poles of most taxa. The
75 many hypotheses invoked to explain the latitudinal gradient have been elegantly distilled by Schluter
76 (5) into two – one mainly ecological (ecological opportunity), and the other historical (age and area).
77 The former argues that diversity patterns are underpinned by differences in ecological opportunity
78 associated with gradients in habitat heterogeneity, productivity and the intensity of biotic interactions,
79 all of which influence the length of niche axes: this hypothesis predicts a positive relationship
80 between diversity and speciation rate. The age and area hypothesis posits that high diversity is a
81 consequence of areas – sufficiently large to support viable populations of the focal taxa - having high
82 environmental stability over evolutionary time scales, which reduces extinction rates, and results in
83 the accumulation of species, both in old lineages and more recent radiations (2, 5, 7). Area and
84 stability combine to increase rates of speciation and reduce rates of extinction. Large areas, being
85 more heterogeneous, provide longer niche axes than small areas and offer more opportunities for
86 speciation and reduced risks of extinction and overall will affect the total number of species (8–10).
87 Environmental stability promotes high speciation rates owing to increased opportunities for niche
88 differentiation in stable selective mosaics, but also ensures lower rates of extinction, and will affect
89 the total number of species and their spatial arrangement (11–13). Although these two hypotheses
90 have primarily been tested against species richness patterns, the recent increase and availability of
91 regional species and phylogenetic datasets has enabled the testing of predictions for other diversity
92 metrics, such as beta and phylogenetic diversity, which are central to our understanding of global
93 diversity patterns (7, 14–18).

94 The age and area hypothesis predicts that biotas would have high beta diversity (changes in species
95 composition along ecological gradients) owing to the accumulation of habitat specialists associated
96 with both early- and later-diverging lineages. In this case, spatial turnover (species replacement),

97 rather than species loss (nestedness), should prevail as the driver of beta diversity (17, 19, 20) (Fig.
98 1A, B). The ecological opportunity hypothesis predicts the same patterns, but for a different reason:
99 richness accumulates in areas of high ecological opportunity that foster rapid, ecological speciation in
100 numerous clades (Fig. 1A, C). Beta diversity is largely driven by recently evolved species that have
101 subdivided the long niche axes characteristic of high-opportunity regions. Spatial turnover should be
102 high in areas of high ecological opportunity and high stability, allowing for the evolution of numerous
103 range-restricted, habitat-specialist species, whereas areas of high ecological opportunity and low
104 stability should have higher nestedness due to recolonization of empty niches after events of
105 instability (19).

106 The two hypotheses make different predictions for phylogenetic diversity-based metrics. For
107 equivalent species richness, the age and area hypothesis predicts high phylogenetic diversity, owing to
108 the preservation of older lineages, which are widely dispersed on phylogenetic trees (Fig. 1B),
109 whereas ecological opportunity predicts lower phylogenetic diversity owing to the preponderance of
110 younger, recently evolved species swarms, which are mostly clustered on phylogenetic trees (Fig. 1C)
111 (2, 7, 16, 21–23). Phylogenetic beta diversity, which measures phylogenetic turnover (i.e. turnover in
112 branch length) (24), will vary depending on the proportion of range-restricted species present in a
113 given area and their distribution within the phylogenetic tree (i.e. the phylogenetic distance separating
114 them). For areas with similar species richness, phylogenetic beta diversity is predicted to be similar
115 under the age and area hypothesis and the ecological opportunity hypothesis (15, 17, 20), although
116 driven by different phylogenetic patterns, i.e. fewer deeper branches for the former (Fig. 1B) and
117 many shallower branches for the latter (Fig. 1C). However, one would expect a larger proportion of
118 widespread taxa to be present under the age and area hypothesis because of the longer time for range
119 expansion to occur (Fig. 1B). Environmental stability fosters the large-scale preservation of clades
120 (i.e. low extinction (Fig. 1A, B)), whereas in regions of high ecological opportunity, high
121 diversification rates produce fewer, but more species-rich, phylogenetic groups (Fig. 1C, D) (1, 5, 7,
122 21–23).

123 The two hypotheses, however, are not necessarily mutually exclusive (5). A system where both
124 hypotheses have traction (i.e. a stable biome with high ecological heterogeneity) would show high
125 beta diversity, and both high phylogenetic diversity and phylogenetic beta diversity, a consequence of
126 high speciation and low extinction rates (Fig. 1A). In this scenario, phylogenetic beta diversity can
127 also be low if most narrow-ranged species are recently-evolved (Fig. 1A(1)). On the other hand, a
128 stable biome with an ecologically homogeneous environment, and an unstable biome with an
129 ecologically heterogeneous environment, would both have high phylogenetic diversity, but it would
130 be over-dispersed in the former (i.e. principally formed of isolated lineages) (Fig. 1B) and clustered in
131 the latter (i.e. generally comprising fewer, but more speciose lineages) (Fig. 1C). Likewise, under
132 these two scenarios phylogenetic beta diversity would be high, although higher in the first case, driven
133 principally by deep branches (Fig. 1B), than in the second case, which will be driven mostly by
134 shallower branches (Fig. 1C).

135 The age and area and ecological opportunity hypotheses have seldom been tested simultaneously and
136 never for a diversity gradient within an extratropical megadiversity centre; most research has focused
137 on the latitudinal gradient, which conflates the predictions of historical and ecological hypotheses:
138 The productive tropical rainforest biomes, which offer high opportunities for ecological speciation
139 (e.g. epiphytes in tall, multi-layered forests) (4, 25, 26), have also experienced the highest stability
140 throughout the Cenozoic (2, 5, 27, 28). This problem can be overcome by researching diversity
141 gradients where environmental stability and ecological heterogeneity are uncoupled, as occurs along
142 many longitudinal diversity gradients. Examples include comparisons of diversity in temperate
143 biomes of south-eastern North America and eastern Asia (3, 29), between Europe and eastern
144 Asia/North America (30), and among the Mediterranean-climate regions across the globe (13). These
145 studies conclude that historical events and biogeographic idiosyncrasies, play a more important role in
146 explaining diversity than ecological factors associated with contemporary environments. However,
147 the world's most diverse regions, the mountainous areas of the tropical Asia and the Neotropics (1, 5,
148 7, 31), combine the environmental features predicted by both the age and area and the ecological
149 opportunity hypotheses to be associated with megadiversity.

150 The Cape Floristic Region (CFR), a Mediterranean-climate region, provides an excellent opportunity
151 to investigate simultaneously the ecological and historical drivers of diversity (32). Firstly, the CFR
152 flora is the richest extratropical flora in the world, comprising 9,383 species (68% endemic) in just
153 90,760 km². Secondly, the CFR flora is well-known taxonomically, spatially and phylogenetically.
154 Thirdly, biological heterogeneity is relatively homogeneous throughout the region; the diversity and
155 structure of plant communities are relatively similar for analogous landscapes throughout the CFR.
156 Fourthly, the region shows a pronounced longitudinal gradient in regional-scale (1 – 10,000 km²)
157 diversity: The numbers per unit area of taxa associated with clades endemic to the CFR, as well as
158 regional scale richness of entire floras, decline markedly in a longitudinal pattern, from south-west to
159 south-east (32). Fifthly, longitudinal gradients of Pleistocene climatic and biome stability are evident
160 across the CFR, with more stable climates in the west where Mediterranean climates persisted over
161 much of the region, and less stable climates in the east where the CFR flora was replaced at times by a
162 subtropical flora (33–35).

163 Here, we use the longitudinal plant diversity gradient in the CFR to test the predictions of the age and
164 area, and ecological opportunity hypotheses to explain the longitudinal plant diversity gradient in the
165 CFR by modelling several key diversity metrics, incorporating both species richness and evolutionary
166 history, in relation to variables reflecting ecological and historical phenomena. Our analysis was
167 conducted at the regional scale; our mapping unit is a two-minute grid cell (ca. 12 km²), sufficiently
168 large to include, in all parts of the CFR, substantial environmental gradients and several floristically
169 distinct plant communities. Since our focus is on the evolution of CFR plant diversity, we included in
170 our analysis only species associated with “Cape clades”, groups largely endemic to the CFR and
171 which have their diversity centred within the region (36). Our comprehensive data set includes
172 modelled occurrences across 8,347 two-minute grid cells for 4,813 species (~51% of total CFR
173 species) and dated molecular phylogenies for 21 Cape clades. Patterns of Cape clade species richness
174 are strongly correlated with overall CFR plant richness (See SI Appendix, Fig. S1) and we therefore
175 consider them reflective of taxonomic patterns for the entire flora. We used measures of topographical
176 heterogeneity, productivity (evapotranspiration) and rainfall seasonality as surrogates for ecological

177 opportunity (4, 6, 25, 37). For historical measures, climatic and biome stability were assessed using an
178 ensemble of general circulation model experiments to calculate climatic variability and biome
179 persistence over the last 140ky (35). This time span is appropriate for our study since many Cape
180 clades have speciated massively during the Pleistocene (38); almost half (48.6%) of all divergence
181 events in the current study took place in the last 2 Ma.

182 If the ecological opportunity hypothesis explains the CFR's species and evolutionary diversity
183 gradients, we would expect significant positive relationships between richness, and both topographical
184 heterogeneity and productivity, and a negative relationship between richness and rainfall seasonality
185 (more seasonal environments precipitation becomes limiting in different seasons (i.e. precipitation
186 only during the cool-season vs precipitation only during the warm-season) whereas less seasonal
187 environments provide greater opportunities for niche specialization to warm- and cool-season
188 precipitation) (32). We also expect similar relationships for beta diversity because rapid, ecological
189 speciation should result in high spatial turnover of ecological specialists along habitat gradients. For
190 evolutionary diversity, we expect richness hotspots to be correlated with low phylogenetic diversity
191 per species (made up of fewer, but more speciose lineages) and relatively low phylogenetic beta
192 diversity, owing to the predominance of recently radiating clades likely comprising range-restricted
193 species. On the other hand, for the age and area hypothesis, we expect that richness, the spatial
194 turnover component of beta diversity, and phylogenetic diversity all to be associated with areas of
195 high climatic and biome stability, owing to the preservation of clades, a consequence of low
196 extinction rates. For the same reason, phylogenetic beta diversity is more likely to be positively
197 associated with climate and biome stability because of the prevalence of deeper branches, despite
198 species being also more likely to exhibit wider distributions. We also predict that in regions with
199 stable biomes and climates, and with ecologically heterogeneous landscapes, both hypothesised
200 mechanisms will have influenced diversity patterns.

201 **Results**

202 **Ecological and stability predictors**

203 The spatial patterns for the five covariates used to test our predictions are shown in Fig. 2. Two nodes
204 of high Late Pleistocene climate stability were identified, one in the west and a less pronounced one in
205 the east CFR (Fig. 2A). However, a clear west–east gradient of biome stability was retrieved (Fig.
206 2B). The node of high climate stability in the east does not translate into high biome stability since
207 eastern climates are currently marginal for Cape vegetation (32, 34) so that even small climatic shifts
208 can cause biome replacement; thus, biome persistence was lower the eastern CFR. There is little
209 evidence of a topographic heterogeneity gradient across the CFR; areas of high and low values are
210 evenly spread across the region (Fig. 2C). Productivity was highest in the south-eastern and south-
211 western CFR, and medium to low in the central and interior regions (Fig. 2D). A strong west–east
212 seasonality gradient exists (Fig. 2E), with the west showing predominance of a winter seasonal
213 moisture regime (See SI Appendix, Fig S1), whereas precipitation seasonality was less pronounced in
214 the south-west, and low in the east where rainfall occurs throughout the year.

215 **Species and evolutionary diversity patterns**

216 The spatial patterns across the region for species and evolutionary diversity of CFR-centred plant
217 clades are shown in Fig. 3. We recovered a marked west–east gradient in species richness across the
218 southern CFR with highest concentrations of species in the southwest (> 380 species per grid cell)
219 (Fig. 3A). Species richness declined eastwards into the year-round rainfall region (See SI Appendix,
220 Fig. S2) where we recorded 65-100 species per grid cell. Total taxonomic beta diversity showed
221 consistently high values (~0.65) across almost the entire CFR (Fig.3B) and was predominantly the
222 result of species turnover (See SI Appendix, Fig. S3A & Fig. S3B). Nodes of high beta diversity were
223 associated with lower mountain slopes and adjacent lowlands, areas of rapid transition of the CFR's
224 major vegetation types, namely fynbos, renosterveld and succulent karoo (39).

225 Highest values of phylogenetic diversity were concentrated in the south-western CFR (Fig. 3C) and
226 were broadly concordant with the patterns of species richness. Residuals of phylogenetic diversity
227 over species richness showed a clear concentration of positive residuals in the eastern CFR (Fig. 3E),
228 indicating that phylogenetic diversity is generally over-dispersed in the east and more clustered in the
229 west. High values of phylogenetic-beta diversity were somewhat patchily distributed across the CFR

230 (Fig. 3D) but showed an obverse pattern to phylogenetic diversity; the south-western CFR had
231 comparatively low phylogenetic beta diversity, most likely caused by a concentration of closely
232 related and narrow ranged endemics (40) (as in Fig. 1A, scenario 1). Positive residuals of
233 phylogenetic beta diversity over taxonomic beta diversity were mostly concentrated in northern parts
234 of the CFR (Fig. 3F), where high phylogenetic beta diversity occurs without high taxonomic beta
235 diversity (Fig. 3B). Areas of high positive residuals indicate high phylogenetic beta diversity
236 associated with turnover of deeper branches on the phylogenetic tree (as in Fig. 1A, scenario 2). This
237 suggests that these areas hold a high proportion (but a low absolute number) of small-ranged species
238 belonging to older clades.

239 **Spatial regression models**

240 A separate full model including all covariates was run for each of the four metrics of diversity,
241 removing one covariate at a time, and covariate support was assessed using credible intervals and
242 wAIC statistics (*Materials and Methods*; Table 1; See SI Appendix, Table S1). The direction of the
243 relationship and the strength of the effect the covariate has on a diversity variable are summarized in
244 Table 1 and Fig. 4 (full details in SI Appendix, Fig. S4, Table S1, S2).

