Environmental heterogeneity patterns plant species richness and turnover in two hyperdiverse floras

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Running title: Environmental heterogeneity and plant species richness

1 ## Abstract

2 **Aim:** To quantify the explanatory power of environmental heterogeneity in predicting plant species richness

3 and turnover in two mediterranean-type biodiversity hotpots, the southwestern Cape of South Africa and

4 southwest Australia (SWA), due to habitat diversity's stimulating speciation and supporting diverse

5 assemblages. In each region, we compare different forms of environmental heterogeneity, species turnover and

6 the relative importance of different forms of heterogeneity better predict species richness and turnover. We

7 expected the Cape to be more heterogeneous in most environmental axes, and at a finer grain, such that the

8 consequent high levels of species turnover explain the Cape's greater species richness per unit area. We also

9 conjectured that edaphic heterogeneity would be an important factor in predicting species richness patterns in

10 SWA.

11 **Location:** The Greater Cape Floristic Region in southwest Africa (the Cape), and the Southwest Australia

12 Floristic Region (SWA)

13 **Taxon:** Vascular plants

14 **Methods:** Geospatially explicit floral and environmental data, non-parametric statistics, boosted regression
15 tree modelling

16 **Results:** The Cape is more environmentally heterogeneous and has higher levels of floristic turnover than
17 SWA. We find that environmental heterogeneity is the main predictor of species richness in the Cape, and
18 somewhat less so for SWA. Edaphic conditions are found to be of more biologically important in the Cape,
19 though this is contingent on the quality of the data modelled.

20 **Main conclusions:** The Cape was found to have generally more environmentally heterogenous than SWA,
21 though SWA does possess edaphic heterogeneity as great as that in the Cape at coarse spatial scales, and greater
22 levels of floristic turnover in vascular plant communities between grid-cells than SWA. Vascular plant species
23 richness and turnover in the Cape was associated more strongly with environmental heterogeneity than in SWA,
24 and particularly edaphic heterogeneity, than species richness in SWA. In SWA, patterns of species richness and
25 turnover are more strongly associated with climatic axes. The relative strengths of association of different
26 environmental variables with patterns of species richness and turnover was found to vary with spatial scale.

27 *Keywords:* biodiversity, boosted regression trees, BRTs, environmental heterogeneity, fynbos, Greater Cape
28 Floristic Region, kwongan, macroecology, species richness, species turnover, vascular plants, Southwest
29 Australia Floristic Region

Acknowledgements

1   Introduction

Biodiversity represents the variety of species and the ecological and evolutionary processes that bring about those species (**???**; Bøhn & Amundsen, 2004). Studying the distribution of biodiversity in space is a major avenue of biological research (**???**; Kreft & Jetz, 2007). Region-scale geographic patterns in species richness have long been studied, particularly in biodiversity hotspots (**???**; Cook et al., 2015). Indeed, "primary geographic patterns" such as these (sensu **???**) are arguably central when studing the distribution of biota across space. The spatial distribution of species richness can be and often is explained in terms of the physical environment. Certain properties of the environment have been suggested to influence species richness in three ways: (i) available resources and energy, which can determine the number of species able to co-exist in an area (Gaston, 2000; Kreft & Jetz, 2007; Mouchet et al., 2015); (ii) environmental stability through time, which enables species' persistence; and (iii) spatial heterogeneity, which can both stimulate ecological speciation and possible barriers to gene flow and can facilitate greater levels of species' co-existence (Thuiller et al., 2006; Mouchet et al., 2015; Cramer & Verboom, 2016). The physical environment, then, can be used to explain species richness in both a local-deterministic and historical sense (Ricklefs, 1987).

The maintenance of species richness, particularly the coexistence of high numbers of species in biodiversity hotspots, is often regarded as "paradoxical" (Hart et al., 2017), and is a central problem in macro-ecology and biogeography (Ricklefs, 1987; Kreft & Jetz, 2007; Hart et al., 2017). Species richness is constrained by the ability of habitats to support a variety of species—its ecological carrying capacity (Mateo et al., 2017). This is exemplified in modelling approches, wherein species richness is a function of environmental predictors in a correlative framework ("macro-ecological models"; Mateo et al., 2017). Macro-ecological models of species richness implicitly assume that communities are saturated, following species-area and species-energy relationships, and at equilibrium with the environment (Mateo et al., 2017).

A solution to the "paradox" of species co-existence is environmental heterogeneity (EH): a more heterogeneous environment exhibits a larger environmental space, thus facilitating co-existence between more species. Heterogeneity in the physical environment is known to be positively associated with species richness (Rensburg et al., 2002; Hart et al., 2017), and has been demonstrated to do so across many taxa—e.g. Canadian butterflies (**???**), European vertebrates (Mouchet et al., 2015), South African birds (Rensburg et al., 2002), in communities along marine continental margins (Levin et al., 2010), French scarab beetles (Lobo et al., 2004), and for global terrestrial plants (Kreft & Jetz, 2007). The spatial scale of heterogeneity, or "grain" of the environment, is also important to consider (Hart et al., 2017), as spatial scale in absolute environmental

67 conditions has also been explored (**???**; Baudena et al., 2015; Mouchet et al., 2015). Species co-existence and

68 biodiversity maintenance is indeed suggested to be scale-dependent (Hart et al., 2017).

69 EH is often under-represented in macro-ecological models of species richness, and has recently been found to

70 explain up to ca. 95% of biome level species richness across South Africa (Cramer & Verboom, 2016). Indeed,

71 models that include EH yield better estimates of the richness of the Cape flora (Thuiller et al., 2006; Cramer &

72 Verboom, 2016). Mediterranean-type terrestrial biodiversity hotspots, such as the Cape flora included in the

73 models by Cramer & Verboom (2016), present interesting study systems in which to investigate the relationship

74 between the environment and species richness. These systems exhibit far greater species richness than

75 predicted by their areas, productivities and latitudes (Cowling et al., 1996; Kreft & Jetz, 2007). There are five

76 Mediterranean biodiversity hotspots on Earth: the California Floristic Province, the Mediterranean Basin, the

77 Chilean Winter Rainfall-Valdivian Forests, the Greater Cape Floristic Region, and the Southwest Australia

78 Floristic Region (Cowling et al., 1996; Hopper & Gioia, 2004; Cook et al., 2015). These ecosystems have

79 regular fire-cycles (Cowling et al., 1996), climatic buffering, and long term stability (Kreft & Jetz, 2007),

80 shrubby, sclerophyllous flora (Hopper & Gioia, 2004). Together, they account for ca. 20% of global vascular

81 plant species, yet only ca. 5% of global land surface areas (Cowling et al., 1996). Various hypotheses have

82 been proposed to explain the high levels of plant species richness in these regions (Cook et al., 2015). The

83 species accumulation hypothesis states that the stability of these regions has allowed many species to accrue.

84 The species co-existence hypothesis states that these hotspots may facilitate greater degrees of species

85 co-existence in smaller spatial areas, due to fine-scale heterogeneity in their environments. Indeed, EH has

86 evolutionary implications too, stimulating ecological speciation across sharp environmental gradients.

87 Both the Southwest Australia Floristic Region (SWA) and the Greater Cape Floristic Region (Cape) are

88 Mediterranean-type biodiversity hotspots, particularly in terms of plant species. Where the Cape (with an area

89 of ca. 189,000 km^2) is known to contain about 11,400 plant species (about 0.060 species per km^2), SWA (area

90 of ca. 270,000 km^2) has about 3,700 species (0.014 species per km^2) (**???**). So, the Cape has ca. 4.3 times as

91 many species per km^2 as SWA. The Cape and SWA are appropriately often compared, due to the similarities

92 between their environments (e.g. oligotrophic soils, an oceanically buffered moderate climate) and their plants'

93 ecologies (Hopper & Gioia, 2004). These two regions present unique flora out of the five Mediterranean

94 systems, with high levels of endemism (Cowling et al., 1996), and many obligate fire-adapted species (Cowling

95 et al., 1996). Similarities withstanding, SWA is topographically and edaphically distinct from the Cape. The

96 former is topographically rather uniform (i.e. flat)—uniquely so among the world's five Mediterranean-climate

97 regions (Hopper & Gioia, 2004)). SWA possesses a mesoscale chronosequence dune system (Laliberte et al.,

98   2014; Cook et al., 2015), while the Cape is mountainous, topographically heterogeneous, and therefore

99   associated with a large degree of spatial climatic variability, with a fine-scale mosaic of geologies and soils

100   (Cowling et al., 1996; Cramer et al., 2014; Verboom et al., 2017).

101   Both regions have sources of edaphic heterogeneity, but at different scales. This edaphic variability may aid in

102   explaining the species richness in these regions (Beard et al., 2000; Verboom et al., 2017). EH of many forms

103   will likely be important in macro-ecological models in both regions, as both regions have been relatively

104   environmentally stable over evolutionary time-scales (Wardell-Johnson & Horwitz, 1996; Hopper & Gioia,

105   2004; Lambers et al., 2010; Cramer et al., 2014; Laliberte et al., 2014; Cook et al., 2015). For the Cape, high

106   levels of species richness are thought to result from long term climatic stability, and fine grain variation in

107   geology and soils (Cramer et al., 2014). The question thus arises whether heterogeneity is a significant

108   contributor to SWA species richness. In the absence of topographic variability in SWA, it is proposed that the

109   heterogeneity of that region is due to the juxtaposition of soil types (Laliberte et al., 2014; Cook et al., 2015),

110   creating extreme edaphic variation.

111   Our hypotheses concern the Cape and SWA's environments and floras. Our main hypothesis is that the Cape

112   possesses greater abiotic heterogeneity, and at finer grain, compared to SWA, such as to explain the Cape's

113   greater species richness per unit area, and proposed greater levels of species turnover between areas. We also

114   conjecture that the heterogeneity that predicts species richness in SWA will be more pronounced in terms of

115   edaphic variables. Here we attempt to assess five key predictions of this hypothesis, additionally investigating

116   a seventh prediction to test the conjectured role of edaphic heterogeneity in SWA. Dealing with the two

117   regions' environments, we assess (i) whether the Cape environment is more heterogeneous than that of SWA

118   and (ii) whether the Cape environment has more pronounced heterogeneity at finer scales than that of SWA.

119   Dealing with the distribution of species in the two regions, we assess (iii) whether the Cape exhibits greater

120   levels of species turnover between areas. Relating each regions' environment and flora, we finally assess (iv)

121   whether species richness and species turnover are adequately predicted by EH in both regions and whether (v)

122   species richness and species turnover are better predicted by different forms of EH in either region (e.g. the

123   importance of edaphic heterogeneity in SWA).

