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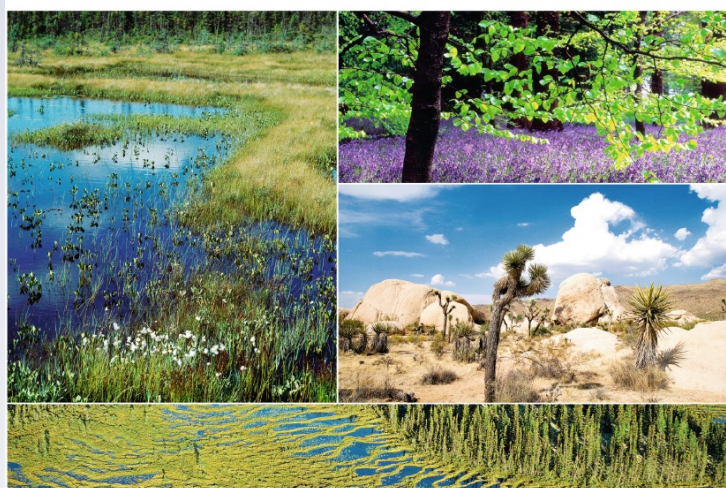
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Multiple processes at different spatial scales determine beta diversity patterns in a mountainous semi-arid rangeland of Khorassan-Kopet Dagh floristic province, NE Iran

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Abstract The study of local and regional mechanisms driving spatial patterns in beta diversity is essential to the understanding of biodiversity. We aimed to predict the roles of multiple mechanisms operating at regional to fine spatial scales in structuring the beta diversity in a mountainous semi-arid rangeland of the Khorassan-Kopet Dagh floristic province located in NE Iran. We evaluated the relative contributions of three main filters, at the regional (stochastic but spatially structured dispersal filter), local (abiotic filter), and fine (biotic filter) spatial scales on beta diversity across communities. We

partitioned beta diversity constrained by spatial, environmental, and biotic variables in 23 communities studied here, and used simple RDA and RDA-based variation partitioning to assess the contributions of studied filters on beta diversity. Moreover, spatial autocorrelation analyses were used to test neutral theory predictions. The relative contributions of the studied ecological filters explained 55% of variation in beta diversity. Although differences in the explained variations between unique fractions are low, the abiotic and biotic filters (signifying the niche-based processes) represent stronger effects directly and indirectly (via impact on significantly of other ecological filters) than dispersal (signifying neutral processes) on beta diversity. In addition, 45% of the variation in beta diversity was not explained by the studied ecological filters. In conclusion, independent and shared impacts of processes at different spatial scales determine beta diversity in our plant communities. However, unexplained variation in beta diversity requires further study of other facets of biodiversity and community assembly processes.

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Keywords Multiple processes · Spatial scales · Beta diversity patterns · Biotic filter · Abiotic filter · Dispersal filter

Introduction

Identifying the mechanisms controlling community diversity has been a particularly important challenge in ecology (Gotelli and Graves 1996). Central to this challenge is the evaluation of the relative contributions of processes operating at distinct spatial scales and their influences on variation in community structure, termed as a type of beta diversity (Harrison et al. 1992; Lennon et al. 2001; Soininen et al. 2007; Mayfield and Levine 2010; Anderson et al. 2011; Shipley 2015). Several theories of community assembly, such as neutral theory and niche-based environmental filtering, suggest that regional, local, and fine-scale factors generate beta diversity in terrestrial ecosystems (Qiao et al. 2015; Mori et al. 2015; Tello et al. 2015). The effects of different filters at one or more specific spatial scales are due to geographic variation in ecological attributes of species in regional species pools that often cause idiosyncratic community responses of communities. Therefore, significant variations in community structures along specific ecological filters are related to the presence of key species (i.e., species that strongly respond to ecological filters) in the species pool. If an ecological filter influences species composition of plant communities at the regional scale, the responses of entire communities to ecological filters are contingent upon environmental affinities of species in the regional pool (Lessard et al. 2012; Myers et al. 2013). Although a deeper understanding of processes shaping beta diversity is required, environmental and spatial factors, nonetheless, have been frequently assessed as the primary determinants of diversity patterns (Lin et al. 2013; Qiao et al. 2015; Yang et al. 2015). The effects of environmental and spatial factors working in conjunction with fine-scale factors such as biotic interactions have rarely been evaluated on beta diversity (Rajaniemi et al. 2009; Soliveres et al. 2012). Thus, the relative contributions of dispersal limitation, abiotic filtering, and biotic filtering remain unknown (Verdú et al. 2009).

In order to assess the effects of multiple filters acting hierarchically at multiple spatial scales on beta diversity, some recent studies introduced mountainous rangeland ecosystems as natural laboratories for investigation (Moura et al. 2016; Soliveres et al. 2012). Several important factors, such as environmental severity, heterogeneous topography, and the

presence of cushion plants, make mountainous rangelands particularly suitable ecosystems for this investigation (Farzam and Ejtehadi 2016). Topographical factors operating at local scales may be particularly important in mountainous rangelands because climate varies strongly with elevation, and so mountainous rangelands often encompass a large climatic range within a small geographical extent. The direct effects of climatic variables (Stein et al. 2014), and indirect effects of elevation on species composition may be large and important (Moura et al. 2016). Annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality are important climatic variables that affect plant distributions (Qian et al. 2017). In addition, strong elevational gradients in mountainous terrain can represent a serious barrier to dispersal. Other topographic variables such as slope aspect may yield differentiation in species composition through the interacting impacts of solar radiation and the duration of snow-free periods on the length of the effective growing season (Lopez-Angulo et al. 2018). In addition, soil quality as another local scale factor may affect large-scale patterns in diversity by enhancing primary productivity and producing heterogeneity in habitats (Miranda et al. 2011). However, abiotic filters operating at the local scale can alter the roles of dominant cushion plants as biotic filters in plant communities (Luzuriaga et al. 2012).

Biotic interactions, such as the facilitation and competition provided by perennials in the role of nurse plants, are important factors impacting community composition at fine spatial scales. Perennial plants usually ameliorate harsh microclimatic conditions under their canopies (Maestre et al. 2003) and improve soil fertility (Cortina and Maestre 2005), and the differences in composition between open/cushion patch types usually increase under more severe environmental conditions (Callaway et al. 2000; Badano and Cavieres 2006). In the same way as climate conditions, soil nutrients, and topography act as environmental filters at the local scale, the amelioration of microhabitats by cushion plants as biotic filters operating at fine spatial scales can also be important to diversity (Soliveres et al. 2012). In addition to the role of perennial plants as biotic filters, biotic interactions among plants such as competition and facilitation may influence plant community diversity, especially in stressful environments (Callaway 2007; Brooker et al. 2008). The interplay

between biotic interactions together and with main environmental factors can influence significantly on factors on community structure and on determination of final beta diversity patterns in mountainous rangeland communities (Cavender-Bares et al. 2009; Pausas and Verdú 2010).

Although processes related to local and fine spatial scales can largely affect diversity patterns of semi-arid communities, processes operating at the regional scale, such as dispersal from the species pool, can also play crucial roles driving community diversity patterns (Ricklefs 2008). Studies suggest clear positive spatial autocorrelations resulting from neutral dynamics and dispersal limitation (Pashirzad et al. 2018; Qian et al. 2017; Dray et al. 2010). Although neutral dynamics may generate significant spatial variation in ecological communities, observed variation can also be explained by unmeasured spatially structured environmental variables. Therefore, the correct recognition of dispersal limitation on diversity patterns requires the incorporation of spatially variable environmental factors in a spatially explicit model based on genetic differentiation models (Velend 2010). Dispersal limitation affects community dynamics and promotes species coexistence near range-limits through the decreasing presence of species in otherwise unsuitable locations, and the expansion of range limits. Consequently, variation in community structure is enhanced, with multiple species cannot coexist due to dispersal limitations (Weinstein et al. 2017). However, dispersal limitation at the regional scale can be balanced by biotic filters at fine spatial scales and heterogeneity produced by soil quality in plant communities at local spatial scales (Luiz et al. 2016). Biotic interactions such as facilitation in more severe environments can expand the niche of dispersed species via amelioration of micro-habitat conditions. However, expansion and contraction of species niches relate to the availability of resources (i.e., abiotic filters) (Pashirzad et al. 2019; Luzuriaga et al. 2012). Therefore, the interplay between neutral factors at the regional scale, and abiotic and biotic filters at the local and fine scales, respectively, can influence final diversity patterns across entire communities (Qian et al. 2017; Qiao et al. 2015).