245 For species richness we found strong evidence (support both from credible intervals and wAIC
246 statistics) for a positive relationship with both biome stability and topographic heterogeneity, and a
247 negative relationship with seasonality (areas with moderate seasonality in the south-western and
248 southern CFR generally had higher richness whereas high-seasonality areas in the north-western CFR
249 were relatively species poor, as were the areas of lowest seasonality in the east) (Fig. 2). Species
250 richness showed marginal positive relationships with productivity and climatic stability.

251 Before controlling for species richness, we found that ecological covariates were the best predictors
252 for taxonomic beta diversity; however, the direction of these relationships did not all match the
253 direction of our predictions (Fig. 1). We recorded a negative effect with topographic heterogeneity
254 and productivity, and a positive effect with seasonality; topographic heterogeneity and seasonality
255 also received support from wAIC statistics. Controlling for species richness altered these relationships

256 and only topographic heterogeneity (negative relationship) was retained as a marginally significant
257 ecological predictor, whereas both historical stability predictors showed well-supported positive
258 effects. Biome stability received additional support from wAIC statistics and therefore emerged as the
259 most robust predictor of taxonomic beta diversity.

260 For metrics of evolutionary diversity, we found a similar pattern for phylogenetic diversity to that
261 observed for species richness, with all covariates having a strong effect (Table 1). Other than
262 seasonality, which was negatively related to phylogenetic diversity, all covariates showed positive
263 relationships with this metric. As was the case for species richness, models excluding climatic
264 stability or productivity received more support from wAIC statistics than the full model, indicating
265 that the positive effects of biome stability and topographic heterogeneity, and the negative effects of
266 seasonality, are best at predicting phylogenetic diversity. However, when controlling for species
267 richness, almost all the strong effects of covariates disappeared, except for the positive relationship
268 with biome stability.

269 For phylogenetic beta diversity, we found well-supported negative relationships with all covariates,
270 except for seasonality. Seasonality showed a well-supported positive relationship, with areas of high
271 seasonality (the strongly winter-rainfall, north-western CFR) having high phylogenetic beta diversity.
272 After accounting for species richness, the model retained a well-supported negative relationship
273 between phylogenetic beta diversity and biome stability and productivity. Climatic stability offered
274 marginal support for a negative relationship with phylogenetic beta diversity, while seasonality
275 retained marginal support for a positive relationship. Phylogenetic beta diversity, therefore, appears
276 highest in less stable and low-productivity environments such as the northern fringes of the eastern
277 CFR.

278 Overall, results from our spatial regression models support our predictions of greater species and
279 phylogenetic diversity (Fig. 1A) and lower phylogenetic beta diversity (Fig.1A, scenario 1) associated
280 with the areas of high biome stability, namely the south-western CFR. These areas support the highest
281 numbers of taxa, many of which are range-restricted and recently-diversified (See SI Appendix, Fig.

282 S3, Table S3). We also found well-supported evidence consistent with the prediction that the turnover
283 component of taxonomic beta diversity would be positively related to biome stability (Fig. 1A, B).
284 We found mostly marginal support for the role of ecological predictors in patterns of diversity, and
285 the directions of the individual diversity-covariate relationships did not always follow expected
286 predictions. Although topographical heterogeneity showed a strong positive relationship with species
287 richness (Fig. 1A), it had a strong negative relationship with beta diversity, contrary to our predictions
288 (Fig. 1A, C). Our prediction that topographical heterogeneity would have a strong, positive
289 relationship with evolutionary diversity metrics (Fig. 1A, C), was also rejected. Our prediction that
290 productivity would be positively related to species-richness was only marginally supported, and we
291 retrieved little support for our prediction of a positive relationship between phylogenetic diversity and
292 productivity (Fig. 1A, C). We also did not find support for the prediction that taxonomic beta diversity
293 would be positively related to productivity; instead we found some support for a negative relationship.
294 Contrary to our predictions (Fig.1A, scenario 2), phylogenetic beta diversity was negatively
295 associated with climatic and biome stability, and productivity.

296

297 **Discussion**

298 As an extratropical centre of plant megadiversity, the diversity of the CFR has puzzled evolutionary
299 biologists for decades. A relatively recent model for predicting global plant diversity patterns, which
300 used measures of productivity and topographic heterogeneity as explanatory variables, while
301 explaining diversity patterns for other bioregions, predicted half the observed species richness of the
302 CFR (37). Here we show that biome stability (age and area), in combination with low seasonality and
303 high topographic heterogeneity (ecological opportunity), were the best predictors of taxonomic plant
304 richness in the CFR (Fig. 1A). Importantly, productivity, widely invoked as a key driver of global
305 patterns of richness (4, 25, 37), played only a marginal role in explaining these patterns (see also 7).
306 We recognize, however, that we have presented a set of verbal predictions that may not fully capture
307 how different processes map to patterns. Further testing of our predictions by simulation with a wider
308 range of parameters would help to confirm the importance of biome stability in shaping regional
309 diversity patterns.

310

311 Our results go to the heart of one of the most enduring patterns in ecology and evolution: areas of high
312 productivity (such as the humid tropics) are repositories of large amounts of diversity. While the CFR
313 has long been seen as an exception to this rule (13, 32), ours is the first study to demonstrate this
314 analytically. The relationship between energy and diversity is largely the historical legacy of a warm
315 and wet world during the Cenozoic (2, 5, 7), which was disrupted since the mid-Miocene by
316 progressive aridification and cooling. Tropical areas may well be diverse not primarily because of
317 high water-energy regimes, but because of age and area; their biotas have persisted in vast equatorial
318 regions for the past 60 My, resulting in a far greater accumulation of species than in the younger
319 temperate and arctic zones (1, 5, 6, 41). In this sense the CFR is not an exception but a robust example
320 of a general model for explaining regional-scale taxonomic diversity gradients: richness patterns can
321 be best predicted by measures of Cenozoic environmental stability.

322

323 Other important metrics of diversity also appear best explained by measures of stability, with positive
324 correlations retrieved for all but one diversity metric, namely phylogenetic beta diversity. High values
325 of species turnover (~ 60% changes in species composition) were recorded throughout the CFR and
326 showed a strong positive correlation with biome stability. Contrary to our predictions (e.g. Fig. 1A),
327 greater ecological opportunity did not necessarily equate to higher values of species turnover. This
328 pattern is likely a consequence of biome stability allowing the persistence in and generation of habitat
329 specialists (greater niche filling) in the south-western CFR, from both young and old lineages. The
330 pattern cannot be attributed to topographical heterogeneity *per se* since this is essentially invariant
331 across the CFR (32, 42). The low ratio of species loss (the nestedness component of beta diversity) in
332 the less stable areas of the eastern CFR is surprising considering the findings by other studies where
333 high nestedness was associated with areas experiencing climatic instability (e.g. see 17, 21, 43, 44).
334 However, by focusing only on Cape clades, which tend to be habitat specialists, we do not fully
335 capture the many habitat generalists associated with widespread clades that are best represented in the
336 eastern CFR (33, 39), and which may contribute more to nestedness.

337

338 Phylogenetic diversity in the CFR shows patterns similar to species richness, with a concentration of
339 high values in the western part of the region. Our results confirm that overall, phylogenetic diversity
340 is more evenly distributed in the phylogenetic tree, and generally on longer branches (i.e.
341 overdispersed), in the eastern CFR (45, 46). Our finding of a strong positive relationship of
342 phylogenetic diversity with biome stability (Table 1) supports this pattern, which can be explained by
343 the presence in the western part of the CFR of a high number of closely related taxa that accumulated
344 over time in a relatively stable environment (see (45)). The strong relationship of phylogenetic
345 diversity with biome stability may suggest high speciation rates coupled to lower extinction rates for
346 the south-western CFR (e.g. (42); Fig 1A). However, owing to the high incidence range-restricted
347 taxa in the western CFR (40, 42), extinction rates may likely be high (47). On the other hand, the
348 eastern CFR has experienced greater biome instability, leading to limited speciation and increased
349 extinction compared to the western part of the region, as exemplified by the presence of fewer species
350 from more disparate lineages positioned on long branches in the phylogenetic tree (e.g. (45); Fig. 1D).
351 Importantly, paleoecological data modelling studies suggest more stable biomes and environments in
352 the western than eastern CFR during the Late Pleistocene; during glacial periods CFR biomes
353 persisted or even expanded in the west, in the east, large areas were replaced by subtropical grassland
354 (e.g. (44, 48–50)).

355

356 The phylogenetic beta diversity patterns revealed here are somewhat more difficult to explain and
357 need to be considered in parallel with taxonomic beta diversity (24). High levels of phylogenetic beta
358 diversity and positive residuals (i.e. excess phylogenetic beta diversity above and beyond that
359 expected from taxonomic beta diversity) were found mostly in the north of the CFR, with low levels
360 of phylogenetic beta diversity (and negative residuals) concentrated in the south-west corner of the
361 region. This suggests that these areas hold a high proportion (but a low absolute number) of small
362 ranged species (40, 42) belonging to older clades (Fig. 1A, scenario 2). However, some species near
363 the northern boundaries of the CFR may be present in only a few localities within the CFR but have a
364 much wider range extending outside of the region. This would bias the results towards higher

365 phylogenetic beta diversity values in the northern part of the CFR because these potentially wider
366 ranges would not be accounted for in the present calculations. On the other hand, the coastal regions
367 of the CFR are mostly characterised by negative residuals and high taxonomic beta diversity (Fig. 3B,
368 E), which indicates the presence of a high proportion of range-restricted species, mostly from recently
369 diversified clades (Fig. 1A, scenario 1).

370

371 Using a region of extraordinarily high plant richness and endemism we conclude that age and area
372 best explains large-scale patterns of plant diversity. We further argue that far from being the
373 exception, the CFR model suggests that environmental stability may be the primary predictor of plant
374 megadiversity. This explanation, retrieved for a longitudinal gradient, is equally applicable to the
375 intensively researched latitudinal diversity gradient (1, 5, 21, 51). Our use of a longitudinal gradient of
376 diversity is important in that it allowed us to explore predictors of regional-scale diversity not
377 necessarily concordant with gradients of productivity. Given sufficient biome stability in combination
378 with high ecological opportunity, we see no reason why megadiversity should not evolve in low-
379 production bioregions. An illustrative example is the extraordinarily high biodiversity of South
380 Africa’s winter-rainfall desert – the Succulent Karoo – which, like the adjacent CFR, enjoyed a
381 relatively stable Pleistocene climate (52).

382

383 **Material & Methods**

384 **Cape plant database**

385 We built a plant species distributional database for South African angiosperms incorporating data
386 from national plant atlas and citizen science projects, and databased herbarium specimens (53–56).

387 The final database comprised 19,622 taxa (ca 96% of South African taxa) (57) and just over 1.8
388 million point locality records. In order to account for the inherent biases in such presence-only or
389 “atlas-type” data, we employed a geospatial modelling technique (58) to interpolate the distribution
390 records for each plant species and to calculate a continuous probability of occurrence surface for each
391 species at a two minute grid cell scale (~ 12km²), with an associated measure of uncertainty. We

392 followed the same modelling procedures (“Spatial Model 1”) described in detail by (58) and using
393 code provided in Spatial Model 1 that built on earlier models by (59). For each species, we built a
394 model at two minute resolution combining point pattern analysis methods with environmental niche
395 information, to account for ecological similarity, inferred observer effort and geographical distance.
396 Briefly, this process involved two stages, each consisting of a number of separate steps. The first stage
397 involved selecting a sample of non-focal species records to act as pseudo-absences (reflecting the
398 pattern of observation in the dataset), and the second stage involved interpolating distributions based
399 on presence and pseudo-absence records. In slightly more detail, the first stage required (1) mapping
400 all records of the focal species and generating a kernel density estimate for records of this species; (2)
401 identifying all records of all other plant species (not just representatives of Cape Clades) > 100m from
402 records of the focal species and generating similar kernel density estimates; (3) computation of the
403 difference in density estimates between focal and non-focal species (an approximate index of the
404 probability of encountering the focal species); (4) computation of an environmental envelope within a
405 principal component analysis of rainfall (mean annual rainfall and rainfall season) (60) and
406 temperature variables (mean winter and mean summer temperature) (60) and soil covariates (61)
407 (means taken from aggregating original soil data resolution of ca. 1km² to our ca. 12km² grid cell size;
408 soil properties: % calcium carbonate, % clay, % silt, % sand; and pH); (5) computing the
409 environmental distance between all two minute raster cells and the centroid of the environmental
410 envelope occupied by the focal species; and (6) sampling records of the non-focal species using the
411 environmental distance and geographic probability of encountering the focal species to bias selection
412 towards locations where absence was most likely. With pseudo-absence records selected, the second
413 stage of analysis involved regression kriging of the presence / absence points onto the two minute
414 raster surface, using the rainfall, temperature and soil covariates. For species recorded from <5
415 locations in the database, we were unable accurately to interpolate distribution and simply generated a
416 raster map with presence (1) and assumed absence (0) directly from the recorded data. We sought to
417 verify distributions for well-known species, sending maps to colleagues with detailed knowledge of
418 the species groups concerned and asking for expert opinion on the map quality. Our estimated species
419 richness patterns were consistent with expert opinion. Once the surfaces for probability of occurrence

420 of all species were calculated, we then selected only those species associated with pre-defined Cape
421 clades (following the criteria of (36): CFR origin and > 50% of species native to the CFR) and for
422 which phylogenetic data were available (Table S3). Finally, the calculated probability of occurrence
423 surfaces for all Cape clade species was clipped to the extent of the CFR as defined by (62). Our final
424 Cape clade database consisted of modelled occurrences across 8,347 two-minute grid cells for 4,813
425 taxa (51% of total CFR species (63)). These probabilities of occurrence surfaces were used in all our
426 metrics of contemporary and evolutionary diversity. All data analyses and geospatial modelling were
427 undertaken in R (64) using packages *spatstat* (65), *sp* (66, 67), *rgdal* (68) and *gstat* (69).

