



Climate and soil attributes determine plant species turnover in global drylands

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ABSTRACT

Aim Geographical, climatic and soil factors are major drivers of plant beta diversity, but their importance for dryland plant communities is poorly known. The aim of this study was to: (1) characterize patterns of beta diversity in global drylands; (2) detect common environmental drivers of beta diversity; and (3) test for thresholds in environmental conditions driving potential shifts in plant species composition.

Location Global.

Methods Beta diversity was quantified in 224 dryland plant communities from 22 geographical regions on all continents except Antarctica using four complementary measures: the percentage of singletons (species occurring at only one site); Whittaker's beta diversity, $\beta(W)$; a directional beta diversity metric based on the correlation in species occurrences among spatially contiguous sites, $\beta(R^2)$; and a multivariate abundance-based metric, $\beta(MV)$. We used linear modelling to quantify the relationships between these metrics of beta diversity and geographical, climatic and soil variables.

Results Soil fertility and variability in temperature and rainfall, and to a lesser extent latitude, were the most important environmental predictors of beta diversity. Metrics related to species identity [percentage of singletons and $\beta(W)$] were most sensitive to soil fertility, whereas those metrics related to environmental gradients and abundance [$\beta(R^2)$ and $\beta(MV)$] were more associated with climate variability. Interactions among soil variables, climatic factors and plant cover were not important determinants of beta diversity. Sites receiving less than 178 mm of annual rainfall differed sharply in species composition from more mesic sites (> 200 mm).

Main conclusions Soil fertility and variability in temperature and rainfall are the most important environmental predictors of variation in plant beta diversity in global drylands. Our results suggest that those sites annually receiving c. 178 mm of rainfall will be especially sensitive to future climate changes. These findings may help to define appropriate conservation strategies for mitigating effects of climate change on dryland vegetation.

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Keywords

Aridity, beta diversity, climatic variability, global environmental change, habitat filtering, latitudinal gradient, plant community assembly, regression analysis, soil fertility, spatial soil heterogeneity.

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INTRODUCTION

Plant species occurrences depend on dispersal and environmental conditions. Changes in these variables generate species turnover across space and time (Whittaker, 1972). This species turnover is a key component of diversity, and characterizing the variables associated with species turnover is crucial for understanding assemblage organization at local, continental and global scales (Buckley & Jetz, 2008; Qian, 2009; Kraft *et al.*, 2011; Svenning *et al.*, 2011; Barton *et al.*, 2013). Indeed, spatial analyses of species turnover, particularly changes in beta diversity (Whittaker, 1972), are increasingly being used to quantify potential responses of natural communities to environmental changes (Clough *et al.*, 2007; Anderson *et al.*, 2011; Blois *et al.*, 2013; Qian *et al.*, 2013). In this paper, we will use the terminology proposed by Vellend (2001) and Tuomisto (2010) and refer to *beta diversity* as the partition of regional (gamma) and local (alpha) diversity and to *species turnover* as the mapping of this partition onto an environmental gradient.

Arid, semi-arid and dry-subhumid regions (drylands hereafter) occupy 41% of terrestrial surface area (Safrieli & Adeel, 2005) and are among the most sensitive ecosystems to climate change (Körner, 2000; Maestre *et al.*, 2012a; Vicente-Serrano *et al.*, 2012). Climate change models for the next century forecast average (median) warming values ranging

from 3.2 °C to 3.7 °C and changing amounts and patterns of rainfall for drylands worldwide (Christensen & Hewitson, 2007). These climatic change models predict the area occupied by drylands to expand globally by 10% by the end of this century (Feng & Fu, 2013), which will be likely to affect species diversity and associated ecosystem services and functions (Maestre *et al.*, 2012a; Delgado-Baquerizo *et al.*, 2013). Despite the global extent and importance of drylands (Reynolds *et al.*, 2007), there are only a handful of published studies of beta diversity in these ecosystems (e.g. Garcillán & Ezcurra, 2003; Goettsch & Hernández, 2006; Fernández-Goñi *et al.*, 2013).

Although existing studies provide important insights at local to regional scales, they are difficult to extrapolate to biogeographical and global scales. For example, the latitudinal gradient commonly observed for species richness (Lomolino *et al.*, 2006; Brown, 2014) and beta diversity (Hawkins & Diniz-Filho, 2004; Qian & Ricklefs, 2007; Buckley & Jetz, 2008) of most plant and animal assemblages has never been examined using dryland plant communities. Large-scale beta diversity assessments exist for a number of other taxa and communities. However, investigating the particular environmental factors that drive species turnover in drylands is necessary to implement conservation efforts more effectively (Buckley & Jetz, 2008), to help to maintain ecosystem services in these environments (Pasari *et al.*, 2013), and

to better understand the environmental drivers of change in these widely distributed plant communities (Blois *et al.*, 2013). Furthermore, regional differences in climatic or biogeographical histories, such as legacy effects of past glaciations (Svenning *et al.*, 2011), contributions of regional floras (Cowling *et al.*, 1996), and human activities can affect patterns of beta diversity measured at small spatial scales. These limitations may be overcome by conducting large-scale biome-wide comparative studies (Gaston *et al.*, 2007; Buckley & Jetz, 2008).

Previous research has highlighted the necessity of studying multiple geographical and environmental factors simultaneously when analysing species diversity patterns (Qian, 2009; Svenning *et al.*, 2011; Fernández-Goñig *et al.*, 2013). For example, differences in soil fertility are an important driver of species turnover in productive environments (Paoli *et al.*, 2006), but not in harsher ones (Fernández-Goñig *et al.*, 2013), and the importance of climatic factors decreases towards higher latitudes (Qian & Ricklefs, 2007) or with increasing plant cover (Vicente-Serrano *et al.*, 2012). Within-year variability in climatic factors (e.g. annual ranges in temperature or rainfall) has also proven crucial for species turnover (Qian, 2009). However, the effect of variability in soil attributes on species turnover in drylands has not been considered previously. This variability may be especially important because soil properties linked to fertility and hydrology show pronounced spatio-temporal heterogeneity (Schlesinger *et al.*, 1996; Maestre & Cortina, 2002; Wilson & Thompson, 2005), which tends to increase with aridity and with anthropogenic disturbances (D'Odorico *et al.*, 2007).

