

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

15 statistics

Results:

Main conclusions:

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

20 Floristic Region

Acknowledgements

This work was funded by the South African Department of Science and Technology (DST) and the National Research Foundation (NRF) under the DST-NRF Innovation Honours Scholarship (to RVM), and by the South African Association of Botanists (SAAB) Honours Scholarship (to

25 RVM).

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

30 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

35 & 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).

40 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
45 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
50 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
55 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 (???;
60 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
65 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

70 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
75 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
80 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
85 (GCFR) are Mediterranean-type biodiversity hotspots, particularly in terms of plant species.

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

100 2017) . Both regions have sources of edaphic heterogeneity, but at different scales. This edaphic variability may aid in explaining the species richness in these regions (Beard et al., 2000; Verboom et al., 2017). EH can stimulate ecological speciation, should the region be stable over evolutionary time-scales, as is likely the case in both the GCFR and the SWAFR (Wardell-Johnson & Horwitz, 1996; Hopper & Gioia, 2004; Lambers et al., 2010; Cramer et al., 105 2014; Laliberte et al., 2014; Cook et al., 2015). For the GCFR, this richness is largely known to result from long term climatic stability, and fine grain variation in geology and soils (Cramer et al., 2014). The question thus arises whether heterogeneity is a significant contributor to SWAFR species richness as is likely the case in the GCFR. In the absence of topographic variability in the SWAFR, it is proposed that the heterogeneity of that region is due to the juxtaposition of soil 110 types (Laliberte et al., 2014; Cook et al., 2015), creating extreme edaphic 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 115 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, 120 due to potential complementarity between neighbouring communities increasing total richness. Thus, 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 125 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
130 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
135 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
140 flora, we finally assess (iv) whether species richness and species turnover are adequately predicted
by EH in both regions and whether (v) 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
145 occurrence datasets.

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

and regional biodiversity.

The GCFR is a megadiverse terrestrial biogeographic region, with high levels of endemism.

Midgley et al. (2003) investigated the responses the now defunct Cape Floristic Region (CFR)

160 flora to climate change. Using bioclimatic envelope models (a form of SDM), they modelled the Fynbos Biome's distribution as a whole, and select Cape-endemic Proteaceae species'

distributions, under current and future climate (climate scenario HadCM2), and again with the impact of land use change. Their Fynbos model was an indicator of regional priority for species level modelling efforts, showing a general southwards contraction of the biome. Their specific

165 Proteaceae models yielded various results: complete extinctions for some species, range contractions for most, improbable range shifts in some, and range expansions in few. The range shifts predicted therein were acknowledged to be improbable, due to the unmodelled limitations of plant dispersal and edaphic dependence. Midgley et al. (2003) concluded that climate change is likely to have severely negative for the CFR flora. However, as will be outlined below, their
170 methods may be overpredicting losses due to climate change.

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The last 20 years have seen much ecological research interest in and development of SDMs, using many statistical and machine-learning-based methodologies (Altwegg et al., 2014; Elith et al., 2008, 2011; Guisan & Thuiller, 2005). Machine-learning-based methods in SDMs include MaxEnt

175 (Elith et al., 2011), genetic algorithms, and adaptive neural networks (Hannah et al., 2005). The use of more advances statistics (e.g. Bayesian frameworks, ordination methods (Hannah et al., 2005)) is also seen. These two avenues of research have intersected in the development of boosted regression trees (BRTs) (originally "gradient boosting machine"; Friedman, 1999) a system of recursively generated, non-linear regression trees, as outlined by Elith et al. (2008). BRTs have
180 been used as SDMs in southern Africa before (e.g. Thuiller et al., 2006), sometimes for conservation purposes (e.g. Coetsee et al., 2009), but BRTs have yet to be used specifically to assess the responses of the regional flora to climate change. BRTs have more flexibility in their predictions than more traditional methods (e.g. GAMs), as they are non-linear and machine-learning-based (Elith et al., 2008).