428 **Taxonomic plant diversity**

429 We calculated two measures of taxonomic species diversity: species richness and beta diversity.
430 Species richness was calculated for each grid cell as the summed probability surfaces for all our Cape
431 clade species. Three different measures of beta diversity were calculated using the indices presented
432 by (19): Sorenson's beta-diversity ($\beta_{\text{sor}} = b + c / (2a + b + c)$) and its two component parts of Simpson's
433 spatial turnover $\beta_{\text{sim}} = \min(b, c) / [a + \min(b, c)]$ and nestedness $\beta_{\text{nes}} = \beta_{\text{sor}} - \beta_{\text{sim}}$. Variable a is the number
434 of species common to a focal and neighbour grid cell, b is the number of species that occur only in the
435 focal grid cell, and c is the number of species that occur only in the adjacent cell. In each case we
436 computed a , b and c based on probabilities of presence: a was simply the sum of the probability of
437 presence of all species; b , the sum of the product of the probabilities that a species was present in the
438 focal cell, but absent in a neighbour; and c , the sum of the product of the probabilities that a species
439 was absent in the focal cell, but present in a neighbour. Using interpolated species distributions
440 offered advantages over and above raw presence-only data, as our beta diversity indices were not
441 overly biased by gaps in the data (i.e. false absences). Calculated beta diversity for each grid cell
442 represented the mean value of probabilities between the focal cell and all its neighbours (maximum of
443 eight). We specifically partitioned beta diversity into its two component parts across the CFR, as the
444 processes associated with species loss and gain (nestedness) and replacement (turnover) can be
445 fundamentally different and can offer contrasting insights into the generation of diversity (17, 19, 43).

446 **Phylogenetic plant diversity**

447 Phylogenetic diversity metrics were computed for 21 Cape clades for which molecular data were
448 available (See SI Appendix, Table S3). Phylogenetic trees were compiled from one of three data
449 sources: 1) trees acquired directly from the publication or provided by the authors; 2) matrices
450 obtained from the publication or from the authors; and 3) sequence data downloaded from GenBank.
451 Trees acquired directly from their published source were made ultrametric using the function *chronos*
452 (70) as implemented in the R package *APE* (71), which implements the penalized likelihood method
453 (72). The “correlated” model of substitution rate variation among branches was applied and the root
454 of the tree was assigned a value of 1.0. If an ultrametric tree was obtained directly from the original
455 publication, it was standardised so that its root was given a value of 1.0. For cases for which either
456 matrices or sequence data were obtained, the software *RAXML* (v. 8.2.8), as implemented on the
457 *Cipres* portal (www.phylo.org), was used to reconstruct a phylogenetic tree under the maximum
458 likelihood (ML) criterion, with 1,000 rapid bootstrap replicates followed by the search of the best ML
459 tree; the *GTRCAT* model was used and all other parameters were set up with their default settings.
460 DNA sequence data were retrieved from GenBank using *Geneious* (version 7.1.2) (73) and aligned
461 using the *MUSCLE* (74) algorithm. The approach used for each Cape clade is described in Table S3.
462 The 21 individual species-level Cape clade trees were grafted onto a previously published genus-level
463 phylogeny of the Cape flora (45). This approach was favoured for several reasons. First, accurately
464 calibrating phylogenetic trees from Cape groups is particularly difficult due to the limited information
465 available in the fossil record for the vast majority of these clades (e.g. (36)). Second, the comparison
466 of phylogenetic diversity metrics between clades would be invalid if all clades were in effect assigned
467 the same age, as performed here (i.e. all root ages assigned a value of 1.0), which they are evidently
468 not (e.g. (38, 49, 75)). Third, embedding all 21 Cape clades in a flora-wide tree allows us to compile
469 overall phylogenetic diversity metrics for all clades and account for their deep history, which is
470 particularly important in the case of phylogenetic beta diversity because the age of a group will
471 significantly affect turnover in branch lengths (i.e. shallow vs deep branches).

472 The function *paste.tree* from the R package *phytools* (76) was used to graft the individual trees onto
473 the Cape flora genus-level tree. For clades comprising more than one genus (e.g. Bruniaceae,
474 Podalyriaceae, Restionaceae), all genera except one (randomly selected) were first pruned so that all 21
475 clades are represented by only one branch in the Cape flora tree. For each clade, the crown node was
476 grafted in the middle of the corresponding branch in the Cape flora tree. Phylogenetic diversity and
477 phylogenetic beta diversity metrics were calculated with the resulting Cape flora genus-level tree
478 comprising the grafted Cape clades, considering only the species found in the Cape clades in the
479 calculations (i.e. the other genera included in the Cape flora tree were not considered here).

480 Phylogenetic diversity was calculated for each grid as the sum of all branches connecting all members
481 of a set of taxa, including the root of the tree. Branch lengths were weighted using the same
482 probabilistic computations used for species diversity (see above), with a terminal branch weighted by
483 the probability of occurrence in a given cell of the species it represents, while all internal branches
484 were weighted by the joint probability of occurrence in a given cell of all the species it subtends.
485 Phylogenetic beta diversity was compiled using Sorenson's index, similarly to taxonomic beta
486 diversity as described above, where variable a is the sum of the branch lengths common to a given
487 grid cell and an adjoining grid cell, b is the sum of the branch lengths that only occur in a given grid
488 cell, and c is the sum of the branch lengths that occur only in the adjacent cell. As for the phylogenetic
489 diversity calculation, branch lengths were weighted using their probability of occurrence in each grid
490 cell.

491 **Surrogate variables for ecological opportunity**

492 We calculated topographic heterogeneity from the Shuttle Radar Topography Mission (SRTM) digital
493 elevation model (DEM; available from <http://earthexplorer.usgs.gov/>) computing the mean absolute
494 difference in altitude between the focal pixel and its eight neighbours at the native 30m resolution
495 (77), then calculating the median value per two minute grid cell (See SI Appendix, Fig. S5). As beta-
496 diversity was measured at two minute resolution, we further compared this measure of topographic
497 heterogeneity with the somewhat cruder analysis generated by first aggregating the DEM data to 2

498 minute resolution and computing the mean altitude, then computing roughness on this using the same
499 algorithm. These two alternative surfaces were correlated at $r = 0.632$, so we used the first in all
500 analyses (See SI Appendix, Fig. S5). Seasonality was calculated using a measure of rainfall
501 concentration (ranging between 0% for zero seasonality to 100% for all rainfall in a single month)
502 (60). We used as a measure of productivity, annual actual evapotranspiration obtained from satellite
503 data (MOD16A2 Version 6 Evapotranspiration/Latent Heat Flux product is an 8-day composite
504 product produced at 500 metre pixel resolution (78)). Actual evapotranspiration is a measure of water-
505 energy balance closely associated with plant productivity (4). We used 8-day values to generate an
506 annual value (mm/a) and aggregated this to our two-minute grid taking the median value for each
507 two-minute cell.

508 **Surrogate variables for environmental stability**

509 We investigated climate and biome changes over the 140ka, a period spanning two major glacial-
510 interglacial cycles (Marine Oxygen Isotope Stages 6 to 1) (35). Results from 78 palaeoclimate
511 experiments and a pre-industrial experiment made with a consistent configuration of the Hadley
512 Centre unified model (79), a fully-coupled atmosphere–ocean general circulation model (80), were
513 used to compute anomalies for monthly mean temperature, precipitation and cloudiness. Thin-plate
514 splines fitted to these anomalies (81) were used to interpolate them to a 0.5° grid. Palaeoclimate
515 scenarios at 0.5° grid resolution were then generated for the 78 time slices by applying the
516 interpolated anomalies to observed recent (1961–90) values in the CRU CL 1.0 dataset (82). Nine
517 bioclimatic variables were computed for each grid cell and time slice, including 1961–90: annual
518 thermal sums above 0°C and 5°C ; mean temperatures of the coldest and warmest months; an estimate
519 of the annual ratio of actual to potential evapotranspiration; annual total intensity of the wet and dry
520 season(s); and maximum wet and dry season intensity (for details see (35)). Values for each
521 bioclimatic variable were then standardised to zero mean and unit standard deviation across all grid
522 cells and time slices, the standardised values being used to compute Euclidean distances between all
523 3081 possible time-slice pairs for each grid cell. Finally, the mean of the Euclidean distances for a

524 grid cell was used as the metric of climatic stability, smaller values indicating greater stability. No
525 two covariates were particularly strongly correlated (all $r < 0.6$; See SI Appendix, Fig. S6).

526 The relationships between the relative extents in each 0.5° grid cell of each of the nine regional
527 biomes (39) and present climate were modelled using quantitative climatic response surfaces (79).
528 Details of the modelling approach are given by (35). These models were used to simulate the relative
529 extent of each biome in each grid cell for each of the 79 time slices. The frequency with which each
530 biome dominated each grid cell (i.e. had the greatest relative extent) across time slices was counted
531 and the biome with the highest frequency of dominance in a grid cell was identified and its frequency
532 used as the metric of biome stability for that grid cell. After computation, we downscaled predictions
533 to our 2-minute raster using bilinear interpolation.

534 **Spatial regression models**

535 To test predictions about drivers of diversity we fitted spatial regression models to each of the
536 taxonomic and phylogenetic diversity surfaces, using covariates (topographic heterogeneity, actual
537 evapotranspiration, rainfall seasonality, and biome and climatic stability) representing the primary
538 hypotheses to predict diversity patterns. Specifically, we fitted intrinsic Continuous Autoregressive
539 (iCAR (83)) models using Integrated Nested Laplace Approximation (INLA (84)) via the R-INLA
540 package (85). iCAR models have been shown to perform well in a variety of spatial regression
541 situations (86) and INLA provides a fast, Bayesian approach to fitting these computationally
542 demanding models. As components of beta diversity (taxonomic and phylogenetic) and phylogenetic
543 diversity measures are strongly influenced by local gradients in species richness (19, 45) we fitted
544 further models to predict these variables that also included species richness as a covariate, expecting
545 that including this covariate would remove relationships that are due primarily to drivers of species
546 richness, rather than beta and phylogenetic diversity *per se*. We expect the models with species
547 richness to be both more conservative and more reliable, but included models without them to
548 facilitate understanding of the simpler relationships. As INLA provides a Bayesian approach to model
549 fitting we assessed support for parameter estimates by identifying whether or not 95% Credible
550 Intervals (CIs) overlapped zero. Although there appears to be potential for a degree of circularity in

551 our use of environmental variables to model species distributions and then relating modelled species
552 data to environmental data in our spatial regression models, it will not necessarily do so and previous
553 work demonstrates that covariates predicting richness can be markedly different to covariates
554 predicting individual distributions (58). If this potential circularity was problematic, we would expect
555 that the environmental data to outperform the other covariates, but as our results did not support this,
556 we can be confident our results are not an artefact.

557 **Data Availability**

558 Plant species and phylogenetic data are available from published sources and online repositories listed
559 in Material & Methods and Supporting Information.

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- 756
- 757

758 **Figure Legends**

759 **Fig.1.** Hypothetical examples depicting the possible scenarios by which the ecological opportunity
760 hypothesis, which focuses upon gradients in, for example, topographic diversity, seasonality and
761 water–energy, and/or the age and area hypothesis, here considered in terms of late-Pleistocene
762 climatic and biome stability, can explain plant diversity patterns in the CFR. Areas where both
763 hypotheses would influence diversity achieve the highest values for all diversity metrics (Box A),
764 except possibly for phylogenetic beta diversity (PBD), which value will vary depending on the
765 proportion of range-restricted species and their distribution on the tree. In Box A, Scenario 1 has a
766 high proportion of range-restricted, recently diverged species and thus a low PBD, while in Scenario 2
767 the range-restricted species are predominantly older, resulting in a higher PBD. The effect of the age
768 and area hypothesis alone is shown in Box B, while the outcomes of the ecological opportunity
769 hypothesis alone are depicted in Box C. In Boxes B and C, PBD will increase with higher proportions
770 of range-restricted species, but will be less affected by the distribution of these species (contrary to the
771 situation in Box A); range-restricted taxa are expected to be more prevalent in Box C. An area that is
772 ecologically homogeneous and with unstable biome and climate (Box D) has the lowest diversity
773 metrics. Black dots and circles depict the distribution on the phylogenetic tree of the species present in
774 each scenario.

775

776 **Fig. 2.** Spatial patterns of the five predictor variables (A-E) plotted for the Cape Floristic Region (F).

777

778 **Fig. 3.** Spatial patterns of the four diversity variables (A-D) and of residuals from linear regressions of
779 phylogenetic diversity on species richness (E) and of phylogenetic-beta diversity on taxonomic beta
780 diversity (F), plotted for the Cape Floristic Region.

781

782 **Fig. 4.** The relationships between species richness predicted from models with (A) climate stability,
783 (B) biome stability, (C) topographic heterogeneity, (D) energy, and (E) seasonality. Figure (F) shows
784 simplified plots of the relationship of these covariates with the remaining diversity variables
785 controlling for species richness (species turnover, phylogenetic and phylogenetic-beta diversity; See

786 SI Appendix, Fig. S4 for detailed plots). Within each plot, the results are shown with median estimate
787 and 95% confidence intervals (shaded). Confidence intervals are computed from models that include
788 all fixed and spatially explicit random effects: the presence of strong spatial effects generates wider
789 scatter in the points than may be expected from plotted confidence intervals. A large asterisk indicates
790 well-supported effects with confidence intervals that exclude zero; a small asterisk indicates that
791 models excluding a specific covariate received more support from wAIC statistics than a full model
792 including all covariates. For example, excluding climate stability or energy received more support
793 from wAIC statistics than the full model suggesting the positive effects of biome stability and
794 topographic heterogeneity and the negative effects of seasonality on species richness are the most
795 robust. [phylo-diversity = phylogenetic diversity; phylo-beta diversity = phylogenetic beta diversity].

