

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

Running title: Environmental heterogeneity and plant species richness

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Abstract

Aim: To quantify the explanatory power of heterogeneity in predicting plant species richness and turnover here in the Greater Cape Floristic Region and in the Southwest Australia Floristic Region. We compare the environmental heterogeneity in each region, how species richness and turnover interact in each region to produce the observed patterns of richness, and what different forms of environmental heterogeneity better predict richness in each region. We expect the Cape to be more heterogeneous in most environmental axes, and at a finer grain, such that the consequent high levels of species turnover explain the Cape's greater species richness per unit area. We also conjecture that edaphic heterogeneity will be an important factor in predicting richness in SW Australia.

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

Taxon: Vascular plants

Methods: Geospatial data, floral occurrence data → regression analyses, non-parametric statistics

Results:

Main conclusions:

Keywords: biodiversity, environmental heterogeneity, fynbos, Greater Cape Floristic Region, kwongan, macroecology, species richness, species turnover, vascular plants, Southwest Australia Floristic Region

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1 Introduction

Biodiversity represents the variety of living things, and the variety of ecological and evolutionary processes responsible for it (Bøhn & Amundsen, 2004). Studying the distribution of biodiversity in space is a major avenue of biological research (???; Kreft & Jetz, 2007). Regional-scale geographic patterns in species richness have long been studied, particularly in biodiversity hotspots (Cook et al., 2015). The spatial distribution of species richness can be explained in terms of the physical environment. Properties of the environment have been suggested to influence species richness in three ways: (i) productivity, water, and energy to enable organismal growth, and resources (i.e. niche space) to support a wider range of species (Gaston, 2000; Kreft & Jetz, 2007; Mouchet et al., 2015); (ii) stability, which enables species' persistence; and (iii) heterogeneity, which enables ecological speciation and possible barriers to gene flow, and with a wider variety of environments to facilitate 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 a local-deterministic sense, and in a historical context (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 ecology (Ricklefs, 1987; Kreft & Jetz, 2007; Hart et al., 2017). Species richness is constrained by the ability of habitats to support

41 a variety of species—its ecological carrying capacity (Mateo et al., 2017). This is exemplified in approaches to
42 modelling species richness as a function of environmental predictors in a correlative framework
43 (“macro-ecological models”; Mateo et al., 2017). Macroecological models of species richness implicitly
44 assume that communities are saturated, following species-area and species-energy relationships, and at
45 equilibrium with the environment (Mateo et al., 2017).

46 A solution to the paradox of species coexistence is environmental heterogeneity (EH): a more heterogeneous
47 environment has a larger environmental space, and can thus facilitate co-existence between species at the scale
48 of that heterogeneity. EH can also stimulate ecological speciation, should the region be environmentally stable
49 over evolutionary time-scales. Heterogeneity in the physical environment is known to be positively associated
50 with species richness (Rensburg et al., 2002; Hart et al., 2017), and has been demonstrated to do so across
51 many taxa—e.g. Canadian butterflies (???), European vertebrates (Mouchet et al., 2015), South African birds
52 (Rensburg et al., 2002), in communities along marine continental margins (Levin et al., 2010), French scarab
53 beetles (Lobo et al., 2004), and for global terrestrial plants (Kreft & Jetz, 2007). The spatial scale of
54 heterogeneity, or “grain” of the environment, is important to consider (Hart et al., 2017), in the same way that
55 the spatial of absolute environmental conditions has also been considered (???; Baudena et al., 2015; Mouchet
56 et al., 2015). Species co-existence and biodiversity maintenance is indeed suggested to be scale-dependent
57 (Hart et al., 2017).

58 EH is often under-represented in macro-ecological models of species richness, and has recently been found to
59 explain up to ca. 95% of biome level species richness across South Africa (Cramer & Verboom, 2016). Models
60 that include EH yield better estimates of the richness of the Cape flora, as they account for the role
61 heterogeneous environments such as those in the Cape facilitate species coexistence (Thuiller et al., 2006;
62 Cramer & Verboom, 2016). Mediterranean-type terrestrial biodiversity hotspots, such as the Cape flora
63 included in the models by Cramer & Verboom (2016), present interesting study systems in which to investigate
64 the relationship between the environment and species richness. These systems exhibit far greater species
65 richness than predicted by their areas, productivities and latitudes (Cowling et al., 1996; Kreft & Jetz, 2007).
66 There are five Mediterranean biodiversity hotspots on Earth: the California Floristic Province, the
67 Mediterranean Basin, the Chilean Winter Rainfall-Valdivian Forests, the Greater Cape Floristic Region, and the
68 Southwest Australia Floristic Region (Cowling et al., 1996; Hopper & Gioia, 2004; Cook et al., 2015). These
69 ecosystems have regular fire-cycles (Cowling et al., 1996), climatic buffering, and long term stability (Kreft &
70 Jetz, 2007), shrubby, sclerophyllous flora (Hopper & Gioia, 2004). Together, they account for ca. 20% of
71 global vascular plant species, yet only ca. 5% of global land surface areas (Cowling et al., 1996). Various

72 hypotheses have been proposed to explain the high levels of plant species richness in these regions (Cook et al.,
73 2015). The species accumulation hypothesis states that the stability of these regions has allowed many species
74 to accrue. The species co-existence hypothesis states that these hotspots may facilitate greater degrees of
75 species co-existence in smaller spatial areas, due to fine-scale heterogeneity in their environments. Indeed, EH
76 has evolutionary implications too, stimulating ecological speciation across sharp environmental gradients.

77 Both the Southwest Australia Floristic Region (SWA) and the Greater Cape Floristic Region (Cape) are
78 Mediterranean-type biodiversity hotspots, particularly in terms of plant species. Where the Cape (with an area
79 of ca. 189,000 km²) is known to contain about 11,400 plant species (about 0.060 species per km²), SWA (area
80 of ca. 270,000 km²) has about 3,700 species (0.014 species per km²) (???). So, the Cape has ca. 4.3 times as
81 many species per km² as SWA. The Cape and SWA are appropriately often compared, due to the similarities
82 between their environments (e.g. oligotrophic soils, an oceanically buffered moderate climate) and their plants'
83 ecologies (Hopper & Gioia, 2004). These two regions present unique flora out of the five Mediterranean
84 systems, with high levels of endemism (Cowling et al., 1996), and many obligate fire-adapted species (Cowling
85 et al., 1996). Similarities withstanding, SWA is topographically and edaphically distinct from the Cape. The
86 former is topographically rather uniform (i.e. flat)—uniquely so among the world's five Mediterranean-climate
87 regions (Hopper & Gioia, 2004)). SWA possesses a mesoscale chronosequence dune system (Laliberte et al.,
88 2014; Cook et al., 2015), while the Cape is mountainous, topographically heterogeneous, and therefore
89 associated with a large degree of spatial climatic variability, with a fine-scale mosaic of geologies and soils
90 (Cowling et al., 1996; Cramer et al., 2014; Verboom et al., 2017).

