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

Acknowledgements

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 a variety of species—its ecological carrying capacity (Mateo et al., 2017). This is exemplified in approaches to modelling species richness as 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 coexistence is environmental heterogeneity (EH): a more heterogeneous environment has a larger environmental space, and can thus facilitate co-existence between species at the scale of that heterogeneity. EH can also stimulate ecological speciation, should the region be environmentally stable over evolutionary time-scales. 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 important to consider (Hart et al., 2017), in the same way that the spatial of absolute environmental conditions has also been considered (**???**; Baudena et al., 2015; Mouchet et al., 2015). Species co-existence and biodiversity maintenance is indeed suggested to be scale-dependent (Hart et al., 2017).

EH is often under-represented in macro-ecological models of species richness, and has recently been found to explain up to ca. 95% of biome level species richness across South Africa (Cramer & Verboom, 2016). Models that include EH yield better estimates of the richness of the Cape flora, as they account for the role heterogeneous environments such as those in the Cape facilitate species coexistence (Thuiller et al., 2006; Cramer & Verboom, 2016). Mediterranean-type terrestrial biodiversity hotspots, such as the Cape flora included in the models by Cramer & Verboom (2016), present interesting study systems in which to investigate the relationship between the environment and species richness. These systems exhibit far greater species richness than predicted by their areas, productivities and latitudes (Cowling et al., 1996; Kreft & Jetz, 2007). There are five Mediterranean biodiversity hotspots on Earth: the California Floristic Province, the Mediterranean Basin, the Chilean Winter Rainfall-Valdivian Forests, the Greater Cape Floristic Region, and the Southwest Australia Floristic Region (Cowling et al., 1996; Hopper & Gioia, 2004; Cook et al., 2015). These ecosystems have regular fire-cycles (Cowling et al., 1996), climatic buffering, and long term stability (Kreft & Jetz, 2007), shrubby, sclerophyllous flora (Hopper & Gioia, 2004). Together, they account for ca. 20% of global vascular plant species, yet only ca. 5% of global land surface areas (Cowling et al., 1996). Various hypotheses have been proposed to explain the high levels of plant species richness in these regions (Cook et al., 2015). The species accumulation hypothesis states that the stability of these regions has allowed many species to accrue. The species co-existence hypothesis states that these hotspots may facilitate greater degrees of species co-existence in smaller spatial areas, due to fine-scale heterogeneity in their environments. Indeed, EH has evolutionary implications too, stimulating ecological speciation across sharp environmental gradients.

Both the Southwest Australia Floristic Region (SWAFR) and the Greater Cape Floristic Region (GCFR) are Mediterranean-type biodiversity hotspots, particularly in terms of plant species. Where the GCFR (with an area of ca. 189,000 km^2) is known to contain about 11,400 plant species (about 0.060 species per km^2), the

86 SWAFR (area of ca. 270,000 km^2) has about 3,700 species (0.014 species per km^2) (**???**). So, the GCFR has
87 ca. 4.3 times as many species per km^2 as the SWAFR. The GCFR and SWAFR are appropriately often
88 compared, due to the similarities between their environments (e.g. oligotrophic soils, an oceanically buffered
89 moderate climate) and their plants' ecologies (Hopper & Gioia, 2004). These two regions present unique flora
90 out of the five Mediterranean systems, with high levels of endemism (Cowling et al., 1996), and many
91 obligate fire-adapted species (Cowling et al., 1996). Similarities withstanding, the SWAFR is topographically
92 and edaphically distinct from the GCFR. The SWAFR former is topographically rather uniform
93 (i.e. flat)—uniquely so among the world's five Mediterranean-climate regions (Hopper & Gioia, 2004)). The
94 SWAFR possesses a mesoscale chronosequence dune system (Laliberte et al., 2014; Cook et al., 2015), while
95 the GCFR is mountainous, topographically heterogeneous, and therefore associated with a large degree of
96 spatial climatic variability, with a fine-scale mosaic of geologies and soils (Cowling et al., 1996; Cramer et al.,
97 2014; Verboom et al., 2017) . Both regions have sources of edaphic heterogeneity, but at different scales. This
98 edaphic variability may aid in explaining the species richness in these regions (Beard et al., 2000; Verboom et
99 al., 2017). EH can stimulate ecological speciation, should the region be stable over evolutionary time-scales,
100 as is likely the case in both the GCFR and the SWAFR (Wardell-Johnson & Horwitz, 1996; Hopper & Gioia,
101 2004; Lambers et al., 2010; Cramer et al., 2014; Laliberte et al., 2014; Cook et al., 2015). For the GCFR, this
102 richness is largely known to result from long term climatic stability, and fine grain variation in geology and
103 soils (Cramer et al., 2014). The question thus arises whether heterogeneity is a significant contributor to
104 SWAFR species richness as is likely the case in the GCFR. In the absence of topographic variability in the
105 SWAFR, it is proposed that the heterogeneity of that region is due to the juxtaposition of soil types
106 (Laliberte et al., 2014; Cook et al., 2015), creating extreme edaphic variation.

