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

**Results:** The Cape is more environmentally heterogeneous and has higher levels of vascualr plant species turnover than SWA. We find that environmental heterogeneity is the main predictor of species richness in the Cape, and somewhat less so for SWA. Species turnover is best predicted by environmental heterogeneity in both regions.

**Main conclusions:**

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

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## 1 Introduction

Biodiversity represents the variety of living things, and the variety of ecological and evolutionary processes responsible for it (Bøhn & Amundsen, 2004). Studying the distribution of biodiversity in space is a major avenue of biological research (**???**; Kreft & Jetz, 2007). Regional-scale geographic patterns in species richness have long been studied, particularly in biodiversity hotspots (Cook et al., 2015). The spatial distribution of species richness can be explained in terms of the physical environment. Properties of the environment have been suggested to influence species richness in three ways: (i) productivity, water, and energy to enable organismal growth, and resources (i.e. niche space) to support a wider range of species (Gaston, 2000; Kreft & Jetz, 2007; Mouchet et al., 2015); (ii) stability, which enables species' persistence; and (iii) heterogeneity, which enables ecological speciation and possible barriers to gene flow, and with a wider variety of environments to facilitate species' co-existence (Thuiller et al., 2006; Mouchet et al., 2015; Cramer & Verboom, 2016). The physical environment, then, can be used to explain species richness in a local-deterministic sense, and in a historical context (Ricklefs, 1987).

The maintenance of species richness, particularly the coexistence of high numbers of species in biodiversity hotspots, is often regarded as "paradoxical" (Hart et al., 2017), and is a central problem in ecology (Ricklefs, 1987; Kreft & Jetz, 2007; Hart et al., 2017). Species richness is constrained by the ability of habitats to support 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). Macroecological 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 (SWA) and the Greater Cape Floristic Region (Cape) are Mediterranean-type biodiversity hotspots, particularly in terms of plant species. Where the Cape (with an area of ca. 189,000 $km^2$) is known to contain about 11,400 plant species (about 0.060 species per $km^2$), SWA (area of ca. 270,000 $km^2$) has about 3,700 species (0.014 species per $km^2$) (**???**). So, the Cape has ca. 4.3 times as many species per $km^2$ as SWA. The Cape and SWA are appropriately often compared, due to the similarities 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, SWA is topographically and edaphically distinct from the Cape. The former is topographically rather uniform (i.e. flat)—uniquely so among the world's five Mediterranean-climate regions (Hopper & Gioia, 2004)). SWA possesses a mesoscale chronosequence dune system (Laliberte et al., 2014; Cook et al., 2015), while the Cape 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., 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 Cape and SWA (Wardell-Johnson & Horwitz, 1996; Hopper & Gioia, 2004; Lambers et al., 2010; Cramer et al., 2014; Laliberte et al., 2014; Cook et al., 2015). For the Cape, 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 SWA species richness as is likely the case in the

Cape. In the absence of topographic variability in SWA, it is proposed that the heterogeneity of that region is due to the juxtaposition of soil 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 these two regions to demonstrate this. As stated above, heterogeneous environments can (i) support diverse species assemblages, and (ii) stimulate ecological speciation. Thus, we expect species richness to covary with heterogeneity. Additionally, as one moves across a heterogeneous landscape, we expect to find greater turnover in community composition, as different environments support different species. Thus, areas of greater turnover should also be more rich, due to potential complementarity between neighbouring communities increasing total richness. Consequently, we expect that EH positively influences species richness and species turnover, and that species turnover itself positively influences species richness.

