Similar axes of environmental heterogeneity drive plant species richness in two hyperdiverse floras

Running title: Environmental heterogeneity and plant species richness

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# Abstract

**Aim:** …

**Location:** The Greater Cape Floristic Region, South Africa (GCFR) and Southwest Australian Floristic Region (SWAFR)

**Taxon:** Vascular plants (Tracheophytes)

**Methods:** …

**Results:** …

**Main conclusions:** …

*Keywords:* …

# 1 Introduction

The species richness of a region is a function of its biogeographic context (e.g. proximity to potential immigrant source areas), its diversification history (e.g. speciation and extinction history) and any locally-deterministic, environmental features (e.g. environmental productivity, heterogeneity) that influence species persistence and coexistence (Ricklefs 1987, 2004). Since all three effects are potentially influenced by environmental heterogeneity (environmental heterogeneity), the latter may be a particularly important driver of regional species richness variation (refs), with physically-heterogeneous regions being especially prone to be species-rich (refs). For example, given that the recruitment success of immigrant lineages into a region is often dictated by the pre-adaptations of those lineages (Ackerly, Donoghue & Crisp), a physically-heterogenous environment may promote diversity by admitting a more functionally-diverse array of immigrant lineages (ref). In addition, by virtue of its central role in powering adaptive divergence and/or promoting population isolation, environmental heterogeneity is a critical requirement for speciation under most models (Wiens 2004a,b; Sobel et al. 2010; Nosil?). Likewise, in the context of long-term environmental change, physically heterogeneity may offer refugia to a wider array of lineages and so confer a greater level of buffering against lineage extinction (refs Byrne?). Finally, environmental heterogeneity has repeatedly been shown to facilitate species coexistence at a variety of scales, and so enhance regional species richness (refs). Differences in environmental heterogeneity may therefore be critically important in accounting for variation in regional species richness, particularly where the regions under comparison are similar in terms of area, their physical properties, and the time-frames within which their biotas have assembled.

The floristically-rich South Western Australian Floristic Region (SWAFR; Hopper & Gioia 2004) and Greater Cape Floristic Region of South Africa (GCFR; Born et al. 2007) constitute a case in point. Situated on the southwestern corners of their respective continents, the climates of both these regions have been oceanically-moderated at least since the Cretaceous, and both are dominated by a contemporary mediterranean-type climate whose origin can be traced to the Early-Middle (SWAFR: Rundel et al. 2016; Lamont & He 2017) or Late Miocene (GCFR: Dupont et al. 2011; Hoffmann et al. 2015). In addition, both regions have been unglaciated since the Permian and are dominated by ancient, weathered landscapes whose soil-nutritional status is amongst the lowest of any landscape on Earth (Stock & Verboom XXXX), hence their designation as “OCBILs” (“old, climatically-buffered infertile landscapes”; Hopper 2009). Owing to these environmental similarities, the SWAFR and GCFR floras are very similar in terms of their functional trait spectra (Cowling & Witkowski 1994), though the presence of a significant tree component in the SWAFR underpins a striking difference in vegetation physiognomy (ref). Moreover, the long-term climatic and geological stability of the two regions ensures that the native floras of both reflect long histories of assembly, extending back to the Palaeocene and possibly even earlier (refs), with evidence of a long history of transoceanic dispersal between the two (refs). In this context, it is unsurprising that the two floras show strong taxonomic affinities and that both are species-rich, with high levels of regional endemism (refs).

Notwithstanding these similarities, the SWAFR and GCFR differ markedly in terms of their vascular plant species richness, particularly when considered in relation to geographical area. Where the SWAFR accommodates ca .7,380 species in an area of ca. 302,600 km2 (i.e. 0.024 species km-2; Hopper & Gioia 2004), the GCFR accommodates ca. 11,430 species in an area of ca. 189,700 km2 (i.e. 0.060 species km-2; Snijman 2013). One explanation for this striking 2.5-fold species richness difference (per area) relates to differences in the physical heterogeneity of the two regions. Where much of the GCFR, particularly the hyper-diverse (ca. 9,400 species in ca. 90,800 km2; 0.104 species km-2) “core” Cape Floristic Region (CFR; Goldblatt 1978), is rugged and mountainous, the SWAFR landscape is much more subdued, comprising an ancient, weathered plateau. Since the strong relief of the GCFR underlies steep climatic and edaphic gradients (refs), it is probable that environmental heterogeneity is generally greater. The central aim of this paper, then, is to test the hypothesis that the observed species richness difference (per area) is a consequence of differences in the physical heterogeneity of these regions. Focusing on the quarter-degree square (QDS), half-degree square (HDS) and degree square (DS) scales (sensu Larsen et al. 2009), we first compare the distribution of species richness between the two regions, and in each region decompose broader-scale richness into average finer-scale richness and between-square turnover. Thereafter, we compare environmental heterogeneity between the two regions across a range of spatial scales. Finally, we use linear models to assess whether differences in environmental heterogeneity are sufficient to explain observed differences in species richness between the two regions.