91 Both regions have sources of edaphic heterogeneity, but at different scales. This edaphic variability may aid in
92 explaining the species richness in these regions (Beard et al., 2000; Verboom et al., 2017). EH can stimulate
93 ecological speciation, should the region be stable over evolutionary time-scales, as is likely the case in both the
94 Cape and SWA (Wardell-Johnson & Horwitz, 1996; Hopper & Gioia, 2004; Lambers et al., 2010; Cramer et al.,
95 2014; Laliberte et al., 2014; Cook et al., 2015). For the Cape, this richness is largely known to result from long
96 term climatic stability, and fine grain variation in geology and soils (Cramer et al., 2014). The question thus
97 arises whether heterogeneity is a significant contributor to SWA species richness as is likely the case in the
98 Cape. In the absence of topographic variability in SWA, it is proposed that the heterogeneity of that region is
99 due to the juxtaposition of soil types (Laliberte et al., 2014; Cook et al., 2015), creating extreme edaphic
100 variation.

1.1 Hypothesis-v1

Our main hypothesis is that the greater abiotic heterogeneity in the Cape, and the finer grain of that heterogeneity, compared to that of the SWA, accounts for the Cape's greater species richness per unit area. We expect the relationships between EH, species richness, and species turnover in these two regions to demonstrate this. As stated above, heterogeneous environments can (i) support diverse species assemblages, and (ii) stimulate ecological speciation. Thus, we expect species richness to covary with heterogeneity. Additionally, as one moves across a heterogeneous landscape, we expect to find greater turnover in community composition, as different environments support different species. Thus, areas of greater turnover should also be more rich, due to potential complementarity between neighbouring communities increasing total richness. Consequently, we expect that EH positively influences species richness and species turnover, and that species turnover itself positively influences species richness.

1.2 Hypothesis-v2

Aim: This study investigates the role EH plays in explaining vascular plant species richness in the Cape and SWA. We compare the relative importance of heterogeneity between the two regions, as heterogeneity has the evolutionary role of facilitating speciation, and the ecological role of supporting diverse species assemblages. Spatial scale of that heterogeneity is also considered, as the heterogeneity-richness relationship can vary with habitat grain-size.

Our hypotheses concern the Cape and SWA's environments and floras. Our main hypothesis is that the Cape possesses greater abiotic heterogeneity, and at finer grain, compared to SWA, such as to explain the Cape's greater species richness per unit area, and proposed greater levels of species turnover between areas. We also conjecture that the heterogeneity that predicts species richness in SWA will be more pronounced in terms of edaphic variables. Here we attempt to assess six key predictions of this hypothesis, additionally investigating a seventh prediction to test the conjectured role of edaphic heterogeneity in SWA. Dealing with the two regions' environments, we assess (i) whether the Cape environment is more heterogeneous than that of SWA and (ii) whether the Cape environment has more pronounced heterogeneity at finer scales than that of SWA. Dealing with the distribution of species in the two regions, we assess (iii) whether the Cape exhibits greater levels of species turnover between areas. Relating each regions' environment and flora, we finally assess (iv) whether species richness and species turnover are adequately predicted by EH in both regions and whether (v) Species

129 richness and species turnover are better predicted by different forms of EH in either region (e.g. the importance
130 of edaphic heterogeneity in SWA).

131 ...

132 We employ classical statistical methods to analyse publicly available geospatial and species occurrence
133 datasets.

134 ...

135 Species distribution models (SDMs), or environmental niche models, are sets of empirical methods that relate
136 observed species presences (or similar data) to environmental and spatial variables, often correlatively (Guisan
137 & Thuiller, 2005). As SDMs rely chiefly on correlating observed species ranges with the conditions thereof,
138 they provide only a model of the realised niche of a species (Raes, 2012), which can cause issues when
139 attempting to predict responses of species to changing climate. Other assumptions of typical SDMs include that
140 the range of species considered is in equilibrium with the environment (Altwegg et al., 2014; Guisan & Thuiller,
141 2005; Hannah et al., 2005), thus limiting the efficacy of these models on dynamically ranged or highly vagile
142 species (Hannah et al., 2007). Regardless, given the dynamic nature of biotic ranges under climate change,
143 SDMs are a valuable tool in identifying the contemporary risks posed to global and regional biodiversity.

144 The GCFR is a megadiverse terrestrial biogeographic region, with high levels of endemism. Midgley et al.
145 (2003) investigated the responses the now defunct Cape Floristic Region (CFR) flora to climate change. Using
146 bioclimatic envelope models (a form of SDM), they modelled the Fynbos Biome's distribution as a whole, and
147 select Cape-endemic Proteaceae species' distributions, under current and future climate (climate scenario
148 HadCM2), and again with the impact of land use change. Their Fynbos model was an indicator of regional
149 priority for species level modelling efforts, showing a general southwards contraction of the biome. Their
150 specific Proteaceae models yielded various results: complete extinctions for some species, range contractions
151 for most, improbable range shifts in some, and range expansions in few. The range shifts predicted therein were
152 acknowledged to be improbable, due to the unmodelled limitations of plant dispersal and edaphic dependence.
153 Midgley et al. (2003) concluded that climate change is likely to have severely negative for the CFR flora.
154 However, as will be outlined below, their methods may be overpredicting losses due to climate change.