1.1 Hypothesis-v1

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

1.2 Hypothesis-v2

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

124 Our hypotheses concern the Cape and SWA's environments and floras. Our main hypothesis is that the Cape
125 possesses greater abiotic heterogeneity, and at finer grain, compared to SWA, such as to explain the Cape's
126 greater species richness per unit area, and proposed greater levels of species turnover between areas. We also
127 conjecture that the heterogeneity that predicts species richness in SWA will be more pronounced in terms of
128 edaphic variables. Here we attempt to assess six key predictions of this hypothesis, additionally investigating
129 a seventh prediction to test the conjectured role of edaphic heterogeneity in SWA. Dealing with the two
130 regions' environments, we assess (i) whether the Cape environment is more heterogeneous than that of SWA
131 and (ii) whether the Cape environment has more pronounced heterogeneity at finer scales than that of SWA.
132 Dealing with the distribution of species in the two regions, we assess (iii) whether the Cape exhibits greater
133 levels of species turnover between areas, such as to (iv) explain the greater species richness per unit area of

the Cape compared to SWA. Relating each regions' environment and flora, we finally assess (v) whether species richness and species turnover are adequately predicted by EH in both regions and whether (vii) Species richness and species turnover are better predicted by different forms of EH in either region (e.g. the importance of edaphic heterogeneity in SWA).

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

2 Materials and methods

2.1 Overview

These analyses required definitions of the boundaries of the two regions, environmental data for each, and geospatially-explicit vascular plant occurrence records, all based on publicly available data. The environmental variables chosen (Table **??**) 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 using 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). Note, at least for the Cape, most plant occurrence records are only accurate to QDS level. Thus, any analysis involving species data was necessary limited to scales above and including QDS. Analyses were performed in R v3.5.0 (R Core Team, 2018). Version-numbers of specific R packages used are presented in the bibliography, or in text where applicable.

2.2 Environmental data sources

Geospatially-explicit raster layers were acquired for a selection of environmental variables (Table **??**), 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 0.05º 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 **??**). 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

178 covariates, including MODIS and STRM sources (see Hengl et al., 2017), using random-forests and other
179 classification-tree-based methods, including gradient-boosting. For the soil data considered here (Table 1),
180 we used depth-interval weighted average values as the value for a particular soil variable in a given place.

181 Climatic and spectral data arise from satellites monitoring properties of the Earth's surface through time.
182 We therefore use the mean annual values for rainfall, surface temperature, and NDVI across space in our
183 analyses. Pronounced seasonality of rainfall is a known feature of Mediterranean systems (**???**). known
184 toand timing, namely precipitation in the driest quarter (PDQ) and temperature in the ... describe!–>

2.3 Plant occurrence data

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

191 We cleaned these data using the R package "taxise" (**???**, (**???**)) to check that these species names had
192 accepted-status among taxonomic databases. I queried two major taxonomic databases: the Global Name
193 Resolver (GNR), and the Taxonomic Name Resolution Service (TNRS). Should one of either service return
194 at least one match for a given name, then that name was deemed accepted. Those names for which no full
195 binomial matches were found in either database were excluded from the final list of species. The number of
196 species names excluded totalled at 1 and 1 for the Cape and SWA respectively. Especially for SWA, these
197 numbers may be deemed appreciably high. But, the occurrence records that would be dropped, as a
198 consequence of these names' removals, seemed to be distributed randomly in geographic space in both
199 regions. As such, any effect of the loss of these records in this analysis is uniform within the two regions.