# 2 Materials and methods

## 2.1 Comparing species richness

To compare vascular plant species richness between the GCFR and SWAFR, geospatially-explicit occurrence records of tracheophytes from within the borders of the GCFR and SWAFR were downloaded from the Global Biodiversity Information Facility (GBIF; see Table 1). For this purpose, the GCFR was treated as the area occupied by the Succulent Karoo and Fynbos Biomes (Mucina & Rutherford 2006), while the SWAFR was treated as the area occupied by Southwest Australia Savanna, Swan Coastal Plain Scrub and Woodlands, Jarrah-Karri Forest and Shrublands, Southwest Australia Woodlands, Esperance Mallee, and Coolgardie Woodlands (Olson et al. 2001) in order to match the current delimitation of the SWAFR (Hopper & Gioia 2004; Gioia & Hopper 2017). The query results were then cleaned as follows. Firstly, we retained only records identified to the species level, and ignored intraspecific taxa. This resulted in the retention of XXX and XXX unique species names for the GCFR and SWAFR, respectively. The R package “taxize” (Chamberlain & Szocs 2013; Chamberlain et al. 2018) was then used to query each species name against two taxonomic databases, the Global Name Resolver (GNR) and the Taxonomic Name Resolution Service (TNRS). Where either or both databases returned a match for a name, the name was retained; where not, it was excluded. Although the number of species thus excluded is high (GCFR: XXX; SWAFR: XXX), the geographically-random distribution of the records associated with these names suggests that exclusion of these names will not significantly influence spatial patterns of species richness. In order to ensure that no species was listed under multiple synonyms, the retained names were then queried against the Tropicos and Integrated Taxonomic Information System (ITIS) for known synonyms, again using “taxize.” We removed all records of species identified as non-native, using lists of invasive plants for South Africa and Australia from the IUCN’s Global Invasive Species Database (<http://www.iucngisd.org/gisd/>). Finally, we removed species with fewer than five total collection records in total, in order to discount low-confidence collections [reword]. The final species richness totals thus obtained were XXX and XXX for the GCFR and SWAFR, respectively. Using R, these cleaned species occurrence record data were collated into QDS, HDS and DS pixels. In addition, following Whittaker’s (ref) original additive decomposition of *γ*-diversity, we decomposed the species richness of each HDS (*S*HDS) into its *α* (“plot” richness) and *β* (turnover) components, using the equations

where QDS and HDS are the average species richness of the four constituent pixels in each HDS and DS respectively (i.e. *α*), and *T*QDS and *T*HDS represent the residual (i.e. turnover-based) richness *β*, determined each as *γ* − *α*.

## 2.2 Comparing environmental heterogeneity

To compare environmental heterogeneity between the GCFR and SWAFR, we acquired a broad suite of geospatially-explicit environmental data in the form of raster layers. For the purpose of analysis, we then selected a subset of ten variables (Table 1) to represent topographic (elevation), climatic (surface T, MAP, PDQ), edaphic (clay content, soil C, pH, CEC) and vegetational (NDVI) gradients. As far as possible, these variables were selected to represent environmental axes which are considered regionally important. For example, the inclusion of PDQ in addition to MAP is justified on the basis that, where the letter captures variation in overall rainfall amount, the former measures the intensity of seasonal aridity which is a key feature of mediterranean-type climates (ref). Variable selection was, however, constrained by the availability of suitable raster-layers. Thus, although soil [P] is probably an important determinant of plant distribution in both the GCFR and SWAFR (refs), this variable could not be included owing to a lack of comparable data layers for the two regions. Indeed, wherever possible, we made use of satellite layers \*\*\*. Where soil variables were summarised as depth-interval weighted averages, climatic and spectral variables were summarised as annual means using the “raster” package for R (Hijmans, 2016). All layers were then projected to a common coordinate reference system (WGS84; ref) using the “rgdal” package (Bivand et al., 2017) and resampled to 0.05º resolution using the “resample” function in “raster,” with the “bilinear” method.

In order to quantify heterogeneity in the variables under study, we developed an index that would account for the spatial configuration of different environmental conditions at a range of scales. Our index, based on raster data, employs nested pixels at various spatial scales. We treated environmental heterogeneity as the variance of the environmental conditions in the four sub-pixels for a given pixel. As such, we calculate heterogeneity based on the twentieth-degree squares’ (0.05°×0.05°), eighth-degree squares’ (EDS), QDS’ and HDS’ environmental conditions within tenth-degree squares (0.10°×0.10°), QDS, HDS and DS respectively. We implemented this measure of heterogeneity using the R functions “var” and “aggregate” (the latter in the R package “raster” (Hijmans 2016)). This index only uses neighbouring pixels to describe heterogeneity, similar to indices implemented in the “terrain” function in “raster”. However, our index describes heterogeneity within pixels as opposed to between pixels as in “terrain”. The former is comparable with species richness data, and is thus used here.