## 1.2 Hypothesis-v2

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

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

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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 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 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) 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 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 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 (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 been used as SDMs in southern Africa before (e.g. Thuiller et al., 2006), sometimes for conservation purposes (e.g. Coetzee 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

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

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

## 2.2 Environmental data sources

Geospatially-explicit raster layers were acquired for a selection of environmental variables (Table 1), for the regions of interest. Here, the GCFR was treated as the areas occupied by the Succulent Karoo and Fynbos biomes in the current delineation of South Africa's biome boundaries (Mucina & Rutherford, 2006). The SWAFR was treated as the areas occupied by the Southwest Australia savanna, Swan Coastal Plain Scrub and Woodlands, Jarrah-Karri forest and shrublands, Southwest Australia woodlands, Esperance mallee, and Coolgardie woodlands in the World Wildlife Fund Terrestrial Ecoregions dataset (Olson et al., 2001) in order to closely match the currently delineated SWAFR (Gioia & Hopper, 2017, Hopper & Gioia (2004)). For the sake of readability, we shall refer to the GCFR and SWAFR simply as the Cape and SWA from hereon.

Raster data were re-projected to a common coordinate reference: WGS84 (NIMA, 2000), using the "rgdal" (**???**) package in R (R Core Team, 2018). All data were re-sampled to 0.05° resolution using the "resample" function in the R package "raster" (**???**), with the "bilinear" method.

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

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

## 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 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 "terrain" function. For a three by three neighbourhood $N$ 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 $x_{focal}$:

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

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, 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 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 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 Quantifying species turnover

Regarding prediction (iii), we wished to compare the general degree of species turnover in each region. To compare the extent of species turnover between the Cape and SWA, we determined two metrics of species turnover. The first, computes the mean species turnover as Jaccard distance (**???**) between each pair of QDS within each HDS ($\overline{J}_{QDS}$, 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 $\beta$-diversity (**???**), where

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

Here, we treat species richness at the HDS-scale ($S_{HDS}$)) as $\gamma$ and at the QDS-scale as $\alpha$. 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 ($\overline{S}_{QDS}$). We compare the distributions of $\overline{J}_{QDS}$ and $T_{HDS}$ using non-parametric Mann-Whitney $U$-tests, in order to guard against non-normality.

#### 2.4.3 Predicting richness and turnover with environmental heterogeneity

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 using boosted regression-tree (BRT) modelling techniques. Allowing us to explore which axes of environmental heterogeneity have most influence on vascular plant species richness and turnover, and the differences in the importance of such axes between the Cape and SWA.

BRTs are a flexible machine learning-based model of response variables and do so without involving normal null-hypothesis significance testing (Elith et al., 2008), and 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 are developed through the iterative generation of non-linear regression trees. BRTs are an ensemble-approach, in which a prediction $\widehat{y_i}$ is based on the weighted sum of the predictions of progressively "less important" regression trees ($t_k$), as opposed to the predictions of one tree (Elith et al., 2008). For $k \rightarrow nt$ number of trees, where each tree is itself a function of the matrix $X$ of $j$ predictor variables ($t_k = f(x_{ij})$),

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

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

BRTs were implemented here to predict both vascular plant species richness and turnover in each HDS, as a function of environmental variables and environmental roughness values in those cells, as Gaussian responses, thus resulting in two BRT-models for each region. We treated richness as $S_{HDS}$ and turnover as $\overline{J}_{QDS}$. The natural logarithm of species richness was used, in order to satisfy the assumptions of a 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. Additionally, BRTs were implemented to predict both vascular plant species richness at the QDS-scale ($S_{QDS}$), thus resulting in a total of six BRT-models presented here.

As recommended by Elith et al. (2008), BRT models were trained on a set of non-collinear predictor variables using "gbm.step" in "dismo" (**???**) and "gbm" (**???**). 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" (**???**) separately for each region, such that variables were no more than 80% collinear (Pearson's $r \geq 0.80$). When faced with a cluster of collinear variables, one variable was chosen manually therefrom. Where possible, the roughness-equivalent of an environmental variable was included if its absolute-equivalent could also be included. When 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.