200 After the unaccepted names were removed, it was important to ensure that a species was not listed under
201 multiple synonyms. Such cases would skew the species richness data used in this study. In light of this, the
202 remaining names were queried in the Tropicos and Integrated Taxonomic Information System (ITIS)
203 databases for their known synonyms, using "taxize". These were collated to produce a nomenclatural
204 "thesaurus" for the Cape and SWA species. This consisted of a list of the accepted species names in a region,
205 each associated with a list of known synonyms. I amended species' names in the GBIF occurrence data, in
206 order ensure species were listed under only one of these synonyms, as follows: For each entry in the
207 thesaurus, for each synonym of that entry, if that synonym appeared in the GBIF species list, I replaced all
208 appearances of that synonym in the species list with the original name from the thesaurus-entry that that
209 synonym came from.

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

213 The final total plant species richness in each region was 12991 and 8074 for the Cape and SWA respectively.
214 These final collections of species occurrence records were converted to raster-layers, wherein pixel-values
215 represented the species, genus and family richness of vascular plants within that pixel. These rasters were
216 produced at QDS, HDS, and 3QDS resolutions.

2.4 Analyses

2.4.1 Quantifying environmental heterogeneity

219 First, in order to assess predictions (i) and (ii), we needed to describe the EH in both regions. Using the R
220 package "raster" (**???**), we used a modified version of the "roughness" index in the "terrain" function: for a
221 three by three neighbourhood of cells, our index of roughness is the average square-root of the squared
222 difference between each of the n neighbour cells' values x_i and the central focal cell's value x_{focal}:

$$Roughness = \frac{1}{n}\sqrt{\sum_{i=1}^{n}\left(x_{focal} - x_i\right)^2} \qquad (1)$$

223 Note, in order to use as much data from within regions' borders as possible, roughnes swas computed if a
224 focal cell had at least one neighbour cell—that is, roughness is defined where $n_{x_{focal}} \geq 1$. Using this index of
225 heterogeneity, we produced raster layers of each of our nine environmental variable's heterogeneity. We
226 compared the distributions of roughness values in each variable in each region with non-parametric
227 Mann-Whitney U-tests, as almost all variables could not be normalised by log-transformations. We also
228 compare the effect size of the Cape vs SWA using the "common language effect size" (CLES), using the R
229 package "canprot". The CLES is the proportion of all pairwise comparisons between two sample groups'
230 observations where one group's value is greater than the other. In our case, of all pairwise comparisons of a
231 variable's roughness values between the Cape and SWA, we calculated the CLES as the proportion of pairs
232 where Cape roughness values were greater than that of SWA. This allowed us to assess prediction (i). To
233 compare the spatial scales of heterogeneity (prediction [(ii)][Hypothesis-v2]) between each region, we repeated
234 this analysis at all four spatial scales. Once again, this entailed recalculating the roughness layer for each
235 variable after the original layer (0.05 degrees resolution) had been rescaled to each of the coarser resolutions.

2.4.2 Relating species richness and species turnover

237 Regarding predictions (iii) and (iv), we wished to compare the relative importance of species turnover in each
238 region as a predictor of species richness.

239 First, for (iii), we compared the degree of species turnover in general in each region by computing all pairwise
240 Jaccard distances (**???**) between QDS' communities. We then regressed these turnover values for each pair
241 of cells against the physical distance between the centres of those cells. The range of turnover values was
242 found to be highest at small distances (Figure 1A), and indeed complete species turnover between cell pairs
243 was observed at all distances. Thus we used quantile regressions of the 5% quantile of species turnover as a
244 function of geographic distances (using "quantreg" (**???**) in R). This allowed us to compare the lower bounds
245 of species turnover between the Cape and SWA.