We used principal components analysis (PCA), applied to the nine environmental variables across both regions, to derive a measure of overall environmental heterogeneity. For this purpose, the layers describing heterogeneity in the nine environmental variables at each spatial scale were first log10-transformed to ensure normality and then subjected to PCA. A separate PCA was done for each spatial scale. The first axis (PC1) extracted from each of the four PCAs represents the major axis of heterogeneity across the nine environmental variables considered in this study.

To compare the nine forms of environmental heterogeneity and the major axis of heterogeneity between the two regions, we employed common language effect sizes (*CLES*) using the R package “canprot” (ref). The *CLES* describes the proportion of pairwise comparisons, between two categories’ quantitative values, where one category’s values exceeds the other’s. Along with this appealing descriptive statistic, we tested for differences in regions’ heterogeneity values using two-sided Mann-Whitney *U*-tests (ref) in R. We performed the *CLES*-calculations and *U*-tests at the four spatial scales considered. The enabled us to assess scale-dependence in the calculation of heterogeneity and to ascertain the spatial scale (if any) at which environmental heterogeneity is [was?] most pronounced.

## 2.3 Environmental heterogeneity as an explanation of species richness

In the absence of strong non-linearity of the relationships between environmental heterogeneity (in the nine selected variables, and the major heterogeneity axis represented by PC1) and species richness at the QDS-, HDS- and DS-scales, we used linear models to assess the explanatory power of environmental heterogeneity as a determinant of species richness across the two regions. These analyses made use of the species richness data collated at the QDS-, HDS- and DS-scales and measures of environmental heterogeneity determined at these same scales. To test the dependence of species richness on environmental heterogeneity and to assess whether the form of this dependence is identical across the two regions, we fitted simple and multiple linear regression models specifying *S*HDS, *S*QDS and *S*DS each as functions of environmental heterogeneity.

For the univariate regressions, we fitted three nested models for each of the nine axes of environmental heterogeneity and the major axis of heterogeneity. For each predictor variable *X*, we fit: a “main effect only” model (*S* ~ *β*0 + *β*1*X*), a “main effect + region” model (*S* ~ *β*0 + *β*1*X* + *β*2*Region*) and a model with an interaction term for region (“main effect × region”; (*S* ~ *β*0 + *β*1*X* + *β*2*Region* + *β*3(*X × Region*)). The best fitting of these three models for each of the ten predictor variables was determined using Akaike’s information criterion (*AIC*; ref), such that the selected model was the simplest model with *∆AIC* < 2 (ref).Using this ANCOVA-like approach, we assess when each form of heterogeneity poorly predicts species richness across the two regions (i.e. when a “main effect + region” model is best fitting but with little support for the main effect), when there is a common relationship between a form of heterogeneity in both regions (i.e. when a “main effect only” or a “main effect + region” model is best fitting) or when species richness in each region relates differently to a form of heterogeneity (i.e. when a “main effect × region” model is best fitting). [reword this explanation/para!]

While the rationale of the univariate models was to describe empirical patterns of covariance between each axis of environmental heterogeneity and species richness, the multivariate models allow us to account for differences in richness across multiple axes of environmental heterogeneity simultaneously [expand?].

# 3 Results

## 3.1 Comparing species richness

Comparison of QDS- and HDS-scale species richness between the GCFR and SWAFR confirms the greater richness of the former,

We partitioned *S*HDS into its - and -components (QDS and *T*QDS respectively), and demonstrate that almost all HDS in both the GCFR and SWAFR are composed of QDS that only account for no more than ca. 50% of *S*HDS (Figure 2a). After accounting for the generally greater *S*HDS in the GCFR (Figure 2b), *S*HDS is more attributable to floristic turnover in in the GCFR than it is in the SWAFR (Figure 2c).

## 3.2 Comparing environmental heterogeneity

Regressions of *CLES* against spatial scale identified the GCFR as being consistently more heterogeneous than the SWAFR for all nine environmental variables, across the full range of spatial scales studied (Fig. 1; Two-sided t test (mean *CLES* > 0.5): t = \*\*\*, df = \*\*\*, P < 0.001) [Across the five spatial scales, all *CLES*-values differed significantly from 0.5 following two-sided *t*-tests (*P* < 0.001).]. The same was true for the major axis of heterogeneity, described by PC1, which accounted for between 43.64% and 46.40% of the variance in all nine variables across the five spatial scales. In addition, for MAP, surface T, CEC, soil C and PC1, *CLES* was negatively related to spatial scale, indicating that the greater heterogeneity of the GCFR was especially pronounced at small spatial scales. The opposite was true of elevation and Clay, in which the greater heterogeneity of the GCFR was more pronounced at large spatial scales. NDVI and pH showed no scale-dependence.