Here we analyse patterns of beta diversity in global drylands by using a unique data set derived from standardized sampling of 224 dryland sites that differ in contemporary abiotic conditions, recent land use and biogeographical histories (Maestre *et al.*, 2012b). Our study addresses the following five hypotheses:

1. Similar to the latitudinal gradients in species richness and beta diversity observed in other biomes and organisms (Qian & Ricklefs, 2007; Qian, 2009), we predict a strong latitudinal gradient in beta diversity in drylands, with higher species turnover closer to the equator.
2. Because dryland communities with higher plant cover are less sensitive to environmental changes (Vicente-Serrano *et al.*, 2012), we predict strong interactive effects of plant cover and environmental factors (soils and climate) on beta diversity.
3. Because soil and climatic factors may simultaneously affect beta diversity (Fernández-Goñig *et al.*, 2013), we predict a stronger effect of soil attributes in more mesic environments and therefore a stronger effect of climatic factors in more arid environments.
4. Because prominent environmental heterogeneity characterizes drylands (Whitford, 2002), we predict that the temporal (climate) or spatial (soils) variance, as well as the mean, of environmental factors will be important predictors of beta diversity (Qian, 2009).

5. We predict that the environmental drivers of beta diversity may exhibit thresholds, with major shifts in species composition (and hence large changes in beta diversity) above and below these environmental thresholds.

MATERIALS AND METHODS

Study sites and sampling protocol

Field data for this study were obtained from 224 dryland sites established in 16 countries from six continents (Argentina, Australia, Brazil, Chile, China, Ecuador, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, USA and Venezuela; see Table 1 and Appendix S1a in Supporting Information). Drylands are characterized by seasonal climatic extremes and unpredictable rainfall patterns; specifically, they include sites with an aridity index (precipitation/potential evapotranspiration) between 0.05 and 0.65 (Middleton & Thomas, 1997). Although broadly classified as 'drylands', the studied sites encompass a wide range of environmental conditions (66–1219 mm average annual rainfall, -1.8 °C– 27.8 °C annual average temperature, 69–4668 m a.s.l., 3%–83% total plant cover, and more than 25 different soil types according to the FAO world classification; IUSS Working Group, 2006) and vegetation types (grasslands, shrublands and savannahs; see Maestre *et al.*, 2012b for details). All of the sites studied were sampled according to a standardized protocol. At each site, we surveyed 20 contiguous $1.5 \text{ m} \times 1.5 \text{ m}$ quadrats located along four 30-m long transects, each separated by 8 m (80 quadrats per site). Within each quadrat, we counted the number of species present and measured the cover of each perennial plant species. Annual species were not included in our study as their composition in drylands is known to change substantially through the year and among different years (Whitford, 2002). Thus, we did not include them in our observational design to avoid confounding effects in our results derived from sampling 'incomplete' annual communities depending on the time of the year that each site was sampled.

To classify sites into homogeneous regional floras, we performed a neighbour-joining cluster analysis of species composition (Sørensen distances as implemented in PAST 3.01; Hammer *et al.*, 2001) that classified each site into one of 22 floristically distinct groups with less than 20% similarity in species composition among groups (Appendix S1b). These groups corresponded to spatially distinct geographical regions (Table 1, Appendix S1b), encompassing different biogeographical and evolutionary histories. The groups (hereafter regions) ranged from anthropogenically dominated communities in the Mediterranean Basin (Puigdefábregas & Mendizabal, 1998) to relatively unimpacted communities in the Americas or Australia that have nevertheless been heavily influenced by the arrival of exotic species during the last two centuries (Mandrini, 2008; Pucheta *et al.*, 2011; Speziale & Ezcurra, 2011). For each of the 22 regions, we constructed a species \times sites matrix containing the relative abundance of

each species in each site, which was defined as the percentage cover of each species divided by the total percentage cover of plants within a site.

Measurement of soil and climatic variables

Using a stratified sampling design, we sampled the top 7.5 cm of areas of bare ground that were devoid of perennial vascular plants to avoid the well-known effect of 'fertile islands' (Reynolds *et al.*, 1999). Five samples from randomly selected bare ground areas were collected per site. Soil samples were air-dried at room temperature and sieved (< 2 mm fraction). For each sample, we measured pH and the contents of sand, organic carbon, available phosphorus, ammonium and nitrate as described in Maestre *et al.* (2012b) and Delgado-Baquerizo *et al.* (2013). These variables were selected because they are either appropriate surrogates of overall soil fertility and nutrient availability for plants in drylands (carbon, nitrogen and phosphorus variables; Schlesinger, 1996; Whitford, 2002), or they are surrogates of important abiotic variables that control nutrient transformations and availability in soils (e.g. pH; Reth *et al.*, 2005). We used average values of soil variables per site for further analyses.

We also obtained climatic data for each site using WorldClim (<http://www.worldclim.org>; Hijmans *et al.*, 2005). From this database, we extracted the annual mean temperature and rainfall, and their annual ranges (max – min) for each site. These climatic variables were selected because they have been shown to influence beta diversity and other important com-

munity attributes in plants (D'Odorico *et al.*, 2007; Qian & Ricklefs, 2007; Vicente-Serrano *et al.*, 2012). Although the topographic slope (measured in degrees) of each site is not a climatic variable per se, we included it as an additional variable because it is directly related to water retention and radiation incidence (e.g. Mohanty & Skaggs, 2001), and thus importantly affects water availability in dryland vegetation (e.g. Reisner *et al.*, 2013). To quantify the potential effects of variability in soil and climate variables on beta diversity, we calculated for each of the 22 regions the coefficient of variation of each environmental variable from the mean and the variance of all sites per region.

Analysis of community structure

Despite renewed interest in the analysis of patterns of beta diversity, there is still no agreement on a single best measure of beta diversity. Different metrics do not always yield consistent results, and the use of multiple complementary metrics has been recommended (Tuomisto, 2010; Anderson *et al.*, 2011). Therefore, we calculated several complementary metrics of beta diversity, including the number of rare species (single site occurrence records), the classic Whittaker (1972) metric of beta diversity, and beta diversity metrics directly related to environmental gradients (species turnover *sensu* Vellend, 2001; or directional metrics *sensu* Anderson *et al.*, 2011), based on both species abundance and species incidence.