246 Regarding prediction (iv), to test how turnover *between* sites predicts richness *across* rites, we regressed the
247 species richness in coarse scale cells against the average richness of and average turnover between the
248 constituent fine scale cells within a the coarse scale cell. Moreover, average turnover between fine scale cells
249 excluded turnover values between a cell j and itself (necessarily 0), and only included turnover values
250 between between cell j and k and not between k and j (as these are necessarily the same). We focussed on
251 this relationship with HDS as the coarse scale and QDS as the fine scale—as there are four QDS within each
252 HDS, and QDS was the highest precision to which our species data were recorded. Average QDS richness for
253 a given HDS-cell ($\overline{S_{QDS_i}}$), then, is based on $j = 4$ QDS-cells, and is treated here as

$$\overline{S_{QDS_i}} = \frac{1}{j}\sum_{j=1}^{4} S_{QDS_j}. \qquad (2)$$

254 Average QDS turnover for a given HDS ($\overline{T_{QDS_i}}$), based on $n = \binom{j=4}{2} = 6$ QDS pairs (namely pairs $QDS_{1,2}$,
255 $QDS_{1,3}$, $QDS_{1,4}$, $QDS_{2,3}$, $QDS_{2,4}$ and$QDS_{3,4}$) is treated here as

$$\overline{T_{QDS_i}} = \frac{1}{n}\sum_{n=1}^{6} T_{QDS_n}. \qquad (3)$$

256 Thus, we regress coarse scale richness as follows:

$$\widehat{S_{HDS_i}} = \beta_0 +$$
$$\beta_1 \overline{S_{QDS}}_i + \beta_2 \overline{T_{QDS}}_i + \beta_3 SWA_i + \tag{4}$$
$$\beta_4 \overline{S_{QDS}}_i SWA_i + \beta_5 \overline{T_{QDS}}_i SWA_i + \epsilon_i$$

where $\epsilon \sim N\left(\overline{x}, \sigma^2\right)$, and $\overline{S_{QDS}}$ is $log(x+1)$-transformed. This model allows us to compare the spatial-scaling drivers of species richness in either region: whether coarse scale increases in species richness are determined more by (a) being composed of richer—but more similar—communities or by (b) being composed of many different communities. These represent the two logical extremes.

2.4.3 Predicting species richness and turnover with environmental heterogeneity

3 Results

3.1 Describing environmental heterogeneity numerically across scales

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

Most obviously, and as expected, topographic heterogeneity is greatest in the Cape (Figure 1a). Though SWA has a slightly wider distribution of elevational roughness values at coarse scales (e.g. 3QDS, Figure 1a) compared to fine scales (0.05º), so does the Cape. As such, the relative difference between the two regions seems invariant with spatial scale ($CLES \approx 0.95$, Figure 1).

This concurs with our expectations, as the Cape is mountainous and known to have steep elevational gradients (**???**), while SWA is much more topographically uniform.

Intuitively, then, elevation serves as a "benchmark test" for our comparisons of EH here, as it is well known and expected that the Cape should be more elevationally heterogeneous than SWA. Additionally, we can conclude that although there are greater extreme values of Cape elevational roughness at 0.05º x 0.05º scales, larger sections of land (i.e. 3QDS-cells) are are more different from each other in the Cape than the same sized sections are different from each other in SWA.

Climatic heterogeneity presents less differentation between the Cape and SWA than elevational roughness, 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 1c).

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

We can differentiate the Cape and SWA environments based on which environmental axes are more heterogeneous in either region, as they differ somewhat in this regard.

3.2 Species richness as determined by species turnover

3.2.1 Quantifying the "general" degree of species turnover in each region

Following quantile regressions of the 5%-quantile of pairwise species turnover against the distance between pairs' sites (Figure 2a), there is evidence that SWA exhibits a lower lowermost-bound of observed species turnover. This is because of the relative positive influence of a site's being "from the Cape", as opposed to SWA, on the 5%-quantile of species turnover ("Cape"-term, $P < 0.001$, Table 2). As expected, species turnover was greatest between distant pairs of QDS ($P < 0.001$, Table 2, Figure 2a).