2 Materials and methods

2.1 Overview

Our analyses required boundaries for each region and geographically explicit environmental data and vascular plant occurrence records. The environmental variables chosen (Table 1) for this study were intended to cover a reasonable spread of climatic, edaphic, and ecologically relevant environmental axes, and are not intended to be exhaustive. We selected variables describing topography (elevation), productivity (NDVI), soil status and climate and climatic seasonality.

We carried out this investigation at four principal spatial scales: 0.05º x 0.05º squares (the finest common resolution among the environmental data sources used), quarter degree squares (QDS) (Larsen et al., 2009), half degree squares (HDS) (Larsen et al., 2009) and three-quarter degree squares (3QDS). For the Cape, most plant occurrence records are only accurate to QDS level. Thus, analyses involving species occurence data were necessary limited to scales including and above QDS.

Analyses were performed in R v3.4.0–3.5.1 (R Core Team, 2018). Version-numbers of specific R packages used are presented in the bibliography.

2.2 Environmental data sources

The GCFR was treated as the area occupied by the Succulent Karoo and Fynbos biomes in the current delineation of South Africa's biome boundaries (Mucina & Rutherford, 2006). The SWAFR was treated as the areas occupied by the Southwest Australia savanna, Swan Coastal Plain Scrub and Woodlands, Jarrah-Karri forest and shrublands, Southwest Australia woodlands, Esperance mallee, and Coolgardie woodlands in the World Wildlife Fund Terrestrial Ecoregions dataset (Olson et al., 2001) in order to closely match the currently delineated SWAFR (Gioia & Hopper, 2017, Hopper & Gioia (2004)). For the sake of readability, we shall refer to the GCFR and SWAFR simply as the Cape and SWA from hereon.

Geospatially-explicit raster layers were acquired for a selection of environmental variables (Table 1), for the regions of interest. Raster data were re-projected to a common coordinate reference: WGS84 (NIMA, 2000), using the "rgdal" (**???**) package in R (R Core Team, 2018). All data were re-sampled to 0.05º resolution using the "resample" function in the R package "raster" (**???**), with the "bilinear" method.

6

150 An emphasis was made on using satellite-derived environmental data in this work, in order to minimise

151 differences in data quality and methodologies between the Cape and SWA. Additionally, satellite-derived data

152 have been shown to benefit regional-scale species distribution models (Deblauwe et al., 2016), thus motivating

153 their use in this regional-scale study. The environmental data used in this study were derived from NASA's

154 SRTM digital elevation model (Farr et al., 2007), NASA's MODIS/Terra spectroradiometric data for land

155 surface temperature and NDVI, the Climate Hazards Group's CHIRPS rainfall dataset (Funk et al., 2015), and

156 the International Soil Reference and Information Centre's SoilGrids250m edaphic dataset (Hengl et al., 2017)

157 (Table 1). SRTM and MODIS are entirely derived from satellite measurements, whereas CHIRPS is

158 interpolated from weather station data with satellite-derived radiometric measurements. SoilGrids250m is a

159 machine-learning derived product, based on soil measurements as a function of many covariates, including

160 MODIS and STRM sources (see Hengl et al., 2017), using random-forests and other classification-tree-based

161 methods, including gradient-boosting. For the soil data considered here (Table 1), we used depth-interval

162 weighted average values as the value for a particular soil variable in a given place.

163 Climatic and spectral data arise from satellites monitoring properties of the Earth's surface through time. We

164 therefore use the mean annual values for rainfall, surface temperature, and NDVI in each pixel in our analyses.

165 Pronounced seasonality of rainfall is a known feature of mediterranean systems (**???**). We describe this

166 seasonality by computing computing the precipitation in the driest quarter (PDQ), using methods based on the

167 "biovars" function in the R package "dismo".

2.3 Plant occurrence data

169 Geospatially-explicit records of vascular plant occurrences were downloaded from the Global Biodiversity

170 Information Facility (GBIF, Table 1). Queries were made for tracheophyte records from within the borders of

171 the Cape and SWA as treated here (GBIF, 24 July 2017, GBIF (24 July 2017)). Only records with defined

172 species and intra-specific ranks were kept. Intra-specific occurrences were treated as simply being

173 representative of their species. This resulted in FIXME unique species names in the Cape, and FIXME in SWA.

174 We cleaned these data using the R package "taxise" (**???**, (**???**)) to check that these species names had

175 accepted-status among taxonomic databases. We queried two major taxonomic databases: the Global Name

176 Resolver (GNR), and the Taxonomic Name Resolution Service (TNRS). Should either one of these services

177 return at least one match for a given name, then that name was accepted. Those names for which no full

178 binomial matches were found in either database were excluded from the final list of species. The number of

7

179 species names excluded totalled at FIXME and FIXME for the Cape and SWA respectively. Especially for

180 SWA, these numbers may be deemed appreciably high. But, the occurrence records that would be dropped, as a

181 consequence of these names' removals, appeared randomly distributed in geographic space in both regions. As

182 such, any effect of the loss of these records in this analysis is likely uniform within the two regions.

183 After the unaccepted names were removed, it was important to ensure that a species was not listed under

184 multiple synonyms. Such cases would skew estimates of species richness and turnover in this study. In light of

185 this, the remaining names were queried in the Tropicos and Integrated Taxonomic Information System (ITIS)

186 databases for their known synonyms, again using "taxize". These were collated to produce a nomenclatural

187 "thesaurus" for the Cape and SWA species. This consisted of a list of the accepted species names in a region,

188 each associated with a list of known synonyms. We amended species' names in the GBIF occurrence data, in

189 order ensure species were listed under only one of these synonyms, replacing all appearances of a species'

190 synonyms with the first synonym used in the list.

191 Lastly, We removed any species from both regions that are invasive aliens or non-indigenous. Alien species

192 lists for plants in South Africa and Australia were acquired from the IUCN's Global Invasive Species Database

193 (http://www.iucngisd.org/gisd/).

194 The final total plant species richness in each region was FIXME and FIXME for the Cape and SWA

195 respectively. These final collections of species occurrence records were converted to raster-layers, wherein

196 pixel-values represented the species richness of vascular plants within that pixel. These rasters were produced

197 at QDS, HDS, and 3QDS resolutions.

198 ## 2.4 Analyses

199 ### 2.4.1 Quantifying environmental heterogeneity

200 In order to assess predictions (i) and (ii), we needed to describe the EH in both regions. Using the R package

201 "raster" (**???**), we used a modified version of the "roughness" index in the "terrain" function. For a three by

202 three neighbourhood $\mathbf{N}$ of cells, our index of roughness R is the average square-root of the squared difference

203 between each of the n neighbour cells' values x_i and the central focal cell's value x_{focal}:

$$R(\mathbf{N}) = \frac{1}{n}\sqrt{\sum_{i=1}^{n}\left(x_{\text{focal}} - x_i\right)^2} \tag{1}$$

204   This value, notionally equivalent to the standard deviation of values relative to the focal value, is ascribed to

205   the focal cell. Note, in order to use as much data from within regions' borders as possible, roughness was

206   computed if a focal cell had at least one neighbour cell. Using this index, we produced raster layers of each of

207   our nine environmental variable's heterogeneity. We compared the distributions of "roughness" values in each

208   variable in each region with non-parametric Mann-Whitney U-tests, as almost all variables were highly

209   non-normal, and could not be normalised by log-transformations. We also compare the effect size of the Cape

210   vs SWA using the "common language effect size" ($CLES$), using the R package "canprot". The $CLES$ is the

211   proportion of all pairwise comparisons between two sample groups' observations where one group's value is

212   greater than the other's. We calculated the $CLES$ as the proportion of pairs where Cape roughness values

213   were greater than that of SWA. This allowed us to assess prediction (i). To compare the spatial scales of

214   heterogeneity (prediction (ii)) between each region, we repeated this analysis at all four spatial scales. This

215   entailed recalculating the roughness layer for each variable after the original layer (0.05 degrees resolution) had

216   been rescaled to each of the coarser resolutions.

2.4.2   Quantifying species turnover

218   Regarding prediction (iii), we wished to compare the general degree of species turnover in each region. To

219   compare the extent of species turnover between the Cape and SWA, we determined two metrics of species

220   turnover. The first, computes the mean species turnover as Jaccard distances (**???**) between each pair of QDS

221   within each HDS ($\overline{J}_{\text{QDS}}$, based on HDS with $2 \leq n \leq 4$ QDS) in both regions. The second is defined in terms

222   of Whittaker's additive definition of β-diversity (**???**), as follows:

$$\gamma = \alpha + \beta \tag{2}$$

223   Here, we treat species richness at the HDS-scale (S_{HDS}) as γ-diversity and at the QDS-scale ($\overline{S}_{\text{QDS}}$) as

224   α-diversity. Intuitively, the species richness of an area is the result of some combination of the richness of sites

225   within that area and the difference in species complements between those sites. Thus, we partition γ-diversity

226   as in Equation (2), such that β-diversity is the difference between γ- and α-diversity. We compare the

227 distributions of $\overline{J}_{\mathrm{QDS}}$ and T_{HDS} using non-parametric Mann-Whitney U-tests, in order to guard against

228 non-normality.

2.4.3 Predicting richness and turnover with environmental heterogeneity

230 Regarding prediction (iii), we wished to compare the general degree of species turnover in each region. For (iv)

231 and (v) we modelled species richness (S) and turnover as a function of various combinations of environmental

232 and environmental heterogeneity variables in both regions using boosted regression-tree (BRT) modelling

233 techniques. This allowed us to explore which axes of environmental heterogeneity are most influential on

234 vascular plant species richness and turnover, and the differences in the importance of such axes between the

235 Cape and SWA.

236 BRTs are a flexible machine learning-based model of response variables and do so without involving normal

237 null-hypothesis significance testing (Elith et al., 2008), and have been employed previously to model species

238 richness (Thuiller et al., 2006; see Mouchet et al., 2015; Cramer & Verboom, 2016) as macro-ecological

239 models. BRTs are developed through the iterative generation of non-linear regression trees. BRTs are an

240 ensemble-approach, in which a prediction $\widehat{y_i}$ is based on the weighted sum of the predictions of progressively

241 "less important" regression trees (t_k), as opposed to the predictions of one tree (Elith et al., 2008). For $k \to nt$

242 number of trees, where each tree is itself a function of the matrix $\mathbf{X}$ of j predictor variables ($t_k = f(x_{ij})$), a

243 BRT-model can be represented as follows:

$$\widehat{y_i} = \sum_{k=1}^{nt} w_k t_k \tag{3}$$

244 BRTs have two major meta-parameters over which users have control (**???**): the learning rate (lr, the rate at

245 which iterative trees reduce predictive deviance during model-training, controlling the contribution of each tree

246 to the final model) and tree complexity (tc, the number of nodes on a given regression-tree, i.e. the maximum

247 interaction depth the model is permitted to fit).