In order to select ideal $lr$ and $tc$ all models (described below) were trained on the final non-collinear predictor sets iteratively for 25 combinations of a range of $tc$ values (1 to 5) and a range of $lr$ values (0.01, 0.005, 0.001, $5 \times 10^{-4}$, $1 \times 10^{-4}$). The function "gbm.step" optimises the number of trees ($nt$) using cross-validation during model training (Elith et al., 2008) by halting iteration when predictions begin to overfit. For all models, we used 10 cross-validation folds (i.e. use 10 different randomly selected training data sets), a tolerance-threshold of 0.001, a bagging-fraction of 0.75 (proportion of training data randomly chosen to generate each tree), and trained models starting with 50 trees, with each iterative step adding 50 trees at a time, up to a maximum of 10,000 trees.

Following this iterative parameter optimisation, Gaussian BRT models were constructed with $tc = 3$ and $lr = 0.001$, along with the other settings described. The 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, using "gbm.simplify" in "dismo".

BRT-model performance can described by measuring the variance in a dataset a BRT-model has explained, quantified here by $R^2_{pseudo}$, which is the proportion of null deviance $D_{null}$ explained by some model $i$ (Equation (4)).

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

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

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

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

# 3 Results

## 3.1 Describing environmental heterogeneity across scales

Across all variables considered, the Cape is more environmentally 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 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 (0.05º), so does the Cape. As such, the relative difference between the two regions seems invariant with spatial scale ($CLES \approx 0.95$, Figure 1b). This concurs with our expectations, as the Cape is mountainous and known to have steep elevational gradients (**???**), while SWA is much more topographically uniform.

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

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

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

### 3.2 Comparing species turnover in the two regions

Following calculations of $\overline{J}_{QDS}$ 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 was defined here ($P < 0.0001$, Figure 2a,b).

### 3.3 Predicting richness and turnover with environmental heterogeneity

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

BRT-models of species richness at the QDS-scale in each region seemed to generally performed best, as these models had generally fit the greatest number of trees ($nt$, Figure 4a), and higher $R^2$-values (Figure 4b,c). Notably, SWA models of species richness and turnover at the HDS-scale out-performed Cape models, while at the QDS-scale the Cape models performed as-well or better (Figure 4, Table 3).

Across our BRT-models of species richness and turnover, the sets of environmental variables important to model predictions differ substantially between the Cape and SWA, both in terms of which aspects of the environment were found to be biologically relevant and in terms of the relative importance of absolute and heterogeneity variables (Figure 3). Most obviously, species richness and turnover in the Cape are predicted in majority by environmental heterogeneity, which is not the case in SWA (piecharts inset Figure 3). Species richness and turnover in the Cape are predicted by a broad suite of environmental variables, with no individual variable contributing more than ca. 20% to any model prediction (Figure 3a–c). The SWA models' predictions, however, are largely determined by MAP (Figure 3d–f).

more strongly predicted by elevational, climatic and edaphic heterogeneity (Figure 3a), richness in SWA is mostly predicted by absolute MAP (Figure 3b). Indeed, Cape species richness is mostly predicted by environmental heterogeneity variables (Figure 3a inset), while SWA species richness is mostly predicted by absolute environmental variables (Figure 3b inset).

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

# 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 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.

# Table captions

Captions are also repeated alongside their respective tables for readability.

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

Table 2: Average percentile-ranks for BRT-model performance measures ($nt$, $R^2_{pseudo}$ (Equation (4)), $R^2_{E-O}$) of 1000 replicate BRT-models relative to 999 BRT-models fit to permuted datasets. Ranks approaching one indicate that a set of replicate BRT-models had greater values than the permuted models.

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

# Figure captions

Captions are also repeated alongside their respective figures for readability.

Figure 1: 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 (0.05º) and coarse (3QDS) scales. Each distribution has under it an area of one. 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 0.05º 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). 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 ($\overline{J}_{QDS}$), (b) additively defined turnover ($T_{HDS}$, Equation (2)) as a proportion of HDS richness ($S_{HDS}$)), compared between the Cape and SWA. Mann-Whitney $U$-tests between the Cape and SWA distributions of $\overline{J}_{QDS}$ and $T_{HDS}$ yielded significant differences.