## 3.3 Environmental heterogeneity as an explanation of species richness

We regressed vascular plant species richness (*S*) against each axis of environmental heterogeneity separately (Table 2, Figure 3) and in multivariate models (Figure 4) at both HDS- (Table 2a, Figure 4a) and QDS-scales (Table 2b, Figure 4b). Heterogeneity in elevation and mean annual surface temperature were consistently positively “main effect only” across scales when considered in univariate models (Table 2). This pattern is mirrored by the major axis of environmental heterogeneity: PC1 (Figure 3), though there is scale-dependence in the slope of that relationship. In a univariate context, all other environmental heterogeneity-variables showed varying degrees of covariance with *S* (Table 2).

Considering the multivariate models of *S*HDS (Figure 4a) and *S*QDS (Figure 4b), the importance of different axes of environmental heterogeneity varies between the HDS- and QDS-scales (Table 3). At the HDS-scale, the GCFR and SWAFR share no “common effects” of environmental heterogeneity on *S*, while at the QDS-scale the relationships between *S* and heterogeneity in elevation, MAP and CEC are common to the two regions.

At the HDS-scale (i.e. for *S*HDS; Table 2a), there is evidence for a difference in the slopes of the GCFR and SWAFR's relationships with heterogeneity in MAP. Heterogeneity in NDVI and clay only present evidence for the same slope in each region, but differing intercepts. Heterogeneity in CEC and pH have non-significant slopes and significant region-effects­­­—suggesting that these variables values' have weak relationships with *S*HDS, and that the region-effect explains more of the variance. Other variables (heterogeneity in elevation, PDQ, surface T and soil C) only present evidence for a continuous effect of that heterogeneity, explaining the difference in the regions' *S*HDS in terms of the roughness values themselves, without the need to invoke a region term. Think of it this way:

* If there is no need for any information concerning the region a cell belongs to, then the environmental roughness "rule" is followed well across the two regions in a similar way.
* If the region-effect is significant, but not the roughness effect, then that roughness axis isn't doing a very good job of explaining anything, and must defer to the region-effect.
* When both the region- and roughness-effect are significant, this represents a softer version of the above, where the roughness axis can explain some variance, but not all.
* When there is a significant interaction between region and roughness, then each region is playing a whole new game with that axes in terms of how richness is being driven.

At the QDS-scale (i.e. for *S*QDS; Table 2b), it is noteworthy that all axes best-supported to have an additive region term only also had non-significant roughness-effects [expand?].

I also regressed against PC1. Like heterogeneity in elevation and surface T, PC1 was the only explanatory variable "needed" in regressions for *S*HDS (also see Figure 3) and *S*QDS Figure 3 shows quite nicely how, in general, the GCFR and SWAFR are following the same "rule" (species richness increases with increasing environmental heterogeneity (PC1)) but occupy different areas along that relationship (the GCFR being more rich and more rough than the SWAFR).

# 4 Discussion

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# Tables

Table 1: Georeferenced environmental data and vascular plant species occurrence data sources used in this study. Data were acquired for the Greater Cape Floristic Region and Southwest Australian Floristic Region, with the temporal extent of data products used described where applicable.

|  |  |  |  |
| --- | --- | --- | --- |
| Dataset(s) | Source | Temporal extent | Citation(s) |
| Plant species occurrences | GBIF |  | GBIF (2017a,b) |
| Elevation | SRTM (v2.0) |  | Farr et al. (2007) |
| NDVI | MODIS (MOD13C2) | Feb. 2000 to Apr. 2017 | NASA (2017a) |
| Surface T | MODIS (MOD11C3) | Feb. 2000 to Apr. 2017 | NASA (2017b) |
| MAP, PDQ | CHIRPS (v2.0) | Jan. 1981 to Feb. 2017 | Funk et al. (2015) |
| CEC, clay, soil C, pH | SoilGrids250m |  | Hengl et al. (2017) |

Abbreviations are as follows: NDVI, normalized difference vegetation index; T, temperature; MAP, mean annual precipitation; PDQ, precipitation in the driest quarter; CEC, cation exchange capacity; C, carbon.