248 BRTs were implemented here to predict both vascular plant species richness and turnover in each HDS, as a

249 function of environmental variables and environmental roughness values in those cells, as Gaussian responses,

250 thus resulting in two BRT-models for each region. We treated richness as S_{HDS} and turnover as $\overline{J}_{\mathrm{QDS}}$. The

251 natural logarithm of species richness was used, in order to satisfy the assumptions of a Gaussian response.

252 Note, this is not strictly because BRTs have any parametric assumptions concerning the distribution of the

253 response variable, but rather to aid in applying the Gaussian-family of BRT algorithms to the richness data

254 available. Additionally, BRTs were implemented to predict vascular plant species richness at the QDS-scale

255 (S_{QDS}), thus resulting in a total of six BRT-models presented here.

256 As recommended by Elith et al. (2008), BRT models were trained on a set of non-collinear predictor variables

257 using "gbm.step" in "dismo" (**???**) and "gbm" (**???**). Collinear predictor variables can skew the interpretation

258 of results, as the relatively influence of mutually collinear variables is reduced. Collinearity among the nine

259 environmental predictor variables and their respective nine roughness-equivalents was assessed using

260 "removeCollinearity" in the R package "virtualspecies" (**???**) separately for each region, such that variables

261 were no more than 80% collinear (Pearson's $r \geq 0.80$). When faced with a cluster of collinear variables, one

262 variable was chosen manually therefrom. Where possible, the roughness-equivalent of an environmental

263 variable was included if its absolute-equivalent could also be included. When interpreting the results of BRTs,

264 it is important to consider the effects of the variables included as representative of the effect of the excluded

265 variables with which it was found to be collinear.

266 In order to select ideal lr and tc all models (described below) were trained on the final non-collinear predictor

267 sets iteratively for 25 combinations of a range of tc values (1 to 5) and a range of lr values (0.01, 0.005, 0.001,

268 5×10^{-4}, 1×10^{-4}). The function "gbm.step" optimises the number of trees (nt) using cross-validation during

269 model training (Elith et al., 2008) by halting iteration when predictions begin to overfit. For all models, we

270 used 10 cross-validation folds (i.e. use 10 different randomly selected training data sets), a tolerance-threshold

271 of 0.001, a bagging-fraction of 0.75 (proportion of training data randomly chosen to generate each tree), and

272 trained models starting with 50 trees, with each iterative step adding 50 trees at a time, up to a maximum of

273 10,000 trees. Following this iterative parameter optimisation, Gaussian BRT models were constructed with

274 $tc = 3$ and $lr = 0.001$, along with the other settings described.

275 The optimum configuration of lr and tc for the final model is a trade-off between model fit (e.g. pseudo-R^2;

276 Equation (4)) and complexity (nt). A tc of 5 was chosen for the final model. This follows the

277 recommendations of Elith et al. (2008), where lr and tc are advised to be adjusted inversely. This was chosen

278 in order to account for the complex interactions determining species richness. To avoid overfitting, an

279 intermediate lr of 0.001 was chosen.

2.4.4 Assessing BRT-predictions' fit

BRT-model performance can be described by measuring the variance in a dataset a BRT-model has explained, quantified here by R^2_{pseudo}, which is the proportion of null deviance D_{null} explained by some model i. Formally, it is defined as follows:

$$R^2_{\text{pseudo}} = 1 - \frac{D_i}{D_{\text{null}}} \tag{4}$$

The derivation of this metric is not easy to interpret, as it is not immediately clear what model deviance is. Alternatively, comparing expected (i.e. model-predicted) and observed data has more heuristic appeal. We employed this metric of BRT-model performance too. We regressed expected against observed richness and turnover, and calculated the R^2-value for those regressions (hereafter $R^2_{\text{E-O}}$).

The BRT-model fitting algorithm contains intrinsic stochasticity, due to the random partitions made in a dataset during cross-validation. Though this randomness is usually negligible (e.g. variables' contributions vary from run-to-run by a few decimal places), we reran each of the six BRT-models (see above) 1000 times in order to account for this stochasticity. Where indicated, we either present the averages of these replicate-models' results or the results of a representative model from each set of replicates.

In order to assess the reliability of the conclusions drawn from these models, we randomly permuted the response data (S_{QDS}, S_{HDS} and $\overline{J}_{\text{QDS}}$) with respect to the environmental and heterogeneity data, and reran all six BRT-models 999 times (with the final non-collinear predictor sets and preconfigurations above). This also allows us to remove any effect of spatial autocorrelation in generating the observed correlations between patterns of species occurrence and environment (**???**), and to allow us to assess the significance of our results relative to a random null. Notably, as the predictor variables themselves are likely spatially autocorrelated, correlation structure in model residuals is accounted for by the correlation structure in the environmental data. Nonetheless, we wished to demonstrate our results more robustly and thus carried out these permutation tests. For all six models, the majority of the 999 permuted models failed to find associations between the response and predictor variables. The results of those that succeeded to fit a model to completion (usually ca. 200 out of 999) are presented. The replicate and permuted BRT-models were compared using various measures of model performance (above; nt, R^2_{pseudo} (Equation (4)), $R^2_{\text{E-O}}$) and the ranks of these values for each replicate BRT-model relative to the 999 permuted models for that region/scope.

3 Results

3.1 Describing environmental heterogeneity across scales

Across all variables considered, the Cape is more environmentally heterogeneous in the majority of pairwise comparisons of grid-cells ($CLES > 0.50$, Mann-Whitney U-test: $P < 0.05$, Figure 1). The degree to which the Cape is more heterogeneous varies between environmental variables. These effects also vary somewhat across spatial scales. In some variables, the differentiation between Cape and SWA heterogeneity lessens at coarser scales (Figure 1b). Indeed, when comparing the overall ranking and medians of Cape vs SWA roughness values for each variable, we only find non-significant differences at the 3QDS scale (Mann-Whitney U tests, $P > 0.05$, Figure 1b).

Most obviously, and as expected, topographic heterogeneity is generally greater in the Cape than in SWA (Figure 1). Though SWA has a slightly wider distribution of elevational roughness values at coarse scales compared to fine scales than the Cape, the relative difference in heterogeneity between the two regions seems invariant with spatial scale ($CLES \approx 0.95$, Figure 1b). This concurs with our expectations, as the Cape is mountainous and known to have steep elevational gradients (**???**), while SWA is much more topographically uniform. Elevational roughness differs between the two regions in the manner we expected, giving us more confidence in the environmental reality of our other results here.

Climatic heterogeneity is less differentiated between the Cape and SWA than with topographic heterogeneity (Figure 1a), though the Cape is indeed more climatically heterogeneous (Figure **??**b). Notably, the difference between roughness in mean annual rainfall (R MAP) and land surface temperature (R Surface T) in the Cape and SWA is less pronounced when considered at coarse spatial scales (Figure **??**b). At all spatial scales considered, roughness in rainfall seasonality (R PDQ), however, is equally more heterogeneous in the Cape than SWA. Biological productivity, as measured by NDVI, is fairly similarly heterogeneous in the Cape and SWA ($CLES < 0.60$, Figure 1). Concerning edaphic variables, the Cape and SWA are similarly heterogeneous at coarser scales, particularly in terms of CEC and Soil C ($CLES \approx 0.50$, Figure 1b).

3.2 Comparing species turnover in the two regions

Following calculations of $\overline{J}_{\mathrm{QDS}}$ and T_{HDS} for each HDS-cell in each region, we also used non-parametric Mann-Whitney U-tests to compare the distributions of values in the Cape and SWA. The Cape possesses

generally greater floristic turnover than SWA, for both measures of turnover defined here ($P < 0.0001$, Figure 2a,b). $\overline{J}_{\mathrm{QDS}}$ measures the average pairwise Jaccard distance between QDS-cells in each HDS-cell. T_{HDS}, however, represents the inferred β component of γ-diversity. As γ-diversity ($= S_{HDS}$) in the Cape has a greater β-diversity component ($= T_{HDS}$) than SWA, the complement is necessarily true: γ-diversity in the Cape has a lesser α-diversity component ($= \overline{S}_{\mathrm{QDS}}$) than SWA.

3.3 Predicting richness and turnover with environmental heterogeneity

We found vascular plant species richness and turnover both to be predicted primarily by environmental heterogeneity in the Cape (Figure 3a–c) and at least in-part by environmental heterogeneity in SWA (Figure 3d–f). Our six BRT-models performed adequately, and detected relationships between patterns of species occurrence and the environment that do not occur in the permuted datasets (Figures 4 and 3, Table 2).

BRT-models of species richness at the QDS-scale in each region generally performed best, as these models had fit greater number of trees (nt, Figure 4a), and possess higher R^2-values (Figure 4b,c). SWA models of species richness and turnover at the HDS-scale out-performed Cape models. At the QDS-scale, the Cape and SWA models performed equally well (Figure 4, Table 3).

Across our BRT-models of species richness and turnover, the importance of different environmental variables in predictions differed substantially between the Cape and SWA. Additonally, the relative importance of absolute and heterogeneity variables also differs between the Cape and SWA (Figure 3). Most obviously, species richness and turnover in the Cape are predicted mostly by environmental heterogeneity, which is not the case in SWA (Figure 3). Species richness and turnover in the Cape are predicted by a broad suite of environmental variables, with no individual variable contributing more than ca. 20% to any model prediction (Figure 3a–c). The SWA models' predictions, however, are largely determined by MAP (Figure 3d–f).

Species richness at QDS-scales ($= \overline{S}_{\mathrm{QDS}}$), and to a lesser extent at HDS-scales ($= S_{\mathrm{HDS}}$), in the Cape is predicted largely edaphic conditions (Figure 3a,b). Species richness in SWA, at both scales, is mostly predicted by MAP and other climatic variables (Figure 3d,e). Interestingly, topograhphic heterogeneity did not feature as highly in contributing to Cape predictions as we expected (Figure 3a–c).

It is important to consider variables not included formally in these BRT-models that were found to be collinear with some of the variables included (see SI). Here, we interpret the effects of variables excluded from the analyses as well as those included, as the forms and importances of these relationships are likely similar. In the

361 Cape (concerning clusters of collinear variables relevant to relevant to those retained during BRT-model

362 fitting), MAP was included in the BRT-analyses as representative of a cluster of collinear variables consisting

363 of itself, NDVI, surface T and soil C at the. Roughness in soil clay content represented itself, roughness in soil

364 pH and roughness in NDVI. In SWA, MAP was select as representative of itself, NDVI and soil C.