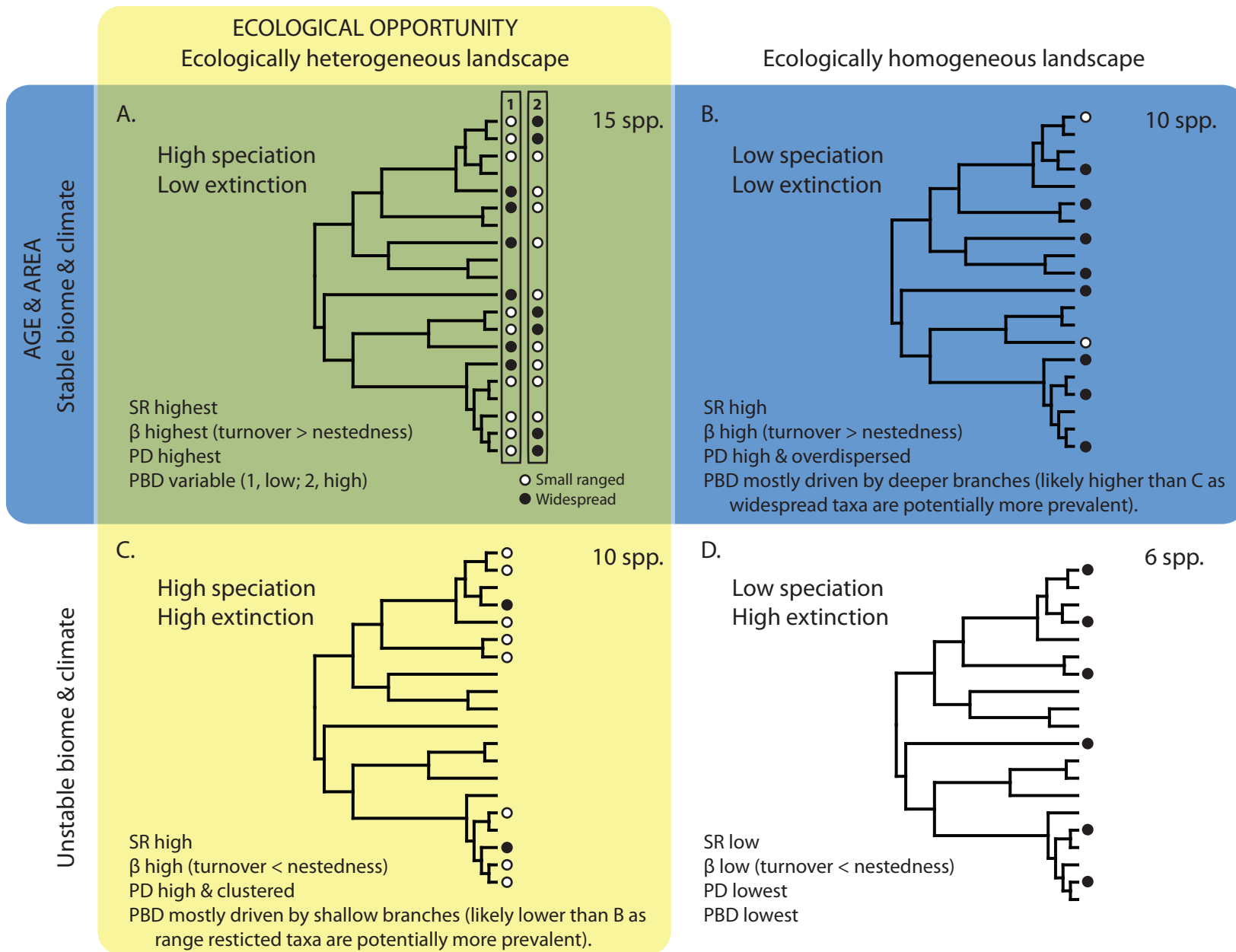
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797 **Tables and Legend**

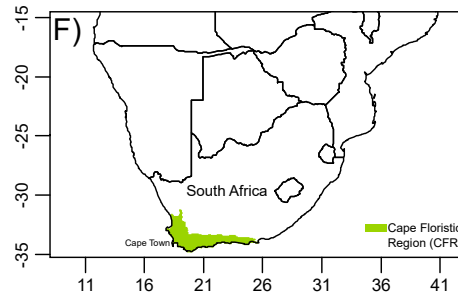
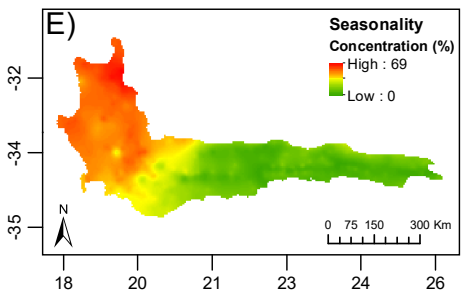
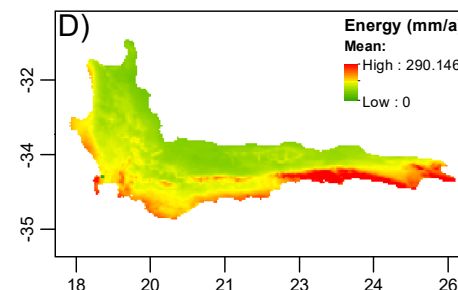
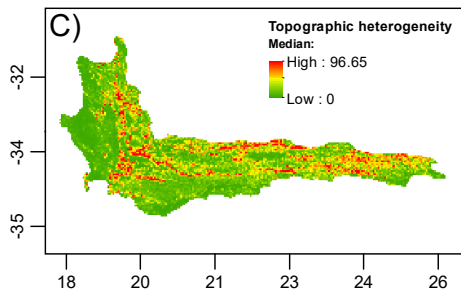
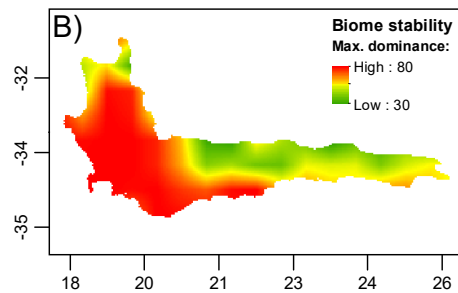
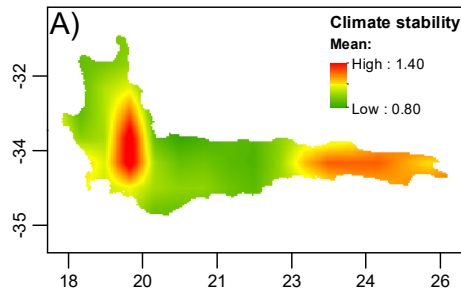
798 **Table 1.** Raw mean effects of the INLA analysis for raw diversity variables and controlling for the
799 effects of species richness (SR). The set of historical and ecological covariates best explaining the
800 spatial diversity patterns are shown by well-supported effects (in bold font) and wAIC values: shaded
801 cells indicate a wAIC value increase of ≥ 3 when a covariate is removed from a model with a full set
802 of covariates (See SI Appendix, Table S1 & S2 for full models results).

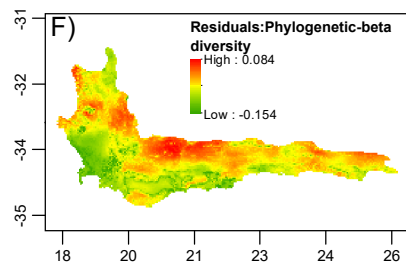
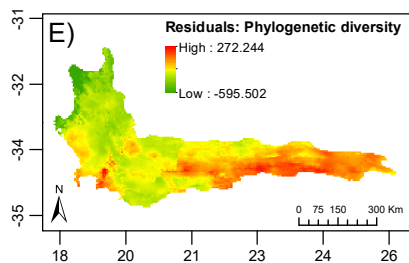
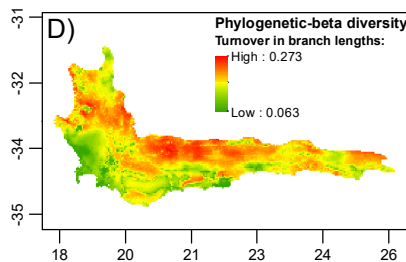
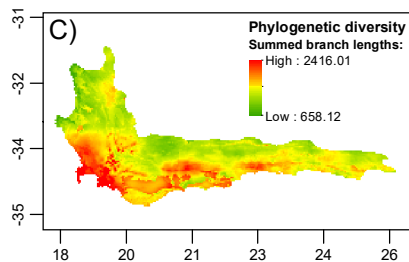
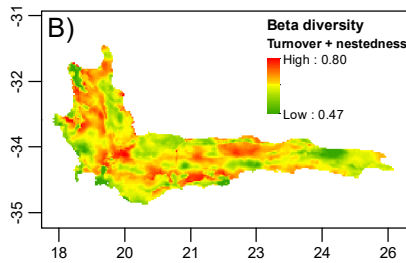
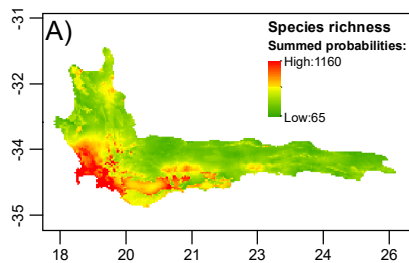
		Age and area		Ecological opportunity		
		Climate stability	Biome stability	Topographic heterogeneity	Productivity	Seasonality
Taxonomic diversity	Species richness	0.110 (0.020, 0.200)	0.219 (0.109, 0.328)	0.078 (0.051, 0.105)	0.079 (0.024, 0.133)	-0.377 (-0.554, -0.120)
	Beta diversity	0.001 (-0.128, 0.147)	0.112 (-0.056, 0.279)	-0.111 (-0.141, -0.082)	-0.080 (-0.152, -0.008)	0.295 (0.046, 0.543)
	Beta diversity SR	0.134 (0.022, 0.247)	0.328 (0.191, 0.465)	-0.047 (-0.075, -0.018)	-0.028 (-0.091, 0.035)	-0.163 (-0.375, 0.050)
Evolutionary diversity	Phylogenetic diversity	0.107 (0.013, 0.202)	0.295 (0.179, 0.410)	0.083 (0.056, 0.111)	0.099 (0.043, 0.156)	-0.524 (-0.708, -0.339)
	Phylogenetic diversitySR	0.022 (-0.032, 0.075)	0.094 (0.029, 0.161)	0.019 (-0.006, 0.044)	0.030 (-0.010, 0.070)	-0.193 (-0.306, -0.079)
	Phylogenetic beta diversity	0.0001 (-0.104, 0.103)	-0.337 (-0.463, -0.210)	-0.086 (-0.114, -0.059)	-0.162 (-0.221, -0.102)	0.220 (0.021, 0.418)
	Phylogenetic beta diversitySR	0.120 (0.053, 0.187)	-0.173 (-0.255, -0.090)	-0.018 (-0.044, 0.008)	-0.090 (-0.136, -0.044)	-0.172 (-0.312, -0.032)

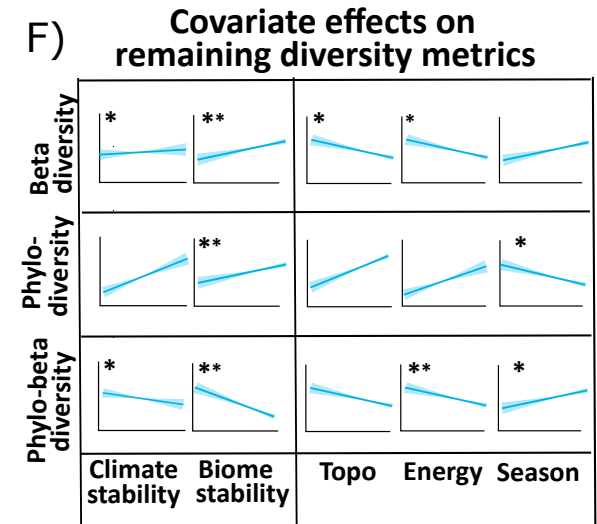
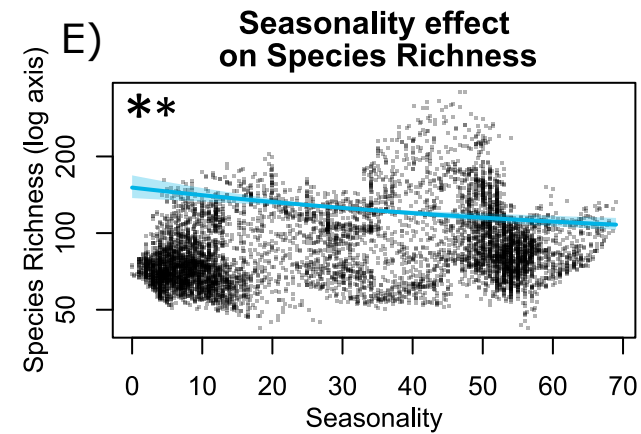
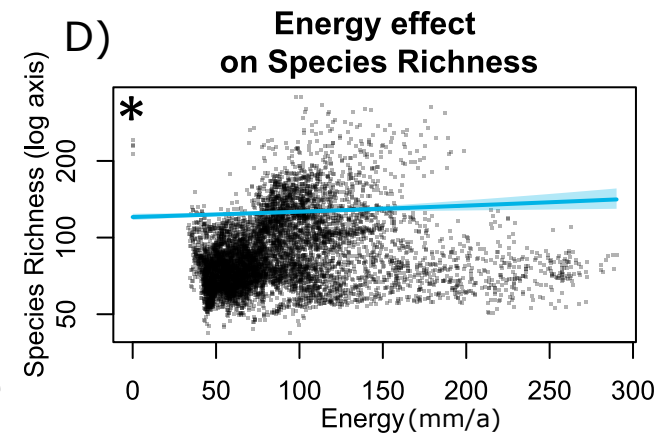
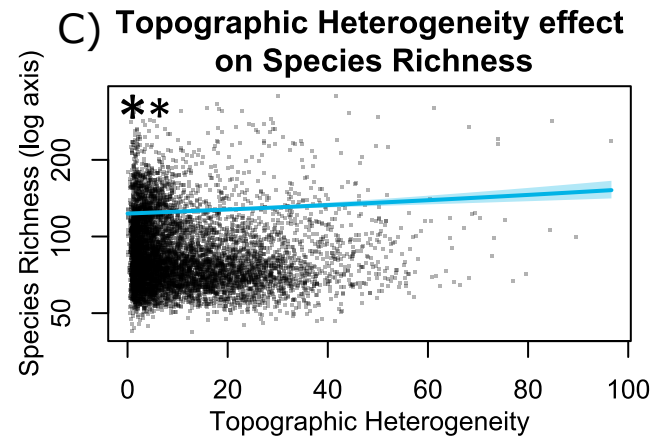
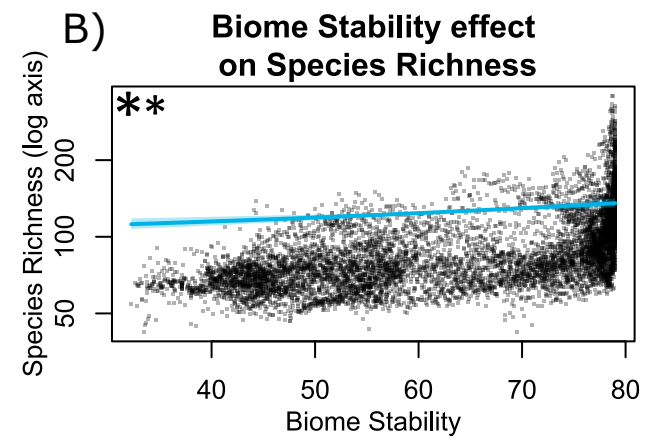
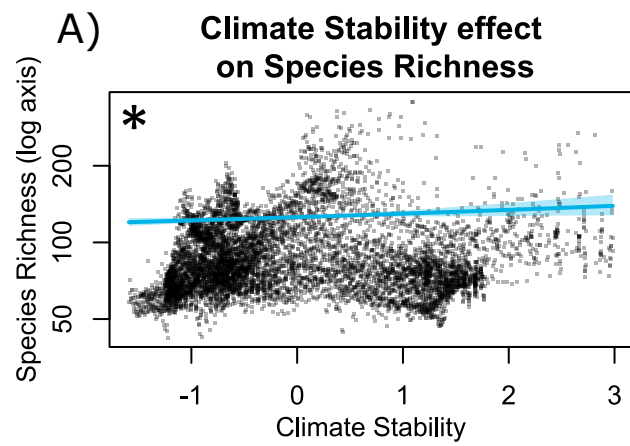
803 [Medians with lower (0.025) and upper (0.975) quantiles are shown in brackets]