We selected a mountainous semi-arid rangeland of the Khorassan-Kopet Dagh floristic province that is located mainly in northeastern Iran and partly in

southern Turkmenistan. This area is a transitional zone among different floristic provinces of the Irano-Turanian region (Memariani et al. 2016a, b). The area consists of arid and semi-arid rangelands with heterogeneous topography, strong geographic barriers, high endemism, and the presence of cushion plants, making it a natural laboratory to investigate the impacts of different ecological filters operating at different spatial scales (Alejandro et al. 2009; Farzam and Ejtehad 2016). Our aim was to determine how spatially restricted dispersal, environmental, and biotic factors operating at regional, local, and fine spatial scales, respectively, shape beta diversity across the landscape (Fig. 1). We examined beta diversity via RDA with Hellinger-transformed abundance-based data as response variables and three ecological filters as explanatory variables. For the first filter, we evaluated the dispersal of species from the regional species pool to the community scale, testing the influence of neutral dynamics on spatial structure of beta diversity. Next, we assessed abiotic filters such as climate, topography, and soil (Chase 2007; Lin et al. 2013). Finally, we evaluated the role of biotic filters, including facilitation via the dominant cushion-like plants that define the final species assembly (Fig. 1). Our specific objectives were to answer the questions: (1) What are the relative contributions of the different filters to determine final beta diversity patterns in plant communities? (2) What critical factors from each ecological filter structure beta diversity? (3) Are there effects of interactions between ecological filters on variation in community structure?

Materials and methods

Study area

Our study region is a 2500-ha mountainous rangeland between 36°40' and 36°55'N, 59°17' and 59°31'E with elevation ranging from 1300 m in the south to 2000 m in the north. It is located in the eastern part of the Khorassan-Kopet Dagh floristic province in the Irano-Turanian region in northeastern Iran (Fig. 2). This floristic province is an important center of plant endemism in the Irano-Turanian region (Memariani et al. 2016a, b). The flora of Khorassan-Kopet Dagh province has evolved from the Eocene to the Holocene under rather constant physiographic and gradual

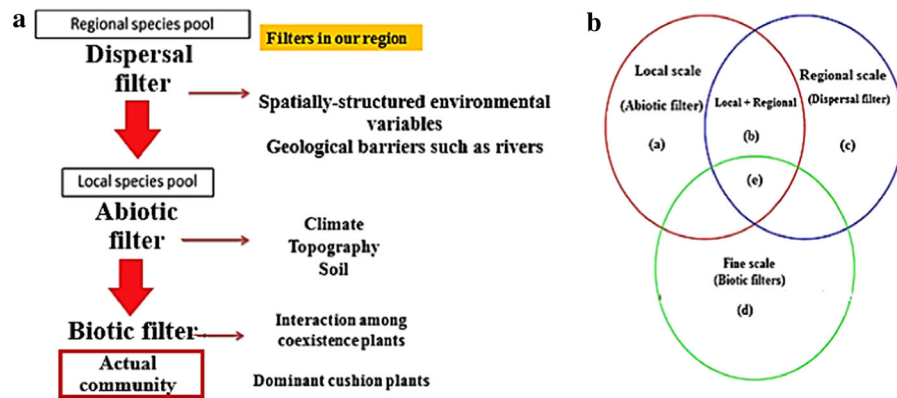


Fig. 1 a Theoretical framework of our studied semi-arid rangeland. Three ecological filters are considered in theoretical framework of our studied semi-arid rangeland. First to third filters relate to regional (i.e., dispersal limitation of the species from regional species pool to community), local (environmental filtering operating by topography, climate, and soil factors), and fine spatial scales (i.e., filter that encompasses the biotic

interactions and microclimatic amelioration promoted by dominant perennial plants) during the species assembly process, respectively. **b** Variation partitioning of beta diversity into fractions explained by three studied filters on beta diversity patterns and unique (i.e., a, c, d fractions) and shared (i.e., b and e fractions) partitions of studied filters

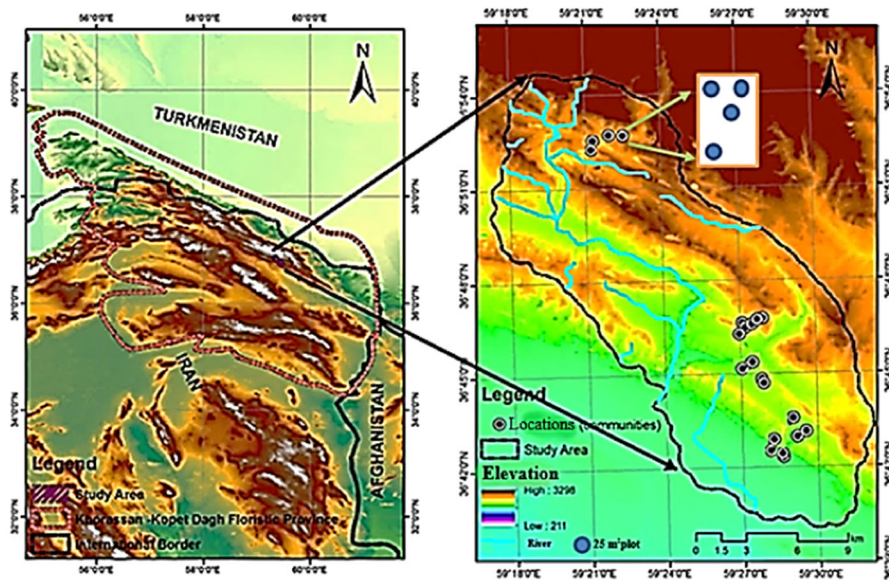


Fig. 2 The study region representing 23 studied locations in eastern part of Khorassan-Kopet Dagh Floristic province that is located in Northeast of Iran. Within each location, four 25 m²

plots were sampled randomly with spacing of approximately 100–150 m between a pair of plots

aridization, leading to a flora dominated by xerophytic plants and plant endemism of 13.8% in the province (Memariani et al. 2016a). Mean monthly precipitation in our study area typically ranges from 0 to 45 mm, and mean monthly temperature ranges from 0 to 28 °C. Significant rainfall occurs in the fall and winter, whereas the spring and summer are dry and hot

(Fig. A1). Plant communities are typically dominated by herbaceous plants and shrubs. The dominant shrub species include *Acantholimon pterostegium* Bunge. (Plumbaginaceae) and *Acanthophyllum diezianum* Hand.-Mazz. (Caryophyllaceae). Other shrub species, such as *Artemisia kopetdaghensis* Krasch., Popov & Lincz. ex Poljakov (Asteraceae), *Juniperus*

polycarpus var. *turcomanica* (B.Fedtsch.) R.P.Adams (Cupressaceae), and *Berberis integerrima* Bunge (Berberidaceae) are only found in certain habitats. In the herbaceous layer, *Holosteum glutinosum* (M.Bieb.) Fisch. & C.A.Mey. (Caryophyllaceae), *Androsace maxima* L. (Primulaceae), *Taeniatherum caput-medusae* (L.) Nevski (Poaceae), *Minuartia meyeri* (Boiss.) Bornm. (Caryophyllaceae), *Carex stenophylla* Wahlenb. (Cyperaceae), *Eremurus stenophyllus* (Boiss. & Buhse) Baker (Asphodelaceae), *Gladiolus atrovioleaceus* Boiss. (Iridaceae), and *Allium giganteum* Regel. (Amaryllidaceae) are indicator species for some topographic habitat types (see Pashirzad et al. 2018 in that paper, topographic habitat types were determined with some topographic variables such as elevation and slope aspects).