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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 1) for this study were intended to cover a reasonable spread of climatic, edaphic, and ecologically relevant environmental axes, and are not intended to be exhaustive. We selected variables describing topography (elevation), productivity (NDVI), soil status, and climate and climatic seasonality.

We carried out this investigation using four principal spatial scales: $0.05^\circ \times 0.05^\circ$ 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 necessarily 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 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.

215 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., 220 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. 225 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.

230 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 across space in our analyses. Pronounced seasonality of rainfall is a known feature of Mediterranean systems (???). known toand timing, namely precipitation in the driest quarter (PDQ) and temperature in the ... describe!->

235 **2.3 Plant occurrence data**

Geospatially-explicit records of vascular plant occurrences were downloaded from the Global Biodiversity Information Facility (GBIF, Table 1). Queries were made for tracheophyte records from within the borders of the Cape and SWA as treated here (GBIF, 24 July 2017, GBIF (24 July 2017)). Only records with defined species and intra-specific ranks were kept. Intra-specific 240 occurrences were treated as simply being representative of their species. This resulted in FIXME unique species names in the Cape, and FIXME in SWA.

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

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

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

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

2.4 Analyses

2.4.1 Quantifying environmental heterogeneity

First, in order to assess predictions (i) and (ii), we needed to describe the EH in both regions.

Using the R package “raster” (???), we used a modified version of the “roughness” index in the

275 “terrain” function: for a three by three neighbourhood of cells, our index of roughness is the average square-root of the squared difference between each of the n neighbour cells’ values x_i and the central focal cell’s value x_{focal} :

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

This value, notionally the standard deviation of values relative to the focal value, is ascribed to the focal cell. Note, in order to use as much data from within regions’ borders as possible,

280 roughness was computed if a focal cell had at least one neighbour cell—that is, roughness is defined where $n_{x_{focal}} \geq 1$. Using this index of heterogeneity, we produced raster layers of each of our nine environmental variable’s heterogeneity. We compared the distributions of roughness values in each variable in each region with non-parametric Mann-Whitney U -tests, as almost all variables could not be normalised by log-transformations. We also compare the effect size of the

285 Cape vs SWA using the “common language effect size” ($CLES$), using the R package “canprot”.

The $CLES$ is the proportion of all pairwise comparisons between two sample groups’ observations where one group’s value is greater than the other. In our case, of all pairwise comparisons of a variable’s roughness values between the Cape and SWA, we calculated the $CLES$ as the

proportion of pairs where Cape roughness values were greater than that of SWA. This allowed us
290 to assess prediction (i). To compare the spatial scales of heterogeneity (prediction (ii)) between

each region, we repeated this analysis at all four spatial scales. Once again, this entailed recalculating the roughness layer for each variable after the original layer (0.05 degrees resolution) had been rescaled to each of the coarser resolutions.

2.4.2 Predicting richness and turnover with environmental heterogeneity

295 Regarding prediction (iii), we wished to compare the general degree of species turnover in each region. For (iv) and (v) we modelled species richness (S) and turnover as a function of various combinations of environmental and environmental heterogeneity variables in both regions.

2.4.2.1 Turnover comparisons

To compare the extent of species turnover between the Cape and SWA, we determined two
300 metrics of species turnover. The first, computes the mean species turnover as Jaccard distance (???) between each pair of QDS 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 of Whittaker's additive definition of β -diversity (???), where

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

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

310 2.4.2.2 Boosted regression trees modelling

2.4.2.2.1 From BIO3013F Protea-SDMs project methods

To explore which axes of environmental heterogeneity have most influence on vascular plant species richness, and differences in the importance of difference axes between the Cape and SWA, we employed boosted regression tree (BRT) modelling techniques. BRTs provide a machine
315 learning-based model of response variables and do so without involving normal null-hypothesis significance testing. Here, two sets of BRT models were developed from the Protea Atlas

occurrence records: BRTs for each of the 203 species of Proteaceae (i.e. SDMs) for which the results thereof were averaged by genus, and BRTs for each of the 13 genera directly, wherein occurrence data was used to create genus-level models. The latter can be thought of as genus
320 distribution models, or GDMs hereafter.