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156 The last 20 years have seen much ecological research interest in and development of SDMs, using many

157 statistical and machine-learning-based methodologies (Altwegg et al., 2014; Elith et al., 2008, 2011; Guisan &
158 Thuiller, 2005). Machine-learning-based methods in SDMs include MaxEnt (Elith et al., 2011), genetic
159 algorithms, and adaptive neural networks (Hannah et al., 2005). The use of more advanced statistics
160 (e.g. Bayesian frameworks, ordination methods (Hannah et al., 2005)) is also seen. These two avenues of
161 research have intersected in the development of boosted regression trees (BRTs) (originally “gradient boosting
162 machine”; Friedman, 1999) a system of recursively generated, non-linear regression trees, as outlined by Elith
163 et al. (2008). BRTs have been used as SDMs in southern Africa before (e.g. Thuiller et al., 2006), sometimes
164 for conservation purposes (e.g. Coetzee et al., 2009), but BRTs have yet to be used specifically to assess the
165 responses of the regional flora to climate change. BRTs have more flexibility in their predictions than more
166 traditional methods (e.g. GAMs), as they are non-linear and machine-learning-based (Elith et al., 2008).

167 ...

168 **2 Materials and methods**

169 **2.1 Overview**

170 Our analyses required definitions of the boundaries of the two regions, environmental data for each, and
171 geospatially-explicit vascular plant occurrence records, all based on publicly available data. The environmental
172 variables chosen (Table 1) for this study were intended to cover a reasonable spread of climatic, edaphic, and
173 ecologically relevant environmental axes, and are not intended to be exhaustive. We selected variables
174 describing topography (elevation), productivity (NDVI), soil status, and climate and climatic seasonality.

175 We carried out this investigation at four principal spatial scales: 0.05° x 0.05° squares (the finest common
176 resolution among the environmental data sources used), quarter degree squares (QDS) (Larsen et al., 2009),
177 half degree squares (HDS) (Larsen et al., 2009) and three-quarter degree squares (3QDS). For the Cape, most
178 plant occurrence records are only accurate to QDS level. Thus, any analysis involving species data was
179 necessarily limited to scales above and including QDS.

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

2.2 Environmental data sources

Geospatially-explicit raster layers were acquired for a selection of environmental variables (Table 1), for the regions of interest. Here, the GCFR was treated as the areas 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.

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 0.05° resolution using the “resample” function in the R package “raster” (???), with the “bilinear” method.

An emphasis was made on using satellite-derived environmental data in this work, in order to minimise differences in data quality and methodologies between the Cape and SWA. Additionally, satellite-derived data have been shown to benefit regional-scale species distribution models (Deblauwe et al., 2016), thus motivating their use in this regional-scale study. The environmental data used in this study were derived from NASA’s SRTM digital elevation model (Farr et al., 2007), NASA’s MODIS/Terra spectroradiometric data for land surface temperature and NDVI, the Climate Hazards Group’s CHIRPS rainfall dataset (Funk et al., 2015), and the International Soil Reference and Information Centre’s SoilGrids250m edaphic dataset (Hengl et al., 2017) (Table 1). SRTM and MODIS are entirely derived from satellite measurements, whereas CHIRPS is interpolated from weather station data with satellite-derived radiometric measurements. SoilGrids250m is a machine-learning derived product, based on soil measurements as a function of many covariates, including MODIS and STRM sources (see Hengl et al., 2017), using random-forests and other classification-tree-based methods, including gradient-boosting. For the soil data considered here (Table 1), we used depth-interval weighted average values as the value for a particular soil variable in a given place.

Climatic and spectral data arise from satellites monitoring properties of the Earth’s surface through time. We therefore use the mean annual values for rainfall, surface temperature, and NDVI in each pixel in our analyses. Pronounced seasonality of rainfall is a known feature of Mediterranean systems (???). We describe this seasonality by computing computing the precipitation in the driest quarter (PDQ), using code from within the

211 “biovars” function in the R package “dismo”.

212 **2.3 Plant occurrence data**

213 Geospatially-explicit records of vascular plant occurrences were downloaded from the Global Biodiversity
214 Information Facility (GBIF, Table 1). Queries were made for tracheophyte records from within the borders of
215 the Cape and SWA as treated here (GBIF, 24 July 2017, GBIF (24 July 2017)). Only records with defined
216 species and intra-specific ranks were kept. Intra-specific occurrences were treated as simply being
217 representative of their species. This resulted in FIXME unique species names in the Cape, and FIXME in SWA.

218 We cleaned these data using the R package “taxise” (???, (???)) to check that these species names had
219 accepted-status among taxonomic databases. I queried two major taxonomic databases: the Global Name
220 Resolver (GNR), and the Taxonomic Name Resolution Service (TNRS). Should one of either service return at
221 least one match for a given name, then that name was deemed accepted. Those names for which no full
222 binomial matches were found in either database were excluded from the final list of species. The number of
223 species names excluded totalled at FIXME and FIXME for the Cape and SWA respectively. Especially for
224 SWA, these numbers may be deemed appreciably high. But, the occurrence records that would be dropped, as a
225 consequence of these names’ removals, seemed to be distributed randomly in geographic space in both regions.
226 As such, any effect of the loss of these records in this analysis is uniform within the two regions.

227 After the unaccepted names were removed, it was important to ensure that a species was not listed under
228 multiple synonyms. Such cases would skew the species richness data used in this study. In light of this, the
229 remaining names were queried in the Tropicos and Integrated Taxonomic Information System (ITIS) databases
230 for their known synonyms, using “taxize”. These were collated to produce a nomenclatural “thesaurus” for the
231 Cape and SWA species. This consisted of a list of the accepted species names in a region, each associated with
232 a list of known synonyms. I amended species’ names in the GBIF occurrence data, in order ensure species were
233 listed under only one of these synonyms, as follows: For each entry in the thesaurus, for each synonym of that
234 entry, if that synonym appeared in the GBIF species list, I replaced all appearances of that synonym in the
235 species list with the original name from the thesaurus-entry that that synonym came from.

236 Lastly, I removed any species from both regions that are invasive aliens or non-indigenous. Alien species lists
237 for plants in South Africa and Australia were acquired from the IUCN’s Global Invasive Species Database
238 (<http://www.iucngisd.org/gisd/>).

239 The final total plant species richness in each region was FIXME and FIXME for the Cape and SWA
 240 respectively. These final collections of species occurrence records were converted to raster-layers, wherein
 241 pixel-values represented the species, genus and family richness of vascular plants within that pixel. These
 242 rasters were produced at QDS, HDS, and 3QDS resolutions.