3.2.2 How species richness is determined by species turnover

Logic: Richness @ coarse scale $\sim \sum$ Richness @ finer scale $+ \sum$ Turnover @ finer scale

4 Discussion

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

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

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

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

The fact that a combination of absolute and roughness variables is also as predicted by the hypothesis in this study. In the models developed by Cramer & Verboom (2016) for South Africa, roughness in topography was largely superseded as an important predictor of species richness by other roughness variables. My models, however, did not show this. Similar to the study by Rensburg et al. (2002), my models revealed roughness in topography and other variables to be important. Although, Rensburg et al. (2002) considered differences within pixels, as opposed to this study, which considered differences between pixels. My models, those of Cramer & Verboom (2016), and those of Rensburg et al. (2002), do not all concur as to the role of roughness

in elevation vs. more biologically meaningful variables in explaining species richness. The source of these discrepancies is unclear, though no doubt complex. The complements of environmental variables and methodologies used in these studies do differ, limiting extensive comparison between these analyses.

The determinants of vascular plant species are shown to be region specific (Figures **??**, **??**, **??**). The importance of MAP and roughness in rainfall seasonality (PCV) in predicting richness in the SWAFR (Figure **??**I, **??**J), aligns with the steep climatic gradients observed there (Cook et al., 2015). The soil variables that determine plant species richness in the model for the SWAFR (Figures **??**K, **??**L) differ to those that determine richness in the GCFR (Figures **??**G, **??**H), further highlighting the edaphic differences between these two regions. 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, Thuiller et al. (2006) also included topographic heterogeneity. Cramer & Verboom (2016) described 68% of species richness at the QDS scale across South Africa. Regarding the GCFR, depending on whether one consults 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.

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

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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 GCFR (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 GCFR was correctly predicted to have, on average, more species per grid-cell at HDS and 3QDS scales than the SWAFR, this was not the case for QDS grid-cells (Table 5). This demonstrates that the GCFR is indeed overall more rich in plant species than the SWAFR, but a given HDS in the SWAFR contains fewer species than a given GCFR HDS. Thus, the greater richness in the GCFR 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 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.

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Biosketches

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

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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.

Table captions

Table 1

Data sources used in this study. Abbreviations are as follows:.

Table 2

Estimated coefficients and significances (P-value) following quantile regression of the 5%-quantile ($\tau = 0.05$) of pairwise species turnover (as Jaccards distance) as a function of the geographic distance (km, log-transformed) between QDS cells. The Cape term represents the difference between Cape and SWA species turnover, for a given geographic distance.

Table 3

Estimated coefficients and significances (P-value) following multiple linear regression of HDS species richness (S_{HDS}) against the mean QDS species richness ($\overline{S_{QDS}}$, Equation (2)) and turnover (Jaccards distance, $\overline{J_{QDS}}$, Equation (3)) within a given HDS, of the form in Equation (4). The Cape was fit as the baseline, hence SWA represents the categorical term here. This was model was better fitting than a similar model without a region category ($\Delta AIC = 90.56$). Note, this model does not represent those curves plot in Figures 2 and **??** (there, the curves are from simple linear regressions of the variables in each panel, separated by region).

Table 4

Comparisons of Akaike information criterion values (small sample-size-corrected, $AICc$) of various geographically weighted regressions (GWR) of log-transformed species richness as a function of various sets of environmental variables. Models were fit for the Cape and SWA richness and environmental data both separately and together. GWR methods preclude the need for a categorical predictor for the Cape vs SWA, as the longitudinal (and to a lesser extent latitudinal) differences between the regions allows local regression coefficients in each region to differ.

Tables

Table 1: Data sources used in this study. Abbreviations are as follows:.