Table 2 (next page): Results of univariate regressions of vascular plant species richness against different axes of environmental heterogeneity and overall environmental heterogeneity (PC1) across the Greater Cape Floristic Region and Southwest Australian Floristic Region (SWAFR), at both (a) HDS- and (b) QDS-scale. For each axis of environmental heterogeneity, we fit three univariate models: *S* as a function of environmental heterogeneity, *S* as a function of environmental heterogeneity with an additive term describing region and *S* as a of environmental heterogeneity with an interaction term for region. We used Akaike’s information criterion (*AIC*; ref) to select which of these three model types fit best for each environmental heterogeneity predictor variable. In each case, the best-fitting model (those presented) was selected as the simplest model with *∆AIC* < 2.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  | Model term (signs and significances) | | | | | | |
| Response | Model type | Predictor | Slope |  | SWAFR effect |  | Slope:SWAFR |  |
| (a) *S*HDS | Main effect × region | MAP | + | \*\*\* | + |  | – | \*\* |
|  | Main effect + region | Clay | + | \* | – | \*\* |  |  |
|  |  | NDVI | + | \*\*\* | – | \* |  |  |
|  | Main effect only | Elevation | + | \*\*\* |  |  |  |  |
|  |  | PDQ | + | \*\*\* |  |  |  |  |
|  |  | Soil C | + | \*\*\* |  |  |  |  |
|  |  | Surface T | + | \*\*\* |  |  |  |  |
|  |  | PC1 | + | \*\*\* |  |  |  |  |
|  | Region only | CEC | – |  | – | \*\* |  |  |
|  |  | pH | + |  | – | \*\* |  |  |
| (b) *S*QDS | Main effect × region | NDVI | + | \*\*\* | – | \*\* | – | \*\*\* |
|  |  | PDQ | + | \*\*\* | + |  | + | \*\*\* |
|  |  | Soil C | + | \*\*\* | – |  | – | \*\* |
|  | Main effect only | Elevation | + | \*\*\* |  |  |  |  |
|  |  | MAP | + | \*\*\* |  |  |  |  |
|  |  | Surface T | + | \*\*\* |  |  |  |  |
|  |  | PC1 | + | \*\*\* |  |  |  |  |
|  | Region only | CEC | – |  | – | \*\*\* |  |  |
|  |  | Clay | + |  | – | \*\*\* |  |  |
|  |  | pH | – |  | – | \*\*\* |  |  |

Abbreviations are as in Table 1.

Table 3: Interpretation of region-specific scale-dependencies of the effects of different axes of environmental heterogeneity on vascular plant species richness (*S*) in the Greater Cape Floristic Region (GCFR) and Southwest Australian Floristic Region (SWAFR) (Figure 4). Here, positive scale-dependence (+) represents a greater magnitude of effect on *S* at broader spatial scales (i.e. at the HDS-scale), while negative scale-dependence (–) represents a greater magnitude at finer spatial scales (i.e. at the QDS-scale).

|  |  |  |
| --- | --- | --- |
|  | Axes of heterogeneity | |
| Scale-dependence | GCFR | SWAFR |
| + | Clay, pH |  |
| None |  | CEC |
| – | NDVI, soil C | PDQ |

Abbreviations of variables are as in Tables 1 and 2.