243 2.4 Analyses

244 2.4.1 Quantifying environmental heterogeneity

245 First, in order to assess predictions (i) and (ii), we needed to describe the EH in both regions. Using the R
 246 package “raster” (???), we used a modified version of the “roughness” index in the “terrain” function. For a
 247 three by three neighbourhood N of cells, our index of roughness is the average square-root of the squared
 248 difference between each of the n neighbour cells’ values x_i and the central focal cell’s value x_{focal} :

$$Roughness(N) = \frac{1}{n} \sqrt{\sum_{i=1}^n (x_{focal} - x_i)^2}, \quad (1)$$

249 This value, notionally the standard deviation of values relative to the focal value, is ascribed to the focal cell.
 250 Note, in order to use as much data from within regions’ borders as possible, roughness was computed if a focal
 251 cell had at least one neighbour cell—that is, roughness is defined where $n_{x_{focal}} \geq 1$. Using this index of
 252 heterogeneity, we produced raster layers of each of our nine environmental variable’s heterogeneity. We
 253 compared the distributions of roughness values in each variable in each region with non-parametric
 254 Mann-Whitney U -tests, as almost all variables could not be normalised by log-transformations. We also
 255 compare the effect size of the Cape vs SWA using the “common language effect size” ($CLES$), using the R
 256 package “canprot”. The $CLES$ is the proportion of all pairwise comparisons between two sample groups’
 257 observations where one group’s value is greater than the other. In our case, of all pairwise comparisons of a
 258 variable’s roughness values between the Cape and SWA, we calculated the CLES as the proportion of pairs
 259 where Cape roughness values were greater than that of SWA. This allowed us to assess prediction (i). To
 260 compare the spatial scales of heterogeneity (prediction (ii)) between each region, we repeated this analysis at
 261 all four spatial scales. Once again, this entailed recalculating the roughness layer for each variable after the
 262 original layer (0.05 degrees resolution) had been rescaled to each of the coarser resolutions.

263 2.4.2 Quantifying species turnover

264 Regarding prediction (iii), we wished to compare the general degree of species turnover in each region. To
265 compare the extent of species turnover between the Cape and SWA, we determined two metrics of species
266 turnover. The first, computes the mean species turnover as Jaccard distance (???) between each pair of QDS
267 within each HDS (\bar{J}_{QDS} , based on HDS with $2 \leq n \leq 4$ QDS) in both regions. The second is defined in terms
268 of Whittaker's additive definition of β -diversity (???), where

$$\gamma = \alpha + \beta \quad (2)$$

269 Here, we treat species richness at the HDS-scale (S_{HDS}) as γ and at the QDS-scale as α . Intuitively, the
270 species richness of an area is the result of the richness of sites within that area and the difference in species
271 complements between those sites. Thus, we use here an additively defined residual turnover (T_{HDS} ; i.e.
272 $\beta = \alpha - \gamma$) as the proportion of S_{HDS} unexplained by the mean species richness of HDS' constituent QDS
273 (\bar{S}_{QDS}). We compare the distributions of \bar{J}_{QDS} and T_{HDS} using non-parametric Mann-Whitney U -tests, in
274 order to guard against non-normality.

275 2.4.3 Predicting richness and turnover with environmental heterogeneity

276 Regarding prediction (iii), we wished to compare the general degree of species turnover in each region. For (iv)
277 and (v) we modelled species richness (S) and turnover as a function of various combinations of environmental
278 and environmental heterogeneity variables in both regions using boosted regression-tree (BRT) modelling
279 techniques. Allowing us to explore which axes of environmental heterogeneity have most influence on vascular
280 plant species richness and turnover, and the differences in the importance of such axes between the Cape and
281 SWA.

282 BRTs are a flexible machine learning-based model of response variables and do so without involving normal
283 null-hypothesis significance testing (Elith et al., 2008), and have been employed previously to model species
284 richness (Thuiller et al., 2006; see Mouchet et al., 2015; Cramer & Verboom, 2016) as macro-ecological
285 models. BRTs are developed through the iterative generation of non-linear regression trees. BRTs are an
286 ensemble-approach, in which a prediction \hat{y}_i is based on the weighted sum of the predictions of progressively
287 "less important" regression trees (t_k), as opposed to the predictions of one tree (Elith et al., 2008). For $k \rightarrow nt$

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

$$\hat{y}_i = \sum_{k=1}^{nt} w_k t_k. \quad (3)$$

289 BRTs have two major metaparameters that users have control over (???): the learning rate (lr , the rate at which
290 iterative trees reduce predictive deviance during model-training, conceptually a “shrinkage factor” controlling
291 the contribution of each tree to the final model) and tree complexity (tc , the number of nodes on a given
292 regression-tree, i.e. the maximum interaction depth the model is permitted to fit).

293 BRTs were implemented here to predict both vascular plant species richness and turnover in each HDS, as a
294 function of environmental variables and environmental roughness values in those cells, as Gaussian responses,
295 thus resulting in two BRT-models for each region. We treated richness as S_{HDS} and turnover as \bar{J}_{QDS} . The
296 natural logarithm of species richness was used, in order to satisfy the assumptions of a Gaussian response. Note,
297 this is not strictly because BRTs have any parametric assumptions concerning the distribution of the response
298 variable, but rather to aid in applying the Gaussian-family of BRT algorithms to the richness data available.

299 As recommended by Elith et al. (2008), BRT models were trained on a set of non-collinear predictor variables
300 using “gbm.step” in “dismo” (???) and “gbm” (???). Collinear predictor variables can skew the interpretation
301 of results, as the relative influence of mutually collinear variables is reduced. Collinearity among the 9
302 environmental predictor variables and their respective 9 roughness-equivalents was assessed using
303 “removeCollinearity” in the R package “virtualspecies” (???) separately for each region, such that variables
304 were no more than 80% collinear (Pearson’s $r \geq 0.80$). When faced with a cluster of collinear variables, one
305 variable was chosen manually therefrom. Where possible, the roughness-equivalent of an environmental
306 variable was included if its absolute-equivalent could also be included. When interpreting the results of BRTs,
307 it is important to consider the effects of the variables included as representative of the effect of the excluded
308 variables with which it is collinear.