Variable	Source (Dataset code)	Citation
Elevation	SRTM v2.0	@Farr2007
NDVI	MODIS (MOD13C2)	@MOD13C2
Climatic variables	NA	NA
Surface T	MODIS (MOD11C3)	@MOD11C3
MAP	CHIRPS v2.0	@Funk2015
PDQ	CHIRPS v2.0	@Funk2015
Edaphic variables	SoilGrids250m	@Hengl2017
pH	PHIKCL_M_250m	NA
CEC	CECSOL_M_250m	NA
Soil C	OCDENS_M_250m	NA
Clay	CLYPPT_M_250m	NA
Plant species occurrence	GBIF	@GBIFCape, @GBIFSWA

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Table 2: Estimated coefficients and significances (P-value) following quantile regression of the 5%-quantile ($\tau = 0.05$) of pairwise species turnover (as Jaccards distance) as a function of the geographic distance (km, log-transformed) between QDS cells. The Cape term represents the difference between Cape and SWA species turnover, for a given geographic distance.

Term	Estimate	P-value
Intercept	-0.311	< 0.001
log(Distance between cells)	0.093	< 0.001
Cape	0.388	< 0.001
log(Distance between cells) $\times$ Cape	-0.026	< 0.001

Table 3: Estimated coefficients and significances (P-value) following multiple linear regression of HDS species richness (S_{HDS}) against the mean QDS species richness ($\overline{S_{QDS}}$, Equation (2)) and turnover (Jaccards distance, $\overline{J_{QDS}}$, Equation (3)) within a given HDS, of the form in Equation (4). The Cape was fit as the baseline, hence SWA represents the categorical term here. This was model was better fitting than a similar model without a region category ($\Delta AIC = 90.56$). Note, this model does not represent those curves plot in Figures 2 and **??** (there, the curves are from simple linear regressions of the variables in each panel, separated by region).

Term	Estimate	P-value
Intercept	-3062.297	0.000
$log(\overline{S_{QDS}} + 1)$	595.574	0.000
$\overline{J_{QDS}}$	338.589	0.534
SWA	2905.604	0.001
$log(\overline{S_{QDS}} + 1) \times$ SWA	-333.908	0.000
$\overline{J_{QDS}} \times$ SWA	-1246.109	0.073

Table 4: Comparisons of Akaike information criterion values (small sample-size-corrected, *AICc*) of various geographically weighted regressions (GWR) of log-transformed species richness as a function of various sets of environmental variables. Models were fit for the Cape and SWA richness and environmental data both separately and together. GWR methods preclude the need for a categorical predictor for the Cape vs SWA, as the longitudinal (and to a lesser extent latitudinal) differences between the regions allows local regression coefficients in each region to differ.

Model predictors	$AICc$	$\Delta AICc$	w_{AICc}
Cape:			
Absolute variables	2112.49	0.00	1.00
Non-elevation variables	2179.35	66.86	0.00
All	2192.59	80.10	0.00
Soil variables	2197.76	85.28	0.00
Roughness variables	2208.43	95.94	0.00
Non-soil variables	2218.08	105.59	0.00
Elevation	2267.30	154.81	0.00
Null	3099.37	986.89	0.00
SWA:			
Absolute variables	826.47	0.00	0.69
Non-elevation variables	828.29	1.82	0.28
All	833.44	6.97	0.02
Soil variables	835.92	9.45	0.01
Non-soil variables	848.57	22.11	0.00
Roughness variables	868.89	42.42	0.00
Elevation	970.19	143.73	0.00
Null	27172.21	26345.74	0.00
Both:			
Absolute variables	1286.27	0.00	1.00
Roughness variables	1338.16	51.89	0.00
Non-elevation variables	1364.26	77.98	0.00
Elevation	1371.30	85.02	0.00
Soil variables	1371.47	85.19	0.00
Non-soil variables	1380.38	94.11	0.00
All	1390.78	104.50	0.00
Null	1404.05	117.78	0.00

Figure captions

Captions are also repeated alongside their respective figures for readability.