Figure 3: Relative influence of environmental variables (including heterogeneity variables—prefixed with "R") in boosted regression tree (BRT) model predictions for the final six models' response variables in Greater Cape Floristic Region (Cape) and Southwest Australia Floristic Region (SWA): vascular plant species richness at the (b,e) QDS-scale, (a,d) HDS-scale and (c,f) turnover ($= \overline{J}_{QDS}$). All BRT-models were permitted to fit three-way interactions between environmental variables. Points denote the average contribution of an environmental variable to model-predictions across the 1000 replicate BRT-models for that region/scope. Horizontal ticks denote the average for the 999 permuted BRT-models. The standard deviations above and below these means are shown with vertical lines. Note that in the case of the replicate models they are very small in most cases, obsfucating them. Colour represents the general category of the environment (keyed) to which a variable belongs, as in Figure 1b. Piecharts inset display the same information (left-most piecharts), and additionally grouped according to whether a variable was absolute or roughness-transformed (right-most

piecharts). $F$-statistics inset are for one-way ANOVAs of differences in variables' relative influences from the replicate ($F_{rep.}$) and permuted ($F_{prm.}$) BRT-models.

Figure 4: Distributions of three measures of boosted regression tree (BRT) model performance (a) the number of trees in the model $nt$, (b) $R^2_{pseudo}$ (Equation (4)), (c) $R^2_{E-O}$ (see text). These measures are presented for the six sets of permuted (pale bars) and six sets of replicate BRT-models (dark bars) as in Figure 3, coloured according to the region of interest as in Figures 1a and 2. In all cases, replicate BRT-models almost entirely out-rank the permuted models in terms of performance (Table 2) and Cape and SWA models had significantly different values for each metric (Table 3). Note, the actual differences between Cape and SWA models' values is not realistically important in some cases.

Figure 5: Differences in the rankings of environmental variables' (including heterogeneity variables) relative influences on boosted regression tree (BRT) model predictions of vascular plant species richness and turnover in (a) Cape and (b) SWA (as in Figure 3). Each point represents an environmental variable's rank in BRT-model importance, decreasing in importance from left to right. Rankings used here are the same as that of the average relative influence for variables across replicate BRT-models, presented in Figure 3. Coloured lines connect points representing the same environmental variable. Points' outlines are coloured according to the general category of the environment (keyed) to which a variable belongs, as in Figuress 1b and 3, while points' centres are coloured according to whether a variable was roughness-transformed or not. The comparisons of variables' rankings of interest are between QDS- and HDS-scale richness (rows nos. 1 and 2) and between HDS-scale richness and turnover (rows nos. 2 and 3). Statistics ($\Delta$- and $P$-values) inset at the top and bottom of each panel refer to these comparisons respectively. $\Delta$-values is the average absolute difference in ranks of across variables between two models' rankings. The associate $P$-value results from ranking the observed $\Delta$-values against 999 $\Delta$-values based on random permutations of variables' rankings (see Supplementary Information).

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# Biosketches

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# Author contributions

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

# Tables

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

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

Table 2: Average percentile-ranks for BRT-model performance measures ($nt$, $R^2_{pseudo}$ (Equation (4)), $R^2_{E-O}$) of 1000 replicate BRT-models relative to 999 BRT-models fit to permuted datasets. Ranks approaching one indicate that a set of replicate BRT-models had greater values than the permuted models.