Data collection

The sampling units used in this study were sampled in 23 locations representing the diverse topography of the area, for example, including different elevations on north and south facing slopes (Fig. 2). Within each location, four 25 m² plots were randomly established at approximate spacing of 100–150 m between a pair of plots. Therefore, 92 plots were sampled across 23 locations in total. In each plot, species abundance was determined by recording the number of individuals of all plants in the plot. Vegetation composition of each sampling location (i.e., the sum of vegetation composition of four plots located in each location) was inferred as vegetation composition each community. Plant specimens were collected for identification, and 129 plant taxa were identified in total. We assessed the vegetation composition at each site in spring and early summer 2017 on the basis of plants falling within four subplots at each of the 23 sampling locations.

Spatial variables

We expected strong effects of processes operating at larger scales, such as neutral dispersion from the regional species pool and spatial structuring due to spatially heterogeneous environmental variables (Dray et al. 2006). To detect positive spatial structure in our study ecosystem, we generated spatial predictors that could explain beta diversity by implementing

a spatial eigenfunction analysis (Legendre and Legendre 2012; Legendre 1993) based on Moran Eigenvector Maps (MEMs) (Dray et al. 2006), which generalize principal coordinates via the neighbor matrices (PCNM) method (Borcard and Legendre 2002). This method consists of eigenvector decomposition of connectivity matrices. The eigenvalues of MEMs represent Moran's I statistic and describes spatial autocorrelation at different spatial scales (Dray et al. 2006).

In MEM analysis, a Gabriel graph is used in the definition of neighborhood to describe spatial relationships among objects. To define linkage between the 23 locations, a spatial weighting matrix (SWM) was constructed for the decomposition of orthogonal spatial variables. Then, eigen decomposition of community data was performed by SWM, providing spatial eigen functions ("MEM-variables") used as spatial predictors in ordination analysis (Muster et al. 2014). We applied a forward selection procedure to the MEM spatial predictors via *ordiR2step* function in R-package "packfor" (those associated with non-significant Moran's indices were removed), and 3 MEMs were significant (Fig. A2). These MEMs were associated with a positive Moran's statistics (positive eigenvalues) and so belong to broad spatial scales. The positive MEMs model positive spatial correlation because they are linearly correlated with Moran's I index, and we included these positive eigenvectors in the spatial matrix (Muster et al. 2014). All spatial analyses were run with the R package "spacemaker" (Dray 2010).

Although broad scale MEMs find signals of stochastic processes and environmental structuring at coarse spatial resolution, nonmeasured environmental variables can also be reflected in this fraction. Therefore, we used the Diniz-Filho et al. (2012) and Luiz et al. (2016) method to assess the impacts on this fraction explained by broad scale processes. This procedure tests explicitly the predictions of neutral theory (i.e., impacts of dispersal limitation). We constructed Moran's I correlograms and produced a matrix of pairwise Manhattan distances among species correlograms (M) to assay the predictions of neutral theory. In addition, other matrices of pairwise correlations among species abundances were also constructed (R). Under neutral dynamics, we expected no correlation between mean pairwise distances of species correlograms (M) (performed by mean ())

function in R-package *vegan*) and of species profiles (R). All values in the R and M matrices were predicted by broad scale MEMs with the *predict* function in the *vegan* package for R (Oksanen et al. 2015). Finally, we conducted a mantel test to evaluate the correlation between M and R matrices.

Environmental variables

We used topography, climate, and soil as proxies of the abiotic factors operating at the local scale. Two topographic variables were used in this study: elevation and slope aspect. Slope aspect refers to the cardinal direction that a slope faces. Additionally, we collected surface-soil samples (0–10 cm) for each community and five parameters; pH, organic carbon (OC), total nitrogen (N), total potassium (K) and electrical conductivity (EC) were measured for each community. Total nitrogen (N) was determined by the Kjeldahl method (Bremner 1996). Organic carbon (OC) was analyzed by the Walkley and Black (1934) method. Soil electrical conductivity (EC) and acidity (pH) were determined using pH and EC meters. Total potassium (K) was analyzed by Flame atomic absorption spectrophotometer (MAPA 1994). Lastly, according to previous studies that have shown eight out of 19 bioclimatic variables are important variables on species composition (Qian et al. 2017), we extracted values of these eight main bioclimatic variables for each 25 m² plot in each community from the WorldClim database (<https://www.worldclim.org>) at a resolution of 30 arc seconds (Hijmans et al. 2005). Then, climatic variables for each community were calculated as mean values of four sampled plots in each community (i.e., location). These bioclimatic variables are annual mean temperature (BIO1), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of the driest quarter (BIO17), and precipitation of the warmest quarter (BIO18). We excluded correlated variables to avoid multicollinearity among these climatic variables (Pearson's $r > 0.85$). This led us to include only precipitation seasonality (BIO15), which ranges from 73 to 76 mm, and annual precipitation (BIO12), which ranges from 281 to 328 mm for each community (Fig. 1a, b). Lastly, we tested for

correlations among all environmental variables to avoid multicollinearity through Variance Inflation Factors (VIF) higher than 10. Due to a lack of higher correlation between environmental variables, we included all of them included the beta diversity analysis. Eventually, we generated a matrix of 23 rows representing communities and nine columns representing abiotic factors including climatic variables (two columns), edaphic variables (five columns) and topographic variables (two columns).

Biotic variables

Three biotic variables were used to determine the variation in community composition by biotic filters at the fine spatial scale. For the first biotic variable, we analyzed species interactions at the community level based on their patterns of species co-occurrence (Gotelli and Graves 1996). To evaluate species co-occurrence patterns in each community, we analyzed 23 matrices (each matrix consist of four 25 m² plots) with the checkerboard score (C-score) index as an indicator of species co-occurrence patterns each location. This index measures how different species pairs appear in the same sites (Gotelli 2000). C_scores were compared to C_score indices derived from 5000 null matrices (Gotelli 2000). The Independentswap algorithm was used to create null matrices at the community level. This algorithm maintains species richness and species frequency at each site (Gotelli 2000). Lastly, we calculated standardized effect sizes (SES) of C_scores for each community (Bowker et al. 2010). Less co-occurrence (competition) and more co-occurrence (facilitation) than expected by chance are resulted by positive and negative SES values of C_score, respectively (Lopez et al. 2013).

According to previous studies (Maestre et al. 2003; Soliveres et al. 2012), dominant perennial plants play important roles in diversity patterns via differentiation of microhabitats in semi-arid rangelands (Badano and Cavieres 2006). Although there are several shrub species in our study region, most were present in only some or in some cases none of our study locations. In contrast, *Acantholimon pterostegium* Hand.-Mazz. and *Acanthophyllum diezianum* Bunge both occurred at all sample sites in high densities. Therefore, we evaluated the degree of microhabitat amelioration provided by those shrubs as our second biotic filter.

Acanthophyllum diezianum and *Acantholimon pterostegium* have dense cushion-like canopy structures. *Acanthophyllum diezianum* is a cushion forming plant covered by long hairs occurring exclusively in the Irano-Turanian region especially in Iran and Afghanistan (Pirani and Rabeler 2017). *Acantholimon pterostegium* is an Iranian endemic species restricted mostly to NE Iran (Memariani et al. 2016a, b). Jankju et al. (2008) found higher soil fertility under the canopy of *Acantholimon* and *Acanthophyllum* as compared with that of open areas. They suggested this difference was due to higher litter accumulation under the canopy of cushion-like nurse species. Consequently, first, we randomly selected four individuals from each dominant cushion plant at each location, and sampled the area under their canopy using 0.5 m × 0.5 m quadrats. Additionally, four paired open areas were randomly selected adjacent to these shrubs (but at least 1 m away from the shrub canopy). Second, the abundance (number of individuals) of all plant species was recorded within each quadrat (Soliveres et al. 2012). Third, we used the Chao–Jaccard abundance-based similarity index (Chao et al. 2005) to evaluate the degree of microhabitat amelioration. Eventually, we estimated similarity values for each nurse species in each location as the mean of the similarity values for each nurse species located in each location. Therefore, 23 similarity values for each nurse species were included in a biotic matrix as the degree of microhabitat amelioration created by each respective nurse species. A lower similarity among cushion/open patches indicates a higher influence of microhabitat amelioration provided by dominant cushion plants (Chao et al. 2005). We calculated similarity indices for each cushion plant/open in each location using “fossil” R-package (Vavrek 2015).