# Figures

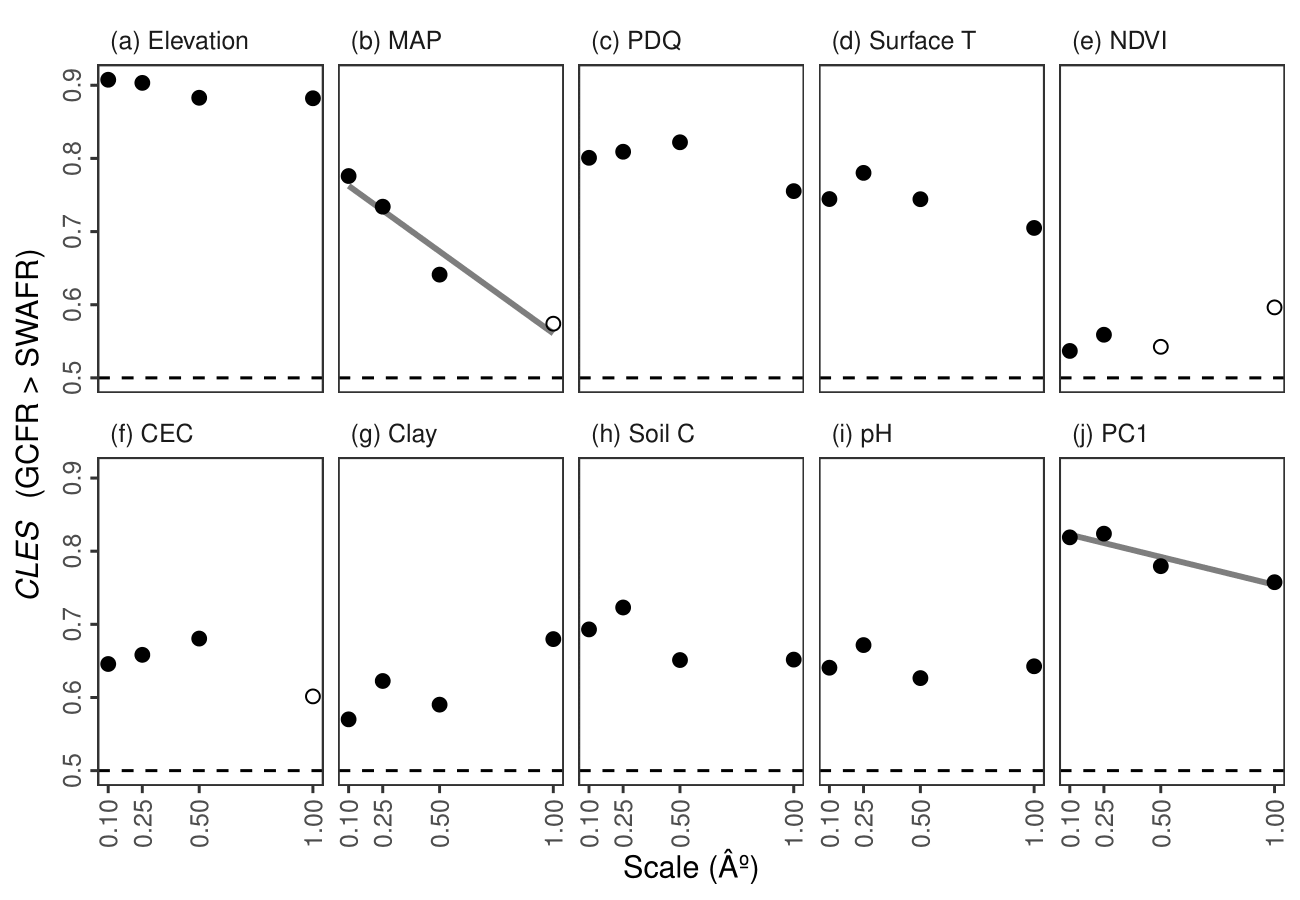


Figure 1: Simple linear regressions of the common language effect size (*CLES*; ref) of (a–i) various forms of environmental heterogeneity and (j) the first principal component of EH (PC1) in the Greater Cape Floristic Region (GCFR) and Southwest Australian Floristic Region (SWAFR). The *CLES* here is treated as the effect of GCFR relative to SWAFR values. Filled points represent comparisons where the GCFR and SWAFR significantly differed in *EH* (*P* ≤ 0.05, Mann-Whitney *U*-tests), while unfilled points represent those that were not significant (*P* > 0.05). Only significant (*P* ≤ 0.05) regression lines are plotted, with the exception of the fit for CEC, which was plotted in light of its marginal significance (*P* = 0.06). Grey bands denote 95% confidence intervals about the fitted lines. PC1 accounted for between 43.64 and 46.40% of the variation in *EH* across the five spatial scales at which it was calculated. Abbreviations of variables are as in Tables 1–3.