BRT model construction was performed, as detailed by Elith et al. (2008) in R (v3.2.4; R Development Core Team, 2014) using the package gbm (v. 2.1.1; Ridgeway, 2007). Following iterative parameter optimisation for learning rate and tree complexity, Gaussian BRT models were constructed with tree complexity = 5 (number of nodes of each tree, i.e. the maximum
325 interaction depth the model is permitted to fit), learning rate = 0.005 (shrinkage factor controlling the contribution of each tree to the final model), bagging fraction = 0.7 (proportion of training data randomly chosen to generate each tree) and cross-fold validation = 10 (i.e. use 10 different randomly selected training data sets). The total explained deviance was calculated as the difference between total and cross-validated deviance divided by the total deviance. The
330 models were developed with all variables (those retained, above) and then simplified using the protocol suggested by Elith et al. (2008) to retain the minimum number of variables contributing to the models of each species or genus.

2.4.2.2.2 From Hons thesis methods

Boosted regression trees are a flexible machine-learning modelling technique (Elith et al., 2008),
335 that allow testing for relationships between a response and a set of predictors without the use of null-hypothesis significance testing (Elith et al., 2008). BRTs have been employed previously to model species richness (Thuiller et al., 2006; see Mouchet et al., 2015; Cramer & Verboom, 2016) as macro-ecological models. BRTs were implemented here to predict vascular plant species richness in each cell, as a function of environmental variables roughness-values in those cells, as a
340 Gaussian response. BRT-models were developed for the GCFR, SWAFR, and for a merged dataset of both regions' data. This combined model included a discrete term for the region. These three regional-scopes were modelled with datasets at the QDS, HDS, and 3QDS resolutions derived from the original environmental data using bilinear resampling (???). The $\log(x + 1)$ -transform of species richness was used, in order to satisfy the assumptions of a
345 Gaussian response. Note, this is not strictly because BRTs have any parametric assumptions concerning the distribution of the response variable, but rather to aid in applying the

Gaussian-family of BRT algorithms to the richness data available.

BRTs are developed through the iterative generation of non-linear regression trees. BRTs are an ensemble-approach, in which a prediction is based on the weighted-sum of the predictions of

350 progressively less important trees, as opposed to the predictions of one tree (Elith et al., 2008).

This is representable as follows, with response \bar{Y}_i , weights w_j , and regression-trees $T(X)_j$ (as functions of some matrix of predictor variables X), for $i \rightarrow nt$ number of trees:

$$\bar{Y}_i = \sum_{j=1}^{nt} w_j T(X)_j \quad (3)$$

As recommended by Elith et al. (2008), BRT models were trained on a set of non-collinear predictor variables, across a range of *tc* and *lr* settings, using `gbm.step` in the `dismo` (???).

355 Collinear predictor variables can skew the interpretation of results, as the relatively influence of mutually collinear variables is reduced. Collinearity among the 9 environmental predictor variables and their respective 9 roughness-equivalents was assessed using `removeCollinearity` in the R package `virtualspecies` v1.4-2 (???), such that variables were no more than 75% collinear (Pearson’s $r \geq 0.75$). When faced with a cluster of collinear variables, one variable was chosen

360 manually therefrom (with the exception of NDVI and MLST, which were collinear, but it was considered desirable to include both, as NDVI was found to be an important predictor of species richness previously (Cramer & Verboom, 2016)). Where possible, the roughness-equivalent of an environmental variable was included if its absolute-equivalent could also be included. For the sake of comparison between regions’ models, the same set of non-collinear predictor variables was used

365 for training all models (Figure ??). The final predictor set consisted of (i) elevation,

rough-elevation, NDVI, and rough-NDVI; (ii) the climatic variables MAP, rough-MAP, PDQ, rough-PDQ, PCV, rough-PCV, MLST, rough-MLST, TCQ, and rough-TCQ; and (iii) the edaphic variables CECSOL, rough-CECSOL, rough-OCDENS, BLDFIE, rough-BLDFIE, CRFVOL, rough-CRFVOL, CLYPPT, rough-CLYPPT, SLTPPT, and SNDPPT. When

370 interpreting the results of BRTs, it is important to consider the effects of the variables included as representative of the effect of the excluded variables with which it is collinear—e.g. any interpretation of the effect of SNDPPT on species richness would then be also considered to be descriptive of the effect of soil pH on species richness (Figure ??).