309 In order to select ideal lr and tc all models (described below) were trained on the final non-collinear predictor
310 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,
311 5×10^{-4} , 1×10^{-4}). The function “gbm.step” optimises the number of trees (nt) using cross-validation during
312 model training (Elith et al., 2008) by halting iteration when predictions begin to overfit. For all models, we
313 used 10 cross-validation folds (i.e. use 10 different randomly selected training data sets), a tolerance-threshold
314 of 0.001, a bagging-fraction of 0.75 (proportion of training data randomly chosen to generate each tree), and

315 trained models starting with 50 trees, with each iterative step adding 50 trees at a time, up to a maximum of
316 10,000 trees.

317 Following this iterative parameter optimisation, Gaussian BRT models were constructed with $tc = 3$ and
318 $lr = 0.001$, along with the other settings described. The models were developed with all variables (those
319 retained, above) and then simplified using the protocol suggested by Elith et al. (2008) to retain the minimum
320 number of variables contributing to the models, using “gbm.simplify” in “dismo”.

321 BRT-model performance can be described by measuring the variance a model has explained and by comparing
322 observed and model-expected species richness (and turnover). For the former, we use R_{pseudo}^2 , which is the
323 proportion of null deviance D_{null} explained by a model i :

$$R_{pseudo}^2 = 1 - \frac{D_i}{D_{null}} \quad (4)$$

324 For the latter, we regressed expected against observed richness and turnover, and calculated the R^2 -value for
325 those regressions (hereafter R_{O-E}^2).

326 **TODO:** In order to assess the reliability of the conclusions drawn from these models, we randomly permuted
327 the response data (S_{HDS} and \bar{J}_{QDS}) with respect to the environmental and heterogeneity data, and refit all 4
328 BRT-models 1000 times (with the final non-collinear predictor sets and preconfigurations above). This also
329 allows us to remove any effect of spatial autocorrelation in generating the observed correlations between
330 patterns of species occurrence and environment (???)

331 **3 Results**

332 **3.1 Describing environmental heterogeneity across scales**

333 Across all variables considered, the Cape is more environmentally heterogeneous in the majority of pairwise
334 comparisons of grid-cells ($CLES > 0.50$, Mann-Whitney U -test: $P < 0.05$, Figure 1). The Cape is thus
335 more environmentally heterogeneous than SWA overall, but the degree to which it is more heterogeneous
336 varies between environmental variables. These effects also vary somewhat with the spatial scale concerned. In
337 some variables, the differentiation between Cape and SWA heterogeneity lessens at coarser scales (Figure 1b).
338 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 coarser 3QDS scale (Mann-Whitney U tests, $P > 0.05$, Figure 1b).

Most obviously, and as expected, topographic heterogeneity is greatest in the Cape (Figure 1). Though SWA has a slightly wider distribution of elevational roughness values at coarse scales (e.g. 3QDS) compared to fine scales (0.05°), so does the Cape. As such, the relative difference 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.

Climatic heterogeneity presents less differentiation between the Cape and SWA than elevational roughness (Figure 1a), though still the Cape predominates (Figure ??b). Notably, the difference between Cape and SWA mean annual rainfall and land surface temperature heterogeneity lessens when considered at coarse spatial scales (3QDS scale, Figure ??b). Rainfall seasonality (PDQ), however, is similarly more heterogeneous in the Cape across all spatial scales considered.

Biological productivity, as measured by NDVI, varies spatially to a similar extent in the Cape and SWA (i.e. is more similarly heterogeneous, $CLES < 0.60$, Figure 1).

Concerning edaphic variables, the Cape and SWA are similarly heterogeneous at coarser scales, particularly in terms of CEC and Soil C (Figure 1b).

3.2 Comparing species turnover in the two regions

Following calculations of \bar{J}_{QDS} and T_{HDS} for each HDS-cell in each region, we 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, no matter how turnover is defined ($P < 0.0001$, Figure 2a,b).

3.3 Predicting richness and turnover with environmental heterogeneity

Vascular plant species richness and turnover are both predicted at least in-part, if not primarily, by environmental heterogeneity in both regions (Figure 3). BRT-models of species richness in each region performed better than the turnover models (e.g. Cape richness vs turnover: $R^2_{pseudo} = 0.30$ vs 0.19 , $R^2_{O-E} = 0.74$ vs 0.71 , respectively; Figure 3).

364 BRT-models found climatic variables to be of most importance when predicting species richness and turnover
365 (Figure 3). Elevational heterogeneity features prominently in all models too, ranking at worst the third most
366 important predictor.

367 Concerning BRT-models of vascular plant species richness, the sets of environmental variables important to
368 predicting species richness differ substantially between the Cape and SWA (Figure 3a,b). While species
369 richness in the Cape is more strongly predicted by elevational, climatic and edaphic heterogeneity (Figure 3a),
370 richness in SWA is mostly predicted by absolute MAP (Figure 3b). Indeed, Cape species richness is mostly
371 predicted by environmental heterogeneity variables (Figure 3a inset), while SWA species richness is mostly
372 predicted by absolute environmental variables (Figure 3b inset).

373 Concerning BRT-models of vascular plant species turnover, elevational heterogeneity is the most important
374 predictor in both the Cape and SWA (Figure 3c,d). Also in both regions land surface temperature heterogeneity
375 is an important predictor, especially in SWA (Figure 3c,d). Moreover, species turnover in SWA was found to
376 only depend on two heterogeneity variables (Figure 3d).

377 **4 Discussion**

378 Conclusion: The Cape is more generally environmentally heterogeneous than the SWA, as expected (see
379 prediction (i)). Though, there are cases where the SWA is arguably at-least-as-heterogeneous as the Cape, and
380 we can observe here extreme regions of high edaphic heterogeneity, at fine scales, in SWA. These surpass the
381 edaphic heterogeneity of the Cape, supporting our seventh prediction/conjecture.

382 We also have support for prediction (ii), as seen in Fig. ??.

383 I have provided support for the hypothesis that the difference in plant species richness between the GCFR and
384 SWAFR is accounted for by the fact that the GCFR is more abiotically heterogeneous than the SWAFR. As
385 expected, the GCFR is shown to possess (i) a quantifiably more heterogeneous environment, and (ii) is
386 heterogeneous at a finer spatial scale than the SWAFR. I have shown that vascular plant species richness (iii)
387 can be explained in terms of environmental conditions, including environmental heterogeneity, in both the
388 GCFR and SWAFR. Also, I have shown that (iv) the set of environmental axes that explain plant species
389 richness, both absolute and as heterogeneity, differs between the GCFR and SWAFR. These findings contribute
390 towards an understanding of the ecological conditions that facilitate species coexistence (and likely stimulate

391 ecological speciation) in these two regions.