Statistical analysis

To assess the impacts of different filters on diversity patterns, we evaluated variations in community structures in response to those filters using canonical redundancy analysis and canonical variation partitioning. Variation in community structure is referred to as “non-directional beta diversity.” Therefore, the term “beta diversity” used in this study is rooted in the concept of variation in community structure. We used the Hellinger-transformed abundance-based data

approach to partition the variation in community structure (Anderson et al. 2011). This approach is appropriate for evaluating the variation in community composition data containing many zeros and long beta-diversity gradients (Legendre and Gallagher 2001; Legendre et al. 2005). The Hellinger-transformation shares all properties necessary for beta diversity assessment (For more information about necessary properties for beta diversity analysis, see Legendre and De Caceres 2013). Data transformed using the Hellinger transformations can be analyzed directly by canonical redundancy analysis (RDA) in variation partitioning method, which is not the case for other coefficients (Legendre and De Caceres 2013; Legendre and Gallagher 2001).

To quantitate the main and interactive effects on beta diversity of the dispersal filter at the regional scale (broad spatial variables), the abiotic filter at the local scale (the environmental variables), and the biotic filter at the fine scale (biotic variables), we used a series of constrained canonical ordinations (RDAs: Borcard et al. 1992; Økland and Eilersten 1994; Økland 2003; Peres-Neto and Legendre 2010) simultaneously with canonical variation partitioning. Because some studies have reported individual effects of regional to fine filters on community structure, we determined canonical ordinations that were appropriate to understand the critical variables of each ecological filter, given our intention to measure community structure related to measured spatial, environmental, and biotic explanatory variables only (McCune and Grace 2002; Carr et al. 2009). Advantages in using Canonical redundancy analysis (RDA) include directly incorporating the environmental, spatial, and biotic variables of interest in the analysis as constraints for the ordination in short gradient in the response matrix (Anderson et al. 2011; Legendre and Legendre 2012). We previously found a short gradient in different facets of biodiversity, and therefore, we used canonical redundancy analysis to decompose beta diversity into fractions explained by our studied filters (Pashirzad et al. 2018, 2019). We performed RDAs with each explanatory set separately (representing each unique fraction obtained in canonical variation partitioning), with significant models and critical factors in each unique fraction recognized by the R square metric (R^2) using ordiR2step function in R-package “packfor.”

The quantitation of interactions from these ecological filters is compatible with canonical variation partitioning (Legendre et al. 2005). We partitioned variation using Hellinger-transformed abundance-based data as the response matrix and the abiotic table, spatial table, and biotic table as explanatory matrices. Then, we divided beta diversity into five components: pure abiotic variation fitted by topographic, edaphic and climate variables independent of spatial variables (a), spatially structured environmental variation fitted by both abiotic and spatial variables (b), pure broad spatial variation fitted by broad spatial variables (c), biotic variables fitted by C_score index and degree of microhabitat amelioration provided by dominant cushion plants (d), and spatially and environmentally structured fine scale biotic filters (e). We used the adjusted R square metric ($R^2_{adj.}$) to represent the relative contribution of each fraction to the total variation. The significance of independent (i.e., unique) fractions was tested by both permutation in RDA through ordiR2step function in R-package “packfor” and permutation in canonical variation partitioning through the anova.cca function of R-package “vegan” (Laliberte et al. 2009). Fractions representing two- and three-way interactions, and the fraction of ‘unexplained’ variation, were calculated indirectly from performed RDAs with each explanatory set only and explanatory sets together and were not statistically testable (Legendre and Legendre 1998; Peres-Neto et al. 2006). Finally, we interpreted niche-based processes via the variation explained by abiotic and biotic factors (a + d) fractions), and neutral processes via the variation explained by broad spatial variables (fraction c) (Legendre et al. 2012) (Fig. 1).

Results

Regional scale (stochastic but spatially structured dispersal filter)

Spatial descriptors including 22MEMs variables retained three MEMs after forward selection (Table 1, Fig. 3a). A total of 43% of the variance in beta diversity was explained by the first two RDA axes (Fig. 3a, $R^2 = 0.18$ $P < 0.001$) when beta diversity was constrained only by significant spatial variables

including MEM1 ($R^2 = 0.11$), MEM2 ($R^2 = 0.06$), and MEM4 ($R^2 = 0.02$) (in descending order; Table 1).

We used the broad spatial fraction that described 12% of the variation (Fig. 4b) in beta diversity to evaluate the influence of neutral dynamics or unmeasured environmental variables in this fraction. The mean of the Manhattan distance between species correlograms (M) was 0.033. The correlation among species profiles (R) was 0.030. The Mantel correlation between M and R was -0.01 ($P = 1.0$) (Fig. A2).

Local scale (abiotic filter)

Variance partitioning suggested that environmental heterogeneity explained the largest proportion of the variance (0.14%) in beta diversity. When beta diversity was constrained only by abiotic variables (i.e., pure abiotic fraction), 45.59% of the variance was explained by the first two axes of the RDA (Fig. 3b, $R^2 = 0.22$, $P < 0.001$). Elevation, climatic variables (most notably annual precipitation (Bio12)), and soil organic carbon were the most important variables in significantly of pure abiotic fraction in the determination of beta diversity patterns (Table 1). The six most important environmental factors that determined beta diversity (in descending order) were elevation ($R^2 = 0.14$), annual precipitation (Bio12) ($R^2 = 0.13$), soil organic carbon (OC) ($R^2 = 0.09$), precipitation seasonality (Bio15) ($R^2 = 0.08$), slope aspect (SA) ($R^2 = 0.04$) and potassium (K) ($R^2 = 0.02$) (Table 1; Fig. 3b).

Fine scale (biotic filter)

The degree of similarity between patches in study communities changed from higher similarity at lower altitudes to lower similarity at higher altitudes (Fig. A3A, B). At the community scale, the degree of co-occurrence among species across communities exhibited positive and negative SES values. Positive SES values of the C_score index indicated less association than expected by chance, which is evidence of competition among species in communities in less stressful environments (Figs. A3, 3c). Strong associations between species (negative SES values), which indicate facilitation, were observed in some

Table 1 The relationships between plant species composition and abiotic, broad space, and biotic variables from 23 communities in studied mountainous semi-arid rangeland

Model	R^2	F	Pr ($> r$)	Significant variables (R^2)
Environment	0.22	4.56	0.001***	Altitude (0.14), Bio12 (0.13), OC (0.09), Bio15 (0.08), asp (0.04), EC (0.007), K (0.02)
Broad space	0.18	3.21	0.01**	MEM1 (0.11), MEM2 (0.06), MEM4 (0.02)
Biotic factors	0.19	3.33	0.01**	Acantholimon (0.12), Acanthophyllum (0.06), C_score (0.02)
All factors	0.3096	4.84	0.001***	Altitude (0.14), Bio 12 (0.13), MEM1 (0.12), OC (0.10), Bio15 (0.08), MEM2 (0.06), C_score (0.05), K (0.04), asp (0.03)

Best model for each factor sets was obtained using lower ALC of Forward selection with ordiR2step () function. R^2 , F value and P value for each model is characterized in Table. Models are characterized in $\alpha = 0.001$ (***), to $\alpha = 0.01$ (**). Forward-selected variables and R^2 each variable are given in the “Significant Variables” column

communities, particularly at higher altitude (Figs. A3, 3c).

The RDA of beta diversity was also constrained by biotic factors (i.e., pure biotic fraction). 44.03% of the variation in beta diversity was explained by the first two RDA axes (Fig. 3c, $R^2 = 0.19$, $P < 0.001$). Biotic interactions (C_score index with $R^2 = 0.12$) and microhabitat amelioration promoted by *Acantholimon* ($R^2 = 0.06$) and *Acanthophyllum* ($R^2 = 0.02$), respectively, played important roles in the determination of beta diversity (Fig. 3c, Table 1).