BRTs have three important parameters that users have control over: the learning rate (lr) (i.e. the
 375 rate at which iterative trees reduce predictive deviance during model-training), tree complexity
 (tc) (i.e. the interaction depth), and the number of trees (nt). In order to select ideal lr , tc and
 nt , 25 candidate BRT-models (for each regional-scope, for each spatial scale) were trained on the
 final predictor set for a range of tc values (1 to 5), and for each of those over a range of lr values
 (0.001, 5×10^{-4} , 1×10^{-4} , 5×10^{-5} , and 1×10^{-5}). The function `gbm.step` optimises nt using
 380 cross-validation during model training (Elith et al., 2008) by halting iteration when predictions
 begin to overfit. For all models, I used 10 cross-validation folds, a tolerance-threshold of 5×10^{-4} ,
 a bagging-fraction of 0.75 (the default in `dismo`), and trained models starting with 1 tree, with
 each iterative step adding 1 tree, up to a maximum of 10,000 trees.

$$pseudo\ R^2 = 1 - \frac{model\ deviance}{null\ deviance} \quad (4)$$

The optimum configuration of lr and tc for the final model is a trade-off between model fit
 385 (pseudo- R^2 ; Equation 3) and complexity (nt) (Figure ??). As the effect of nt on pseudo- R^2 and
 nt is negligibly small (Figure ??A), or non-significant (Figure ??B), a tc of 5 was chosen for the
 final model. This follows the recommendations of Elith et al. (2008), where lr and tc are advised
 to be adjusted inversely. This was chosen in order to account for the complex interactions
 determining species richness. To avoid overfitting, an intermediate lr of 0.001 was chosen (Figure
 390 ??A). Thus, these configured models ($tc = 5, lr = 0.001$), for each regional-scope, for each spatial
 scale, were simplified further (using `gbm.simplify` in `dismo`), in order to remove predictor
 variables that contribute little, specific to each model. These simplified predictor sets produced
 by `gbm.simplify` were then used to re-train the models configured with $tc = 5, lr = 0.001$. These
 final 9 models (i.e. 3 regional-scopes across 3 spatial scales) are interpreted in this study.

395 3 Results

3.1 Describing environmental heterogeneity across scales

Across all variables considered, the Cape is more environmentally heterogeneous in the majority of
 pairwise comparisons of grid-cells ($CLES > 0.50$, Mann-Whitney U -test: $P < 0.05$, Figure 1).

The Cape is thus more environmentally heterogeneous than SWA overall, but the degree to which it is more heterogeneous varies between environmental variables. These effects also vary somewhat with the spatial scale concerned. In some variables, the differentiation between Cape and SWA heterogeneity lessens at coarser scales (Figure 1b). Indeed, when comparing the overall ranking and medians of Cape vs SWA roughness values for each variable, we only find non-significant differences at the 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 Species richness, turnover and environmental heterogeneity

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 (Figure 2).

Species richness and turnover data were related to BRT-models ...

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
430 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
435 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
440 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
445 (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
450 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.,

455 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
460 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
465 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 ??, ??, ??).
470 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
475 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
480 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 of 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; Böhn & 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.

520 The findings here are correlative. There are, however, many proposed mechanisms to explain the correlative signals demonstrated here. My findings support the hypothesis that Mediterranean systems' plant species richness is a function of spatial variability in environmental conditions. This can stimulate diversification, and maintain that diversity by providing a range of habitats for species co-existence. Oligotrophic soils can stimulate an increase in functional diversity, through
525 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
530 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
535 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.