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

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

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

# Figures

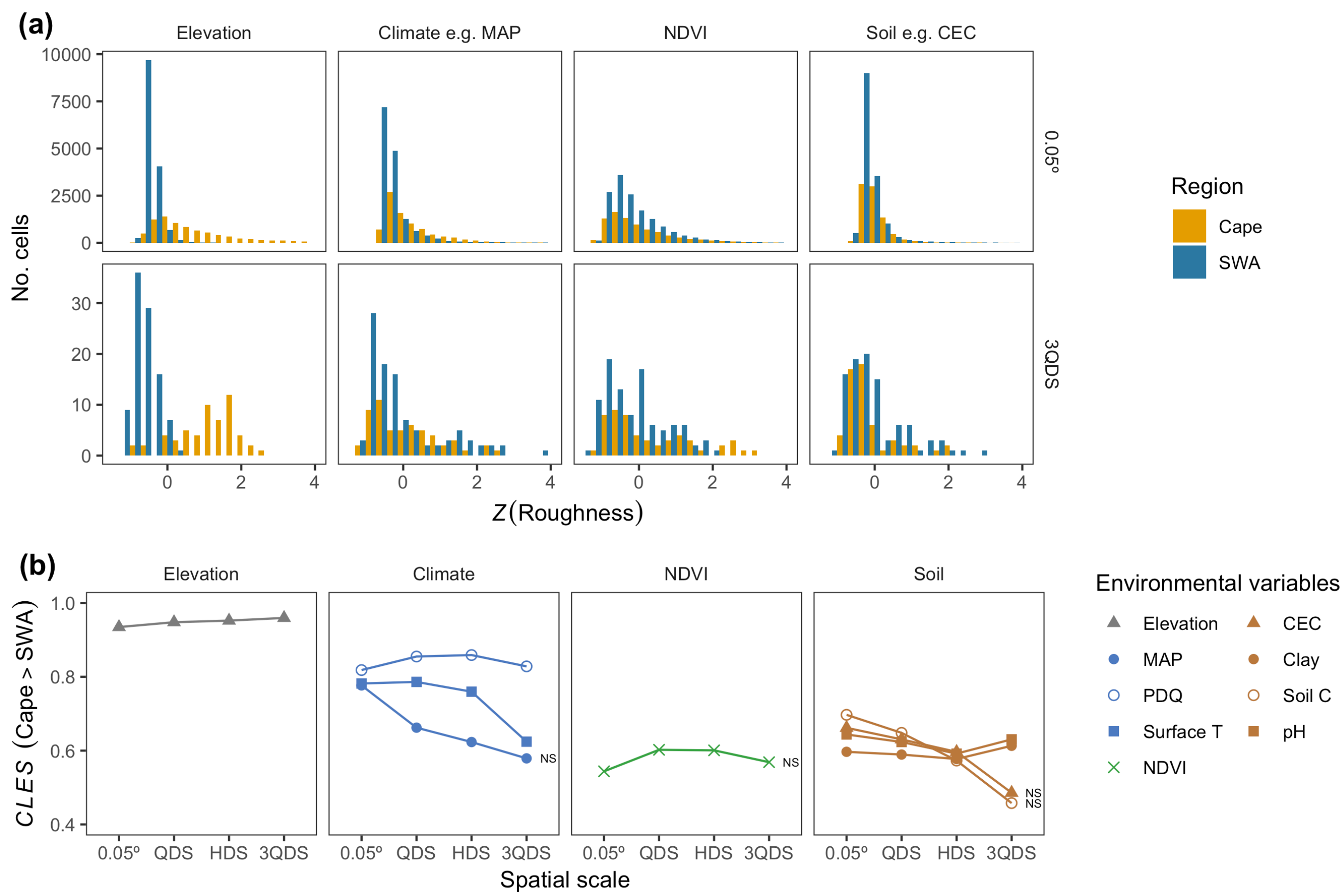


Figure 1: Types of environmental heterogeneity, compared between the the Cape and SWA—namely for (a) elevation, (b) climatic variables, (c) NDVI and (d) soil variables—in each panel consisting of three sub-panels per variable type. The upper row of panels shows example distributions of roughness values (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 an area of one. 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.