RDA tri-plots of beta diversity patterns with all factors

The whole model with broad spatial and biotic factors along with abiotic descriptors together explained 55% of the total variation in beta diversity in the studied semi-arid rangeland (Fig. 4b). All individual fractions of RDA analysis were significant (Fig. 4b). Abiotic descriptors (fraction a) (Fig. 3b) at the local scale explained 14% of the total variation while broad spatial descriptors (fraction c) (Fig. 3a) (MEMs) at the regional scale explained 12% of the total variation in beta diversity. Spatially structured environmental descriptors (fraction b) explained 11% of the total variation in beta diversity. 13% of the total variation was explained by descriptors of biotic filters at the fine spatial scale (fraction d) (Fig. 3c). 5% of total variation was explained by spatially and environmentally structured biotic descriptors (fraction e). Lastly, 45% of the total variation was unexplained by all the studied ecological filters (Figs. 1, 4b).

The two first RDA axes mapped in the study area exhibited the ordination of beta diversity constrained by all predictors and accounted for 28.35% and 17.01% of variation, respectively (Fig. 3d, $R^2 = 0.30$ $P < 0.001$). Therefore, beta diversity is spatially structured [with two significant positive MEMs; MEM1 ($R^2 = 0.12$) and MEM2 ($R^2 = 0.06$)] with respect to all studied factors, but mainly by abiotic variables at the local scale [such as elevation ($R^2 = 0.14$), annual precipitation ($R^2 = 0.13$), organic carbon ($R^2 = 0.10$), biotic variables (such as biotic interaction ($R^2 = 0.06$) at fine spatial scales (Fig. 3d, Table 1).

Discussion

Beta diversity at the community scale in our 2500 ha mountainous semi-arid rangeland in Khorassan-Kopet Dagh province was shaped by regional processes, such as stochastic, spatially structured dispersal, local-scale environmental factors, and biotic interactions at fine spatial scales. We expected that niche-based processes (abiotic and biotic filters) would be the most important drivers structuring plant assemblages in our study site, because our mountainous semi-arid rangeland is characterized by strong environmental severity in climate factors, quite heterogeneous topography especially in altitude, and the presence of cushion plants (Farzam and Ejtehadi 2016). Although beta diversity was dependent on spatially structured dispersal at the regional scale, most of the variation in beta diversity was driven first by purely abiotic filters at the local scale, and second by purely biotic filters at the fine

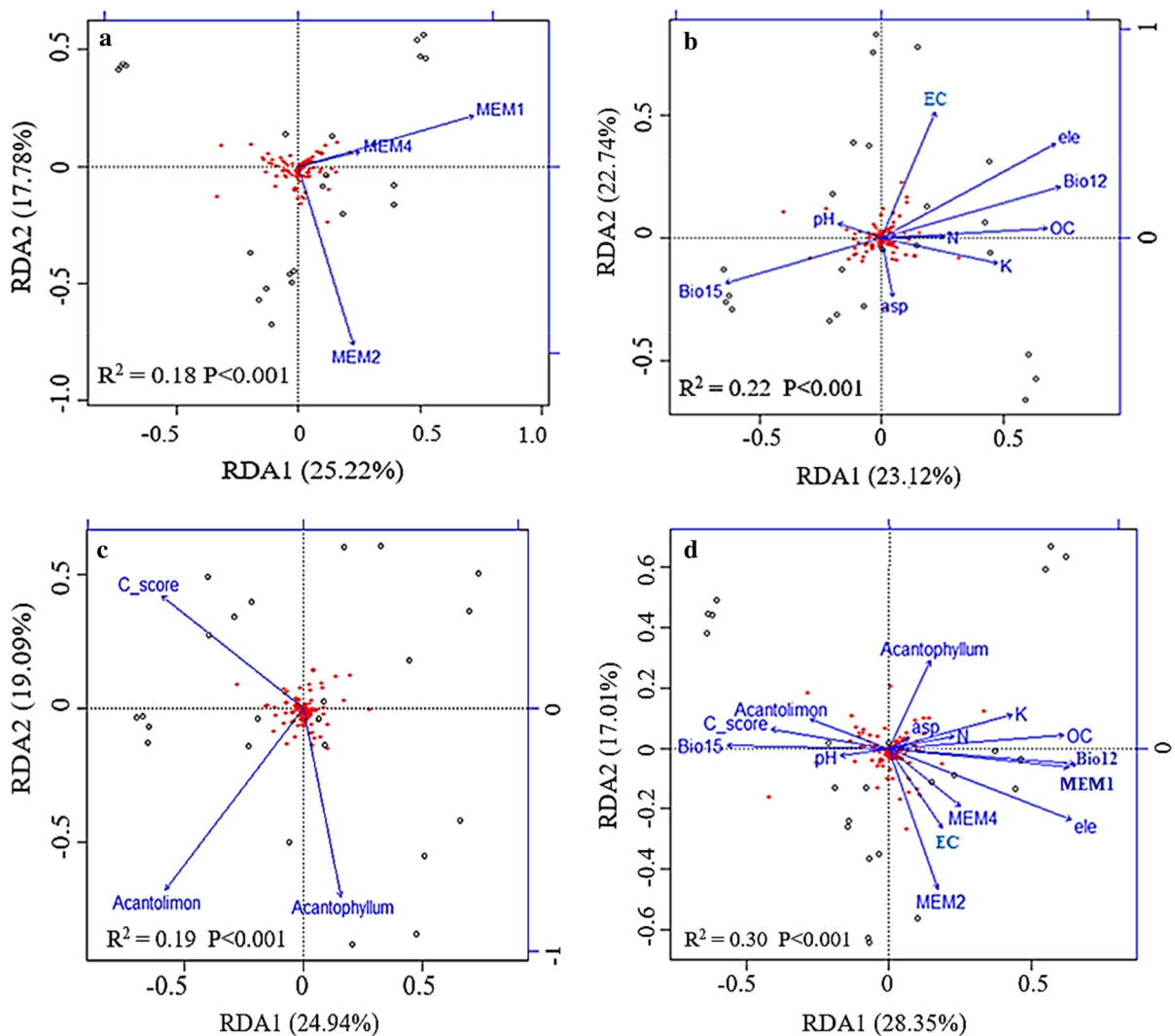


Fig. 3 RDA tri-plots of the beta diversity constrained by the **a** broad scale MEMs, **b** selected environmental variables, **c** biotic variables at fine scale, and **d** environmental variables + broad scale MEMs + biotic variables. ele, Altitude; asp, slope aspect; OC, organic carbon; K, potassium; EC, electric connectivity; N, total nitrogen; Bio12, annual precipitation; Bio15, precipitation of seasonality; C_score, co-

occurrence pattern index; *Acantholimon*, (similarity *Acantholimon*/open); *Acanthophyllum*, (similarity *Acanthophyllum*/open). The bottom and left-hand scales are for the objects and the response variables, respectively; the top and right-hand scales are for the explanatory variables. Red crosses in these graphs represent species scores, while black circles represent site scores

scale, signifying niche-based processes. Therefore, local scale filters contributed more strongly than fine scale filters in community variation, indicating that abiotic filtering processes are more important than biotic filters in signifying niche-based processes. However, the difference between studied ecological filters at multiple spatial scales was marginal and a wide part of variation in community structure was not explained by the studied filters.