We assessed the degree of floristic distinctness of every site within each of the 22 regions using the average degree

Table 1 Basic plant community parameters of 22 regional drylands encompassing the 224 sites studied.

Region	Longitude centroid	Latitude centroid	<i>n</i>	Species	<i>S</i> _{estim}	α	FR	$\beta(W)$	$\beta(R^2)$
Argentina North	-67.4	-31.5	6	26 ± 3.0	43	9.3	0.12	0.64	0.29
Argentina Pampa	-65.8	-38.4	6	74 ± 4.3	75	26.7	0.17	0.61	0.45
Argentina South	-70.4	-41.2	6	46 ± 4.5	50	18.0	0.17	0.55	0.3
Australia Central	142.5	-34.1	12	39 ± 2.5	75	15.7	0.04	0.39	0.03
Australia East	146.7	-31.7	6	76 ± 7.9	105	29.8	0.14	0.6	0.2
Brazil	-40.9	-10.7	6	83 ± 13.5	107	24.0	0.17	0.81	0.76
California	-115.8	33.8	6	13 ± 1.0	43	9.5	0.02	0.15	0.01
Chile Coast	-71.4	-30.2	12	45 ± 2.6	94	13.2	0.06	0.68	0.62
Chile Inland	-71.3	-33.3	6	15 ± 2.8	27	5.3	0.17	0.49	0.33
China	117.4	49.0	6	67 ± 3.0	69	29.7	0.16	0.42	0.29
Ecuador	-79.5	-4.0	16	37 ± 2.8	47	14.1	0.02	0.49	0.25
Iran	57.8	37.2	3	35 ± 4.6	37	16.3	0.43	0.69	0.56
Israel	34.7	31.3	12	8 ± 1.9	18	3.9	0	0.45	0.24
Kenya	37.2	0.5	2	38 ± 13.0	44	22.0	0.54	0.73	0.34
Mexico	-101.2	22.7	11	96 ± 9.0	129	14.6	0.24	0.78	0.77
Morocco	-3.0	34.1	12	48 ± 2.5	72	9.3	0.13	0.71	0.29
Peru	-71.3	-16.3	11	18 ± 2.3	39	5.2	0.1	0.49	0.18
Spain	-2.5	39.3	53	169 ± 8.0	269	16.8	0.05	0.72	0.15
Tunisia	9.8	34.6	10	47 ± 4.1	63	10.2	0.15	0.71	0.31
Utah	-110.9	37.5	10	48 ± 2.9	69	10.6	0.25	0.69	0.55
Venezuela East	-65.1	8.2	6	36 ± 4.4	43	14.0	0.18	0.56	0.3
Venezuela West	-69.8	9.8	6	27 ± 2.0	34	11.2	0.11	0.53	0.51

n, number of sites; Species, observed species richness ± standard deviation; *S*_{estim}, estimated species richness; α , average species richness per site; FR, average frequency of singletons per site; $\beta(W)$, average Whittaker beta diversity; $\beta(R^2)$, species turnover among sites within each region.

of species dissimilarity of a given site in relation to all other sites within its region. Dissimilarity was measured using two different metrics: first, we calculated the average value of the Sørensen coefficient J for each pair of sites within each region. We used the respective complement [$\beta(W) = 1 - J$], which is equivalent to Whittaker's index of species turnover (Whittaker, 1972) and has the advantage of being normalized in the range of zero (no beta diversity) to one (maximum beta diversity). However, this metric does not identify any spatial gradient in species turnover. For an additional metric of floral distinctness, we calculated the proportion of species per site that did not occur in any other site within the same region ('frequency of singletons', FR hereafter). We used this metric because: (1) most species in local assemblages are uncommon, and therefore rare species are an important part of the diversity of natural communities (Cowling *et al.*, 1996; Kunin & Gaston, 1997); and (2) rare species may be more sensitive to environmental change than dominant and generalist species (Thomas, 1994; Blois *et al.*, 2013), and therefore their responses to such changes deserve special attention.

Ulrich & Gotelli (2013) proposed a directional index of beta diversity based upon the correlation in species incidences among spatially contiguous sites [hereafter $\beta(R^2)$]. This beta diversity metric measures how close species incidences are arranged along the left to right matrix diagonal after the incidence matrix has been sorted according to the dominant eigenvalues of a correspondence analysis (Ulrich & Gotelli, 2013). This sorting represents the minimal species overlap among sites, and thus the maximal spatial turnover (Ulrich & Gotelli, 2013). The metric is calculated as the squared coefficient of correlation between the row and column ranks of species in the ordered matrix. Note that in our multivariate comparisons of sites, $\beta(R^2)$ takes identical values for each site within a given region.

The three incidence-based metrics [$\beta(R^2)$, $\beta(W)$ and FR] were not influenced by sampling intensity (all correlations of metric and number of sites per region $r < 0.2$), and were only moderately intercorrelated [$r(\beta(R^2) - \beta(W)) = 0.41$, $r(\text{FR} - \beta(W)) = 0.37$, $r(\beta(R^2) - \beta(W)) = 0.38$]. Hence, they capture different aspects of species turnover.

The relative abundance and evenness among co-occurring species may also play a crucial role in the dynamics and functioning of plant communities (Wilsey & Polley, 2004; Hillebrand *et al.*, 2008). Therefore, to take into account changes in composition other than species identity, we analysed an abundance-weighted species turnover metric [$\beta(\text{MV})$] and used a multiple regression model of climate and soil predictors with the dominant eigenvector of the Bray–Curtis dissimilarity matrix of the species \times sites cover data as the response variable. This eigenvector captures the differences in species abundances among sites and therefore also the variation in plant composition across specific environmental gradients (see Anderson *et al.*, 2006, 2011, for a similar approach).