540 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
545 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. Abbreviations are as follows: MAP, mean annual precipitation; PDQ, precipitation in the driest

quarter; CEC, cation exchange capacity.

Figure captions

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

Figure 1

Types of environmental heterogeneity, compared between the 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
580 values (Equation (1)), showing the different extremes in environmental heterogeneity observed in each region when compared at fine (0.05°) and coarse (3QDS) scales. Each distribution has under it area 1. Histograms were constructed using 20 breaks. 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 0.05° and 3QDS, using non-parametric Mann-Whitney U -tests to test for
585 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). CLES for 0.05° res. is for 5000 random cells in each region, as the Mann-Whitney U -test cannot handle more than a few thousand values per sample when comparing.

590 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.

595 References

- Baudena, M., Sánchez, A., Georg, C.-P., Ruiz-Benito, P., Rodríguez, M.Á., Zavala, M.A., & Rietkerk, M. (2015) Revealing patterns of local species richness along environmental gradients with a novel network tool. *Scientific Reports*, **5**, 11561.
- Beard, J.S., Chapman, A.R., & Gioia, P. (2000) Species richness and endemism in the Western
600 Australian flora. *Journal of Biogeography*, **27**, 1257–1268.
- Bradshaw, P.L. & Cowling, R.M. (2014) Landscapes, rock types, and climate of the Greater Cape Floristic Region. *Fynbos: Ecology, evolution and conservation of a megadiverse region* (ed. by N. Allsopp, J.F. Colville, and G.A. Verboom), pp. 26–46. Oxford University Press, Oxford.
- Bøhn, T. & Amundsen, P.-A. (2004) Ecological Interactions and Evolution: Forgotten Parts of
605 Biodiversity? *BioScience*, **54**, 804.
- Cardillo, M. (2012) The phylogenetic signal of species co-occurrence in high-diversity shrublands: different patterns for fire-killed and fire-resistant species. *BMC Ecology*, **12**, 21.
- Cook, L.G., Hardy, N.B., & Crisp, M.D. (2015) Three explanations for biodiversity hotspots: small range size, geographical overlap and time for species accumulation. An Australian case
610 study. *New Phytologist*, **207**, 390–400.
- Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., & Arianoutsou, M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, **11**, 362–366.
- Cramer, M.D. & Verboom, G.A. (2016) Measures of biologically relevant environmental heterogeneity improve prediction of regional plant species richness. *Journal of Biogeography*, 1–13.
- 615 Cramer, M.D., West, A.G., Power, S.C., Skelton, R., & Stock, W.D. (2014) Plant ecophysiological diversity. *Fynbos: Ecology, evolution and conservation of a megadiverse region* pp. 248–272. Oxford University Press, Oxford.
- Deblauwe, V., Droissart, V., Bose, R., Sonké, B., Blach-Overgaard, A., Svenning, J.C., Wieringa, J.J., Ramesh, B.R., Stévant, T., & Couvreur, T.L.P. (2016) Remotely sensed temperature and
620 precipitation data improve species distribution modelling in the tropics. *Global Ecology and*

Biogeography, **25**, 443–454.

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

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

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

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

GBIF (24 July 2017) GBIF Occurrence Download..

GBIF (24 July 2017) GBIF Occurrence Download..