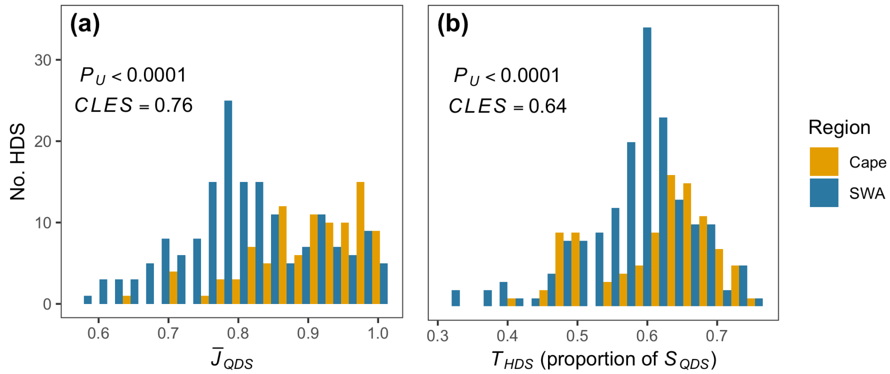


Figure 2: Species turnover, described in two forms ((a) mean Jaccard distance between QDS in each HDS ($\overline{J}_{QDS}$), (b) additively defined turnover ($T_{HDS}$, Equation (2)) as a proportion of HDS richness ($S_{HDS}$)), compared between the Cape and SWA. Mann-Whitney $U$-tests between the Cape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