SR: species diversity β : beta diversity PD: phylogenetic diversity PBD: phylogenetic beta diversity

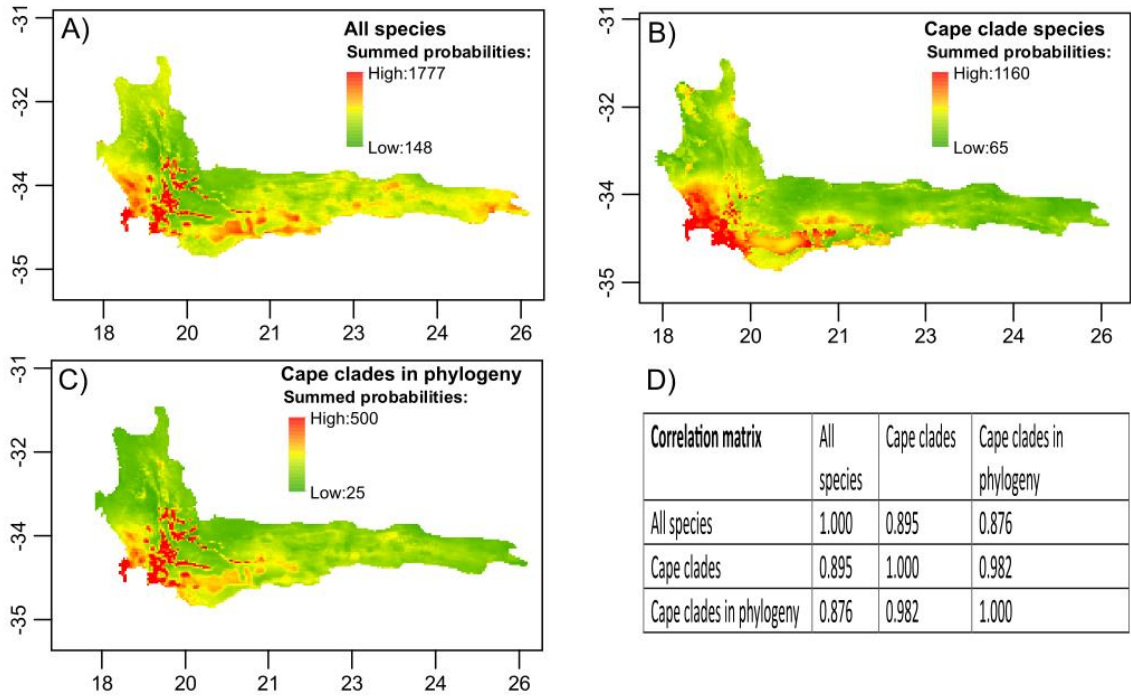






1 **Supporting Information**

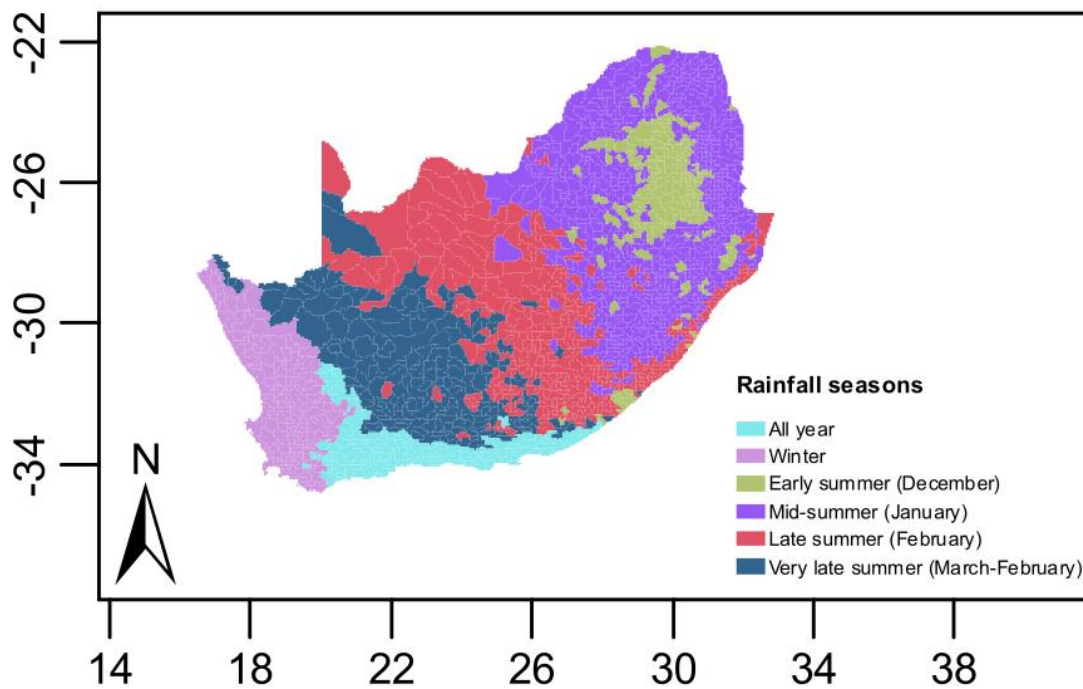
2 Fig S1. (A) Total CFR plant species, (B) Cape clade species and (C) the Cape clade species included
3 in our phylogeny show (D) strongly correlated spatial patterns of richness with each other ($r \sim 0.9$).



4

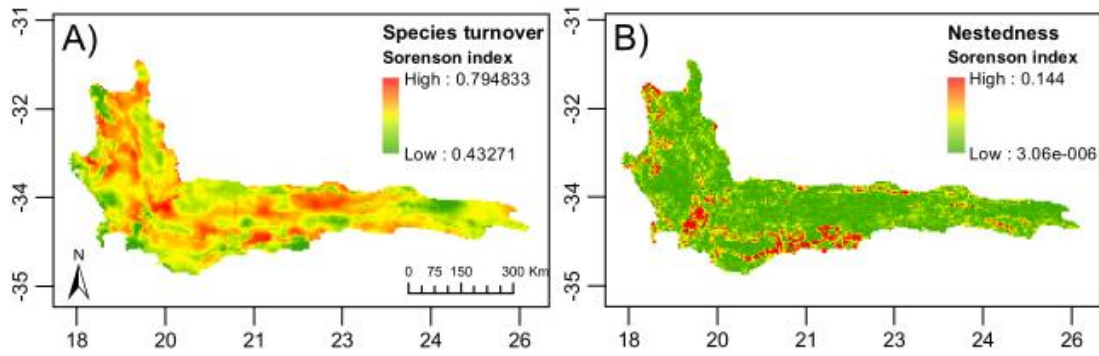
5

6 Fig. S2. Rainfall seasonality regions over South Africa following Schulze & Maharaj (2007).



7
8 [Schulze, R.E. and Maharaj, M. 2007. Rainfall Seasonality. In: Schulze, R.E. (Ed). 2007. South African Atlas of
9 Climatology and Agrohydrology. Water Research Commission, Pretoria, RSA, WRC Report 1489/1/06, Section 6.5.]
10

11 Fig S3. Spatial patterns of (A) species turnover and (B) nestedness plotted for the Cape Floristic
12 Region. Taxonomic beta diversity was dominated by species turnover for the CFR, with nestedness
13 making up only a small proportion of total taxonomic beta diversity.



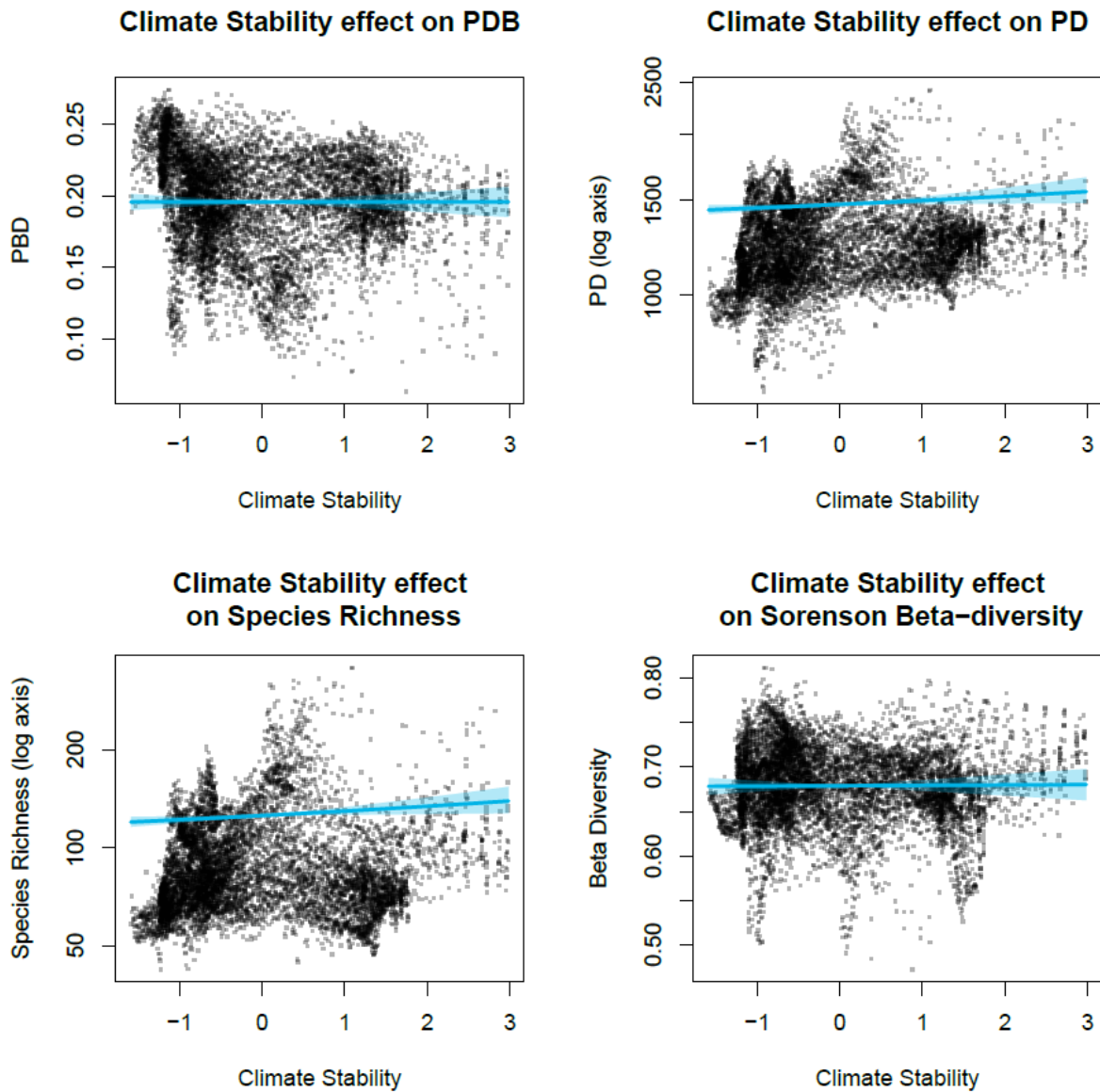
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16 Table S1. wAIC values for the full model with all five covariates, and for models where a single
 17 covariate is removed. Grey shading indicates the importance of a covariate with an increase of ≥ 3 in
 18 the wAIC value when removed from the model with the lowest wAIC (shown in bold font)]. wAIC is
 19 a measure of model support equivalent to the well-known AIC score but appropriate to Bayesian
 20 models that can be used to compare relative support for different models of the same data. Deviance
 21 information criterion (dic) values, a Bayesian alternative to Akaike's information criterion (AIC), are
 22 also given. [Full model = climatic stability + biome stability + topographic heterogeneity +
 23 productivity + seasonality; SR = model controlling for the effects of species richness.]