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

405 The fact that a combination of absolute and roughness variables is also as predicted by the hypothesis in this
406 study. In the models developed by Cramer & Verboom (2016) for South Africa, roughness in topography was
407 largely superseded as an important predictor of species richness by other roughness variables. My models,
408 however, did not show this. Similar to the study by Rensburg et al. (2002), my models revealed roughness in
409 topography and other variables to be important. Although, Rensburg et al. (2002) considered differences
410 within pixels, as opposed to this study, which considered differences between pixels. My models, those of
411 Cramer & Verboom (2016), and those of Rensburg et al. (2002), do not all concur as to the role of roughness in
412 elevation vs. more biologically meaningful variables in explaining species richness. The source of these
413 discrepancies is unclear, though no doubt complex. The complements of environmental variables and
414 methodologies used in these studies do differ, limiting extensive comparison between these analyses.

415 The determinants of vascular plant species are shown to be region specific (Figures ??, ??, ??). The importance
416 of MAP and roughness in rainfall seasonality (PCV) in predicting richness in the SWAFR (Figure ??I, ??J),
417 aligns with the steep climatic gradients observed there (Cook et al., 2015). The soil variables that determine
418 plant species richness in the model for the SWAFR (Figures ??K, ??L) differ to those that determine richness in
419 the GCFR (Figures ??G, ??H), further highlighting the edaphic differences between these two regions.

420 Although both are nutrient leached systems, the SWAFR is flat, with soil-chronosequences (Laliberte et al.,

2014; Cook et al., 2015), while the GCFR is mountainous (Cowling et al., 1996; Cramer et al., 2014; Verboom et al., 2017). The importance of roughness in soil density, and absolute texture, in the SWAFR (Figures ??K, ??L) highlights the changes in soil that are associable with age of the substrate (e.g. particle size) as being biologically relevant to species richness. The positive effect of soil clay content on species richness in the SWAFR aligns with the findings of Laliberte et al. (2014) that richness in the SWAFR increases with soil age.

NDVI is more heterogeneous across the GCFR than the SWAFR (Figures ??A). The fact that thermal variables tend to be more rough in the GCFR (Figure ??A) is likely due to possible covariance of the MODIS/Terra products with topography, as MODIS data used here describes land surface temperature. As the GCFR is topographically rugged, the roughness of NDVI may arise from this. Despite this, NDVI is an integrating variable, which captures information about productivity, light availability, and soil nutrients (Power et al., 2017). The fact that absolute NDVI contributes to predicting species richness in the GCFR, especially at finer spatial scales (Figure ??E) demonstrates the role of ecological productivity in facilitating the coexistence diverse species assemblages. Environmental heterogeneity, then, is integral to explaining patterns of species richness, but must be considered along with resource- and energy-availability axes. In so much as a diverse environmental space supports more species, the materials and productivity required for biota to thrive are also needed to support species (???; Gaston, 2000; Bøhn & Amundsen, 2004; Kreft & Jetz, 2007). As such, my findings, along with those of previous studies (Rensburg et al., 2002; Thuiller et al., 2006; Kreft & Jetz, 2007; Cramer & Verboom, 2016), suggest that there is ecological and evolutionary consequence to resource availability *and* environmental heterogeneity, in that they tend to be positively associated with species richness.

The combined BRT-model of species richness for both regions reveals soil clay content as an important predictor, at coarse spatial scales, despite this variable not being particularly important within each region separately (Figure ??). Though this model does not strictly consider the regions as separate, this finding may indicate that the relationship between clay content and species richness differs between the regions. So far as clay content can be used to predict species richness, it matters more to those predictions when applied to large sections (i.e. coarse scales) of each regions.

Kreft & Jetz (2007) modelled global terrestrial vascular plant species richness, which focussed on primarily absolute environmental values, underestimated the richness of the Cape flora. Though Kreft & Jetz (2007) did include topographic heterogeneity in their predictor set, topography is often a proxy for more biologically meaningful variables (Cramer & Verboom, 2016). This explains why the inclusion of these variables (e.g. roughness in mean annual precipitation) yields more accurate predictions of species richness. Indeed,

451 Thuiller et al. (2006) also included topographic heterogeneity. Cramer & Verboom (2016) described 68% of
452 species richness at the QDS scale across South Africa. Regarding the GCFR, depending on whether one
453 consults pseudo- R^2 (Table 3), the ratio of mean predicted to observed richness per grid-cell (Table 5), or the
454 distributions of predicted vs. observed richness values per grid-cell (Figure ??), I have achieved a similarly
455 suitable level of predictive accuracy. There is, though, still unexplained species richness in light of my models.
456 As Cramer & Verboom (2016), Rensburg et al. (2002), Thuiller et al. (2006), and Mouchet et al. (2015) have
457 done, these macro-ecological models are a-historical. Evolutionary considerations of species richness in
458 geographic space are worthwhile, especially in regions with environments stable over evolutionary time.

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

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

477 Following from the understanding that functionally diverse assemblages, which are more likely to be more
478 species rich, are likely to arise and/or occur in areas with diverse ecological pressures (Molina-Venegas et al.,
479 2015), one would expect, then, heterogeneous habitats such as those in Mediterranean-type biodiversity
480 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 SWAFR 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.

I have demonstrated support for the idea that environmental heterogeneity is positively associated with species richness, particularly Mediterranean systems. In the SWAFR and the GCFR, high levels of endemism and biodiversity are also likely the results of long-term landscape and climatic stability (Hopper, 1979). Thus, the roles of environmental variability through space, and stability through time, are the two main ways in which the environment relates to biodiversity in these regions.

Table captions

Captions are also repeated alongside their respective tables for readability.

Table 1: Georeferenced vascular plant species occurrence and environmental data sources used in this study. The temporal extent of data used is described where applicable. Abbreviations are as follows: MAP, mean annual precipitation; PDQ, precipitation in the driest quarter; CEC, cation exchange capacity.

