Species Richness Capture Plant Functional and Phylogenetic Diversity Variations Along Different Ecosystems on the Hillsides of Damavand Mountain (Iran)

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Research Article

Keywords: community weighted means. Functional richness. Grassland.LHS scheme. Mean pairwise dissimilarities. Plants traits. Shrubland; Soil nutrients

Posted Date: July 13th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-673779/v1>

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Abstract

Aims Plants vary in their functional traits and thus in their preference towards edaphic conditions. Plants displaying tougher, long-living leaves, which better conserve nutrients in the tissues, are expected to grow better in acidic soils, which are frequently nutrient poor.

Methods We used a trait-based approach, quantifying variations in the Leaf-height-seed (LHS) scheme and functional and phylogenetic indices in semi-arid communities from three different habitats (grasslands, shrubland and mixed habitats). Three traits, including specific leaf area (SLA), Plant height (H) and Seed Mass (SM), in 350 plots across the three habitats in the southern hillsides of Damavand Mountain. We only included the species that occurred in more than 20 plots throughout the dataset for the following analyses (i.e., 44 species). We calculated at the plot scale, community weighted means (CWM) for each trait, species richness, Faith's phylogenetic diversity index (PD), functional richness (Frich), functional and phylogenetic mean pairwise dissimilarities (MPD) and nutrient concentration.

Results The results showed that the higher soil nutrient concentration and pH were significant and positive related with species and functional richness and Faith's phylogenetic distance, while not significant results were obtained for any functional trait at community level (SLACWM, VHCWM and SMCWM) or for the functional and phylogenetic mean pairwise distance.

Conclusions In addition, the phylogenetic and functional patterns responded more to the taxonomic richness variations than to trait-based assembly processes.

Introduction

The importance of soil and vegetation management to achieve the United Nations Goals for sustainability (Keesstra et al. 2016) has been highlighted in the last decade due to the central role that both elements play in ecosystem services. Plant-soil interactions provide mechanistic information on the ecosystem's adaptation to the environment (Berdugo et al. 2017), especially in drylands in montane ecosystems, where the soil resources and land use are key factors that explain vegetation structure evolution (Eldridge et al., 2016; Salgado-Luarte et al. 2019; Vaieretti et al. 2018). In this regard, the functional trait-based approach has emerged as a powerful tool to evaluate the evolutionary history and adaptations of plants to a wide range of abiotic factors (Lavorel and Garnier. 2002; Jafarian et al. 2019). In addition, many studies have provided information on the potential impact of the global change on vegetation using functional trait analysis of plant communities along environmental gradients across different biomes (e.g. Pérez-Ramos et al. 2012; Junk et al. 2014) or at global scale (e.g. Yang et al., 2015; Wiczyński et al., 2018). However, notwithstanding the relevant information obtained by these studies, additional empirical information on functional trait variation in plant communities is needed to accurately infer their sensitivity to ongoing global change (Pérez-Ramos et al., 2017).

Arid and semi-arid regions will be among the areas on the planet most affected by global change (Delgado-Baquerizo et al. 2013). However, the current knowledge of the effects of global change on plant

communities has been biased to certain regions of the planet (e.g. Mediterranean-climate regions; León-Sánchez et al. 2020; Pérez-Ramos et al. 2017; Sardans et al. 2011), while others, such as western Asia, have been generally overlooked (but see Bergholz et al. 2017). In Iran, rangelands occupy nearly 54.6% of the landscape with high plant diversity due to its climate conditions. However, human activities (e.g. land use and climate change) and the lack of a proper environmental policy are responsible of the shifts in the ecosystem properties of the rangelands from Iran. For instance, recent studies from Iran have shown that global change caused a shift in vegetation composition and soil biogeochemical cycles (Ashrafzadh and Erfanzadeh. 2014). But, the impact from a functional and phylogenetic point of view has been largely ignored (Jafarian et al. 2019).