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

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

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

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

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

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

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

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

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

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

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

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

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

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

- Mucina, L. & Rutherford, M.C. (2006) *The vegetation of South Africa, Lesotho and Swaziland*.
675 South African National Biodiversity Institute,
- NIMA (2000) Amendment 1. 3 January 2000. Department of Defense World Geodetic System
1984. Its Definition and Relationships with Local Geodetic Systems. 1–3.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood,
E.C., D’amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., & Others (2001) Terrestrial
680 Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions
provides an innovative tool for conserving biodiversity. *BioScience*, **51**, 933–938.
- Power, S.C., Verboom, G.A., Bond, W.J., & Cramer, M.D. (2017) Environmental correlates of
biome-level floristic turnover in South Africa. *Journal of Biogeography*, **44**, 1745–1757.
- R Core Team (2018) *R: A Language and Environment for Statistical Computing. Version 3.5.0*.
685 R Foundation for Statistical Computing, Vienna, Austria.
- Rensburg, B.J. van, Chown, S.L., & Gaston, K.J. (2002) Species Richness, Environmental
Correlates, and Spatial Scale: A Test Using South African Birds. *The American Naturalist*, **159**,
566–577.
- Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*,
690 *New Series*, **235**, 167–171.
- Thuiller, W., Midgley, G.F., Rouget, M., Cowling, R.M., F. Midgley, G., Rougeti, M., & M.
Cowling, R. (2006) Predicting patterns of plant species richness in megadiverse South Africa.
Ecography, **29**, 733–744.
- Verboom, G.A., Stock, W.D., & Cramer, M.D. (2017) Specialization to extremely low-nutrient
695 soils limits the nutritional adaptability of plant lineages. *The American Naturalist*, **In press**.
- Wardell-Johnson, G. & Horwitz, P. (1996) Conserving biodiversity and the recognition of
heterogeneity in ancient landscapes: a case study from south-western Australia. *Forest Ecology
and Management*, **85**, 219–238.

Biosketches

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

Michael D. Cramer

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Author contributions

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

Tables

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

Variable	Source	Citation
Plant species occurrences	GBIF	??, ??
Elevation	SRTM v2.0	??
NDVI	MODIS (MOD13C2)	??
Climatic variables		
MAP	CHIRPS v2.0	??
PDQ	CHIRPS v2.0	
Surface T	MODIS (MOD11C3)	??
Soil variables (SoilGrids250m)		
CEC	CECSOL M 250m	??
Clay	CLYPPT M 250m	
Soil C	OCDENS M 250m	
pH	PHIKCL M 250m	