	Model	wAIC	dic	Difference between model with lowest wAIC
Species richness	Full model	16020.02074	16396.06631	1.048
	Full model – climatic stability	16020.79628	16399.70405	1.823
	Full model – biome stability	16023.5865	16407.49952	4.614
	Full model – productivity	16018.9728	16400.69428	--
	Full model – seasonality	16029.73992	16410.44291	10.767
	Full model – topographic heterogeneity	16050.12553	16425.61027	31.153
Taxonomic beta diversity	Full model	17041.62868	17798.26508	0.980
	Full model – climatic stability	17041.21901	17797.33856	0.570
	Full model – biome stability	17041.24787	17798.5425	0.599
	Full model – productivity	17040.64871	17800.2544	--
	Full model – seasonality	17049.17655	17803.02755	8.528
	Full model – topographic heterogeneity	17064.87193	17841.74798	24.223
	Full modelSR	16013.46376	16612.4569	3.035
	Full model – climatic stabilitySR	16010.42889	16615.04852	--
	Full model – biome stabilitySR	16017.56591	16628.92278	7.137
	Full model – productivitySR	16013.43766	16611.79949	3.009
	Full model – seasonalitySR	16010.51185	16612.3853	0.083
	Full model – topographic heterogeneitySR	16013.54935	16618.77517	3.120
Phylogenetic diversity	Full model	15926.48838	16353.83571	--
	Full model – climatic stability	15926.86926	16356.74216	0.381
	Full model – biome stability	15933.324	16373.34072	6.836
	Full model – productivity	15927.00528	16361.82408	0.517
	Full model – seasonality	15943.04467	16379.95724	16.556
	Full model – topographic heterogeneity	15956.00152	16386.46558	29.513
	Full modelSR	14651.41871	14770.87755	1.283
	Full model – climatic stabilitySR	14650.1358	14769.8164	--
	Full model – biome stabilitySR	14654.26908	14776.59751	4.133
	Full model – productivitySR	14652.53905	14771.2953	2.403
	Full model – seasonalitySR	14652.8451	14778.6903	2.709
	Full model – topographic heterogeneitySR	14651.16078	14770.83809	1.025
Phylogenetic-beta diversity	Full model	16448.12959	16926.18894	0.358
	Full model – climatic stability	16447.7712	16925.16497	--
	Full model – biome stability	16450.84972	16945.98474	3.079
	Full model – productivity	16459.3285	16948.50771	11.557
	Full model – seasonality	16452.88221	16929.73907	5.111
	Full model – topographic heterogeneity	16478.44714	16959.88247	30.676
	Full modelSR	15567.37618	15766.48978	0.414
	Full model – climatic stabilitySR	15566.96256	15774.92335	--
	Full model – biome stabilitySR	15571.87702	15779.6292	4.914
	Full model – productivitySR	15579.72643	15779.45668	12.764
	Full model – seasonalitySR	15567.0543	15769.84668	0.092
	Full model – topographic heterogeneitySR	15569.18265	15766.63675	2.220

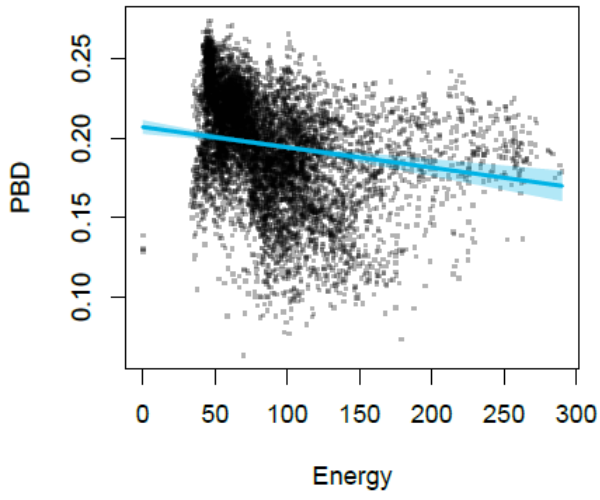
25 Fig. S4. The relationships between plant diversity variables predicted from models with climate
26 stability, biome stability, topographic heterogeneity, productivity, and seasonality. Within each plot,
27 the results are shown with median estimate and 95% confidence intervals (shaded). Confidence
28 intervals are computed from models that include all fixed and spatially explicit random effects: the
29 presence of strong spatial effects generates wider scatter in the points than may be expected from
30 plotted confidence intervals. [PD = phylogenetic diversity; PBD = phylogenetic beta diversity;
31 Sorenson Beta-diversity = beta diversity]. These plots should be read in conjunction with Table S1.



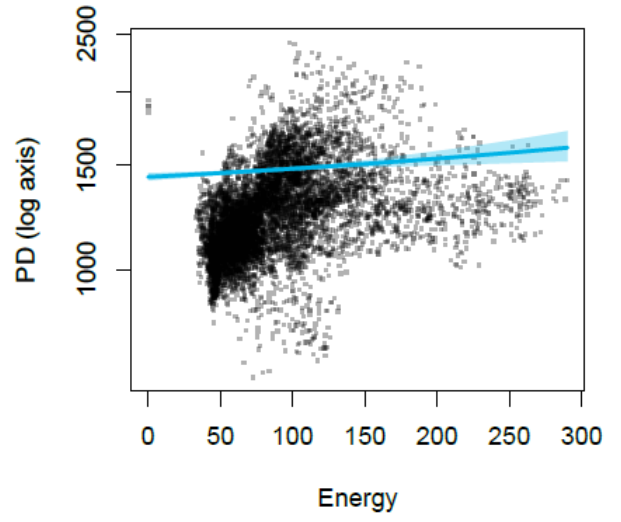
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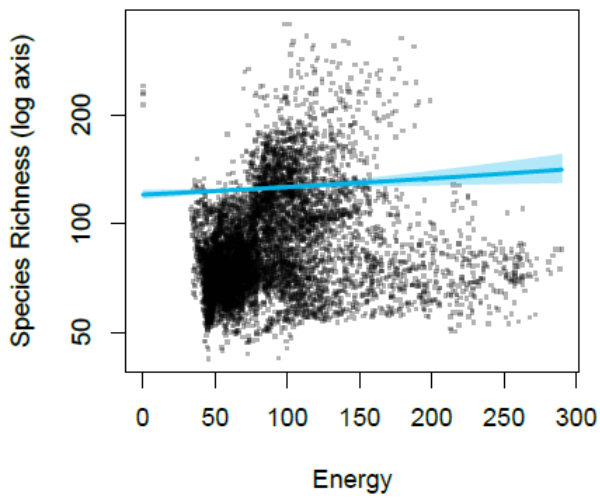
Energy effect on PDB



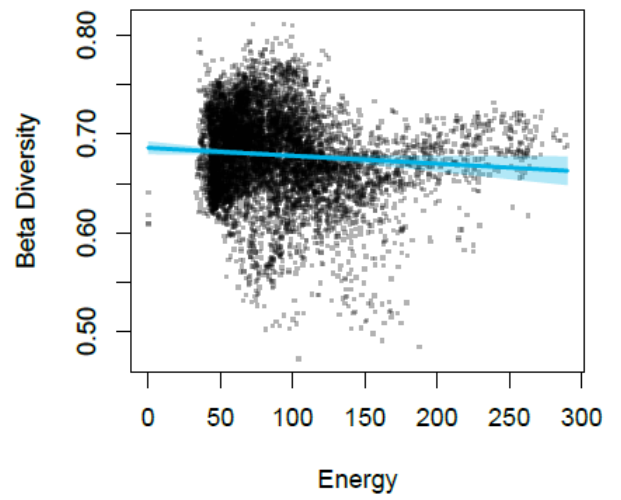
Energy effect on PD



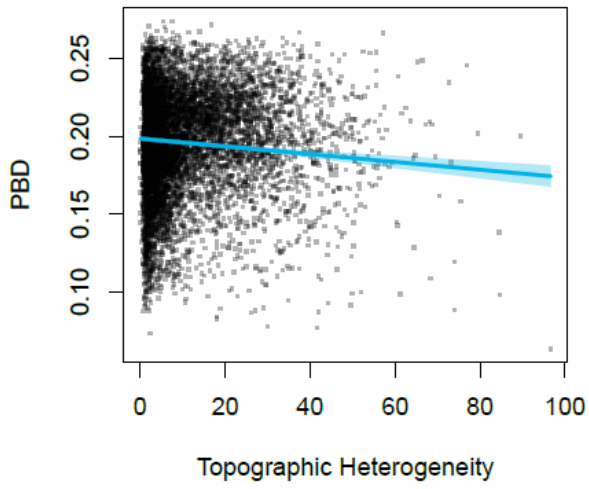
Energy effect on Species Richness



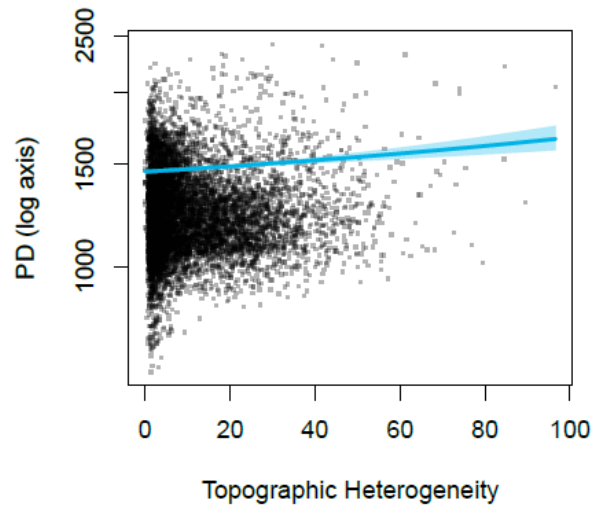
Energy effect on Sorenson Beta-diversity



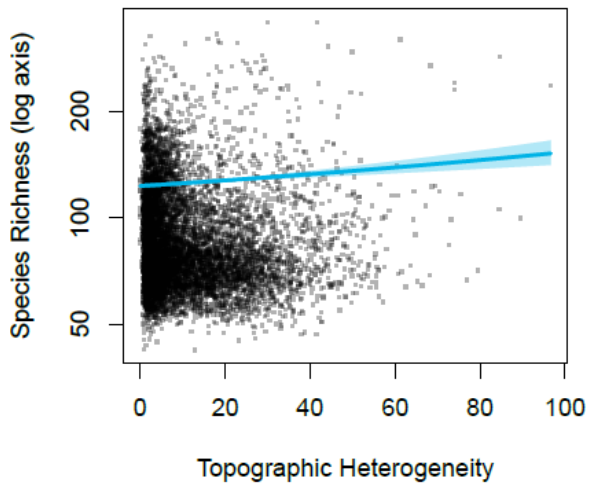
Topographic Heterogeneity effect on PDE



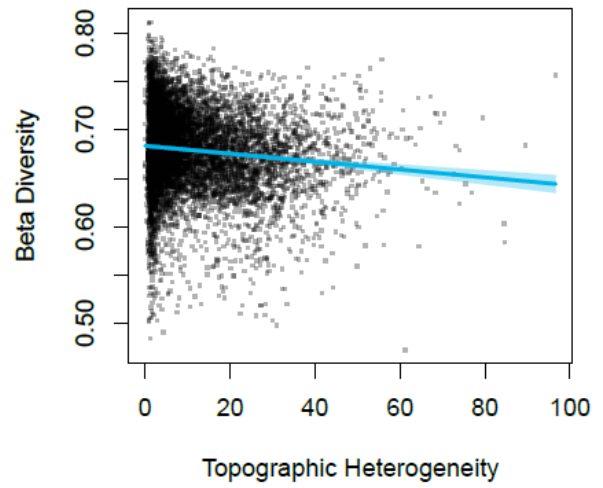
Topographic Heterogeneity effect on PD



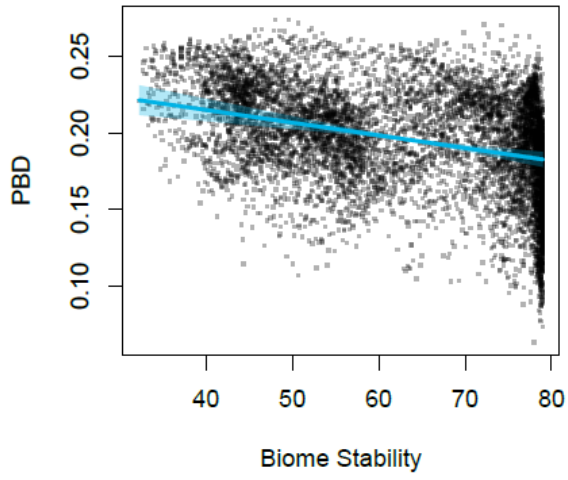
Topographic Heterogeneity effect on Species Richness



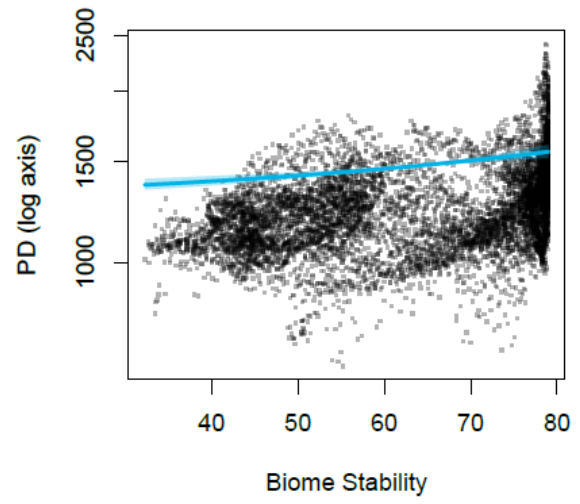
Topographic Heterogeneity effect on Sorenson Beta-diversity



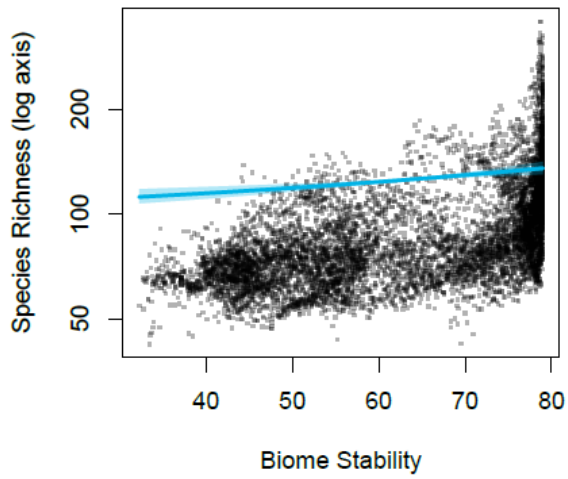
Biome Stability effect on PDB



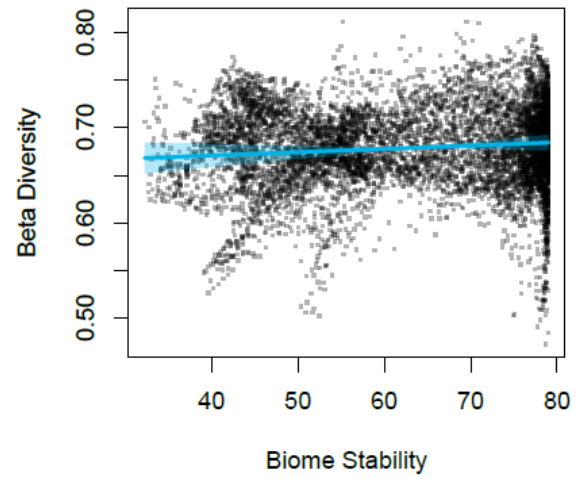
Biome Stability effect on PD



Biome Stability effect on Species Richness



Biome Stability effect on Sorenson Beta-diversity



36

37

38 Table S2. INLA model fixed effects summaries for each diversity model run, and for models
39 controlling for species richness (SR). Pseudo- R^2 values are given for each of the full models
40 incorporating all five covariates. Joint estimation of the spatial error term and fixed effects enables
41 accurate computation of fixed effects but the relatively strong spatial effects modelled mean
42 comparison of the raw data with the confidence intervals of the parameters may be misleading: to the
43 naïve eye, confidence intervals may be more precisely estimated than raw data seems to imply
44 possible.