506 Figure captions

507 Captions are also repeated alongside their respective figures for readability.

508 Figure 1: Types of environmental heterogeneity, compared between the the Cape and SWA—namely for (a)
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510 per variable type. The upper row of panels shows example distributions of roughness values (Equation (1)),
511 showing the different extremes in environmental heterogeneity observed in each region when compared at fine
512 (0.05°) and coarse (3QDS) scales. Each distribution has under it an area of one. Histograms were constructed
513 using 20 breaks. In the lower row of panels, these distributions of roughness values were compared between
514 the Cape and SWA at each of the four spatial scales, not just 0.05° and 3QDS, using non-parametric
515 Mann-Whitney U -tests to test for differences. The “common language effect size” ($CLES$, see text) describes
516 these differences (b). U -tests for almost all environmental variables yielded significant differences ($P < 0.05$)
517 between Cape and SWA values (NS, non-significant differences). $CLES$ for 0.05 res. is for 5000 random cells
518 in each region, as the Mann-Whitney U -test cannot handle more than a few thousand values per sample when
519 comparing.

520 Figure 2: Species turnover, described in two forms ((a) mean Jaccard distance between QDS in each HDS
521 (\bar{J}_{QDS}), (b) additively defined turnover (T_{HDS} , see Equation (2)) as a proportion of HDS richness (S_{HDS})),
522 compared between the Cape and SWA. Mann-Whitney U -tests between the Cape and SWA distributions of
523 \bar{J}_{QDS} and T_{HDS} yielded significant differences.

524 Figure 3: Contributions of environmental variables (including heterogeneity variables) to boosted regression
525 tree (BRT) model predictions for the final four models’ response variables in Greater Cape Floristic Region
526 (Cape) and Southwest Australia Floristic Region (SWA): vascular plant species (a,b) richness and (c,d)
527 turnover. All BRT-models were permitted to fit three-way interactions between environmental variables.
528 Coloured bars denote the general category of the environment (keyed) to which a variable belongs, as in Figure
529 1. Inset piecharts display the same information, but grouped according to whether a variable was absolute or
530 roughness-transformed. Summary statistics for each BRT-models are also inset: R_{pseudo}^2 (Equation (4));
531 R_{O-E}^2 , the R^2 of the regression of expected values as a function of observed values; nt , the number of
532 regressions trees used in a BRT-model.

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616 **Biosketches**

617 **Ruan van Mazijk** is a Masters student broadly interested in comparative biology and ...

618 **Michael D. Cramer**

619 **G. Anthony Verboom**

620 **Author contributions**

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

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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)	TODO	??”
Clay	SoilGrids250m (CLYPPT M 250m)		
Soil C	SoilGrids250m (OCDENS M 250m)		
pH	SoilGrids250m (PHIKCL M 250m)		