Important effects of the abiotic environment as the strongest filter explaining the variation in community structure were most likely attributable to heterogeneity of topography, spatial zonality of soil variables and determination the presence of specific plants in different areas of important gradients. Some of these factors impact beta diversity directly and others influence beta diversity via impact on other variables of different spatial scales (i.e., indirectly). For

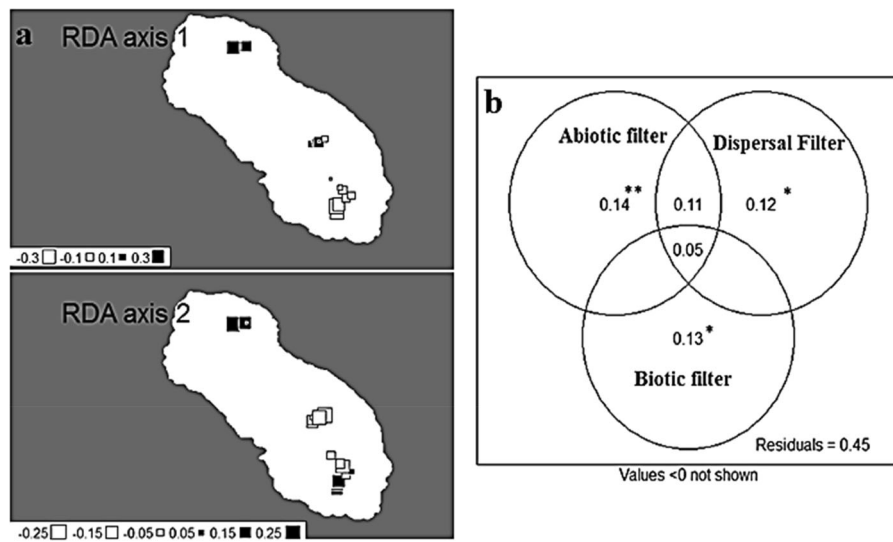


Fig. 4 **a** Study region with site scores of the two first axes of canonical redundancy analysis (RDA). Scores of the two first axes of canonical redundancy analysis were constrained by all predictors: abiotic, dispersal, and biotic factors. The cell size represents scores of axes, and white and black colors represent negative and positive, respectively. The first axis **a** described 28.35% and the second **b** described 17.01% of variation in beta

diversity-species compositional patterns in semi-arid plant communities. **b** Variation partitioning of beta diversity into fractions explained by environmental, broad scale variables and biotic variables at fine scale reported as R^2_{adj} . (*) means significant fractions after permutations tests (* $P < 0.05$, ** $P < 0.01$)

example, elevation was the most important local scale-factor structuring beta diversity with its effects solely and coupled with other variables of different spatial scales (Moura et al. 2016). We believe that several possibilities explain the most important impacts of this variable. First, along with elevation, climatic and some topographic factors act as strong filters, for example: via high precipitation in cold environments, and short growing seasons, and excessive radiation at high elevation. These factors likely select for species with particular traits adapted to harsh, stressful environments, in turn influencing beta diversity (Pashirzad et al. 2018; Peters et al. 2013; Soliveres et al. 2012). Although the change in the amount of annual precipitation along elevation in our study region is relatively low (approximately 47 mm in range), this variation could strongly impact plant communities. Important influence of this variable in coupled with elevation can be performed via the changing roles of dominant species on species under their canopies (Pashirzad et al. 2019). Therefore, these local scale abiotic factors can play important roles in significantly of some biotic variables in fine spatial scale (Butterfield et al. 2013; Lopez et al. 2013).

Further, some soil factors such as organic carbon, climatic factors such as precipitation seasonality and topographic variables such as slope aspect, also affected beta diversity. In mountainous rangelands, significant impacts of slope aspect are related to major abiotic factors such as elevation and annual precipitation (Piston et al. 2016). The better climatic conditions of north-facing, mesic slopes support the presence of more productive plant species that are also more sensitive to disturbance, whereas harsher conditions along south-facing, drier slopes lead to the establishment of spiny, stress-tolerant shrubs (Farzam and Ejtehadi 2016). Therefore, slope aspect plays strong roles on variation in community structure through the establishment of cushion-like species in xeric rather than mesic exposures (Alejandro et al. 2009). Cushion-like species could directly improve soil environments (i.e., enhancing nutrient availability) via the increased presence of other plant species in harsh environments (Butterfield et al. 2013; Erktan and Rey 2013). Reasons for some soil factors affecting diversity patterns may include the altitudinal zonality of soil (Wang et al. 2015), and the indirect effects of dominant cushion-like species on soil fertility (i.e., changing some soil factors such as organic carbon via

microhabitat differentiation promoted by cushion-like species) (Soliveres et al. 2012). Therefore, abiotic filters at local scale and some biotic filters at fine spatial scale simultaneously affect significantly of each other.

At fine spatial scales, direct biotic interactions and microhabitat differentiation provided by the dominant cushion plants i.e., *Acantholimon* and *Acanthophyllum* were important filters exerting influence on beta diversity. Our results suggest important roles of the dominant shrub species on plant community assembly by altering micro-environmental conditions in their vicinities (e.g. increased soil fertility) and by filtering (Cortina and Maestre 2005). However, biotic filter effects at the fine spatial scale on beta diversity are strongly related to the main filters at the local scale. In plant communities at lower elevation, we did not observe any positive effects of the dominant shrubs on variation in community structure; indeed, a high similarity between canopy/open patches suggest competition between dominant shrubs and the plant species under their canopies (Luzuriaga et al. 2012). Although the competitive effects of the dominant shrubs, for example via belowground depletion of water and nutrients under their canopies, have been reported in less harsh environments (Armas and Pugnaire 2011), facilitative effects have also been observed in communities with extreme environments. Some studies have shown both the positive and negative impacts of dominant cushion plants on beta diversity (Luzuriaga et al. 2012; Lopez et al. 2013). In mountainous landscapes, biotic interactions—when present—are expected to vary with elevation (Pottier et al. 2013): the frequency of positive and negative interactions is predicted to change across the stress gradient, with facilitation being more common in places with high abiotic stress such as cold and limiting availability of nutrients (Bertness and Callaway 1994; He et al. 2013; Chamberlain et al. 2014). Moreover, facilitation among plants has often been demonstrated in severe environments, such as high elevations due to decreasing of temperature (Carlsson and Callaghan 1991; Choler et al. 2001; Callaway et al. 2002). Although local scale filters play important roles on significantly of biotic filters, there is the possibility that abiotic filters may have exerted a stronger influence, and the presence of cushion plants reduced these impacts via the amelioration of microhabitats (Lortie et al. 2004; Valiente-Banuet et al.

2006). In accordance with this possibility, variation in biotic interactions from competitive interactions (positive C_score and high similarity indices) in lower elevation communities to facilitative interactions (negative C_score and low similarity indices) in higher elevation communities could explain the high importance of dominant shrubs on abiotic filters, and finally on beta diversity (Pashirzad et al. 2019; Soliveres et al. 2011; Lopez et al. 2013). Therefore, the interplay between abiotic and biotic filters leads to the decreasing importance of the main abiotic filters such as elevation and annual precipitation, and the increasing importance of some biotic filters and other abiotic filters that are affected directly by biotic filters, such as organic carbon.

Broad scale spatial variables (fraction c) may have influenced observed patterns in beta diversity. However, this fraction may reflect either the impacts of spatially structured unmeasured environmental variables, or neutral processes in plant communities (Luiz et al. 2016). A low mean distance in our correlogram and no significant relationship between Manhattan distances (M) and abundance distances ($r = -0.01$) suggests strong roles for neutral processes on beta diversity (Diniz-Filho et al. 2012; Luiz et al. 2016). Neutral processes such as stochastic spatially structured dispersal may be imposed by environmental variables related to limitations on dispersal, such as elevation (Qian et al. 2017). The spatial structure of environmental variables can be a possible major determinant, given the significance of the environmental factors with and without correction for spatial autocorrelation. This suggests that the prevalent environmental filters could determine changes in beta diversity via their spatial structure or by interacting with other processes, especially biotic filters promoting niche differentiations (Kraft and Ackerly 2014). In concordance with this explanation, we found increasing importance of spatial components and biotic filters related to competition and facilitation. In addition to the role of spatially structured environmental variables in dispersal, geological barriers such as rivers may also affect the variation in community structure (Li and Sun 2017). River networks are hierarchical dendritic habitats embedded within the terrestrial landscapes and are recognized as a physical organization influencing the dispersal of organisms, which ultimately affect biodiversity patterns (Tonkin et al. 2018).