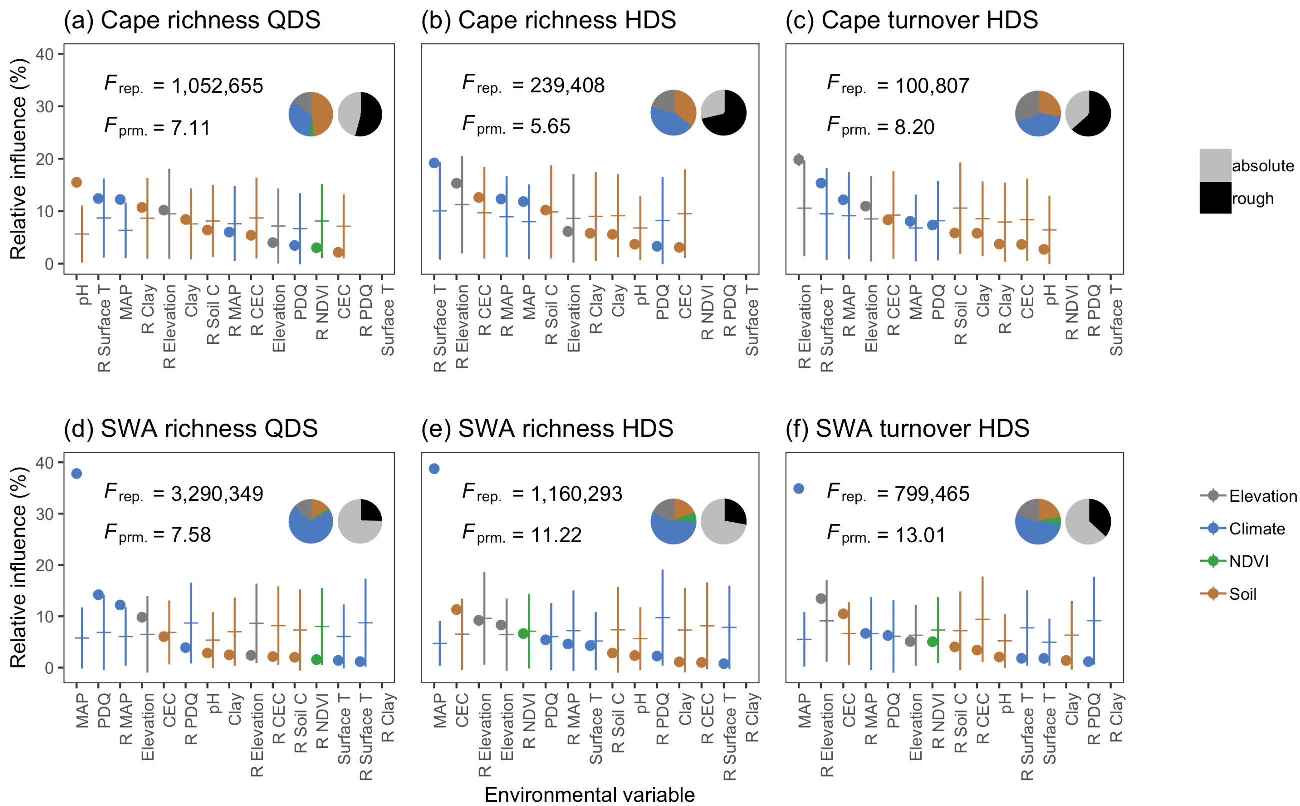


Figure 3: Relative influence of environmental variables (including heterogeneity variables—prefixed with "R") in boosted regression tree (BRT) model predictions for the final six models' response variables in Greater Cape Floristic Region (Cape) and Southwest Australia Floristic Region (SWA): vascular plant species richness at the (b,e) QDS-scale, (a,d) HDS-scale and (c,f) turnover ($= \overline{J}_{QDS}$). All BRT-models were permitted to fit three-way interactions between environmental variables. Points denote the average contribution of an environmental variable to model-predictions across the 1000 replicate BRT-models for that region/scope. Horizontal ticks denote the average for the 999 permuted BRT-models. The standard deviations above and below these means are shown with vertical lines. Note that in the case of the replicate models they are very small in most cases, obsfucating them. Colour represents the general category of the environment (keyed) to which a variable belongs, as in Figure 1b. Piecharts inset display the same information (left-most piecharts), and additionally grouped according to whether a variable was absolute or roughness-transformed (right-most piecharts). $F$-statistics inset are for one-way ANOVAs of differences in variables' relative influences from the replicate ($F_{rep.}$) and permuted ($F_{prm.}$) BRT-models.