Figure 1

Comparisons of different types of environmental heterogeneity in the Cape and SWA—namely for (a) elevation, (b) climatic variables, (c) NDVI and (d) soil variables—in each panel consisting of three sub-panels per variable type. The upper row of panels shows example distributions of roughness values (Equation (1)), showing the different extremes in environmental heterogeneity observed in each region when compared at fine (0.05º) and coarse (3QDS) scales. Each distribution has under it area 1. Distributions were constructed with Gaussian kernels, with bandwidth following Silverman's "rule of thumb" [@Silverman1986]. In the lower row of panels, these distributions of roughness values were compared between the Cape and SWA at each of the four spatial scales, not just 0.05º and 3QDS, using non-parametric Mann-Whitney U-tests to test for

564 differences. The "common language effect size" ($CLES$, see text) describes these differences (b). U-tests for
565 almost all environmental variables yielded significant differences ($P < 0.05$) between Cape and SWA values
566 (NS, non-significant differences).

Figure 2

568 Regressions involving plant species richness and turnover. Species turnover (as Jaccards distance) between
569 QDS-pairs increases as pairs are more geographically separated (a). Species turnover was calculated for all
570 possible pairs of cells, but only the turnover values for a random 5000 pairs in each region have been plotted,
571 for clarity. Fitted lines represent the 5%-quantile regressions of turnover as a function of log-distance for each
572 region separately. Following a 5%-quantile regression of turnover as a function of log-distance with region as
573 a categorical variable (Table 2), a significant interaction between distance and region was found ($P < 0.001$),
574 such that the Cape positively effects the distance slope term. Scatter-plots of HDS-scale species richness
575 against the average QDS-scale richness in a given HDS (b) and the average species turnover between QDS in
576 a given HDS (c). Curves represent simples linear regressions of HDS richness against these two respective
577 independent variables (note, mean QDS richness was log(x + 1)-transformed), separately for each region, for
578 illustration of the two regions' differences, for interpretation alongside Table 3.
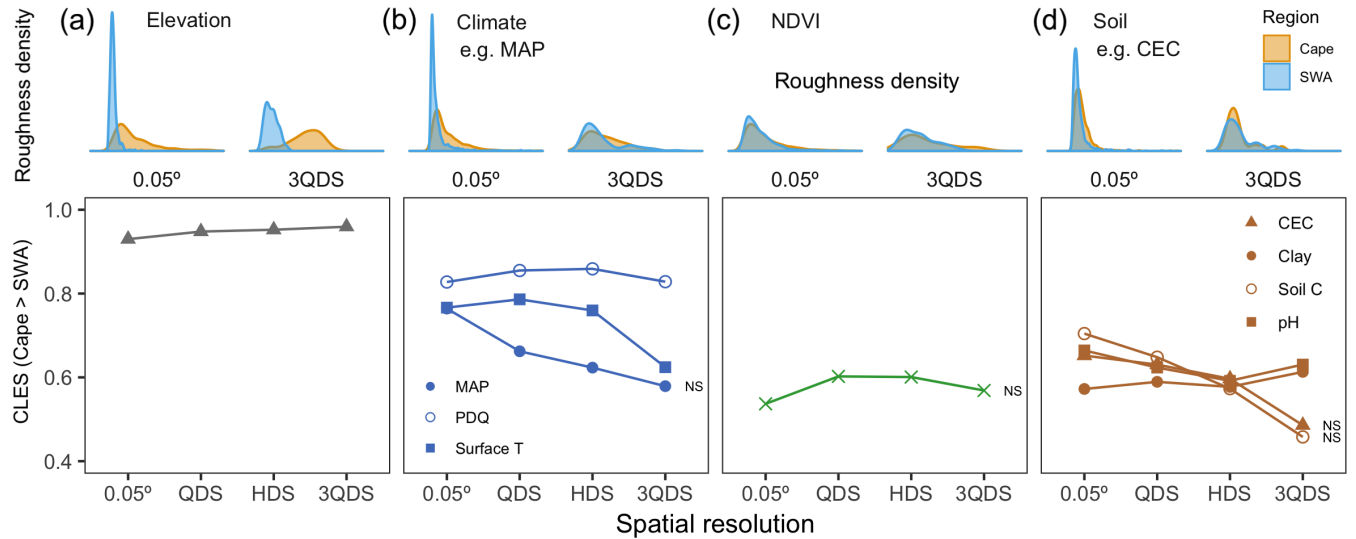
Figures