625 Figures

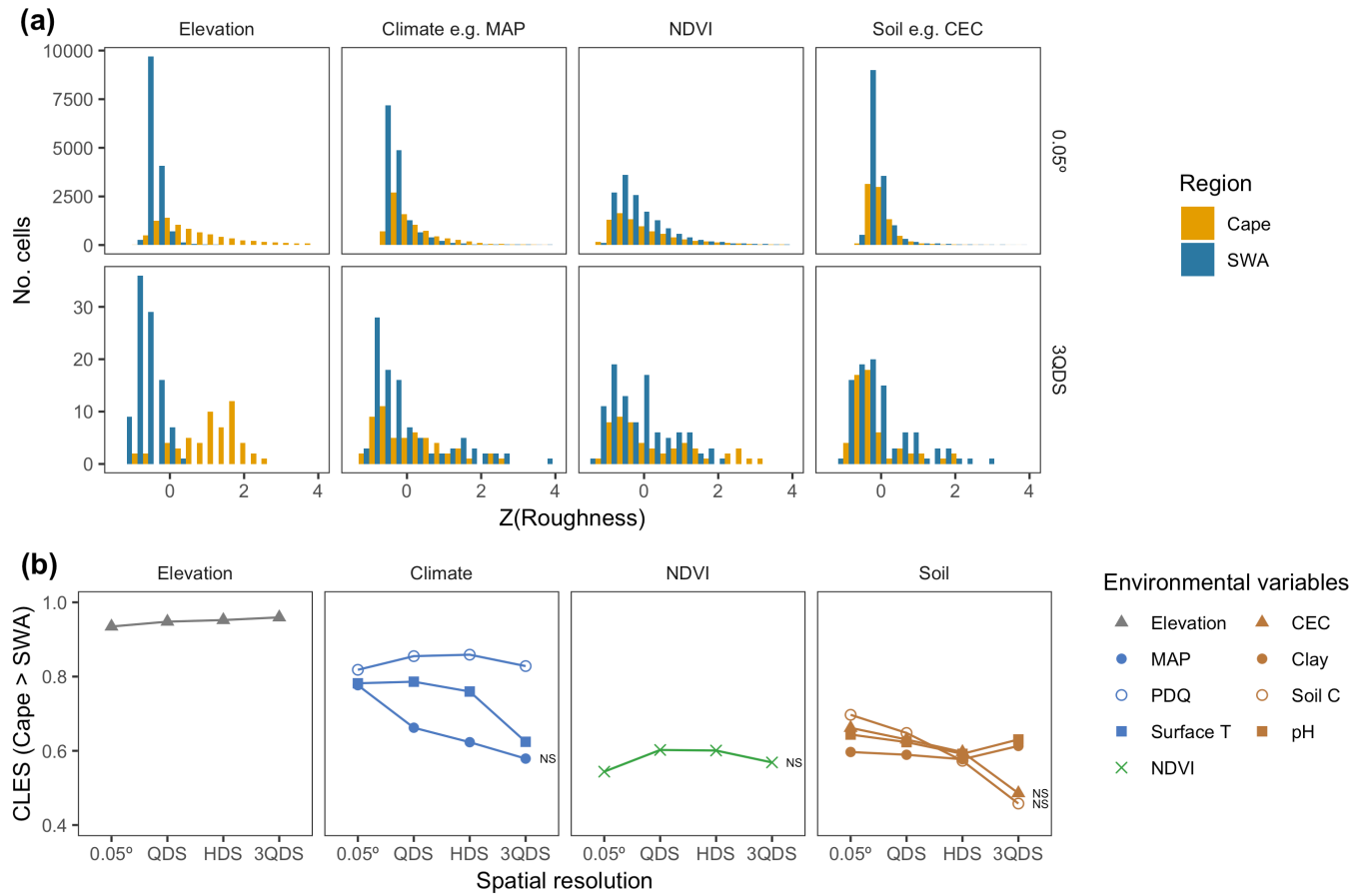


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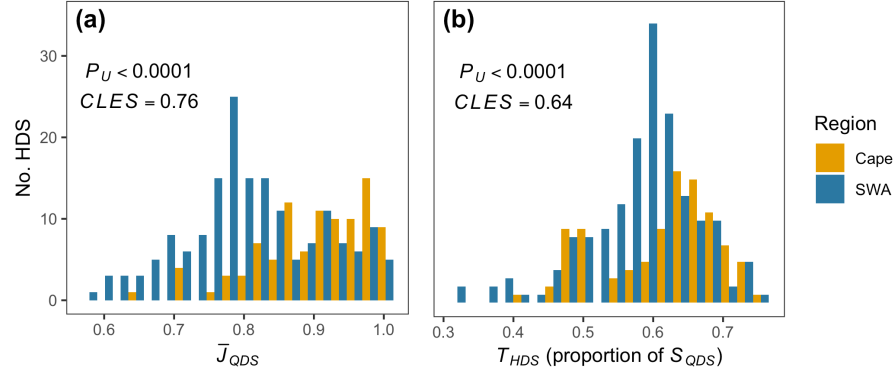


Figure 2: Species turnover, described in two forms ((a) mean Jaccard distance between QDS in each HDS (\bar{J}_{QDS}), (b) additively defined turnover (T_{HDS} , see Equation (2)) as a proportion of HDS richness (S_{HDS})), compared between the Cape and SWA. Mann-Whitney U -tests between the Cape and SWA distributions of \bar{J}_{QDS} and T_{HDS} yielded significant differences.

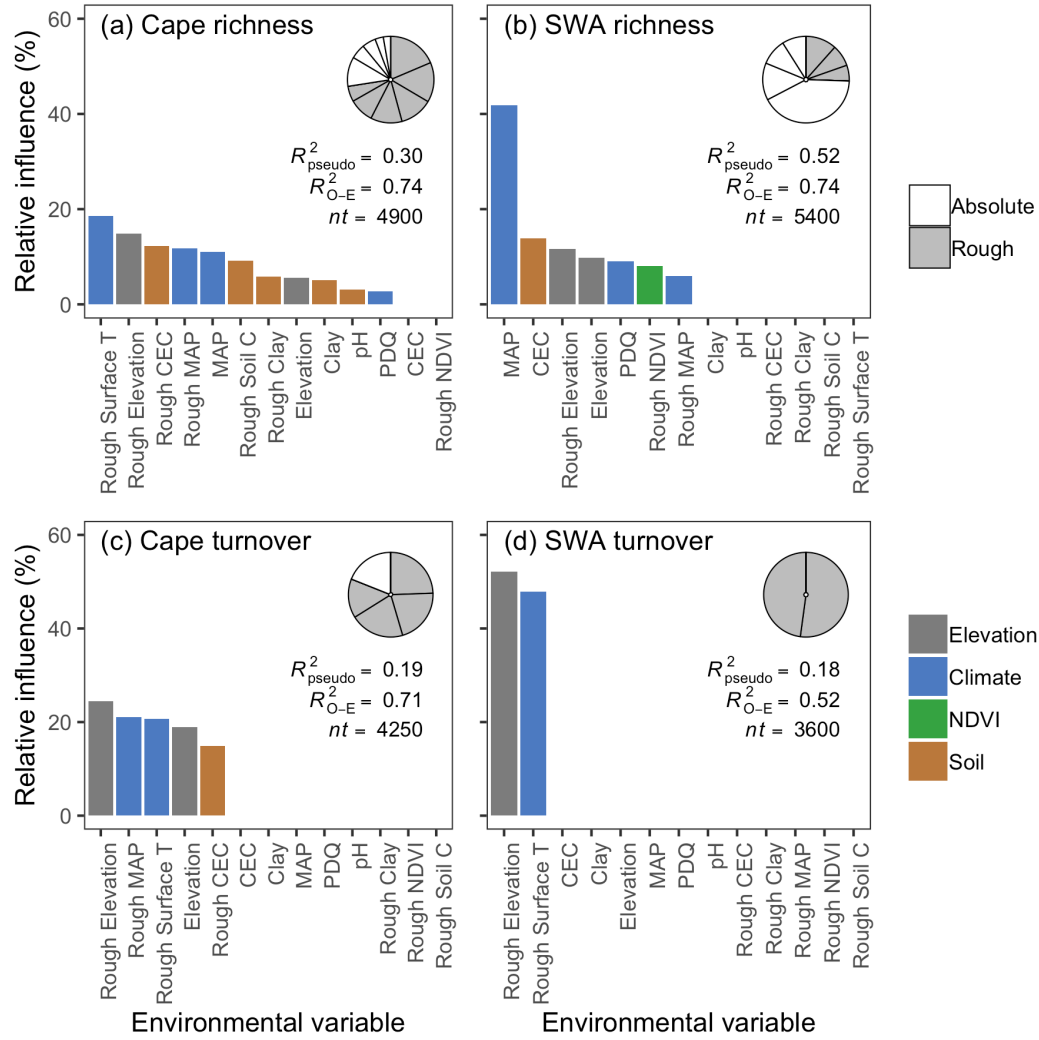


Figure 3: Contributions of environmental variables (including heterogeneity variables) to boosted regression tree (BRT) model predictions for the final four models' response variables in Greater Cape Floristic Region (Cape) and Southwest Australia Floristic Region (SWA): vascular plant species (a,b) richness and (c,d) turnover. All BRT-models were permitted to fit three-way interactions between environmental variables. Coloured bars denote the general category of the environment (keyed) to which a variable belongs, as in Figure 1. Inset piecharts display the same information, but grouped according to whether a variable was absolute or roughness-transformed. Summary statistics for each BRT-models are also inset: R^2_{pseudo} (Equation (4)); R^2_{O-E} , the R^2 of the regression of expected values as a function of observed values; nt , the number of regressions trees used in a BRT-model.