Given that plants all use the same types of resources (e.g. nutrients and water), the resource uptake traits may be a way to more accurately discriminate between species with regard to ecological strategies. For instance, the leaf economics spectrum (LES, Wright et al. 2004) represents the trade-off between acquisition and conservation of resources, being the specific leaf area (SLA; light-capturing area deployed per dry mass allocated) one of the best predictors of the LES (Wright et al. 2004). However, the leading dimensions of ecological variation among plants include not only traits related with resource uptake but also those associated with competition for light and reproductive ability (Díaz et al. 2016). To this end, Westoby (1998) proposed the leaf-height-seed (LHS) strategy scheme, which captures the strategy of plants by three trait-related independent dimensions of ecological variation. Hence, the LHS scheme assumes that leaf economics is essentially independent of the dimensions of plant height and seed production (Laughlin et al. 2010).

Moreover, the community assembly patterns cannot be assessed by a single measure of functional composition (i.e. the dominant trait values expressed by the community weighted means; Garnier et al. 2004) but rather needs a multi-faceted approach (de Bello et al., 2013). Other descriptors of functional and phylogenetic structure may allow inferring relevant processes and can help predict community responses to global change (Salgado-Luarte et al., 2019; Chang et al., 2019). Investigating the functional and phylogenetic structure of communities can thus provide useful insight to understand the outcome of both environmental and historical factors involved in the species assembly. Thus, while the phylogenetic structure provides tools to explore the role of the different evolutionary histories of the species in the community assembly, the functional structure is closely related to the different ecological strategies used to cope with environmental filters (Tanaka and Sato, 2015; Xu et al., 2017). For instance, phylogenetic and/or functional overdispersion can occur among communities situated in similar habitats as a direct consequence of competitive exclusion between similar species, while strong abiotic filtering may promote phylogenetic and/or functional clustering by the selection of certain traits or clades imposed by the environmental constraints (Cavender-Bares et al. 2009; Xu et al. 2017).

In this study, we test the relationship between the simple traits of the LHS model and quantify the variation of the functional and phylogenetic indices of plant communities along natural resource gradient in the southern hillsides of Damavand Mountain. To this end, we have measured the species richness and several metrics of the functional and phylogenetic structure in 350 plots from three different habitats

associated with different intensity of grazing (grasslands, shrubland and mixed habitats) and nutrient concentration. At the community level, the LHS model seems to represent most of the variation in species composition in a grazing context (Golodets et al. 2009): heavy grazing could favor higher rates of resource capture from the environment to support high growth rates (high SLA) and shorter plants with large seeds, which favors seedling establishment in the disturbed environment (Cingolani et al. 2005; Golodets et al. 2009). Grazing might also increase the functional or phylogenetic redundancy by filtering out species that lack traits, such as low stature and/or seed mass, to persist under grazing disturbance (de Bello et al. 2006). Alternatively, higher resource availability may enhance the establishment of species having traits associated with higher growth rate and competition (higher SLA and plant height), which could promote higher functional and phylogenetic dissimilarity between dominant species (de Bello et al., 2013; de la Riva et al. 2019). We tested these predictions: firstly, by examining the responses of the functional LHS trait composition at community level between habitats along the soil nutrient gradient; secondly, by comparing the species richness and the functional and phylogenetic diversity indices with the above mentioned factors.

Materials And Methods

Study site

Of the total land area of Iran, about 52.4% are rangelands; 8.6% are forests and 19.5% are deserts including bare salty lands. There are three main climatic zones in Iran, including arid and semi-arid regions of the interior and far south, Mediterranean climate (mainly in the western Zagros Mountains, the high plateau of Azerbaijan, and the Alborz mountains) and humid and semi-humid regions (mainly in the Caspian, but also in west Azerbaijan and the southwest Zagros). The study area is located in plant geography zone of Europe - Siberia (the Hyrcanian area). The study area, the southern hillsides of Damavand Mountain, is located in the North part of Iran (52°11'–52°5' N; 35°46'–35°49' E). It covers ca. 6000 ha and has an elevation stretching from 2500 m asl to 34600 m asl. The climate is semi-arid cold. Minimum monthly mean – 0.3°C and Maximum monthly mean 19.2°C. The mean annual temperature of 12.7°C; and the mean annual precipitation of 652 mm. The climatic variables were computed from the mean annual precipitation, mean annual moisture and mean annual temperature data recorded for the period 1985–2010 by the Rineh network of meteorological stations (35°54'; 52°04'E) (Fig. 1). The soil type of the study area is sandy-loamy and silty soil. The bedrock is primarily calcareous. The soils are variable, ranging from deep brown soils to shallow lithological soils, the latter exerting a greater influence on vegetation. Basic cations and carbonates promote an alkaline pedogenesis that can be followed by an acidic pedogenesis after carbonate lixiviation.