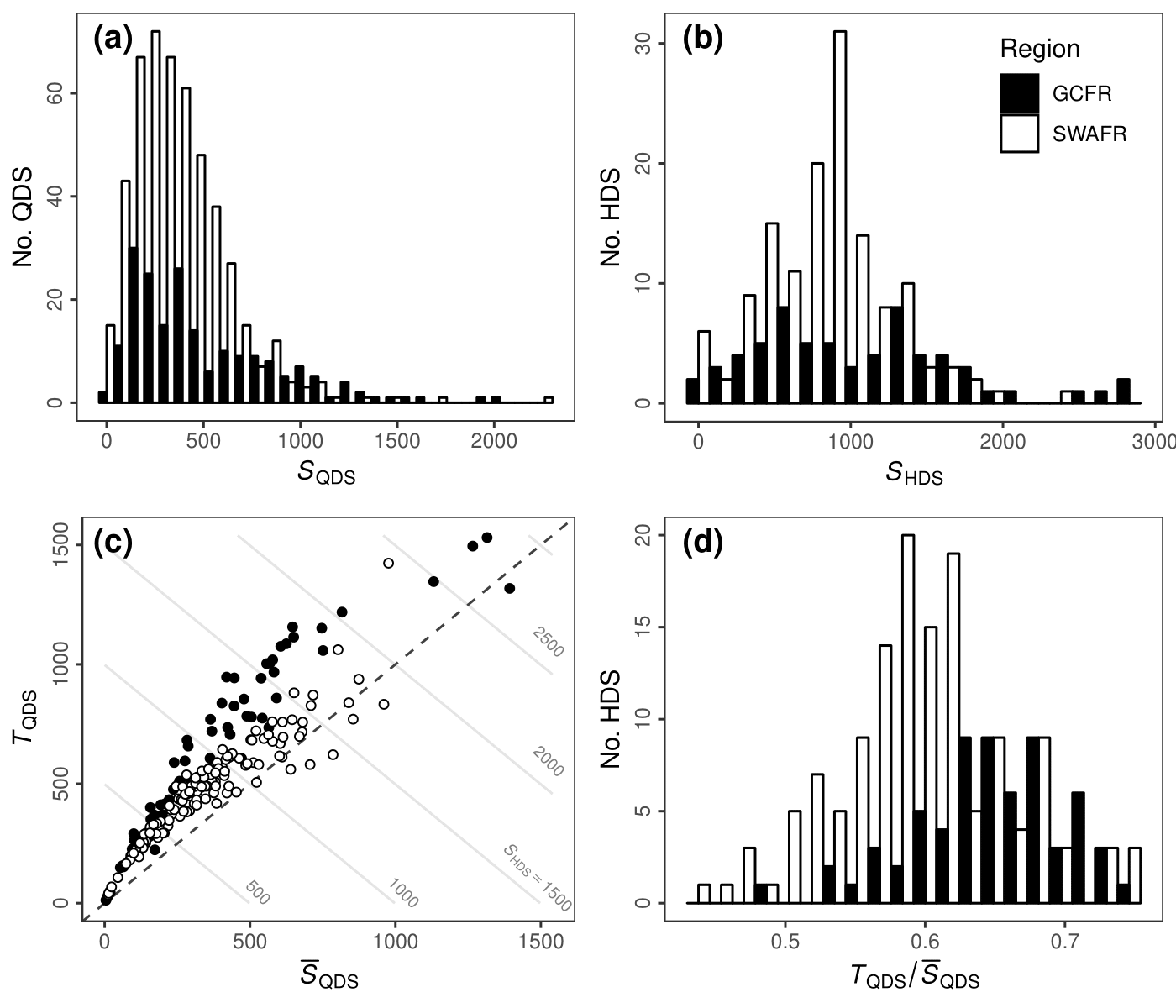


Figure 2: Distributions of (a) HDS- and (b) QDS-scale vascular plant species richness in the Greater Cape Floristic Region (GCFR) and Southwest Australian Floristic Region (SWAFR). (c) Scatter plot of mean QDS-scale richness (QDS) and turnover (*T*QDS; Equation 1) with contour lines denoting the *S*HDS that arises as their sum (i.e. increasing from lower-left to upper-right). (d) The distribution of the turnover partition of *S*HDS, expressed as a proportion (*T*QDS / *S*HDS). *P*-values inset (a,b,d) are from two-sided Mann-Whitney *U*-tests. Common language effect size (*CLES*) values inset (a,b,d) are for comparisons where GCFR values are greater than SWAFR values, as in Figure 1.

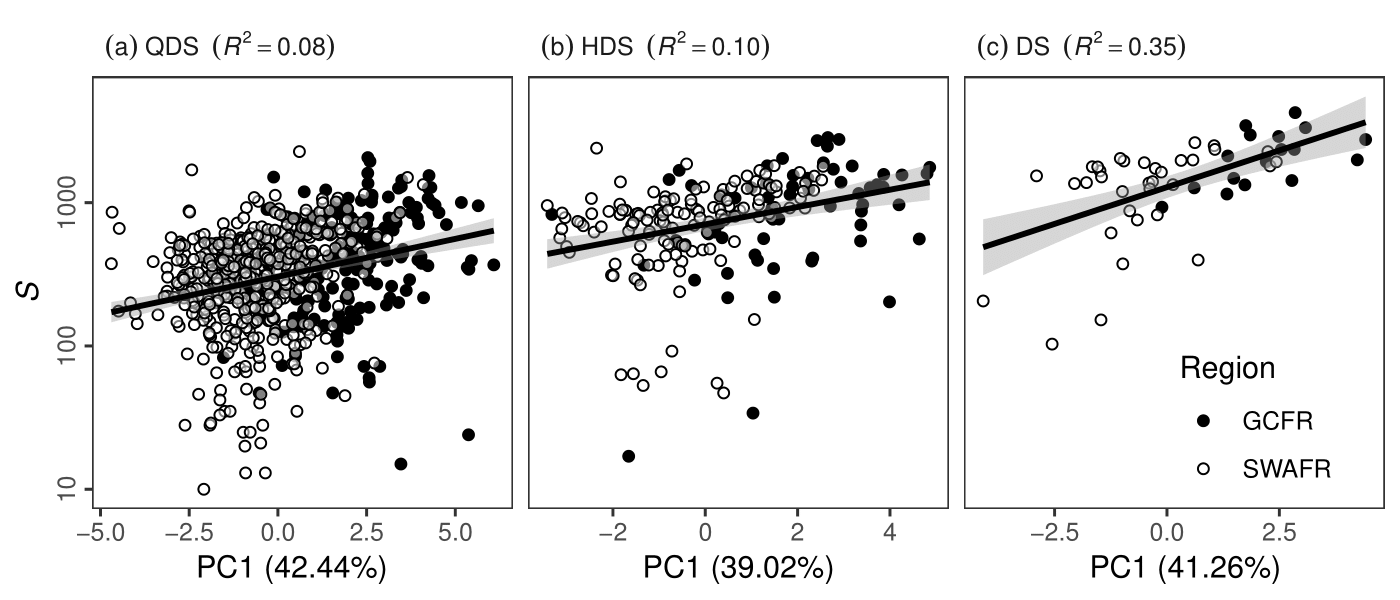


Figure 3: Simple linear regressions of vascular plant species richness as (a) *S*HDS (*R*2 = 0.23) and (b) *S*QDS (*R*2 = 0.15) against each respective scale’s first principle component (PC1) of environmental heterogeneity (*EH*; Equation 3) in the Greater Cape Floristic Region (GCFR) and Southwest Australian Floristic Region (SWAFR). Grey bands denote 95% confidence intervals about the fitted lines. When calculated at the QDS-scale, PC1 explained 39.86% of the variation in EH, while at the HDS-scale PC1 explained 41.55% of the variation in *EH*.