In conclusion, both niche and neutral processes operating at different spatial scales are important determinants of diversity patterns, and the balance between niche processes and neutral processes drives beta diversity. However, there were stronger effects of pure abiotic and biotic filters as proxies of niche-based deterministic processes relative to pure dispersal filters as processes of neutral dynamics on beta diversity patterns in our communities. This result is consistent with expectation, because mountainous semi-arid ecosystems consist of heterogeneous topography simultaneous with the dominance of cushion plants. However, geographic barriers such as rivers and spatial structures of some environmental variables such as elevation in our studied area can be a strong explanation for strongly neutral processes (Myers et al. 2013). Explanations for the stronger effects of niche-based deterministic processes can depend on which factors were studied. Studies incorporating few variables operating at only one spatial scale may suggest that dispersal-based processes determine beta diversity. Therefore, the inclusion of abiotic along with biotic factors reversed these results in signifying niche-based processes (Chang et al. 2013; Qiao et al. 2015). In addition, our results suggest that some factors affecting each ecological filter exhibit scale-dependence in their impacts on beta diversity, but some others act across different spatial scales and directly and indirectly via impact on other factors of different spatial scales influence beta diversity. Therefore, we argue that studies should incorporate many effective variables operating at different spatial scales to yield the most robust results to understand the processes structuring beta diversity in mountainous semi-arid rangelands (Luzuriaga et al. 2012).

Multiple facets of biodiversity must be studied to deal effectively with scale-dependence in community assembly processes. A wide part of the unexplained variation in beta diversity may be due to the studied explanatory variables and to dependence of community assembly processes to multiple facets of biodiversity. Therefore, we recommend future research partitioning phylogenetic and functional beta diversity with a vast range of explanatory factors acting different spatial scales, in order to provide additional insight about the processes that structure beta diversity patterns.

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Data accessibility Data will be made available in the Dryad Digital Repository.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest to disclose.

References

- Alejandro GFB, Chinchilla FA, Magrach A, Romero V, Reyos M, Velilla M, Amador-Vargas Serrano JM, S, (2009) Slope orientation enhances the nurse effect of a paramo shrub, *Hypericum irazuense* (Hypericaceae) in Costa Rica. *J Trop Ecol* 25:331–335
- Anderson MJ, Crist TO, Chase JM, Vellend M, &, et al (2011) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14:19–28
- Armas C, Pugnaire FI (2011) Belowground zone of influence in a tussock grass species. *Acta Oecol* 37:284–289
- BA Carlsson, Callaghan TV (1991) Positive plant interactions in tundra vegetation and the importance of shelter. *J Ecol* 79:973–983. <https://doi.org/10.2307/2261092>
- Badano EI, Cavieres LA (2006) Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *J Biogeogr* 33:304–313
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends in Ecol Evol* 9(5):191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Model* 153:51–68
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Bowker MA, Maestre FT, Escolar C (2010) Biological crusts as a model system for examining the biodiversity–ecosystem function relationship in soils. *Soil Biol Biochem* 42:405–417
- Bremner JM (1996) In: Sparks DL, et al. (eds) Nitrogen-Total Methods of soil analysis. Science Society of America Inc, American Society of Agronomy Inc, Madison, pp 1085–1122

- Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis MJM, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire FI, Saccone P, Schiffer K, Seifan M, Touzard B, Michalet R, (2008) Facilitation in plant communities: the past, the present, and the future. *J Ecol* 96:18–34
- Butterfield BJ, Cavieres LA, Callaway RM, Cook BJ, Kikvidze Z, Lortie CJ, Brooker RW (2013) Alpine cushion plants inhibit loss of phylogenetic diversity in severe environments. *Ecol Lett* 16:478–486. <https://doi.org/10.1111/ele.12070>
- Callaway RM (2007) Positive interactions and interdependence in plant communities. Springer, New York
- Callaway RM, Kikvidze D, Kikvidze Z (2000) Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains. *Oikos* 89:275–282
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R et al (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844–848. <https://doi.org/10.1038/nature00812>
- Carr SC, Robertson KM, Platt WJ, Peet RK (2009) A model of geographical, environmental and regional variation in vegetation composition of pyrogenic grasslands of Florida. *J Biogeogr* 36:1600–1612
- Cavender-Bares J, Kozak K, Fine P, Kembel S (2009) The merging of community ecology and phylogenetic biology. *Ecol Lett* 12:693–715
- Chamberlain SA, Bronstein JL, Rudgers JA (2014) How context dependent are species interactions? *Ecol Lett* 17(7):881–890. <https://doi.org/10.1111/ele.12279>
- Chang LW, Zelen D, Li CF, Chiu ST, Hsieh C-F (2013) Better environmental data may reverse conclusions about niche- and dispersal-based processes in community assembly. *Ecology* 94:2145–2151
- Chao A, Chazdon RL, Colwell RK, Shen T (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol Lett* 8:148–159
- Chase JM (2007) Drought mediates the importance of stochastic community assembly. *PNAS* 104:17430–17434
- Choler P, Michalet R, Callaway RM (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308
- Cortina J, Maestre FT (2005) Plant effects on soils in drylands: implications for community dynamics and ecosystem restoration. In: Binkley D, Menyailo O (eds) Tree species effects on soils: implications for global change. NATO Science Series, Kluwer Academic Publishers, Dordrecht, 85–118.
- Diniz-Filho JAF, Siqueira T, Padial AA, Rangel TF, Landeiro VL, Bini LM (2012) Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in meta communities. *Oikos* 121(2):201–210
- Dray S (2010) SpacemakeR: Spatial modelling. R package version 0.0–5. <https://r-forge.r-project.org/sedar>. Accessed 2 June 2013
- Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Model* 196:483–493
- Erktan A, Rey F (2013) Linking sediment trapping efficiency with morphological traits of *Salix* tiller barriers on marly gully floors under ecological rehabilitation. *Ecol Eng* 51:212–220
- Farzam M, Ejtehadi H (2016) Effects of drought and canopy facilitation on plant diversity and abundance in a semiarid mountainous rangeland. *J Plant Ecol* 10(4):626–633
- Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecol* 81:2606–2621
- Gotelli NJ, Graves GR (1996) Null models in Ecology. Smithsonian Institution Press, Washington DC
- Harrison S, Ross SJ, Lawton JH (1992) Beta diversity on geographic gradients in Britain. *J Anim Ecol* 61:151–158
- He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett* 16(5):695–706
- Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Clim* 25:1965–1978
- Jankju M, Delavari A, Ganjali A (2008) Interseeding *Bromus kopetdaghensis*, in shrublands. *Rangeland J Iran Soc Range Manag* 2:314–328
- Kraft NJB, Ackerly DD (2014) Assembly of plant communities. In: Monson RK (ed) Ecology and the environment, the plant sciences, vol 8. Springer, New York, NY, pp 67–88
- Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. *Funct Ecol* 29:592–599
- Laliberté E, Paquette A, Legendre P, Bouchard A (2009) Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. *Oecologia* 159(2):377–388
- Legendre P (1993) Spatial autocorrelation: trouble or new paradigm. *Ecology* 74:1659–1673
- Legendre P, De Caceres M (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol Lett* 16:951–963
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Legendre L (1998) Numerical Ecology, 2nd edn. Elsevier, Amsterdam
- Legendre P, Legendre L (2012) Numerical ecology, Third English edition. Elsevier, Amsterdam
- Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75:435–450
- Legendre P, Borcard D, Roberts DW (2012) Variation partitioning involving orthogonal spatial eigenfunction sub-models. *Ecol* 93(5):1234–1240
- Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *J Anim Ecol* 70:966–979
- Lessard JP, Belmaker J, Myers JA, Chase JM, Rahbek C (2012) Inferring local ecological processes amid species pool influences. *Trends Ecol Evol* 27(11):600–607
- Li X, Sun H (2017) Phylogenetic pattern of alpine plants along latitude and longitude in Hengduan Mountains Region. *Plant Divers* 39:37–43