Statistical analyses

We evaluated the separate effects of soil fertility, climatic variables and topographic slope on $\beta(W)$, $\beta(R^2)$ and FR using multiple ordinary least squares (OLS) regressions, as implemented in SAM 4.0 (Rangel *et al.*, 2010). To account for nonlinear latitudinal trends, we included latitude and latitude² into the models. Because $\beta(W)$, $\beta(R^2)$ and FR were moderately spatially autocorrelated (Moran's $I < 0.5$), we also included the eigenvector with the largest eigenvalue (the dominant eigenvector) of the associated geographical (latitude and longitude) distance matrix as an additional predictor variable (Hawkins, 2012). This eigenvector explained 84% of total variance in the geographical distance matrix, and captured mainly the coarse-grain spatial structure of the study sites. All other eigenvectors explained less than 15% of the variance and were not significant when included in regression analyses. To control for differences in geographical extent (area) of the study regions, we also used the maximum distance between the sites within each region as an additional explanatory variable. Correlation coefficients among the climate, soil, species richness and spatial predictors introduced in the multiple regressions were nearly always < 0.60 (variance inflation factor < 3); thus multicollinearity was unlikely to affect the results (Appendix S2). Although mean annual rainfall and rainfall variability were strongly correlated ($r = 0.84$, cf. Appendix S2), we nevertheless included both of these potentially important climate variables into the models. None of the regression models was significantly affected by non-normal error structures (Kolmogorov–Smirnov tests) and autocorrelation (Durbin–Watson tests).

Because species richness directly influences beta diversity (Cowling *et al.*, 1996; Kraft *et al.*, 2011), we used observed species richness as additional covariate in all OLS regressions. We also estimated asymptotic species richness per site using the first-order jackknife (Smith & van Belle, 1984). However, observed and extrapolated richness among sites were highly linearly correlated ($r = 0.92$, $P < 0.0001$, data not shown) and consequently the results did not change qualitatively when using asymptotic species richness as the covariate. Therefore, we used simple counts of species per site ('species density', *sensu* Gotelli & Colwell, 2001) in all analyses.

Individual environmental variables, and interactions among multiple variables, are known to affect ecological patterns. For example, dryland plant communities with cover $< 30\%$ are more sensitive to environmental changes than those with cover $> 30\%$ (Vicente-Serrano *et al.*, 2012). Other studies have suggested that soil and climatic factors interact to determine patterns of beta diversity in dryland plant communities (Fernández-Goñig *et al.*, 2013). Therefore, in a subsequent set of OLS regressions, we included multiplicative soil \times cover, climate \times cover, and soil \times climate \times cover interaction terms as potential predictor variables.

Given the large number of main effects and possible interactions, we used a principal components analysis (PCA) to reduce the number of climatic predictors included in the analyses. The first two components of this PCA explained 99% of the variance in climatic data, and loaded highest for annual temperature range, rainfall and annual rainfall range (component 1), and for annual mean temperature (component 2). We also reduced soil variables to two PCA components, which collectively explained 72% of the variance in soil data. The first component of this PCA was related to sand and organic carbon content, whereas the second component was related to available nitrogen and ammonium. These four PCA components, together with interaction terms for cover, climate (PCA components 1 and 2) and soil (PCA components 1 and 2), were used as predictors in a second OLS model.

Finally, we conducted separate regression tree analyses (De'ath & Fabricius, 2000) using each of the presence/absence beta diversity metrics [$\beta(W)$, $\beta(R^2)$, FR] as the dependent variables, and the spatial eigenvector and the measures of soil fertility, climate and topographic slope (15 predictors in total) as the predictor variables. Regression trees are a flexible technique with relatively few analytical assumptions that allowed us to: (1) evaluate the presence of thresholds in species turnover; and (2) identify region-specific responses to environmental predictors. We used 10-fold cross-validation to fit the most parsimonious model to each dataset (De'ath & Fabricius, 2000). Regression tree analyses were performed with the `TREE` package in R (B.D. Ripley: <http://cran.r-project.org/web/packages/tree/tree.pdf>).

RESULTS

The 22 regional floras identified by the neighbour-joining analysis differed widely in average species richness per site and beta diversity (Table 1). Alpha diversities were lowest in Israel (average of 3.92 species per site) and highest in eastern Australia (29.83 species per site). Observed regional species richness varied between 8 species (Israel) and 169 species (Spain) (Table 1) and was typically below 100 species except for the Spanish sites. The percentage of singletons ranged from 0% (Israel) to 54% (Kenya), with a median of 7% singletons within the 22 regions (Table 1).

Of the different beta diversity metrics, $\beta(W)$ and $\beta(R^2)$ significantly decreased with distance to the equator (Table 2). Latitude explained 7% and 9% of variance in $\beta(W)$ and $\beta(R^2)$, respectively. FR and $\beta(MV)$, instead, did not show any significant latitudinal gradient (Table 2). Soil and climate variables had significant effects, but their importance depended on the beta diversity metric considered (Fig. 1). Soil pH, phosphorus, ammonium, organic carbon and sand content explained 14%, 7%, 7% and 14% of the variation in FR, $\beta(W)$, $\beta(R^2)$ and $\beta(MV)$, respectively (Fig. 2). A higher availability of phosphorus and higher soil pH generally increased beta diversity, while higher ammonium concentrations or sand contents generally decreased beta diversity (Fig. 1).

The coefficient of variation of rainfall was positively correlated with all metrics of beta diversity (Fig. 1), indicating more variable community composition in more variable environments. With respect to species composition and turnover, relatively homogeneous communities (lower beta diversity) were found in drier sites (Fig. 1). Temperature variation increased FR and $\beta(MV)$, but decreased $\beta(W)$ (Fig. 1). Overall, higher beta diversity was correlated with higher temperature (Fig. 1).

Regions with higher species richness or plant cover generally showed higher beta diversity, although these predictors explained less than 6% of the variation. The exception to this general pattern was $\beta(W)$, which decreased at higher species richness (Table 2, Fig. 1). This metric was also the most sensitive to the extent of the region studied; larger regions showed substantially higher values of $\beta(W)$ (Figs 1 & 2).