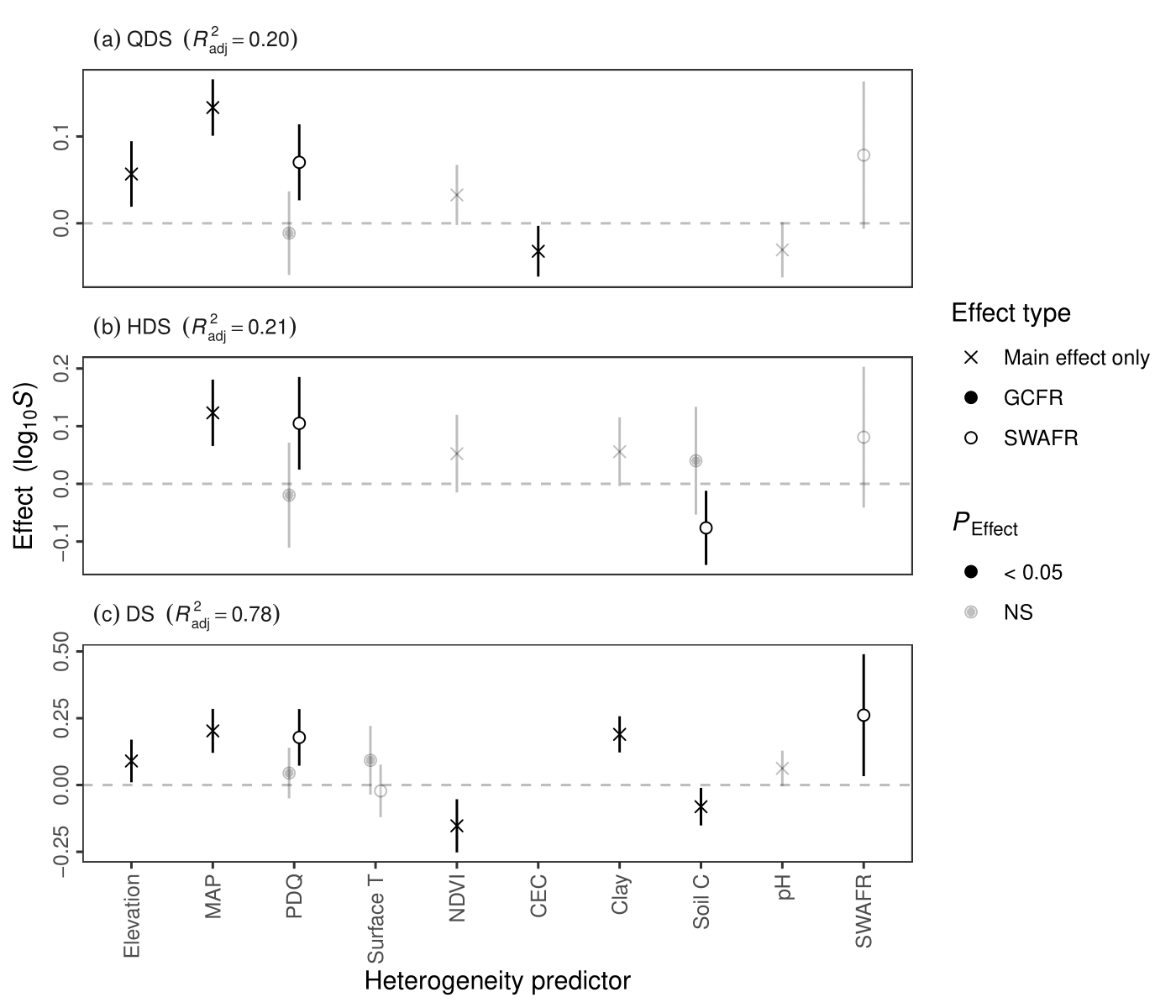


Figure 4: Slope estimates from multiple linear regressions of vascular plant species richness as (a) *S*HDS (*R*2adj = 0.49) and (b) *S*QDS (*R*2adj = 0.33) against the various forms of environmental heterogeneity across the Greater Cape Floristic Region (GCFR) and Southwest Australian Floristic Region (SWAFR). Each model was simplified, from a starting model with all predictors and their interactions with region, using reverse stepwise regression model selection based on *AIC*-scores in R. Points with error bars denote slope estimates and their 95% confidence intervals. Estimates illustrated in black were significant (*P* < 0.05), while those in grey were not, but still retained during stepwise model selection. Abbreviations of variables are as in Tables 1–3 and Figure 1.

# Data availability statement

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# Biosketches

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# Author contributions

MDC and GAV conceived the study question, which RvM investigated and developed under their supervision for his BSc Hons project. RvM collated the data and carried out the GIS work. All authors contributed to the the analyses, which were then carried out by RvM, who wrote the first draft of the manuscript. All authors contributed equally to the writing thereafter.