- Lin G, Stralberg D, Gong G, Huang Z, Ye W, Wu L (2013) Separating the effects of environment and space on tree species distribution: from population to community. *PLoS ONE* 8(2):e56171. <https://doi.org/10.1371/journal.pone.0056171>
- Lopez RP, Valdivia S, Rivera ML, Rios RS (2013) Co-occurrence patterns along a regional aridity gradient of the subtropical andes do not support stress gradient hypotheses. *PLoS ONE* 8:1–10
- Lopez-Angulo J, Swenson NG, Cavieres LA (2018) Interactions between abiotic gradients determine functional and phylogenetic diversity patterns in Mediterranean type climate mountains in the Andes. *J Veg Sci* 29(2):245–254
- Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Callaway FI, Pugnaire RM (2004) Rethinking plant community theory. *Oikos* 107:433–438
- Luiz AM, Leao-Pires TA, Sawaya RJ (2016) Geomorphology drives amphibian beta diversity in Atlantic forest Lowlands of southeastern Brazil. *PLoS ONE* 11(5):e0153977
- Luzuriaga AL, Sanchez AN, Maestre FT, Escudero A (2012) Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PLoS ONE* 7(7):e41270
- Maestre FT, Bautista S, Cortina J (2003) Positive, negative and net effects in grass–shrub interactions in Mediterranean semiarid grasslands. *Ecology* 84:3186–3197
- MAPA (1994) Métodos Oficiales de Análisis. Tomo III. Servicio de Publicaciones del Ministerio de Agricultura. Pesca y Alimentación, Madrid, pp. 662. (In French)
- Mayfield MM, Levine JM (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol Lett* 13:1085–1093
- McCune B, Grace J (2002) Multivariate analysis of ecological communities. MjM Software, Gleneden Beach
- Memariani F, Akhiani H, Joharchi MR (2016) Endemic plants of Khorassan-Kopet Dagh floristic province in Irano-Turanian region: diversity, distribution patterns and conservation status. *Phytotaxa* 249(1):031–117
- Memariani F et al (2016) A review of plant diversity, vegetation and phytogeography of the Khorassan-Kopet Dagh floristic province in the Irano-Turanian region (northeastern Iran – southern Turkmenistan). *Phytotaxa* 249(1):8–30
- Michale R (2006) Highlighting the multiple drivers of change in interactions along stress gradients. *New Phytol* 173:3–6
- Miranda JD, Armas C, Padilla FM, Pugnaire FI (2011) Climatic change and rainfall patterns: effects on semi-arid plant communities of the Iberian Southeast. *J Arid Environ* 75:1302–1309
- Mori AS et al (2015) Null model approaches to evaluating the relative role of different assembly processes in shaping ecological communities. *Oecologia* 178:261–273
- Moura MR, Villalobos F, Costa GC, Garcia PCA (2016) Disentangling the role of climate, topography and vegetation in species richness gradients. *PLoS ONE* 11(3):e0152468
- Muster C, Meyer M, Sattler T (2014) Spatial arrangement overrules environmental factors to structure native and non-native assemblages of synanthropic harvestmen. *PLoS ONE* 9(3):e90474
- Myers JA et al (2013) Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol Lett* 16:151–157
- Økland RH (2003) Partitioning the variation in a plot-by-species data matrix that is related to n sets of explanatory variables. *J Veg Sci* 14:693–700
- Økland RH, Eilersten O (1994) Canonical correspondence analysis with variation partitioning: some comments and an application. *J Veg Sci* 5:117–126
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, et al. (2015) *Vegan: Community Ecology Package*. R package version 2.0–9. <https://CRAN.R-project.org/package=vegan>. Accessed 16 Sept 2015
- Pashirzad M, Ejtehadi H, Vaezi J, Shefferson RP (2018) Spatial scale-dependent phylogenetic signal in species distributions along geographic and elevation gradients in a mountainous rangeland. *Ecol Evol* 8(21):10364–10373. <https://doi.org/10.1002/ece3.4293>
- Pashirzad M, Ejtehadi H, Vaezi J, Shefferson RP (2019) Plant-plant interactions influence phylogenetic diversity at multiple spatial scales in a semi-arid mountain rangeland. *Oecologia* 189:1–11
- Pausas JG, Verdú M, (2010) The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *Bioscience* 60:614–625
- Peres-Neto PR, Legendre P (2010) Estimating and controlling for spatial structure in the study of ecological communities. *Glob Ecol Biogeogr* 19(2):174–184
- Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625
- Peters H, O'Leary BC, Hawkins JP, Carpenter KE, Roberts CM (2013) Conus: first comprehensive conservation red list assessment of a marine gastropod mollusc genus. *PLoS ONE* 8(12):e83353. <https://doi.org/10.1371/journal.pone.0083353>
- Pirani A, Rabeler RK (2017) Nomenclatural notes on *Acanthophyllum* (Caryophyllaceae, Caryophyllaceae). *Phytotaxa* 303(2):197–198
- Piston N, Schob C, Armas C, Prieto I, Pugnaire F (2016) Contribution of co-occurring shrub species to community richness and phylogenetic diversity along an environmental gradient. *Perspect Plant Ecol Evol Syst* 19:30–39
- Pottier J, Dubuis A, Pellissier L, Maiorano L, Rossier L, Randin CF, Guisan A (2013) The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. *Glob Ecol Biogeogr* 22(1):52–63
- Qian H, Chen SH, Zhang JL (2017) Disentangling environmental and spatial effects on phylogenetic structure of angiosperm tree communities in China. *Sci Rep* 7:5864
- Qiao X, Li Q, Jiang Q, Lu J, Franklin S et al (2015) Beta diversity determinants in Badagongshan, a subtropical forest in central China. *Sci Rep* 5:17043
- Rajaniemi TK, Turkington R, Goldberg D (2009) Community-level consequences of species interactions in an annual plant community. *J Veg Sci* 20:836–846
- Ricklefs RE (2008) Disintegration of the ecological community. *Am Nat* 172(6):741–750
- Shipley B (2015) Describing, explaining and predicting community assembly: a convincing trait-based case study. *J Veg Sci* 26:615–616

- Soininen J, Lennon JJ, Hillebrand H (2007) Multivariate analysis of beta diversity across organisms and environments. *Ecology* 88(11):2830–2838
- Soliveres S, Eldridge DJ, Maestre FT, Bowker MA, Tighe M, Escudero A (2011) Microhabitat amelioration and reduced competition among understory plants as drivers of facilitation across environmental gradients: towards a unifying framework. *Perspect Plant Ecol Evol Syst* 13:247–258
- Soliveres S, Torices R, Maestre F (2012) Environmental conditions and biotic interactions acting together promote phylogenetic randomness in semiarid plant communities: new methods help to avoid misleading conclusions. *J Veg Sci* 23:822–836
- Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol Lett* 17(7):866–880
- Tello JS et al (2015) Elevational gradients in β -diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. *PLoS ONE* 10:e0121458
- Tonkin JD, Altermatt F, Finn DS, Heino J, Olden JD, Pauls SU (2018) The role of dispersal in river network metacommunities: patterns, processes, and pathways. *Freshw Biol* 63(1):141–163. <https://doi.org/10.1111/fwb.13037>
- Valiente-Banuet A, Vital A, Verdú M, Callaway RM, (2006) Modern quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proc Nat Acad Sci USA* 103:16812–16817
- Vavrek MJ (2015) Fossil package.
- Vellend M (2010) Conceptual synthesis in community ecology. *Q Rev Biol* 85(2):183–206
- Verdú M, Rey PJ, Alcantara JM, Siles G, Valiente-Banuet A (2009) Phylogenetic signatures of facilitation and competition in successional communities. *J Ecol* 97:1171–1180
- Walkley A, Black IA (1934) An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci* 37:29–38
- Wang B et al (2015) Relationship between topography and the distribution of understory vegetation in a *Pinus massoniana* forest in Southern China. *Int Soil Water Conserv Res* 3:291–304
- Weinstein BG, Catherine H, Parra JL (2017) The role of environment, dispersal and competition in explaining reduced co-occurrence among related species. *PLoS ONE* 12(11):e0185493. <https://doi.org/10.1371/journal.pone.0185493>
- Yang J, Swenson NJ, Zhang G et al (2015) Local-scale partitioning of functional and phylogenetic beta diversity in a tropical tree assemblage. *Sci Rep* 5:12731

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