Species richness: Full model (pseudo-$R^2 = 0.922$)	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	2.95E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.110318	0.045802	0.020324	0.110333	0.200147
biome stability	0.218661	0.055949	0.108722	0.218681	0.328382
topographic heterogeneity	0.0777	0.013758	0.05069	0.0777	0.10469
productivity	0.078684	0.027898	0.023823	0.078711	0.133344
seasonality	-0.3768	0.090239	-0.55405	-0.37678	-0.1998
Species richness: Full model – climatic stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	2.95E-10	0.01135	-0.02228	-3.19E-07	0.022265
biome stability	0.251593	0.054439	0.144605	0.251618	0.358339
topographic heterogeneity	0.081068	0.013695	0.05418	0.081068	0.107933
productivity	0.074932	0.027927	0.020016	0.07496	0.129649
seasonality	-0.35949	0.090221	-0.53674	-0.35947	-0.18256
Species richness: Full model – biome stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	3.07E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.153947	0.044844	0.065824	0.153966	0.241884
topographic heterogeneity	0.074893	0.013761	0.047877	0.074892	0.10189
productivity	0.116109	0.026349	0.064245	0.116151	0.167691
seasonality	-0.36328	0.090891	-0.54185	-0.36325	-0.18504
Species richness: Full model – productivity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	3.36E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.103429	0.04607	0.012908	0.103445	0.193782
biome stability	0.273936	0.052767	0.170145	0.273991	0.377326
topographic heterogeneity	0.079022	0.013766	0.051995	0.079021	0.106027
seasonality	-0.4186	0.089529	-0.59438	-0.41862	-0.24293
Species richness: Full model – seasonality	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	1.83E-11	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.094774	0.045959	0.004485	0.094784	0.184922
biome stability	0.209097	0.056273	0.098546	0.209109	0.319475
topographic heterogeneity	0.079444	0.013767	0.052417	0.079443	0.106451
productivity	0.097205	0.02766	0.042796	0.097237	0.151385
Species richness: Full model – topographic heterogeneity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	3.14E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.136571	0.04566	0.046856	0.136585	0.226123

biome stability	0.201623	0.055986	0.091603	0.201647	0.311411
productivity	0.083788	0.027905	0.028922	0.083813	0.138471
seasonality	-0.39212	0.090358	-0.56965	-0.39209	-0.21493
Taxonomic beta diversity: Full model (pseudo-$R^2 = 0.924$)	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.51E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.009601	0.070171	-0.12828	0.00963	0.147194
biome stability	0.111702	0.085325	-0.05588	0.111712	0.279075
topographic heterogeneity	-0.11146	0.01497	-0.14084	-0.11147	-0.08208
productivity	-0.08014	0.036724	-0.15221	-0.08015	-0.00806
seasonality	0.294752	0.126702	0.046265	0.294648	0.543587
Taxonomic beta diversity: Full model – climatic stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.38E-10	0.01135	-0.02228	-3.20E-07	0.022265
biome stability	0.114552	0.082759	-0.04802	0.114572	0.276867
topographic heterogeneity	-0.11133	0.014928	-0.14063	-0.11134	-0.08203
productivity	-0.08047	0.036643	-0.15238	-0.08049	-0.00855
seasonality	0.295689	0.126434	0.047719	0.295588	0.543991
Taxonomic beta diversity: Full model – biome stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.47E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.031826	0.068114	-0.10203	0.031858	0.165377
topographic heterogeneity	-0.11225	0.01496	-0.14161	-0.11226	-0.08289
productivity	-0.06578	0.035059	-0.13459	-0.06579	0.003024
seasonality	0.298034	0.12672	0.049504	0.297932	0.546897
Taxonomic beta diversity: Full model – productivity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.66E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.019151	0.070181	-0.11875	0.01918	0.156763
biome stability	0.056181	0.081623	-0.10409	0.056176	0.216331
topographic heterogeneity	-0.1128	0.014963	-0.14216	-0.11281	-0.08343
seasonality	0.331643	0.125795	0.084906	0.331549	0.578671
Taxonomic beta diversity: Full model – seasonality	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-1.90E-12	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.019456	0.069971	-0.11803	0.019483	0.156663
biome stability	0.115483	0.085224	-0.05191	0.115494	0.282656
topographic heterogeneity	-0.11299	0.014951	-0.14232	-0.11299	-0.08364
productivity	-0.0914	0.036378	-0.1628	-0.09142	-0.02
Taxonomic beta diversity: Full model – topographic heterogeneity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.71E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	-0.02883	0.071091	-0.16849	-0.02881	0.110592
biome stability	0.137732	0.086582	-0.03233	0.137745	0.307564
productivity	-0.09169	0.037071	-0.16445	-0.09171	-0.01893
seasonality	0.3402	0.128199	0.088783	0.340093	0.591978
Taxonomic beta diversity: Full model.SR (pseudo-$R^2 = 0.948$)	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	13.87861	0.372267	13.14779	13.87857	14.60896

climatic stability	0.134676	0.057272	0.022041	0.134732	0.246892
biome stability	0.328313	0.069891	0.190997	0.328337	0.465373
topographic heterogeneity	-0.0466	0.014486	-0.07503	-0.0466	-0.01817
productivity	-0.02796	0.032115	-0.09102	-0.02796	0.035043
seasonality	-0.16241	0.108194	-0.37453	-0.16252	0.05014
log(SR)	-3.1164	0.083553	-3.28046	-3.11639	-2.9525
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Taxonomic beta diversity: Full model – climatic stability.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	13.8369	0.372437	13.10579	13.83685	14.56763
biome stability	0.367212	0.068176	0.233216	0.367251	0.500865
topographic heterogeneity	-0.04379	0.014446	-0.07215	-0.0438	-0.01545
productivity	-0.03268	0.032143	-0.0958	-0.03268	0.030376
seasonality	-0.14264	0.108233	-0.35488	-0.14274	0.069951
log(SR)	-3.10703	0.083591	-3.27118	-3.10703	-2.94307
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Taxonomic beta diversity: Full model – biome stability.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	13.74174	0.372543	13.01045	13.74167	14.4727
climatic stability	0.197368	0.056205	0.086823	0.197427	0.307485
topographic heterogeneity	-0.04995	0.014498	-0.0784	-0.04995	-0.02149
productivity	0.019501	0.030686	-0.04079	0.019514	0.079667
seasonality	-0.14168	0.108974	-0.35537	-0.14177	0.072368
log(SR)	-3.08566	0.083615	-3.24986	-3.08565	-2.92166
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Taxonomic beta diversity: Full model – productivity.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	13.89564	0.371728	13.16587	13.89561	14.62493
climatic stability	0.137801	0.057149	0.025411	0.137857	0.249781
biome stability	0.308992	0.066261	0.178794	0.309019	0.438925
topographic heterogeneity	-0.04702	0.014477	-0.07543	-0.04703	-0.01861
seasonality	-0.14939	0.107133	-0.35942	-0.1495	0.061085
log(SR)	-3.12022	0.083431	-3.28405	-3.12022	-2.95656
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Taxonomic beta diversity: Full model – seasonality.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	13.82605	0.370941	13.0979	13.826	14.55386
climatic stability	0.128131	0.057242	0.015576	0.12818	0.240307
biome stability	0.324548	0.07001	0.187013	0.324565	0.461856
topographic heterogeneity	-0.04599	0.014487	-0.07442	-0.04599	-0.01756
productivity	-0.02129	0.031857	-0.08386	-0.02129	0.041188
log(SR)	-3.1046	0.083255	-3.26809	-3.10459	-2.9413
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Taxonomic beta diversity: Full model – topographic heterogeneity.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	14.0495	0.369197	13.32463	14.04949	14.77377
climatic stability	0.119832	0.057401	0.006964	0.119881	0.232321
biome stability	0.340947	0.070157	0.203095	0.340974	0.478517
productivity	-0.03143	0.032212	-0.09468	-0.03143	0.031761
seasonality	-0.15261	0.108637	-0.3656	-0.15273	0.060807
log(SR)	-3.15477	0.082863	-3.31746	-3.15477	-2.99221
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Phylogenetic diversity: Full model (pseudo-$R^2 = 0.934$)	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile

(Intercept)	4.08E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.107332	0.048229	0.012568	0.107348	0.201916
biome stability	0.294842	0.058892	0.179128	0.294862	0.410335
topographic heterogeneity	0.083446	0.013878	0.056196	0.083447	0.110668
productivity	0.099357	0.028815	0.042705	0.099381	0.155823
seasonality	-0.52358	0.094012	-0.70821	-0.52358	-0.33916
Phylogenetic diversity: Full model – climatic stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	4.59E-10	0.01135	-0.02228	-3.19E-07	0.022265
biome stability	0.326839	0.057265	0.214305	0.326865	0.439126
topographic heterogeneity	0.086408	0.013822	0.059266	0.08641	0.11352
productivity	0.095674	0.028826	0.039	0.095698	0.152163
seasonality	-0.5075	0.093955	-0.69204	-0.50749	-0.32321
log(SR)	4.59E-10	0.01135	-0.02228	-3.19E-07	0.022265
Phylogenetic diversity: Full model – biome stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	4.03E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.165955	0.047434	0.072743	0.165976	0.258969
topographic heterogeneity	0.079737	0.013891	0.052462	0.079737	0.106986
productivity	0.147587	0.02738	0.093705	0.147627	0.201198
seasonality	-0.50709	0.095031	-0.69376	-0.50707	-0.32071
Phylogenetic diversity: Full model – productivity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	4.47E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.098022	0.048566	0.002595	0.09804	0.193264
biome stability	0.364493	0.05577	0.254819	0.364544	0.473783
topographic heterogeneity	0.085043	0.013889	0.057771	0.085044	0.112286
seasonality	-0.57499	0.093448	-0.75844	-0.57501	-0.39161
Phylogenetic diversity: Full model – seasonality	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	2.19E-11	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.086277	0.04866	-0.00931	0.086287	0.181722
biome stability	0.282514	0.059548	0.165541	0.282524	0.39932
topographic heterogeneity	0.085753	0.013898	0.058463	0.085754	0.113015
productivity	0.123782	0.028694	0.067352	0.123812	0.179996
Phylogenetic diversity: Full model – topographic heterogeneity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	4.55E-10	0.01135	-0.02228	-3.19E-07	0.022265
climatic stability	0.135363	0.048294	0.040466	0.135382	0.230068
biome stability	0.276184	0.059166	0.159929	0.276205	0.392213
productivity	0.105097	0.028895	0.048296	0.105118	0.161729
seasonality	-0.54171	0.09442	-0.72717	-0.54169	-0.35652
Phylogenetic diversity: Full model.SR (pseudo-R² = 0.984)	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-13.2888	0.274862	-13.8279	-13.2891	-12.749
biome stability	0.101016	0.032649	0.036801	0.101044	0.165018
topographic heterogeneity	0.020471	0.012753	-0.00458	0.020475	0.045477
productivity	0.029161	0.020377	-0.01083	0.029154	0.069156
seasonality	-0.18626	0.057174	-0.29833	-0.18635	-0.07384

log(SR)	2.983968	0.061667	2.862731	2.984016	3.104822
Phylogenetic diversity: Full model – climatic stability.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-13.2888	0.274862	-13.8279	-13.2891	-12.749
biome stability	0.101016	0.032649	0.036801	0.101044	0.165018
topographic heterogeneity	0.020471	0.012753	-0.00458	0.020475	0.045477
productivity	0.029161	0.020377	-0.01083	0.029154	0.069156
seasonality	-0.18626	0.057174	-0.29833	-0.18635	-0.07384
log(SR)	2.983968	0.061667	2.862731	2.984016	3.104822
Phylogenetic diversity: Full model – biome stability.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-13.3787	0.274359	-13.9166	-13.3789	-12.8397
climatic stability	0.039474	0.026878	-0.01353	0.039546	0.092036
topographic heterogeneity	0.015418	0.012823	-0.00977	0.01542	0.040567
productivity	0.052852	0.018713	0.016089	0.052856	0.089553
seasonality	-0.17279	0.057747	-0.28604	-0.17286	-0.05929
log(SR)	3.004133	0.061554	2.883082	3.004194	3.124736
Phylogenetic diversity: Full model – productivity.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-13.3189	0.273588	-13.8555	-13.3191	-12.7816
climatic stability	0.020813	0.027417	-0.03327	0.020892	0.074416
biome stability	0.11447	0.030644	0.054288	0.114463	0.174625
topographic heterogeneity	0.018716	0.012869	-0.00656	0.018719	0.043956
seasonality	-0.21107	0.056293	-0.32131	-0.21119	-0.10029
log(SR)	2.990712	0.06138	2.870052	2.990754	3.111019
Phylogenetic diversity: Full model – seasonality.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-13.3691	0.2766	-13.9115	-13.3694	-12.8259
climatic stability	0.008103	0.027592	-0.04623	0.008146	0.062138
biome stability	0.081668	0.033918	0.01512	0.081641	0.148299
topographic heterogeneity	0.018673	0.012903	-0.00667	0.018676	0.043978
productivity	0.044155	0.020097	0.004664	0.044164	0.083563
log(SR)	3.001993	0.062057	2.879983	3.002044	3.123605
Phylogenetic diversity: Full model – topographic heterogeneity.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-13.3069	0.274852	-13.8462	-13.3071	-12.7673
climatic stability	0.027528	0.02722	-0.02618	0.027611	0.080734
biome stability	0.090046	0.033479	0.024279	0.090047	0.155746
productivity	0.02912	0.020396	-0.01091	0.029111	0.069158
seasonality	-0.19269	0.057852	-0.306	-0.1928	-0.07887
log(SR)	2.988025	0.061664	2.866841	2.988057	3.108914
Phylogenetic beta diversity: Full model (pseudo-$R^2 = 0.910$)	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-1.88E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	-0.00019	0.052834	-0.10401	-0.00018	0.103416
biome stability	-0.337	0.064485	-0.4635	-0.33704	-0.21036
topographic heterogeneity	-0.08643	0.014099	-0.11411	-0.08643	-0.05877
productivity	-0.16194	0.030499	-0.22179	-0.16195	-0.10208
seasonality	0.219788	0.101125	0.021441	0.219708	0.418387