365 **In the equations below, collinear groups of variables are listed as predictors enclosed within braces.**

366 **Cape:**

$$\overline{S}_{\text{QDS}} \sim pH + RSurfT + \begin{Bmatrix} MAP \\ NDVI \\ SurfT \\ SoilC \end{Bmatrix} + \begin{Bmatrix} RClay \\ RpH \end{Bmatrix} + RElev$$

$$S_{\text{HDS}} \sim RSurfT + RElev + RCEC + \begin{Bmatrix} RMAP \\ RPDQ \\ RNDVI \end{Bmatrix} + \begin{Bmatrix} MAP \\ NDVI \\ SurfT \\ SoilC \end{Bmatrix}$$

$$T_{\text{HDS}} \sim RElev + RSurfT + \begin{Bmatrix} RMAP \\ RPDQ \\ RNDVI \end{Bmatrix} + Elev + RCEC$$

367 **SWA:**

$$\overline{S}_{\text{QDS}} \sim \begin{Bmatrix} MAP \\ NDVI \\ SoilC \end{Bmatrix} + PDQ + RMAP$$

$$S_{\text{HDS}} \sim \begin{Bmatrix} MAP \\ NDVI \\ SoilC \end{Bmatrix} + CEC + RElev$$

$$T_{\text{HDS}} \sim \begin{Bmatrix} MAP \\ NDVI \\ SoilC \end{Bmatrix} + RElev + CEC$$

368   Our BRT-models of species richness in both regions rank environmental variables somewhat differently at

369   QDS- and HDS-scales (Figure 3a,b,d,e). These differences in rankings are similar to those between two

370   unrelated lists ($P_{1-2} > 0.05$, Figure 5). This suggests some scale-dependence of different environmental

371   variables' associations with species richness.

372   It is noteworthy that BRT-models of species turnover ($= \overline{J}_{\text{QDS}}$, at HDS-scales) (Figure 3c,f) rank variables

373   similarly to models of richness at HDS-scales ($P_{2-3} \leq 0.005$, Figure 5). This is likely due to the fact that

374   proportional floristic turnover covaries with species richness. As such, though the signs of relationships

375   determining turnover may differ from those determining richness, the importances of different variables would

376   be similar.

377   In addition to different variables being more strongly associated with species richness and turnover in the Cape

378   compared to SWA (Figure 3), the forms of those relationships vary (Figure 6). We found MAP, and roughness

379   therein, to relate positively with species richness in both regions at both scales (Figure 6a,b,d,e). As MAP is

380   collinear with NDVI and soil C in both regions (and surface T in the Cape), this can be interpreted as the signal

381   of a biological productivity and resource availability associating with high levels of species richness.

382   The positive association of heterogeneity variables in the Cape as opposed to SWA (Figure 6a,b vs d,e) concurs

383   with their greater importance in BRT-model predictions (Figure 3).

384   The fact that species turnover ($T_{HDS} = \overline{J}_{QDS}$) in the Cape and SWA is largely predicted by the same

385   variables as species richness, but with opposite signs to its relationships (Figure 6c,f), is indicative of the

386   richness-dependence of the measure of floristic turnover used here (Jaccard distances) to quantify turnover at

387 the HDS-scale.

4 Discussion

389 We have support for the hypothesis that the difference in plant species richness between the Cape and SWA is
390 accounted for by the greater abiotic heterogeneity in the Cape. As expected, the Cape is shown to possess (i) a
391 quantifiably more heterogeneous environment that is (ii) generally heterogeneous at a finer spatial scale than
392 SWA, with (iii) greater levels of floristic turnover. We have shown that vascular plant species richness (iv) can
393 be explained in terms of environmental conditions including environmental heterogeneity in both the Cape and
394 SWA. Also, we have shown that (v) the sets of environmental axes that explain plant species richness differ
395 between the Cape and SWA. These findings contribute towards an understanding of the ecological conditions
396 associated with high levels of species co-existence in these two regions, and strengthens the generality of a
397 positive relationship between environmental heterogeneity and biodiversity.

398 These two regions present differentiable environmental spaces, each with varying degrees of heterogeneity
399 across spatial scale. The clear separation of the regions' topographic features is as expected (Figures **??**A, **??**),
400 particularly regarding topography. The Cape region has been found previously to have the second highest
401 median topographic heterogeneity of the five Mediterranean-climate regions (Bradshaw & Cowling, 2014).
402 The Cape has a much wider range of scales exhibited in the heterogeneity across its environmental axes.
403 Notably, each region has finer scale heterogeneity in some variables, and coarser scale in others—neither
404 region is more fine or coarse than the other over all environmental axes. BRT-models of species richness in
405 both regions reveal species richness to depend on those environmental axes that differentiate the two regions
406 (Figures **??**), **??**). The importance of variables is also shown to vary with spatial scale (Figure **??**), as
407 previously suggested may be the case when modelling geographic patterns of biodiversity (Baudena et al.,
408 2015). Indeed, as Cowling et al. (1996) describes differing patterns of species richness across spatial scales, so
409 do the predictors of those patterns vary with scale (Hart et al., 2017).

410 In line with our hypotheses, a combination of absolute and roughness variables are associated with species
411 richness and turnover. In the models developed by Cramer & Verboom (2016) for South Africa, roughness in
412 topography was largely superseded as an important predictor of species richness by other roughness variables.

413 …

414   The determinants of vascular plant species are shown to be region specific (Figures **??**, **??**, **??**).

415   …

416   NDVI is more heterogeneous across the Cape than SWA (Figures **??**A). The fact that thermal variables tend to

417   be more rough in the Cape (Figure **??**A) is likely due to possible covariance of the MODIS/Terra products with

418   topography, as MODIS data used here describes land surface temperature. As the Cape is topographically

419   rugged, the roughness of NDVI may arise from this. Despite this, NDVI is an integrating variable, which

420   captures information about productivity, light availability, and soil nutrients (Power et al., 2017). The fact that

421   absolute NDVI contributes to predicting species richness in the Cape, especially at finer spatial scales (Figure

422   **??**E) demonstrates the role of ecological productivity in facilitating the coexistence diverse species

423   assemblages. Environmental heterogeneity, then, is integral to explaining patterns of species richness, but must

424   be considered along with resource- and energy-availability axes. In so much as a diverse environmental space

425   supports more species, the materials and productivity required for biota to thrive are also needed to support

426   species (**???**; Gaston, 2000; Bøhn & Amundsen, 2004; Kreft & Jetz, 2007). As such, my findings, along with

427   those of previous studies (Rensburg et al., 2002; Thuiller et al., 2006; Kreft & Jetz, 2007; Cramer & Verboom,

428   2016), suggest that there is ecological and evolutionary consequence to resource availability *and*

429   environmental heterogeneity, in that they tend to be positively associated with species richness.

430   The combined BRT-model of species richness for both regions reveals soil clay content as an important

431   predictor, at coarse spatial scales, despite this variable not being particularly important within each region

432   separately (Figure **??**). Though this model does not strictly consider the regions as separate, this finding may

433   indicate that the relationship between clay content and species richness differs between the regions. So far as

434   clay content can be used to predict species richness, it matters more to those predictions when applied to large

435   sections (i.e. coarse scales) of each regions.

436   Kreft & Jetz (2007) modelled global terrestrial vascular plant species richness, which focussed on primarily

437   absolute environmental values, underestimated the richness of the Cape flora. Though Kreft & Jetz (2007) did

438   include topographic heterogeneity in their predictor set, topography is often a proxy for more biologically

439   meaningful variables (Cramer & Verboom, 2016). This explains why the inclusion of these variables

440   (e.g. roughness in mean annual precipitation) yields more accurate predictions of species richness. Indeed,

441   Thuiller et al. (2006) also included topographic heterogeneity.@Cramer2016 described 68% of species

442   richness at the QDS scale across South Africa. Regarding the Cape, depending on whether one consults

443   pseudo-R^2 (Table 3), the ratio of mean predicted to observed richness per grid-cell (Table 5), or the

distributions of predicted vs. observed richness values per grid-cell (Figure **??**), I have achieved a similarly
suitable level of predictive accuracy. There is, though, still unexplained species richness in light of my models.
As Cramer & Verboom (2016), Rensburg et al. (2002), Thuiller et al. (2006), and Mouchet et al. (2015) have
done, these macro-ecological models are a-historical. Evolutionary considerations of species richness in
geographic space are worthwhile, especially in regions with environments stable over evolutionary time.

…

Jaccard distances, as used here as $\overline{J}_{\mathrm{QDS}}$, are highly richness dependent. Although they represent the
proportional floristic turnover between cells, this proportion itself is sensitive to the richness of sites under
comparison. For example, the turnover between two low richness sites has is likely to be greater by chance,
due to the absence or presence of a few species, than the turnover between two high richness sites, where the
absence or presence of a few species does not greatly affect the turnover calculated.

…

The findings here are correlative. There are, however, many proposed mechanisms to explain the correlative
signals demonstrated here. My findings support the hypothesis that Mediterranean systems' plant species
richness is a function of spatial variability in environmental conditions. This can stimulate diversification, and
maintain that diversity by providing a range of habitats for species co-existence. Oligtrophic soils can stimulate
an increase in functional diversity, through the evolution of diverse nutrient acquisition strategies (Lambers et
al., 2010; Verboom et al., 2017)—e.g. sclerophylly (Cramer et al., 2014; Cook et al., 2015). An aspect of the
environment I have neglected to consider is fire, shown to also contribute to predictions here in the Cape
(Cramer & Verboom, 2016). Cardillo (2012) have shown the structuring forces behind species co-occurrence
patterns, and thus likely species richness,differ between species-pairs with different post-fire responses and
those with similar post-fire responses.

Though the Cape was correctly predicted to have, on average, more species per grid-cell at HDS and 3QDS
scales than SWA, this was not the case for QDS grid-cells (Table 5). This demonstrates that the Cape is indeed
overall more rich in plant species than SWA, but a given HDS in SWA contains fewer species than a given Cape
HDS. Thus, the greater richness in the Cape is a product of greater turnover in species at spatial scales no more
coarse than the HDS. Species turnover is an interesting aspect to species richness studies, as it species turnover
is implicit to species-area and co-existence-area relationships (Hart et al., 2017). One could expect patterns of
endemism and species turnover to concur with patterns in environmental heterogeneity to some degree.