Apart from the effect of average climate and soil variables, the coefficient of variation in some soil variables (values obtained at the regional, not at the site level) was positively correlated with beta diversity (Fig. 3). In particular, $\beta(W)$ and $\beta(R^2)$ increased with variability in soil organic carbon and pH (Fig. 3), whereas the relationship with FR was never significant ($P > 0.1$).

In multiple regressions that included interaction terms among the predictor variables (Fig. 4), we found weak soil \times climate interaction effects on FR and $\beta(W)$, but not on $\beta(R^2)$ and $\beta(MV)$. These interactions revealed a positive joint influence of precipitation variability and soil sand content on the fraction of singletons, and a weaker positive joint effect of soil nitrogen content and average precipitation on $\beta(W)$. However, these interactions explained less than 5% of variance in FR and $\beta(W)$. The interactions between the environment (soil and climate PCA components) and cover were also typically weak (Fig. 4). The only exceptions were the interactions between cover and soil sand content (component 1) and nitrogen content (component 2) that significantly affected $\beta(R^2)$.

Table 2 Beta values of ordinary least squares regression of four metrics of species turnover versus latitude and latitude² for plants at 224 sites in 22 regional drylands worldwide. The dominant spatial eigenvector, spatial extent of each region, and observed species richness served as additional covariates.

Variable	FR	$\beta(W)$	$\beta(R^2)$	$\beta(MV)$
Latitude	0.03	0.06	-0.13	-0.12
Latitude ²	-0.12	-0.46***	-0.49***	0.14
Spatial eigenvector	0.09	-0.06	0.18**	0.06
Extent	0.07	0.96***	0.47***	-0.17
Species	0.29***	-0.14**	0.03	0.02
R^2 (model)	0.08	0.57	0.28	0.04
P (model)	0.002	< 0.001	< 0.001	> 0.05

FR, fraction of singletons; $\beta(W)$, average Whittaker score; $\beta(R^2)$ species turnover; $\beta(MV)$, squared r of abundance weighted turnover. ** $P < 0.01$, *** $P < 0.001$.

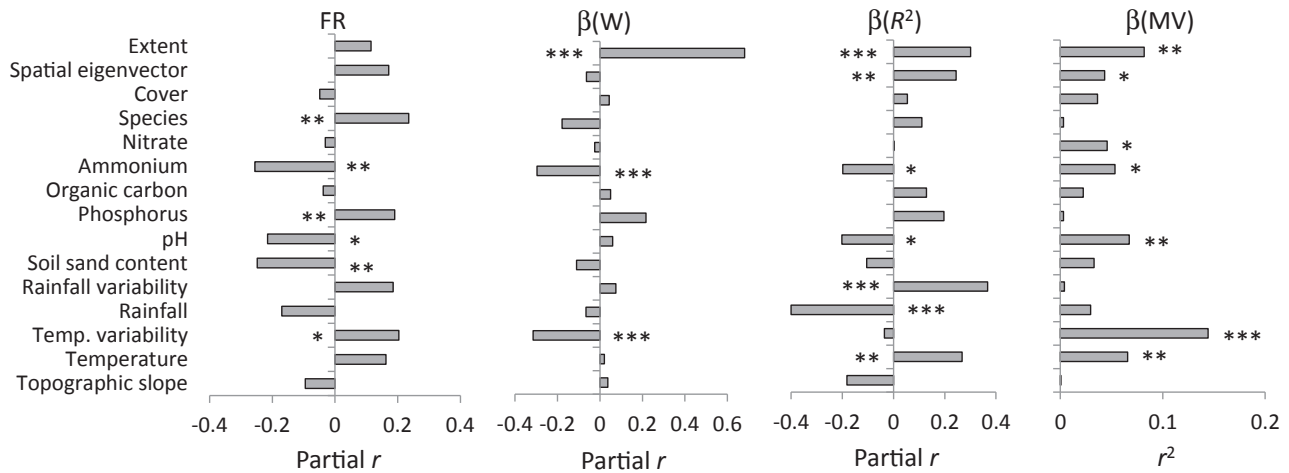


Figure 1 Partial correlation coefficients r of the fraction of singletons (FR) at each dryland study site ($n = 224$), and average Whittaker score ($\beta(W)$), species turnover ($\beta(R^2)$) and squared r of abundance weighted turnover ($\beta(MV)$) of plants within each region with geographical, climatic and soil variables as well as species richness, the dominant spatial eigenvector of the geographical distance matrix, and spatial extent of sites. Bonferroni corrected significance levels refer to the associated ordinary least squares multiple regression using all variables. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Total explained variances: FR: 0.29; $\beta(W)$: 0.61; $\beta(R^2)$: 0.42; $\beta(MV)$: 0.31, all with P -values < 0.001 .

Regression tree analysis revealed that the response of non-directional beta diversity metrics [$\beta(W)$ and the percentage of rare species (FR)] to soil variables varied widely depending on the region studied (Fig. 5). For example, FR was affected by soil variables in China, Kenya, Australia, Argentina and the United States (those with spatial eigenvector values > 0.55 ; Fig. 5), but not in the other 13 regions studied. In contrast, $\beta(W)$ was affected by soil characteristics in only three of the studied regions (organic C in the United States, and pH in Australia and China). The directional species turnover metric [$\beta(R^2)$] showed less idiosyncratic results. Irrespective of region, climatic variables, particularly rainfall (negative effect) and annual temperature variability (positive effect), were the strongest correlates of $\beta(R^2)$. Regression tree analysis (Fig. 5) and pairwise comparisons showed that $\beta(W)$, and particularly $\beta(R^2)$ were significantly higher among sites receiving < 178 mm of rainfall than among sites receiving > 178 mm [one-way ANOVA: both P -values < 0.03 ; $\beta(R^2)$: $n = 22$; $\beta(W)$: $n = 224$]. Species turnover was also highest among sites with higher annual temperature variability (where the difference between maximum and minimum temperature was > 23 °C; Fig. 4).