Phylogenetic beta diversity: Full model – climatic stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.06E-10	0.01135	-0.02228	-3.20E-07	0.022265
biome stability	-0.3371	0.062484	-0.45969	-0.33714	-0.2144
topographic heterogeneity	-0.08644	0.014039	-0.114	-0.08644	-0.05889
productivity	-0.16195	0.030438	-0.22169	-0.16197	-0.10221
seasonality	0.219666	0.100813	0.021927	0.219589	0.417649
Phylogenetic beta diversity: Full model – biome stability	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-1.85E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	-0.06815	0.052108	-0.17051	-0.06814	0.034063
topographic heterogeneity	-0.08271	0.014124	-0.11044	-0.08271	-0.055
productivity	-0.21373	0.029146	-0.27087	-0.21376	-0.15647
seasonality	0.207022	0.102482	0.006043	0.206933	0.40831
Phylogenetic beta diversity: Full model – productivity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.57E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.015609	0.053396	-0.08929	0.015622	0.12034
biome stability	-0.44987	0.061598	-0.57066	-0.44994	-0.32885
topographic heterogeneity	-0.0892	0.014119	-0.11692	-0.0892	-0.0615
seasonality	0.302598	0.100917	0.104599	0.30254	0.500734
Phylogenetic beta diversity: Full model – seasonality	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.29E-11	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	0.008125	0.052666	-0.09536	0.008144	0.11141
biome stability	-0.33266	0.064416	-0.45903	-0.33271	-0.20616
topographic heterogeneity	-0.08749	0.014088	-0.11515	-0.08749	-0.05985
productivity	-0.17199	0.030137	-0.23113	-0.172	-0.11283
Phylogenetic beta diversity: Full model – topographic heterogeneity	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	-2.33E-10	0.01135	-0.02228	-3.20E-07	0.022265
climatic stability	-0.02968	0.052941	-0.1337	-0.02966	0.074148
biome stability	-0.31702	0.064799	-0.44414	-0.31707	-0.18976
productivity	-0.16903	0.030591	-0.22907	-0.16904	-0.10899
seasonality	0.24246	0.101583	0.043253	0.242368	0.441993
Phylogenetic beta diversity: Full model.SR (pseudo-R² = 0.948)	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	12.23145	0.307333	11.62677	12.23186	12.83331
climatic stability	0.120052	0.034258	0.052579	0.120115	0.187114
biome stability	-0.17281	0.041966	-0.25519	-0.17283	-0.09041
topographic heterogeneity	-0.01824	0.013277	-0.04431	-0.01823	0.007805
productivity	-0.09006	0.023282	-0.13584	-0.09005	-0.04443
seasonality	-0.17215	0.071265	-0.31184	-0.17224	-0.03207
log(SR)	-2.74653	0.068963	-2.88166	-2.74663	-2.61099
Phylogenetic beta diversity: Full model – climatic stability.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	12.13304	0.308157	11.52698	12.13338	12.73671
biome stability	-0.13794	0.041472	-0.21939	-0.13794	-0.05655
topographic heterogeneity	-0.01314	0.013235	-0.03914	-0.01314	0.012813

productivity	-0.09392	0.023509	-0.14014	-0.0939	-0.04785
seasonality	-0.143	0.071844	-0.28393	-0.14306	-0.00188
log(SR)	-2.72444	0.069149	-2.85998	-2.72451	-2.58858
Phylogenetic beta diversity: Full model – biome stability.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	12.36294	0.308163	11.75637	12.36345	12.96619
climatic stability	0.085629	0.033851	0.018967	0.085687	0.151903
topographic heterogeneity	-0.01425	0.013277	-0.04033	-0.01425	0.011784
productivity	-0.12668	0.021748	-0.16939	-0.12668	-0.08402
seasonality	-0.19326	0.072189	-0.33465	-0.1934	-0.05127
log(SR)	-2.77606	0.06915	-2.91149	-2.77618	-2.6401
Phylogenetic beta diversity: Full model – productivity.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	12.34498	0.306652	11.74147	12.34545	12.94536
climatic stability	0.125182	0.034315	0.057632	0.125232	0.192386
biome stability	-0.23477	0.03892	-0.31124	-0.23476	-0.15841
topographic heterogeneity	-0.01852	0.013288	-0.04462	-0.01852	0.00754
seasonality	-0.12021	0.0702	-0.25781	-0.1203	0.017784
log(SR)	-2.77202	0.068811	-2.90681	-2.77213	-2.63675
Phylogenetic beta diversity: Full model – seasonality.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	12.14176	0.306113	11.53962	12.14212	12.74134
climatic stability	0.110386	0.034289	0.042887	0.110436	0.177542
biome stability	-0.18077	0.042169	-0.26349	-0.18081	-0.09793
topographic heterogeneity	-0.01818	0.013291	-0.04429	-0.01818	0.007883
productivity	-0.07989	0.023012	-0.12516	-0.07986	-0.03482
log(SR)	-2.72639	0.068689	-2.86101	-2.72648	-2.59142
Phylogenetic beta diversity: Full model – topographic heterogeneity.SR	mean	sd	0.025 quantile	0.5 quantile	0.975 quantile
(Intercept)	12.28369	0.304617	11.68449	12.28406	12.88034
climatic stability	0.11455	0.033967	0.04763	0.114618	0.181027
biome stability	-0.16824	0.041766	-0.25021	-0.16826	-0.08622
productivity	-0.09015	0.023263	-0.13589	-0.09013	-0.04456
seasonality	-0.17179	0.071168	-0.31129	-0.17189	-0.0319
log(SR)	-2.75826	0.068353	-2.89222	-2.75835	-2.62395

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46

47 **Table S3.** Cape clades sampled for the calculation of phylogenetic diversity and phylogenetic beta
 48 diversity metrics of the Cape flora of South Africa. Numbers of species in total, species native to the
 49 Cape and Cape endemic species are based on (1).

Clade	Family	No species total	No species Cape	No species endemic	No species included	Data obtained	References
<i>Babiana</i>	Iridaceae	92	60	46	66	Dated tree	2
Bruniaceae	-	79	79	77	53	GenBank sequences	3,4
<i>Cliffortia</i>	Rosaceae	140	125	113	117	GenBank sequences	5
Coryciinae ¹	Orchidaceae	112	44	30	25	Published matrix	6
<i>Disa</i>	Orchidaceae	170	100	82	76	GenBank sequences	7,8
<i>Ehrharta</i>	Poaceae	36	20	12	19	Dated tree	9,10
<i>Erica</i>	Ericaceae	860	680	659	309	GenBank sequences	11
<i>Gladiolus</i>	Iridaceae	250	108	86	94	Dated tree	12,13
<i>Heliophila</i>	Brassicaceae	75	61	38	38	Dated tree	10,15
<i>Lachnaea</i>	Thymelaeaceae	40	40	40	38	GenBank sequences	Direct submission to GenBank, M. van der Bank (U. of Johannesburg)
Metalasia clade ²	Asteraceae	61	61	54	57	GenBank sequences	15-17
<i>Moraea</i>	Iridaceae	220	122	84	110	Dated tree	2
<i>Muraltia</i>	Polygalaceae	118	109	101	68	Dated tree	9,18
<i>Pelargonium</i>	Geraniaceae	250	150	85	98	Dated tree	9,19
Penaeaceae	-	23	23	23	18	Published matrix	20
<i>Pentameris</i>	Poaceae	83	62	49	58	Dated tree	9, 21
Phyliceae ³	Rhamnaceae	152	134	127	40	GenBank sequences	22
Podalyrieae ⁴	Fabaceae	125	117	109	95	Dated tree	2, 23
<i>Protea</i>	Proteaceae	115	70	65	71	Dated tree	2, 24
Restionaceae	-	545	342	313	261	Dated tree	25
Stilbaceae	-	39	20	17	16	GenBank sequences	26
Total	-	3,585	2,527	2,210	1,727		

50 ¹ Includes genera *Ceratandra*, *Disperis*, *Evotella*, and *Pterygodium*.

51 ² Includes genera *Atrichantha*, *Calotesta*, *Dolichotheix*, *Hydroidea*, *Lachnospermum*, *Metalasia*, and
 52 *Phaenocoma*.

53 ³ Includes genera *Noltea*, *Phylica* and *Trichocephalus*.

54 ⁴ Includes genera *Amphithalea*, *Calpurnia*, *Cyclophia*, *Liparia*, *Podalyria*, *Stirtonanthus*, *Virgilia* and
 55 *Xiphotheca*.

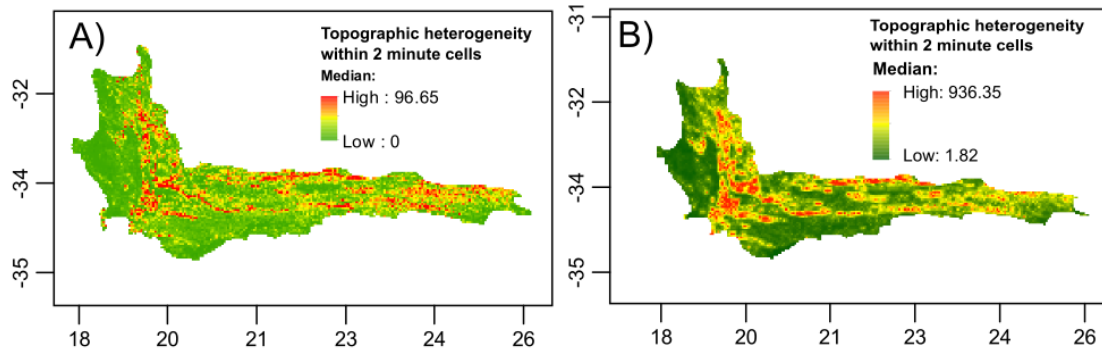
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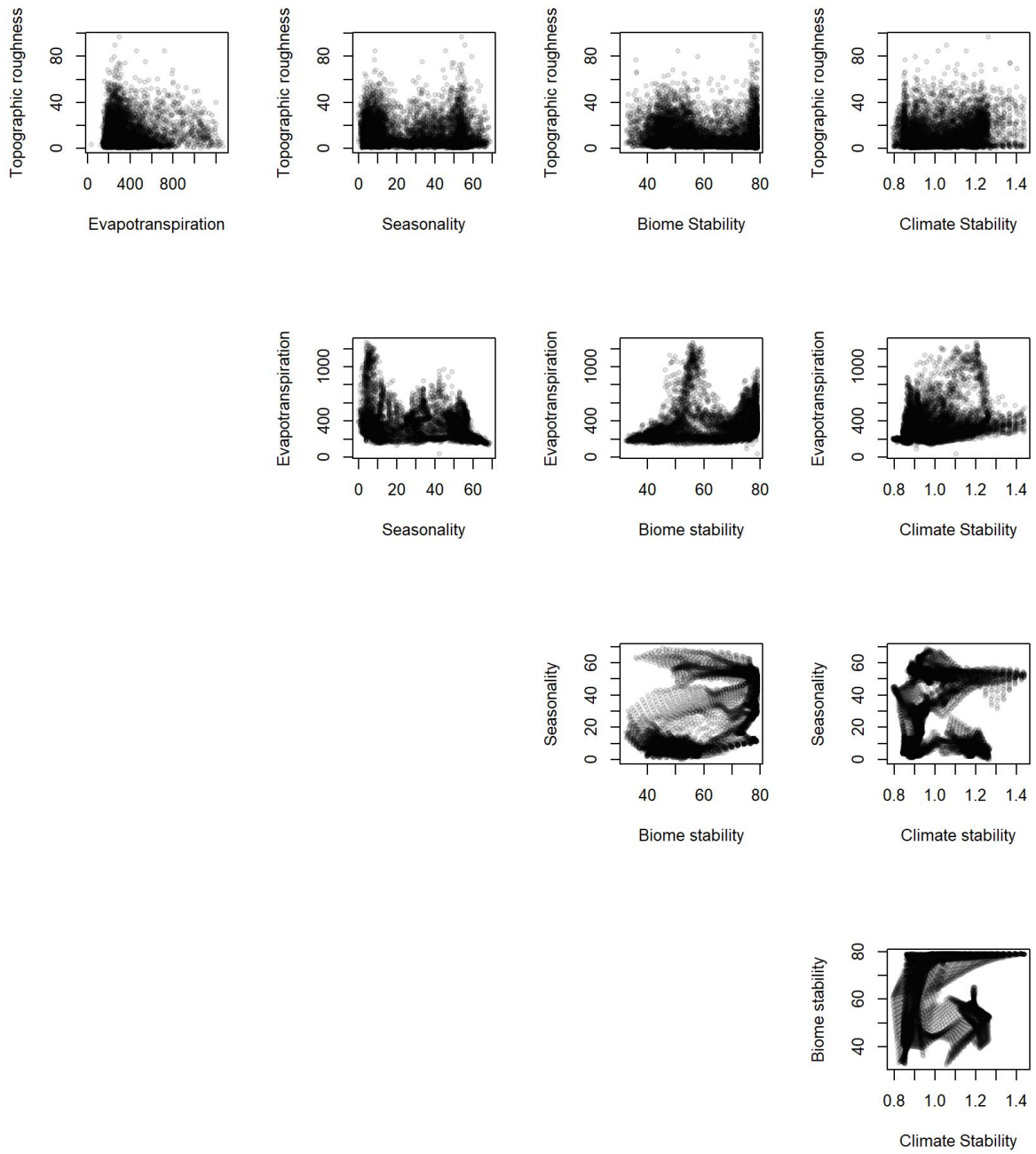
118 Fig. S5. Topographic heterogeneity (A) within two minute grid cells and (B) between neighbouring
119 sets (up to eight) of two minute cells (see Materials & Methods). Within cell topographic
120 heterogeneity for the CFR is correlated with between cell topographic heterogeneity ($r = 0.632$); the
121 former measure was used as a covariate in our spatial regression models.



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124 Fig. S6: Bivariate plots of the relationships between the five covariates (all $r < 0.6$).



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