Following from the understanding that functionally diverse assemblages, which are more likely to be more species rich, are likely to arise and/or occur in areas with diverse ecological pressures (Molina-Venegas et al., 2015), one would expect, then, heterogeneous habitats such as those in Mediterranean-type biodiversity hotspots to exhibit high levels functional beta diversity along steep environmental gradients (Molina-Venegas et al., 2015). If the niches concerning these functions are phylogenetically conserved among those biota, then one would also expect high levels of species and phylogenetic beta diversity along these gradients (Molina-Venegas et al., 2015). This concurs with the notion put forward by Power et al. (2017), wherein megadiverse systems such as these represent the results of "phylogenetic niche conservatism on a heterogeneous landscape". Thus, species and phylogenetic turnover should covary with environmental heterogeneity in some way. Indeed, endemism, at certain scales, could also follow this pattern. Thuiller et al. (2006) demonstrated that there is phylogenetic and biome related determinants of species richness. This makes sense, in light of the difficulty of crossing biome boundaries in Mediterranean systems (Power et al., 2017). NDVI and light availability, and the heterogeneity therein, are associated with high levels of floristic turnover (Power et al., 2017). This may be indicative of ecological specialisation precluding species from crossing these boundaries, thus increasing the level of endemism within a region, while also increasing the level of turnover, and thus likely species richness, along environmental gradients. Although, this may be debated. Beard et al. (2000) state that the high levels of endemism in SWA are function of habitat specialisation to soil mosaics. Cf. Laliberte et al. (2014), who say that this endemism is likely due to environmental filtering along these soil turnover sequences, as opposed to the juxtaposition of specialised species along soil gradients.

Summarily, we have demonstrated support for the generality of as a meaningful predictor of patterns of species richness and turnover in mediterranean-type ecosystems. In SWA and the Cape, high levels of are also likely the results of long-term landscape and climatic stability (Hopper, 1979). Thus, the roles of environmental variability through space that persists through deep time are two important ways in which the environment relates to biodiversity in these regions. The efficacy of environmental stability through geological time should be explored further, comparing the Cape and SWA.

4.1 Future studies (a.k.a. "to do after first review maybe")

- 3QDS scale BRTs
- $S_{\text{HDS}} \sim \overline{S}_{\text{QDS}} + \overline{\delta_{ij}}_{??}$ (= "$\gamma = \alpha + \beta$"-analysis) (see `explore-turnover-metrics.pdf` note, where $\overline{\delta_{ij}}(\mathbf{N})_{??} = \overline{\alpha_i}(\mathbf{N}) \times \overline{\beta_{ij}}(\mathbf{N}) = \overline{S}_{\text{QDS}} \times \overline{J}_{\text{QDS}})$

20

- Expanding the analyses to other/all mediterranean-type regions

- Investigating environmental stability through time (e.g. WorldClim LGM vs today)

- Phylogenetics/mega-trees in different flora? β_{phylo}?

- Teasing apart co-existance and evolution

- Teasing about turnover into turnover-sensu-stricto and nestedness

- Functional diversity $\sim$ EH? Functional turnover?

Table captions

Captions are also repeated alongside their respective tables for readability.

Table 1: Georeferenced vascular plant species occurence and environmental data sources used in this study. Data were acquired for the Cape and SWA regions, with the temporal extent of data products used described where applicable. Abbreviations are as follows: MAP, mean annual precipitation; PDQ, precipitation in the driest quarter; CEC, cation exchange capacity.

Table 2: Average proportional-ranks for BRT-model performance measures (nt, R^2_{pseudo} (Equation (4)), $R^2_{\mathrm{E-O}}$ (see text)) of the 1000 replicate BRT-models relative to 999 BRT-models fit to permuted datasets. Each of the 1000 replicate BRT-mdels was ranked against the 999 permuted BRT-models. The average rank of each, as a proportion, is presented.

Table 3: Estimated differences between replicate Cape and SWA BRT-models' performance measures (nt, R^2_{pseudo} (Equation (4)), $R^2_{\mathrm{E-O}}$ (see text)) following two-sided t-tests. Positive values indicate that the Cape models had greater values. In all cases, the Cape and SWA had highly significantly different values for these quality measures ($P < 0.0001$).

Figure captions

Captions are also repeated alongside their respective figures for readability.

Figure 1: Comparisons of different types of environmental heterogeneity between the the Greater Cape Floristic Region (Cape) and the Southwest Australia Floristic Region (SWA). We present (a) distributions of roughness values (Equation (1)) for example variables from each broad category of the environment concerned.

527 (b) The common language effect size ($CLES$; see text) of Cape versus SWA roughness values is shown for all

528 variables, grouped by broad categories of the environment, describing differences in the distributions of Cape

529 and SWA roughness values. We used Mann-Whitney U-tests to assess differences in these distributions.

530 Non-significant differences ($P_U > 0.05$) are denoted as such ("NS"). Note, U-tests were performed using only

531 a random set of 5000 cells at the 0.05-degree-scale, as the U-test as implemented in R cannot handle more than

532 that many values to compare.

533 Figure 2: Species turnover, described in two forms ((a) mean Jaccard distance between QDS in each HDS

534 ($\overline{J}_{\text{QDS}}$), (b) additively defined turnover (T_{HDS}, Equation (2)) as a proportion of HDS richness (S_{HDS})),

535 compared between the Cape and SWA. Mann-Whitney U-tests between the Cape and SWA distributions of

536 $\overline{J}_{\text{QDS}}$ and T_{HDS} yielded significant differences (see P-values and common language effect sizes ($CLES$)

537 inset).

538 Figure 3: Relative influence of environmental variables (including heterogeneity variables—prefixed with "R")

539 in boosted regression tree (BRT) model predictions in the Greater Cape Floristic Region (Cape, a–c) and the

540 Southwest Australia Floristic Region (SWA, b–d) of vascular plant species richness at the (b,e) QDS-scale

541 ($= \overline{S}_{\text{QDS}}$), (a,d) HDS-scale ($= S_{\text{HDS}}$) and (c,f) turnover ($= \overline{J}_{\text{QDS}}$). All BRT-models were permitted to fit

542 three-way interactions between environmental variables. Points denote the mean contribution of an

543 environmental variable to model-predictions across the 1000 replicate BRT-models for that region/scope.

544 Horizontal ticks denote the mean for the 999 permuted BRT-models. Standard deviations above and below

545 these means are shown with vertical lines. Note, in the case of the replicate, standard deviations are so small

546 such that the vertical lines are obscured by the points. Colours represent the general category of the

547 environment to which a variable belongs (keyed), as in Figure 1b. Left-most piecharts inset in each panel

548 display the same information. Right-most piecharts group contributions according to whether a variable was

549 absolute or roughness-transformed (keyed). F-statistics inset are for one-way ANOVAs of differences in

550 variables' relative influences—for both the replicate ($F_{\text{rep.}}$) and permuted ($F_{\text{prm.}}$) BRT-models.

551 Figure 4: Distributions of three measures of boosted regression tree (BRT) model performance: (a) the number

552 of trees in the model nt, (b) R^2_{pseudo} (Equation (4)), (c) $R^2_{\text{E}-\text{O}}$ (see text). These measures are presented for the

553 six sets of permuted (pale bars) and six sets of replicate BRT-models (dark bars) as in Figure 3, coloured

554 according to the region of interest as in Figures 1a and 2. In all cases, replicate BRT-models almost entirely

555 out-rank the permuted models in terms of performance (Table 2) and the Greater Cape Floristic Region (Cape)

556 and Southwest Australia Floristic Region (SWA) models had significantly different values for each metric

557   (Table 3). Note, the actual differences between Cape and the SWA models' values is not realistically significant

558   in some cases (e.g. the difference in nt between the Cape and SWA QDS richness models is statistically

559   significant, but are observedly so similar as not to affect interpretation).

560   Figure 5: Differences in the rankings of environmental variables' (including heterogeneity variables) relative

561   influences on boosted regression tree (BRT) model predictions of vascular plant species richness and turnover

562   in (a) the Greater Cape Floristic Region (Cape) and (b) Southwest Australia Floristic Region (SWA) (as in

563   Figure 3). Each point represents an environmental variable's rank in BRT-model importance, decreasing in

564   importance from left to right. Rankings used here are the same as that of the average relative influence for

565   variables across replicate BRT-models, presented in Figure 3. Coloured lines connect points representing the

566   same environmental variable. Points' outlines are coloured according to the general category of the

567   environment (keyed) to which a variable belongs, as in Figuress 1b and 3, while points' centres are coloured

568   according to whether a variable was roughness-transformed or not. The comparisons of variables' rankings of

569   interest are between QDS- and HDS-scale richness ($= \overline{S}_{\mathrm{QDS}}$ and S_{HDS} respectively; rows nos. 1 and 2) and

570   between HDS-scale richness and turnover ($= \overline{J}_{\mathrm{QDS}}$) (rows nos. 2 and 3). Statistics (Δ- and P-values) inset at

571   the top and bottom of each panel refer to these comparisons respectively. Δ-values represent the average

572   absolute difference in ranks across variables between two models' rankings. The associate P-value results from

573   ranking the observed Δ-values against 999 Δ-values based on random permutations of variables' rankings

574   (SI1), such that more significant P-values denote rankings more similar than would be expected by chance.

575   Figure 6: Marginal effects of environmental conditions and heterogeneity on vascular plant species richness at

576   the QDS-scale ($= \overline{S}_{\mathrm{QDS}}$; a,d), HDS-scale ($= S_{\mathrm{HDS}}$; b,e) and turnover ($= \overline{J}_{\mathrm{QDS}}$; c,f) in response variables in

577   the Greater Cape Floristic Region (Cape; a–c) and Southwest Australia Floristic Region (SWA; d–f) following

578   boosted regression tree (BRT) modelling. Marginal effect functions presented are derived from a representative

579   BRT-model from the set of replicate BRT-models (for each of the six modelling cases) (see SI regarding how

580   representative BRT-models were selected). Marginal effects represent the effect of a predictor variable when all

581   other predictors are set at their means. Marginal effect functions are shown for environmental variables that

582   contributed $\geq 10\%$ to a model's predictions. Functions are coloured as keyed, with solid lines representing

583   absolute environmental variables and dotted representing heterogeneity variables ("rough"). Environmental

584   variables were all rescaled here such as to be centred on zero (i.e. Z-transformed), facilitating comparison of

585   functions' forms.

References

Baudena, M., Sánchez, A., Georg, C.-P., Ruiz-Benito, P., Rodríguez, M.Á., Zavala, M.A., & Rietkerk, M. (2015) Revealing patterns of local species richness along environmental gradients with a novel network tool. *Scientific Reports*, **5**, 11561.