Figures

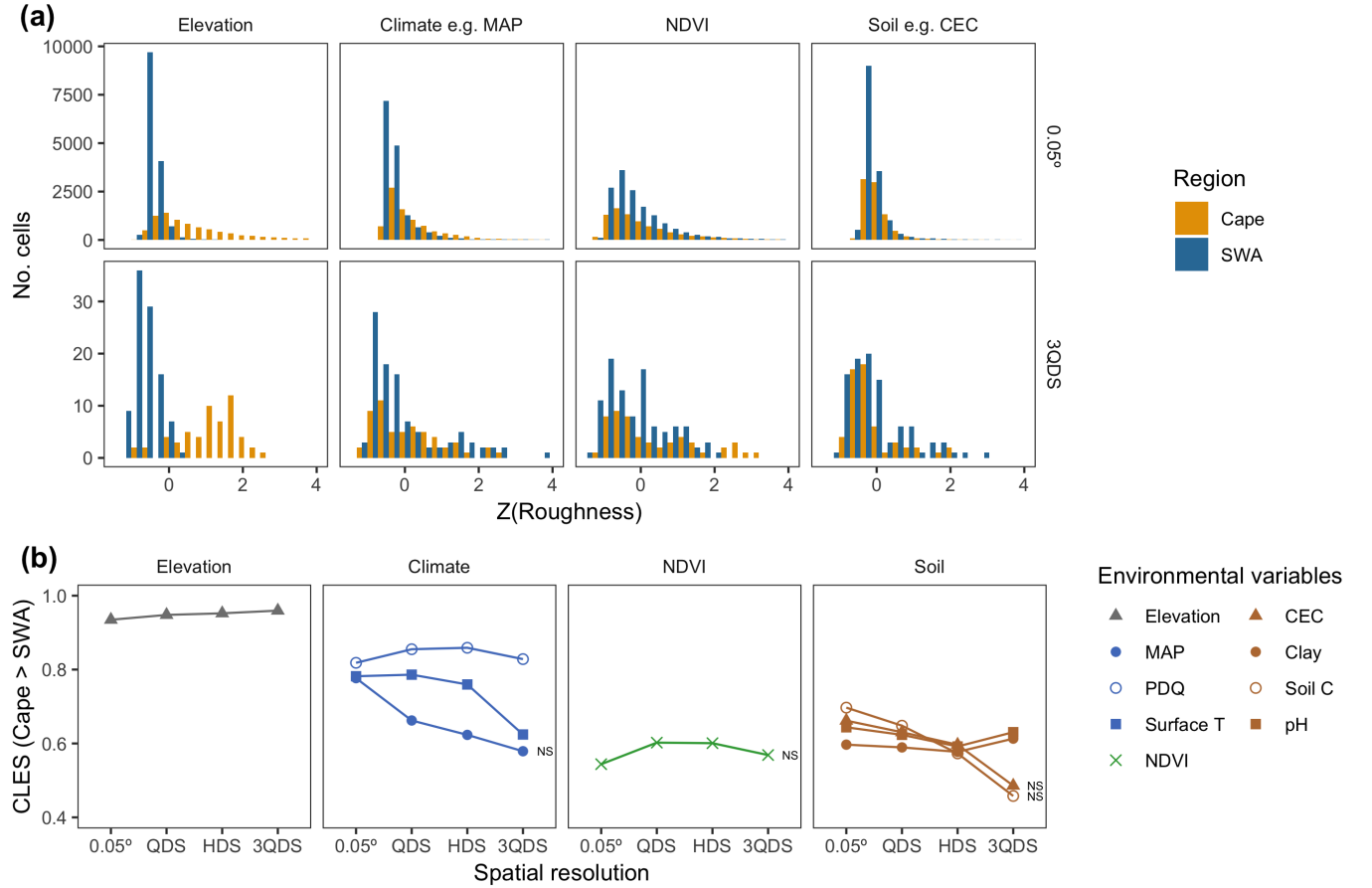


Figure 1: Types of environmental heterogeneity, compared between the the Cape and SWA—namely for (a) elevation, (b) climatic variables, (c) NDVI and (d) soil variables—in each panel consisting of three sub-panels per variable type. The upper row of panels shows example distributions of roughness values (Equation (1)), showing the different extremes in environmental heterogeneity observed in each region when compared at fine (0.05°) and coarse (3QDS) scales. Each distribution has under it area 1. Histograms were constructed using 20 breaks. 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 0.05° 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). $CLES$ for 0.05 res. is for 5000 random cells in each region, as the Mann-Whitney U -test cannot handle more than a few thousand values per sample when comparing.

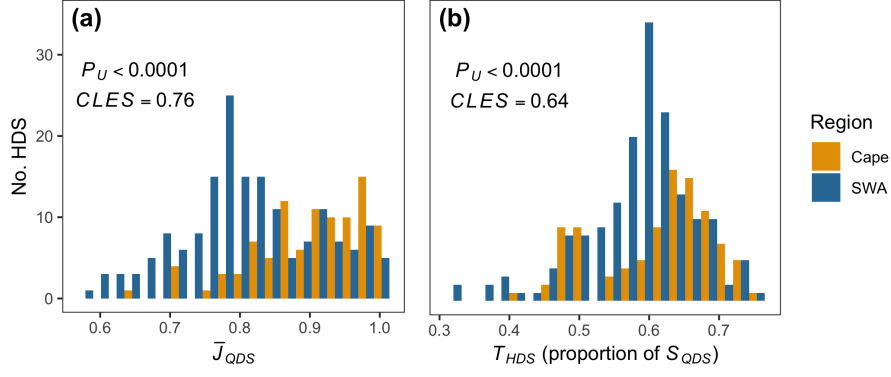


Figure 2: Species turnover, described in two forms ((a) mean Jaccard distance between QDS in each HDS (\bar{J}_{QDS}), (b) additively defined turnover (T_{HDS} , see Equation (2)) as a proportion of HDS richness (S_{HDS})), compared between the Cape and SWA. Mann-Whitney U -tests between the Cape and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