DISCUSSION

Latitudinal gradients in dryland beta diversity

Strong latitudinal gradients in species richness and beta diversity have been previously observed in plant and animal assemblages (Koleff *et al.*, 2003; Hawkins & Diniz-Filho, 2004; Qian & Ricklefs, 2007; Qian *et al.*, 2013). These patterns are commonly explained by contemporary climate gradients in both hemispheres of decreasing temperature and

increasing seasonality from the equator towards higher latitudes (Janzen, 1967; Lomolino *et al.*, 2006; Buckley & Jetz, 2008; Brown, 2014). As predicted by our first hypothesis, we found a significant increase in $\beta(W)$ and $\beta(R^2)$ at lower latitudes (Table 2) in line with the findings of Qian & Ricklefs (2007). However, we did not find significant latitudinal trends in the fraction of singletons and the abundance weighted turnover (Table 2). Therefore the interpretation of observed latitudinal patterns in beta diversity can depend on metric choice, reinforcing the importance of using multiple metrics.

These relatively weak effects of latitude on beta diversity in comparison with previous studies might be explained by

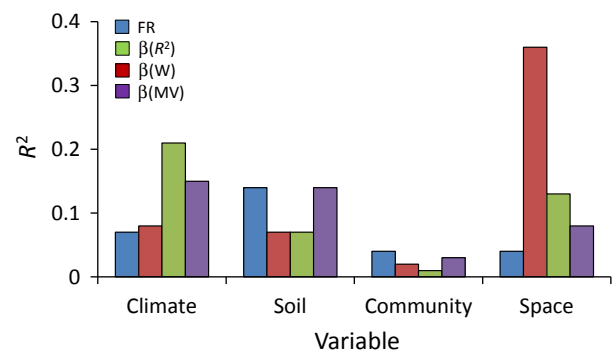


Figure 2 Variance partitioning of the ordinary least squares (OLS) regression model of Fig. 1 for climate, soil, plant community (species richness, cover), and spatial (dominant spatial eigenvector, spatial extent) variables as predictors of the fraction of singletons (FR), Whittaker diversity ($\beta(W)$), species turnover ($\beta(R^2)$), and abundance weighted species turnover ($\beta(MV)$) at 224 sites in 22 dryland regions worldwide.

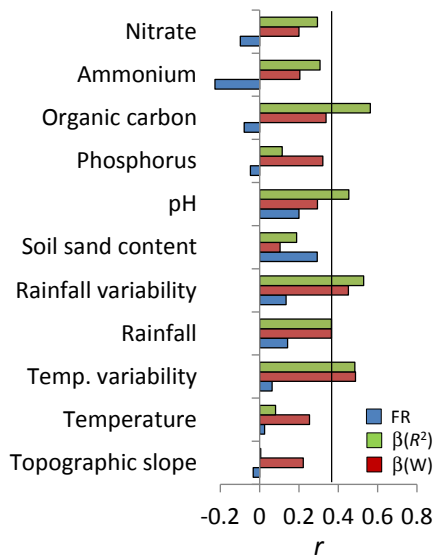


Figure 3 Variability in climate and soil variables (measured by the coefficient of variation) was generally positively correlated (Pearson's r) with the fraction of singletons (FR), Whittaker diversity ($\beta(W)$), species turnover ($\beta(R^2)$) of plants in the dryland sites. The vertical line shows the parametric two-sided 5% significance level.

the variable relationships between important environmental factors and latitude in our database. Although temperature variability decreased towards the equator at these sites ($r^2 = 0.68$; $P < 0.001$; data not shown), rainfall variability showed the opposite trend, and was greater in tropical than

in temperate drylands ($r^2 = 0.42$; $P < 0.001$; data not shown). Rainfall variability plays an important role in defining plant species turnover (e.g. Qian & Ricklefs, 2007), and the higher values found at latitudes close to the equator may well explain the lack of strong latitudinal trends in beta diversity of dryland plants. In spite of this, there was an increase in beta diversity in drylands with higher variability in rainfall and temperature (Fig. 5), as predicted by our fourth hypothesis. These findings agree with previous studies conducted with animals (Buckley & Jetz, 2008; Qian, 2009; Svenning *et al.*, 2011) and North American vascular plants (Qian & Ricklefs, 2007), and may indicate a general pattern of increasing beta diversity in more climatically variable environments, regardless of whether or not these environmental factors follow a latitudinal trend.

Effects of soil, climate and vegetation cover on dryland beta diversity

Our results suggest that climatic and soil predictors may act on components of beta diversity [soil: rare species (FR) and beta diversity metrics ($\beta(W)$); climate: directional species turnover ($\beta(R^2)$], hence independently contributing to changes in plant composition among regions (Fig. 1). The focus of environmental management and monitoring actions, therefore, will depend on the particular community attributes of interest. For example, the generally negative effects of nutrient availability on the fraction of rare species (FR) agree with previous findings (Scholes, 1989; Fernández-Goñi *et al.*, 2013), and indicate that rarity in drylands may be