Beard, J.S., Chapman, A.R., & Gioia, P. (2000) Species richness and endemism in the Western Australian flora. *Journal of Biogeography*, **27**, 1257–1268.

Bradshaw, P.L. & Cowling, R.M. (2014) Landscapes, rock types, and climate of the Greater Cape Floristic Region. *Fynbos: Ecology, evolution and conservation of a megadiverse region* (ed. by N. Allsopp, J.F. Colville, and G.A. Verboom), pp. 26–46. Oxford University Press, Oxford.

Bøhn, T. & Amundsen, P.-A. (2004) Ecological Interactions and Evolution: Forgotten Parts of Biodiversity? *BioScience*, **54**, 804.

Cardillo, M. (2012) The phylogenetic signal of species co-occurrence in high-diversity shrublands: different patterns for fire-killed and fire-resistant species. *BMC Ecology*, **12**, 21.

Cook, L.G., Hardy, N.B., & Crisp, M.D. (2015) Three explanations for biodiversity hotspots: small range size, geographical overlap and time for species accumulation. An Australian case study. *New Phytologist*, **207**, 390–400.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., & Arianoutsou, M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, **11**, 362–366.

Cramer, M.D. & Verboom, G.A. (2016) Measures of biologically relevant environmental heterogeneity improve prediction of regional plant species richness. *Journal of Biogeography*, 1–13.

Cramer, M.D., West, A.G., Power, S.C., Skelton, R., & Stock, W.D. (2014) Plant ecophysiological diversity. *Fynbos: Ecology, evolution and conservation of a megadiverse region* pp. 248–272. Oxford University Press, Oxford.

Deblauwe, V., Droissart, V., Bose, R., Sonké, B., Blach-Overgaard, A., Svenning, J.C., Wieringa, J.J., Ramesh, B.R., Stévart, T., & Couvreur, T.L.P. (2016) Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics. *Global Ecology and Biogeography*, **25**, 443–454.

Elith, J., Leathwick, J.R., & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.

Farr, T., Rosen, P., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007) The shuttle radar topography mission. *Reviews of Geophysics*, **45**, 1–33.

Funk, C.C., Peterson, P.J., Landsfeld, M., Pedreros, D.H., Verdin, J., Shukla, S., Husak, G., Rowland, J.D., Harrison, L., Hoell, A., & Michaelsen, J. (2015) The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. *Scientific Data*, **2**, 150066.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

616   GBIF (24 July 2017) GBIF Occurrence Download..

617   GBIF (24 July 2017) GBIF Occurrence Download..

618   Gioia, P. & Hopper, S.D. (2017) A new phytogeographic map for the Southwest Australian Floristic Region after an exceptional decade
619   of collection and discovery. *Botanical Journal of the Linnean Society*, **184**, 1–15.

620   Hart, S.P., Usinowicz, J., & Levine, J.M. (2017) The spatial scales of species coexistence. *Nature Ecology & Evolution*, **1**, 1066–1073.

621   Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M., Blagoti?, A., Shangguan, W., Wright, M.N.,
622   Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E.,
623   Wheeler, I., Mantel, S., & Kempen, B. (2017) SoilGrids250m: Global gridded soil information based on machine learning.
624   *PLoS ONE*, **12**, e0169748.

625   Hopper, S.D. (1979) Biogeographical Aspects of Speciation in the Southwest Australian Flora. *Annual Review of Ecology and*
626   *Systematics*, **10**, 399–422.

627   Hopper, S.D. & Gioia, P. (2004) The Southwest Australian Floristic Region: Evolution and Conservation of a Global Hot Spot of
628   Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 623–650.

629   Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of*
630   *Sciences*, **104**, 5925–5930.

631   Laliberte, E., Zemunik, G., & Turner, B.L. (2014) Environmental filtering explains variation in plant diversity along resource gradients.
632   *Science*, **345**, 1602–1605.

633   Lambers, H., Brundrett, M.C., Raven, J.A., & Hopper, S.D. (2010) Plant mineral nutrition in ancient landscapes: high plant species
634   diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil*, **334**, 11–31.

635   Larsen, R., Holmern, T., Prager, S.D., Maliti, H., & Røskaft, E. (2009) Using the extended quarter degree grid cell system to unify
636   mapping and sharing of biodiversity data. *African Journal of Ecology*, **47**, 382–392.

637   Levin, L.A., Sibuet, M., Gooday, A.J., Smith, C.R., & Vanreusel, A. (2010) The roles of habitat heterogeneity in generating and
638   maintaining biodiversity on continental margins: an introduction. *Marine Ecology*, **31**, 1–5.

639   Lobo, J.M., Jay-robert, P., Lumaret, J.-p., Lobo, J.M., Jay-robert, P., & Lumaret, J.-p. (2004) Modelling the Species Richness
640   Distribution for French Aphodiidae (Coleoptera, Scarabaeoidea). *Ecography*, **27**, 145–156.

641   Mateo, R.G., Mokany, K., & Guisan, A. (2017) Biodiversity Models: What If Unsaturation Is the Rule? *Trends in Ecology &*
642   *Evolution*, **32**, 556–566.

643   Molina-Venegas, R., Aparicio, A., Slingsby, J.A., Lavergne, S., & Arroyo, J. (2015) Investigating the evolutionary assembly of a
644   Mediterranean biodiversity hotspot: Deep phylogenetic signal in the distribution of eudicots across elevational belts. *Journal*
645   *of Biogeography*, **42**, 507–518.

646 Mouchet, M., Levers, C., Zupan, L., Kuemmerle, T., Plutzar, C., Erb, K., Lavorel, S., Thuiller, W., & Haberl, H. (2015) Testing the
647   effectiveness of environmental variables to explain European terrestrial vertebrate species richness across biogeographical
648   scales. *PLoS ONE*, **10**, 1–16.

649 Mucina, L. & Rutherford, M.C. (2006) *The vegetation of South Africa, Lesotho and Swaziland.* South African National Biodiversity
650   Institute,

651 NIMA (2000) Amendment 1. 3 January 2000. Department of Defense World Geodetic System 1984. Its Definition and Relationships
652   with Local Geodetic Systems. 1–3.

653 Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand,
654   H.E., Morrison, J.C., & Others (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of
655   terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, **51**, 933–938.

656 Power, S.C., Verboom, G.A., Bond, W.J., & Cramer, M.D. (2017) Environmental correlates of biome-level floristic turnover in South
657   Africa. *Journal of Biogeography*, **44**, 1745–1757.

658 R Core Team (2018) *R: A Language and Environment for Statistical Computing. Version 3.5.0.* R Foundation for Statistical
659   Computing, Vienna, Austria.

660 Rensburg, B.J. van, Chown, S.L., & Gaston, K.J. (2002) Species Richness, Environmental Correlates, and Spatial Scale: A Test Using
661   South African Birds. *The American Naturalist*, **159**, 566–577.

662 Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science, New Series*, **235**, 167–171.

663 Thuiller, W., Midgley, G.F., Rouget, M., Cowling, R.M., F. Midgley, G., Rougeti, M., & M. Cowling, R. (2006) Predicting patterns of
664   plant species richness in megadiverse South Africa. *Ecography*, **29**, 733–744.

665 Verboom, G.A., Stock, W.D., & Cramer, M.D. (2017) Specialization to extremely low-nutrient soils limits the nutritional adaptability
666   of plant lineages. *The American Naturalist*, **In press**,.

667 Wardell-Johnson, G. & Horwitz, P. (1996) Conserving biodiversity and the recognition of heterogeneity in ancient landscapes: a case
668   study from south-western Australia. *Forest Ecology and Management*, **85**, 219–238.

Biosketches

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Author contributions

MDC and GAV conceived the study question, which RVM investigated under their supervision for his BSc Hons project. The analyses and programming work were largely devised by RVM, with input from the other authors, and was carried out by RVM. RVM wrote the first draft of the manuscript and all authors contributed equally thereafter.

Tables

Table 1: Georeferenced vascular plant species occurence and environmental data sources used in this study. Data were acquired for the Cape and SWA regions, with the temporal extent of data products used described where applicable. Abbreviations are as follows: MAP, mean annual precipitation; PDQ, precipitation in the driest quarter; CEC, cation exchange capacity.

Variable	Source	Temporal extent	Citation
Plant species occurrences	GBIF	TODO	**??, ??**
Elevation	SRTM v2.0		**??**
NDVI	MODIS (MOD13C2)	Feb. 2000 to Apr. 2017	**??**
Climatic variables			
Surface temperature	MODIS (MOD11C3)	Feb. 2000 to Apr. 2017	**??**
MAP	CHIRPS v2.0	Jan. 1981 to Feb. 2017	**??**
PDQ	CHIRPS v2.0	Jan. 1981 to Feb. 2017	**??**
Soil variables			
CEC	SoilGrids250m (CECSOL M 250m)		**??**
Clay	SoilGrids250m (CLYPPT M 250m)		
Soil C	SoilGrids250m (OCDENS M 250m)		
pH	SoilGrids250m (PHIKCL M 250m)		

Table 2: Average proportional-ranks for BRT-model performance measures (nt, R^2_{pseudo} (Equation (4)), $R^2_{\text{E}-\text{O}}$ (see text)) of the 1000 replicate BRT-models relative to 999 BRT-models fit to permuted datasets. Each of the 1000 replicate BRT-mdels was ranked against the 999 permuted BRT-models. The average rank of each, as a proportion, is presented.

Model	nt	R^2_{pseudo}	R^2_{E-O}
QDS-richness			
GCFR	1.000	1.000	1.000
SWAFR	1.000	1.000	1.000
HDS-richness			
GCFR	0.987	1.000	0.988
SWAFR	1.000	1.000	1.000
HDS-turnover			
GCFR	0.977	0.992	0.979
SWAFR	0.997	1.000	1.000

Table 3: Estimated differences between replicate Cape and SWA BRT-models' performance measures (nt, R^2_{pseudo} (Equation (4)), $R^2_{\text{E}-\text{O}}$ (see text)) following two-sided t-tests. Positive values indicate that the Cape models had greater values. In all cases, the Cape and SWA had highly significantly different values for these quality measures ($P < 0.0001$).