Figure 1: Comparisons of different types of environmental heterogeneity in the Cape and SWA—namely for (a) elevation, (b) climatic variables, (c) NDVI and (d) soil variables—in each panel consisting of three sub-panels per variable type. The upper row of panels shows example distributions of roughness values (Equation (1)), showing the different extremes in environmental heterogeneity observed in each region when compared at fine (0.05º) and coarse (3QDS) scales. Each distribution has under it area 1. Distributions were constructed with Gaussian kernels, with bandwidth following Silverman's "rule of thumb" [@Silverman1986]. In the lower row of panels, these distributions of roughness values were compared between the Cape and SWA at each of the four spatial scales, not just 0.05º and 3QDS, using non-parametric Mann-Whitney U-tests to test for differences. The "common language effect size" ($CLES$, see text) describes these differences (b). U-tests for almost all environmental variables yielded significant differences ($P < 0.05$) between Cape and SWA values (NS, non-significant differences).
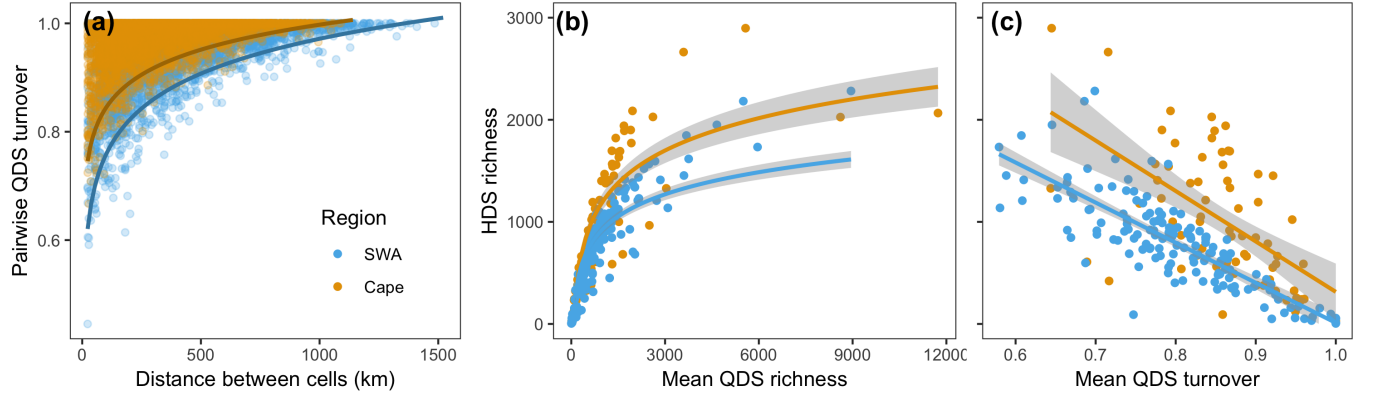
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Figure 2: Regressions involving plant species richness and turnover. Species turnover (as Jaccards distance) between QDS-pairs increases as pairs are more geographically separated (a). Species turnover was calculated for all possible pairs of cells, but only the turnover values for a random 5000 pairs in each region have been plotted, for clarity. Fitted lines represent the 5%-quantile regressions of turnover as a function of log-distance for each region separately. Following a 5%-quantile regression of turnover as a function of log-distance with region as a categorical variable (Table 2), a significant interaction between distance and region was found ($P < 0.001$), such that the Cape positively effects the distance slope term. Scatter-plots of HDS-scale species richness against the average QDS-scale richness in a given HDS (b) and the average species turnover between QDS in a given HDS (c). Curves represent simples linear regressions of HDS richness against these two respective independent variables (note, mean QDS richness was $\log(x + 1)$-transformed), separately for each region, for illustration of the two regions' differences, for interpretation alongside Table 3.