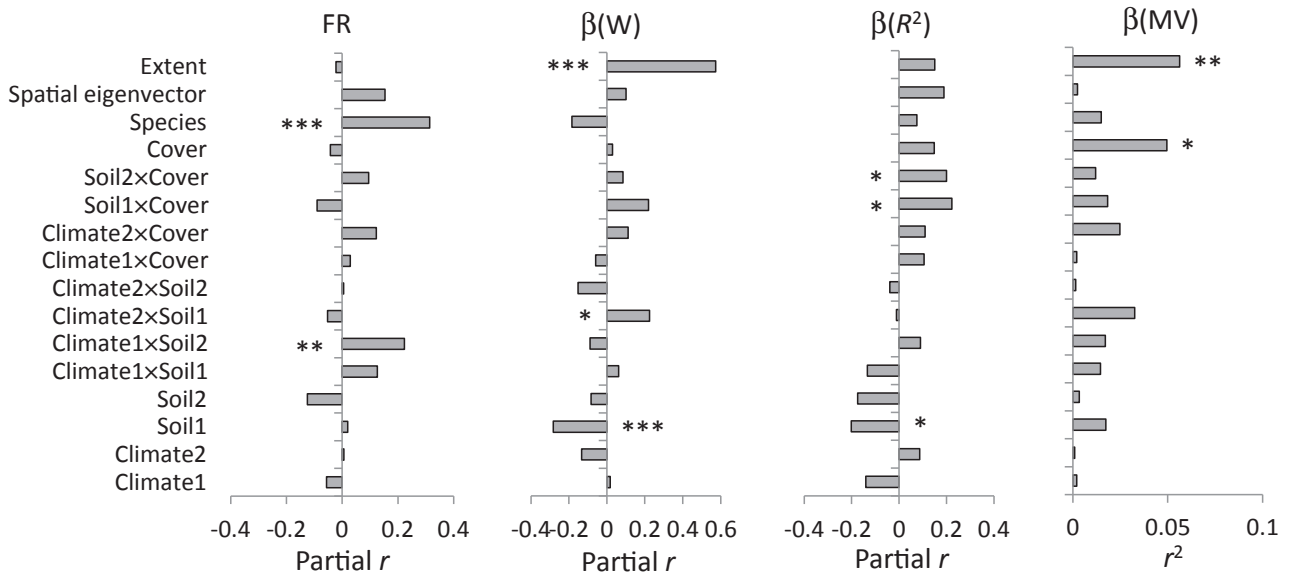


Figure 4 Partial correlation coefficients (r) of the fraction of singletons (FR) at each dryland study site ($n = 224$), and average Whittaker score ($\beta(W)$), species turnover ($\beta(R^2)$) and squared r of abundance weighted species turnover ($\beta(MV)$) of plants within each region for the first two eigenvectors of climatic and soil variables, their first order multiplicative interaction terms, as well as species richness, the dominant eigenvector of the geographical distance matrix, and spatial extent of sites. Bonferroni corrected significance levels refer to the associated ordinary least squares multiple regression using all these variables: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Total explained variances: FR: 0.23; $\beta(W)$: 0.56; $\beta(R^2)$: 0.35; $\beta(MV)$: 0.22, all with $P < 0.001$.

more related to reduced soil fertility than to climatic factors per se.

Interestingly, we found that the fraction of rare species increased with P availability and diminished with ammonium content. Sites with high N:P ratios may reflect more disturbance from grazing or domination by a few nitrogen-fixing or abundant species (Suding *et al.*, 2005; Riginos *et al.*, 2009). In such cases, rare species may be excluded, either by shifts in N:P ratios (Suding *et al.*, 2005) or by competition from dominant species that respond strongly to enhanced fertility and might monopolize limited phosphorus (Riginos *et al.*, 2009; Dawson *et al.*, 2012).

Rare species play a crucial role for several ecosystem attributes and functions, including the resistance to invasions by exotic species (Lyons & Schwartz, 2001) and the maintenance of high functional diversity (Mouillot *et al.*, 2013). Future research should aim to assess whether the loss of ecosystem functioning in drylands resulting from desertification, and its associated loss of ecosystem services (Safriel & Adeel, 2005), might be buffered by a greater proportion of rare species under such less fertile conditions, or might be exacerbated by the strong changes in species composition that we observed under more arid and variable environments.

Previous studies have reported that low soil fertility can increase species turnover under benign, but not under harsh, environmental conditions (Paoli *et al.*, 2006; Fernández-Goñig *et al.*, 2013). Similarly, sites of low plant cover (< 30%) are more sensitive to environmental change than those with higher cover (Vicente-Serrano *et al.*, 2012). We expected, therefore, to detect strong climatic, soil and cover interactions on our metrics of beta diversity. However, we found relatively weak evidence for such interactions in the best-fitting multiple regression models (Fig. 4), and no interactions among soil and climatic factors in the regression trees, which were dominated by either soil or climatic variables depending on the metric analysed (Fig. 5). Our results suggest, instead, that both soil and climate are important drivers of beta diversity, but that they act independently of one another and affect separate aspects of beta diversity.

Several potential mechanisms might explain this lack of effect of the soil \times climate or cover \times soil \times climate interactions. First, soil \times climate interactions have been found to be important for species turnover in drylands when soil types differ markedly in biogeochemistry (e.g. serpentine and non-serpentine soils; Fernández-Goñig *et al.*, 2013). Interactions are thus less likely to be important when comparing fertility levels within similar soil types, which is supported by the relatively weak soil \times climate interactions for the frequency of singletons, $\beta(R^2)$ and $\beta(MV)$ (Fig. 4). Second, decreasing plant cover might affect the sensitivity of dryland plant communities to environmental changes within the same vegetation type or within a given region (Vicente-Serrano *et al.*, 2012), but this effect seems to wane when mixing a variety of habitat

types and biogeographical regions. Overall, our results suggest that these cover \times environment and climate \times soil interactions, known to be important at the regional level, might be less important at the global scale. We note that our sampling design focused on rainfall gradients within the same soil type and land use within each region, which could reduce the possibility of detecting soil \times climate or cover \times environment interactions at regional scales. However, the high variability in both soil types and land uses covered globally should suffice to reveal such interactions if they were important.

Threshold effects on beta diversity

Regression tree analysis (Fig. 5) and bivariate comparisons identified a clear threshold in annual rainfall as a driver of change in community composition. Regardless of region or soil characteristics, areas with annual rainfall below 178 mm have higher beta diversity among sites than more mesic regions (Fig. 5). These results suggest that the expected increase in aridity may be especially relevant for plant communities in sites that currently are just above the 178 mm rainfall value. It is likely that only a few drought-tolerant species will be able to live under such conditions (see also Fernández-Goñig *et al.*, 2013). Species-poor assemblages are sensitive to the invasion of new species and to local extinctions caused by disturbances (i.e. drought or overgrazing in already water-stressed environments; e.g. Vicente-Serrano *et al.*, 2012). This might cause the replacement of one assemblage of drought-tolerant species by another, therefore increasing species turnover under extremely arid conditions (but see Fernández-Goñig *et al.*, 2013). Further empirical and modelling studies are, however, needed to confirm our hypothesis that species turnover and, therefore, community composition change for those communities that cross the 178 mm threshold.