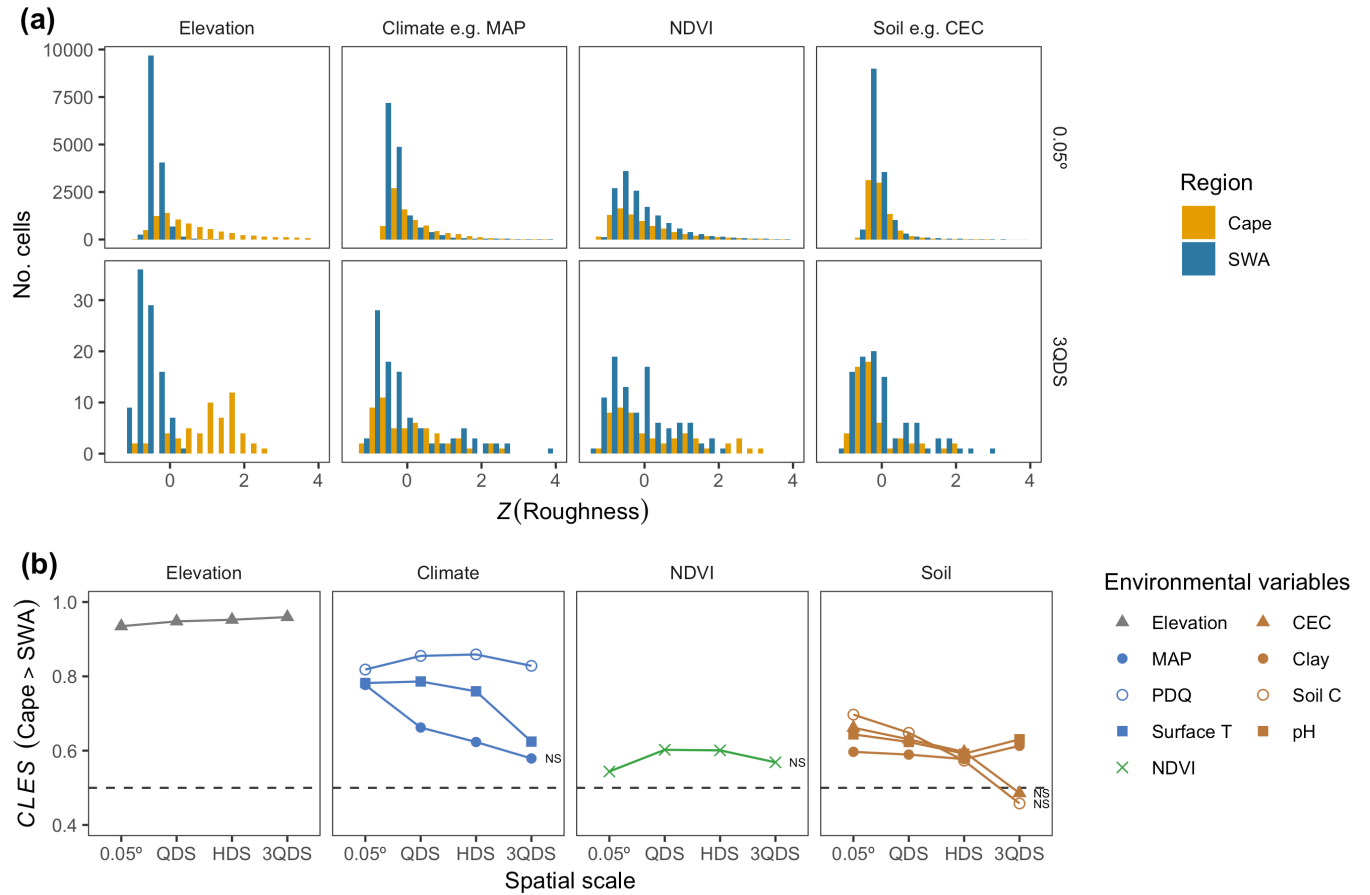| Model	nt	R^2_{pseudo}	$R^2_{\text{E}-\text{O}}$
QDS-richness	542.938	0.063	-0.005
HDS-richness	-808.994	-0.064	-0.233
HDS-turnover	-997.045	-0.052	-0.296

Figures

(a)

(b)