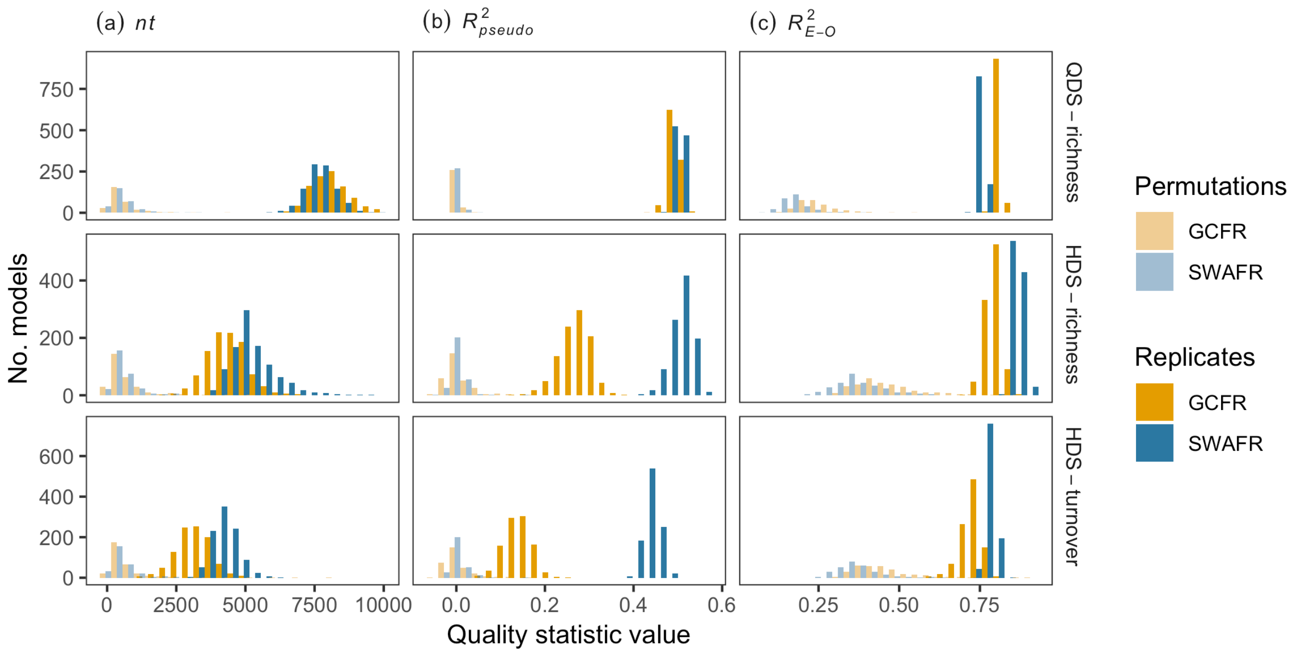


Figure 4: Distributions of three measures of boosted regression tree (BRT) model performance (a) the number of trees in the model $nt$, (b) $R^2_{pseudo}$ (Equation (4)), (c) $R^2_{E-O}$ (see text). These measures are presented for the six sets of permuted (pale bars) and six sets of replicate BRT-models (dark bars) as in Figure 3, coloured according to the region of interest as in Figures 1a and 2. In all cases, replicate BRT-models almost entirely out-rank the permuted models in terms of performance (Table 2) and Cape and SWA models had significantly different values for each metric (Table 3). Note, the actual differences between Cape and SWA models' values is not realistically important in some cases.

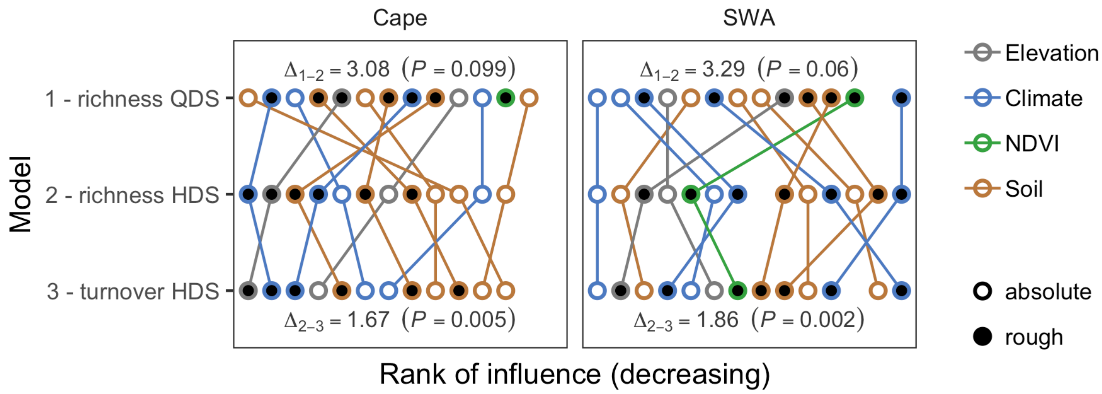


Figure 5: Differences in the rankings of environmental variables' (including heterogeneity variables) relative influences on boosted regression tree (BRT) model predictions of vascular plant species richness and turnover in (a) Cape and (b) SWA (as in Figure 3). Each point represents an environmental variable's rank in BRT-model importance, decreasing in importance from left to right. Rankings used here are the same as that of the average relative influence for variables across replicate BRT-models, presented in Figure 3. Coloured lines connect points representing the same environmental variable. Points' outlines are coloured according to the general category of the environment (keyed) to which a variable belongs, as in Figuress 1b and 3, while points' centres are coloured according to whether a variable was roughness-transformed or not. The comparisons of variables' rankings of interest are between QDS- and HDS-scale richness (rows nos. 1 and 2) and between HDS-scale richness and turnover (rows nos. 2 and 3). Statistics ($\Delta$- and $P$-values) inset at the top and bottom of each panel refer to these comparisons respectively. $\Delta$-values is the average absolute difference in ranks of across variables between two models' rankings. The associate $P$-value results from ranking the observed $\Delta$-values against 999 $\Delta$-values based on random permutations of variables' rankings (see Supplementary Information).