Beta diversity metrics and regional responses to environmental factors

Effects of environmental conditions (especially soil attributes) on FR and $\beta(W)$ were highly idiosyncratic, and the results depended on the region studied (Figs 1 & 5). This pattern reflects interactions between the spatial filters and environmental conditions, in accordance with previous findings for species richness (Qian & Ricklefs, 2007). The only consistent pattern was that regions with higher gamma diversity (Table 2) or variability in soil or climatic attributes (Fig. 5) showed a higher proportion of rare species and non-directional species turnover. This finding corroborates a large recent study that showed that gradients in beta diversity when measured by $\beta(W)$ co-vary with gradients in gamma diversity (Kraft *et al.*, 2011).

We also demonstrated that different metrics of beta diversity are necessary to fully understand the effects of environmental and geographical factors on plant communi-

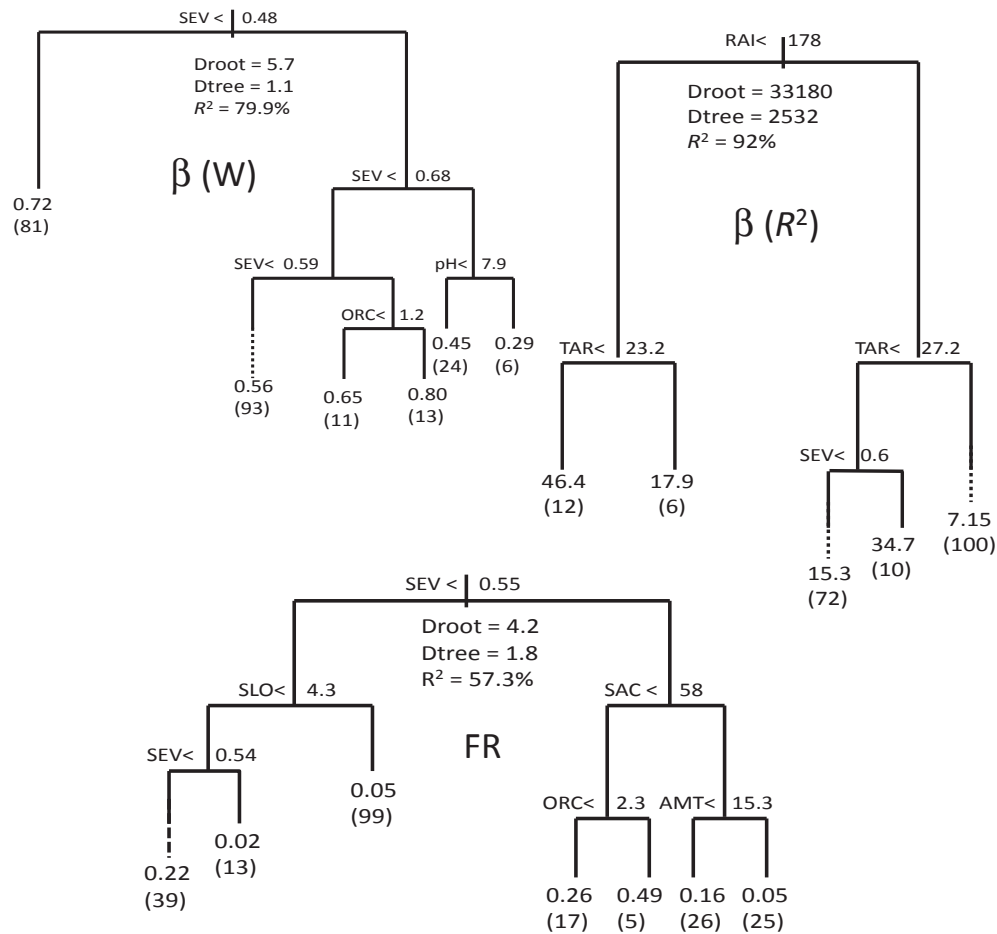


Figure 5 Regression tree results for the three presence–absence species turnover metrics of plants in the dryland study sites ($n = 224$): proportion of singletons (FR), Whittaker's beta diversity metric ($\beta(W)$) and directional species turnover ($\beta(R^2)$). These trees show thresholds in the predictors that best define homogeneous sets of the response variables: left branches are those in which the condition is satisfied (i.e. the predictor is below the given threshold), right branches are those in which the condition is not satisfied. Average values of the response variable for each homogeneous subset are given at the end of each branch, with the number of samples in brackets. The residual (Droot) and final deviance (Dtree), together with the total amount of variance explained (R^2), are given with each tree. Abbreviations are: SEV, spatial eigenvector; SLO, topographic slope; SAC, sand content; ORC, organic C; AMT, annual mean temperature; RAI, annual rainfall; TAR, temperature annual range. Discontinuous lines mean that there are more branches but they are not shown for simplicity. Full results are given in Appendix S1c.

ties (Tuomisto, 2010; Anderson *et al.*, 2011). In this respect, some metrics were more robust than others and therefore more recommendable to extract general conclusions. $\beta(W)$ was most sensitive to the geographical extent. The fraction of singletons, although more informative, necessarily decreases with increasing gamma diversity, which may also prevent its general use. $\beta(R^2)$, instead, was best able to identify environmental covariates and was more robust to region-specific idiosyncrasies. Therefore, we recommend this metric for comparative studies. Finally, β (MV) effectively measured the effects of the environmental conditions on abundance weighted beta diversity and might be the most integrative measurement available to date (see also Anderson *et al.*, 2011; Fernández-Goñi *et al.*, 2013).

CONCLUDING REMARKS

Beta diversity is a fundamental component of diversity and an important attribute by which to assess the response of communities to environmental changes (Buckley & Jetz, 2008; Kraft *et al.*, 2011; Blois *et al.*, 2013). Surprisingly, few studies have focused on beta diversity across global scales (Gaston *et al.*, 2007; Buckley & Jetz, 2008), and the present study is, to our knowledge, the first global assessment of patterns in dryland beta diversity. Our analyses indicate that soil fertility and, particularly, variability in temperature and rainfall are the most important predictors of beta diversity in global drylands, dominating simple latitudinal gradients or interactions among other factors. The results are central to efforts aimed to understand the effects of environmental

change in drylands, which constitute one of the largest biomes on Earth.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional methodological details and results: (a) maps of the 224 study sites of the global dryland survey, (b) neighbour-joining classification, and (c) full results of the regression trees.

Appendix S2 Correlation matrix of environmental variables.

BIOSKETCH

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