Figure 1: Comparisons of different types of environmental heterogeneity between the the Greater Cape Floristic Region (Cape) and the Southwest Australia Floristic Region (SWA). We present (a) distributions of roughness values (Equation (1)) for example variables from each broad category of the environment concerned. (b) The common language effect size ($CLES$; see text) of Cape versus SWA roughness values is shown for all variables, grouped by broad categories of the environment, describing differences in the distributions of Cape and SWA roughness values. We used Mann-Whitney U-tests to assess differences in these distributions. Non-significant differences ($P_U > 0.05$) are denoted as such ("NS"). Note, U-tests were performed using only a random set of 5000 cells at the 0.05-degree-scale, as the U-test as implemented in R cannot handle more than that many values to compare.
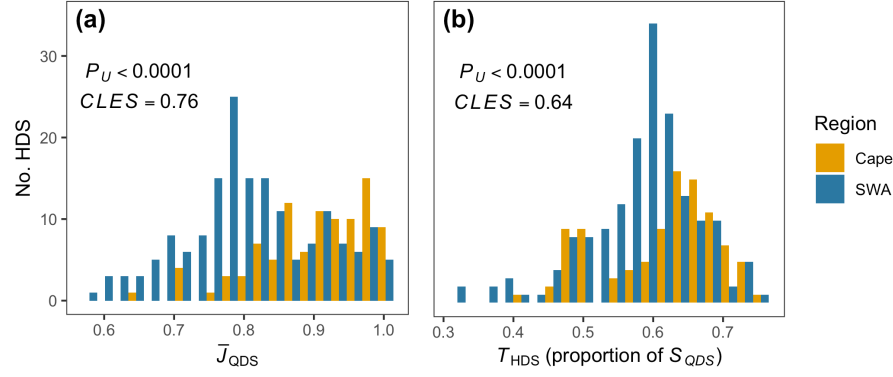
Figure 2: Species turnover, described in two forms ((a) mean Jaccard distance between QDS in each HDS ($\overline{J}_{\mathrm{QDS}}$), (b) additively defined turnover (T_{HDS}, Equation (2)) as a proportion of HDS richness (S_{HDS})), compared between the Cape and SWA. Mann-Whitney U-tests between the Cape and SWA distributions of $\overline{J}_{\mathrm{QDS}}$ and T_{HDS} yielded significant differences (see P-values and common language effect sizes ($CLES$) inset).
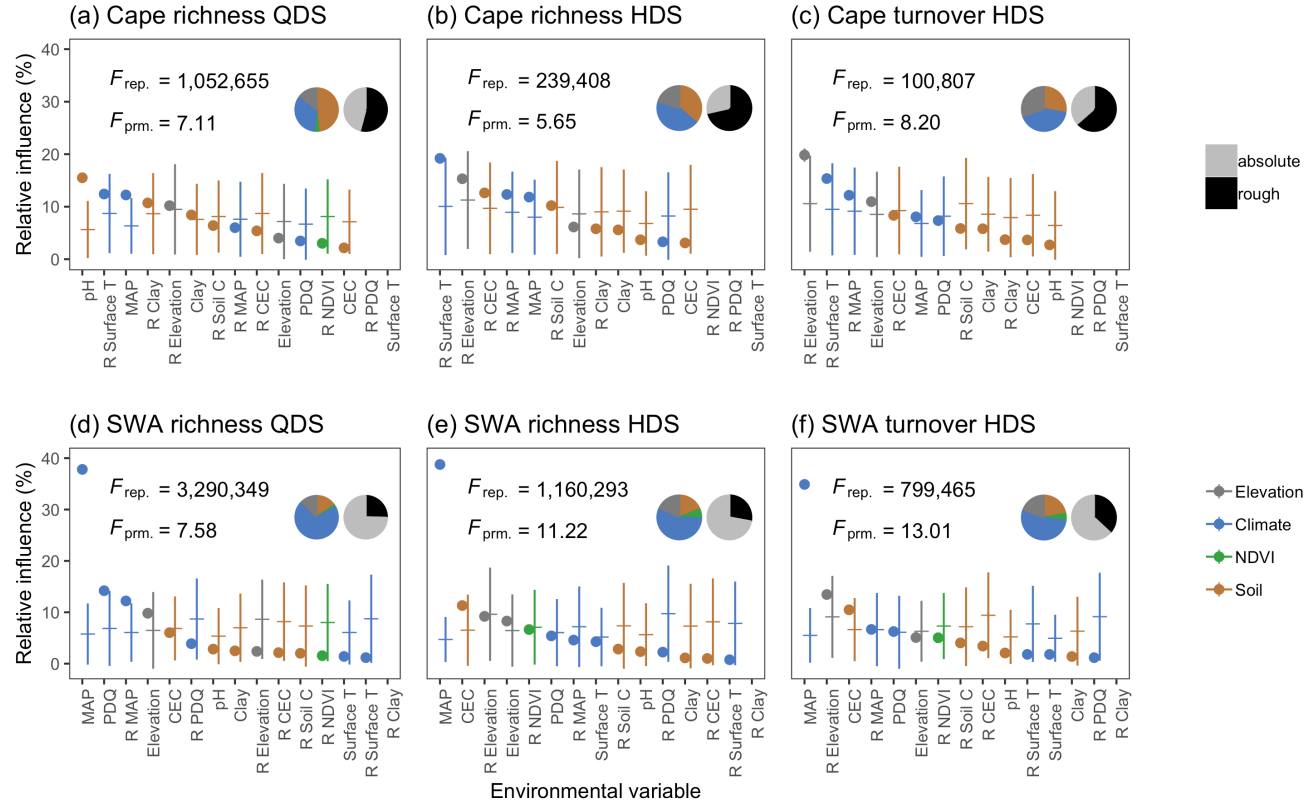
Figure 3: Relative influence of environmental variables (including heterogeneity variables—prefixed with "R") in boosted regression tree (BRT) model predictions in the Greater Cape Floristic Region (Cape, a–c) and the Southwest Australia Floristic Region (SWA, b–d) of vascular plant species richness at the (b,e) QDS-scale ($= \overline{S}_{\mathrm{QDS}}$), (a,d) HDS-scale ($= S_{\mathrm{HDS}}$) and (c,f) turnover ($= \overline{J}_{\mathrm{QDS}}$). All BRT-models were permitted to fit three-way interactions between environmental variables. Points denote the mean contribution of an environmental variable to model-predictions across the 1000 replicate BRT-models for that region/scope. Horizontal ticks denote the mean for the 999 permuted BRT-models. Standard deviations above and below these means are shown with vertical lines. Note, in the case of the replicate, standard deviations are so small such that the vertical lines are obscured by the points. Colours represent the general category of the environment to which a variable belongs (keyed), as in Figure 1b. Left-most piecharts inset in each panel display the same information. Right-most piecharts group contributions according to whether a variable was absolute or roughness-transformed (keyed). F-statistics inset are for one-way ANOVAs of differences in variables' relative influences—for both the replicate ($F_{\mathrm{rep.}}$) and permuted ($F_{\mathrm{prm.}}$) BRT-models.
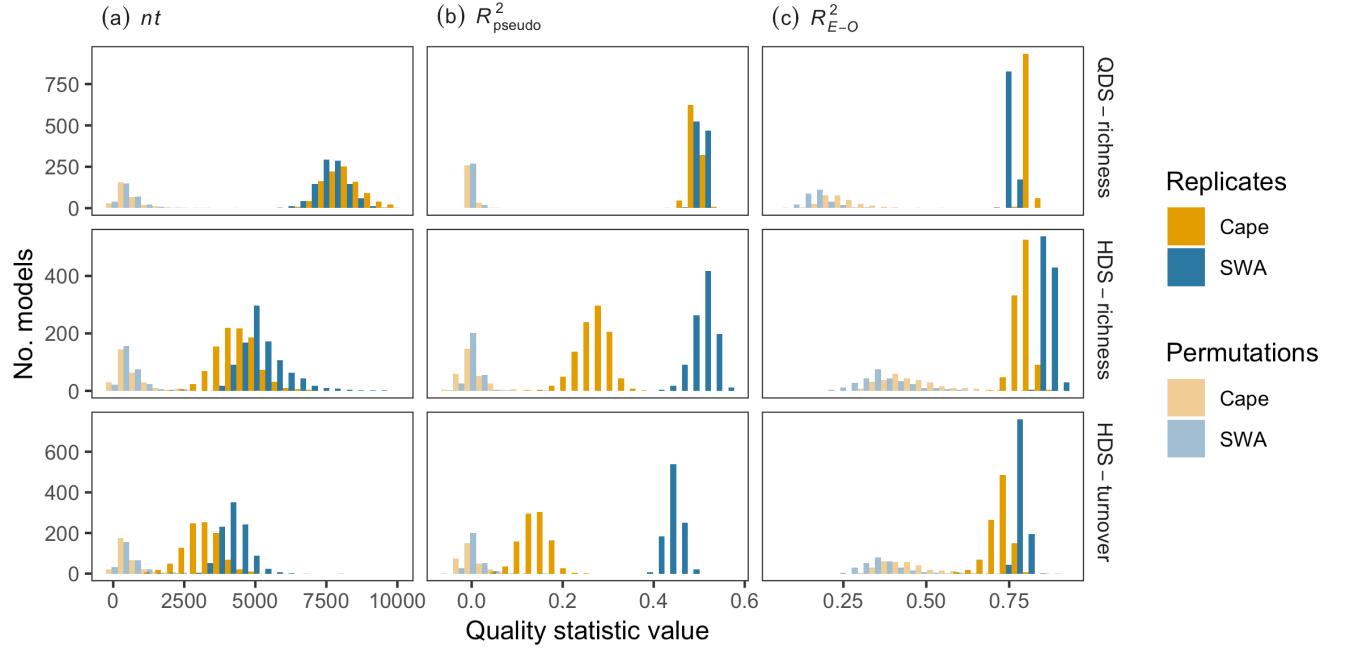
Figure 4: Distributions of three measures of boosted regression tree (BRT) model performance: (a) the number of trees in the model nt, (b) R^2_{pseudo} (Equation (4)), (c) $R^2_{\mathrm{E-O}}$ (see text). These measures are presented for the six sets of permuted (pale bars) and six sets of replicate BRT-models (dark bars) as in Figure 3, coloured according to the region of interest as in Figures 1a and 2. In all cases, replicate BRT-models almost entirely out-rank the permuted models in terms of performance (Table 2) and the Greater Cape Floristic Region (Cape) and Southwest Australia Floristic Region (SWA) models had significantly different values for each metric (Table 3). Note, the actual differences between Cape and the SWA models' values is not realistically significant in some cases (e.g. the difference in nt between the Cape and SWA QDS richness models is statistically significant, but are observedly so similar as not to affect interpretation).
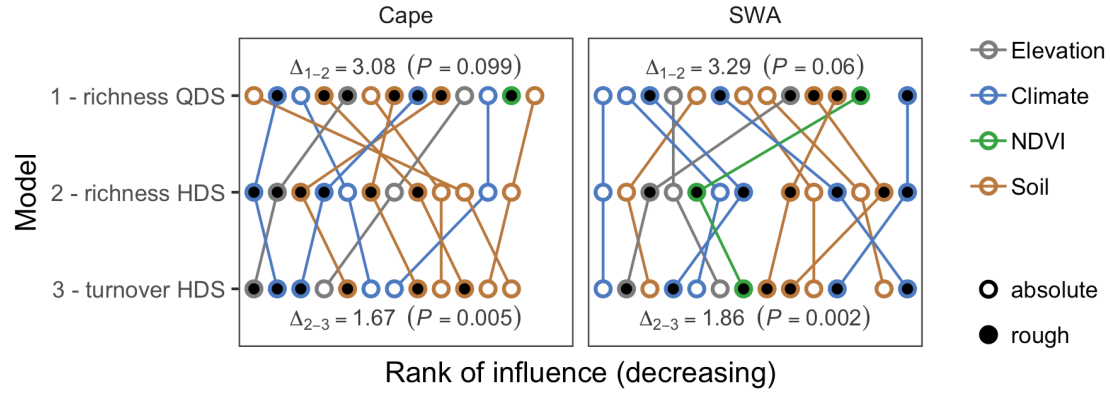
Figure 5: Differences in the rankings of environmental variables' (including heterogeneity variables) relative influences on boosted regression tree (BRT) model predictions of vascular plant species richness and turnover in (a) the Greater Cape Floristic Region (Cape) and (b) Southwest Australia Floristic Region (SWA) (as in Figure 3). Each point represents an environmental variable's rank in BRT-model importance, decreasing in importance from left to right. Rankings used here are the same as that of the average relative influence for variables across replicate BRT-models, presented in Figure 3. Coloured lines connect points representing the same environmental variable. Points' outlines are coloured according to the general category of the environment (keyed) to which a variable belongs, as in Figuress 1b and 3, while points' centres are coloured according to whether a variable was roughness-transformed or not. The comparisons of variables' rankings of interest are between QDS- and HDS-scale richness ($= \overline{S}_{QDS}$ and S_{HDS} respectively; rows nos. 1 and 2) and between HDS-scale richness and turnover ($= \overline{J}_{QDS}$) (rows nos. 2 and 3). Statistics (Δ- and P-values) inset at the top and bottom of each panel refer to these comparisons respectively. Δ-values represent the average absolute difference in ranks across variables between two models' rankings. The associate P-value results from ranking the observed Δ-values against 999 Δ-values based on random permutations of variables' rankings (SI1), such that more significant P-values denote rankings more similar than would be expected by chance.
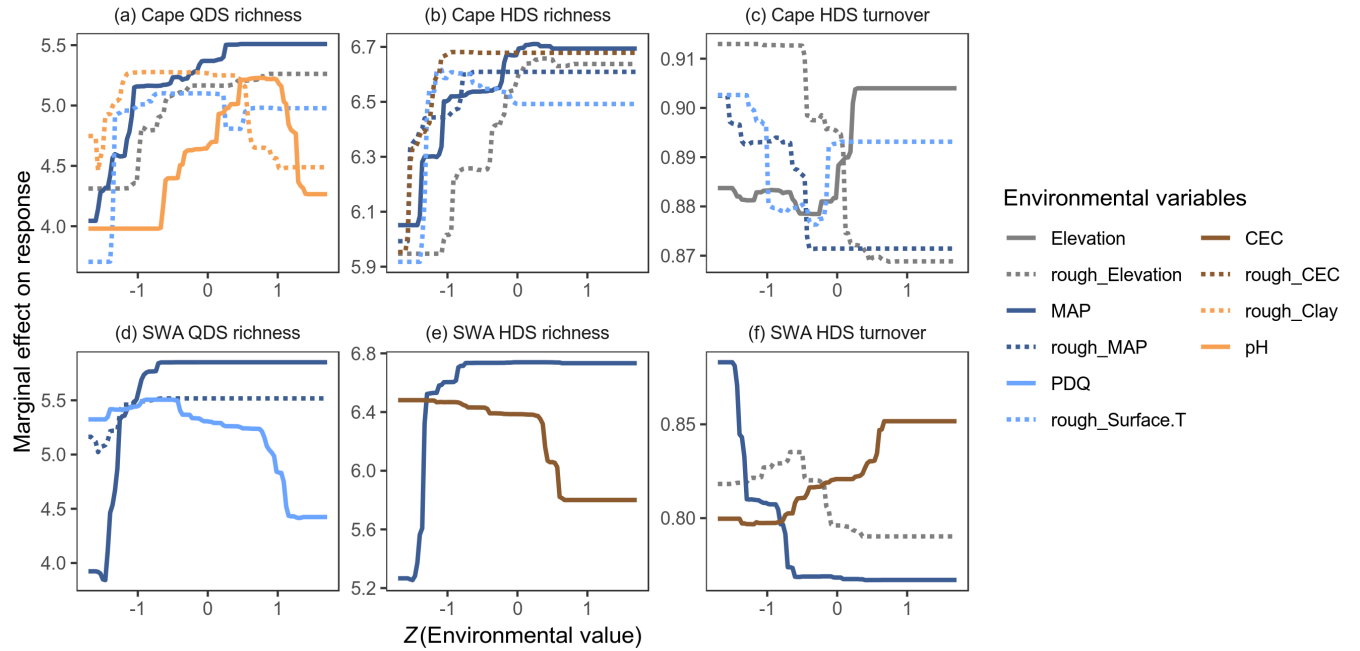
Figure 6: Marginal effects of environmental conditions and heterogeneity on vascular plant species richness at the QDS-scale (= $\overline{S}_{QDS}$; a,d), HDS-scale (= S_{HDS}; b,e) and turnover (= $\overline{J}_{QDS}$; c,f) in response variables in the Greater Cape Floristic Region (Cape; a–c) and Southwest Australia Floristic Region (SWA; d–f) following boosted regression tree (BRT) modelling. Marginal effect functions presented are derived from a representative BRT-model from the set of replicate BRT-models (for each of the six modelling cases) (see SI regarding how representative BRT-models were selected). Marginal effects represent the effect of a predictor variable when all other predictors are set at their means. Marginal effect functions are shown for environmental variables that contributed $\geq 10\%$ to a model's predictions. Functions are coloured as keyed, with solid lines representing absolute environmental variables and dotted representing heterogeneity variables ("rough"). Environmental variables were all rescaled here such as to be centred on zero (i.e. Z-transformed), facilitating comparison of functions' forms.