Experimental design

The experiment was carried out in three different habitats: grassland, dominated by *Agropyron repens*, *Festuca ovina*, *Bromus tectorum* and *Bromus tomentellus*; shrubland, dominated by *Artemisia aucheri*, *Astragalous aegobromus*, *Eringium billardeieri* and *Thymus kotschyanus*; and a transitional fringe

between both habitats, which we called “mixed area”, dominated by *Astragalus ochrodeucus*, *Festuca ovina*, *Onobrychis cornuta* and *Bromus tomentellus*. These habitats are adjacent to each other in our study area and they have different community compositions, structures, and dominant species. From mid spring and summer of 2016, sampling was down in a 1×2 m plots within each habitat. In each habitat, in total 150 sampling plots were selected randomly with the constraint that it was at least 1 m from the margin to avoid edge effects. On the field, each plot was separated at least by 100 m from the others, to avoid spatial autocorrelation. We estimated the cover of each species per plot.

Plant functional trait measurements

We select the 44 most abundant species. Between four and 20 individuals per species were measured in sites. One well-developed entire leaf was collected per individual for trait measurement. The leaves were scanned and analyzed in the lab using the Leaf area matter software to measure their surface. We also measured the leaf dry mass after drying and weighting the leaves. The vegetation height (VH, m) was measured in the field as the distance between the top of the photosynthetic tissue and the ground. Specific leaf area (SLA; mm² mg⁻¹) was calculated as the ratio of the leaf surface to its dry mass. Seed mass (SM; mg) were compiled from seed databases (Goethe University Frankfurt, <http://www.seed-dispersal.info>, and the Royal Botanic Gardens, <http://data.kew.org/sid/>). For the few species that we did not find seed mass values, we estimated the seed mass of each of these species from the average value of the species of the same genus that were registered (de la Riva et al. 2019), because seed mass is strongly conserved through the phylogeny (Lord et al. 1995). Given the multidimensionality of plant functions, we chose these three traits because of their importance in providing information about different independent axes of ecological strategies (see Díaz et al. 2016; Bruelheide et al. 2018). Specifically, we selected SLA, VH and SM as a subrogate of the plant strategies related with resource acquisition, competition for light and reproduction, respectively (Laughlin et al., 2010).

Soil collection and processing

Soil samples of the top 30 cm of depth (where nutrient uptake mostly occurs; Jobbágy and Jackson 2001) were collected from each sampling plot. Soil samples were randomly collected from three points using a bucket auger and mixed into a single soil sample and were brought into the laboratory in airtight plastic bags. All of the soil samples were air-dried and then filtered through a 0.2 mm sieve, discarding the visible roots and other plant debris. Soil pH was measured using a pH meter with a glass electrode (soil / KCl ratio is 1 V 2:5). Soil organic carbon was determined using the Walkley–Black method and a factor of 1.3 was applied to adjust the organic C recovery (Nelson and Sommers, 1982). The soil available nitrogen, phosphorus and potassium were measured using the methods of Miller and Keeney (1982).

Statistical analysis

Following Garnier et al. (2004), the traits were weighted by the relative abundance of their constitutive species to calculate the community weighted mean (CWM) in each plot. The phylogenetic tree was

obtained with the comprehensive Angiosperm species-level phylogeny from Zanne et al. (2014), as updated by Qian and Yin (2015), which is included in the R package 'S. PhyloMaker' (Qian and Yin.2015). The distance of the few species that were not found in the PhytoPhylo were supplanted by the distance of the closest species of the same genus found in the mega-phylogeny tree (de la Riva et al., 2019). For each plot we calculated the species richness (Pielou, 1969), represented by the total number of species per plot, the Faith's phylogenetic diversity index (PD), the functional richness (Frich) and the mean pairwise dissimilarity (MPD) index for both functional and phylogenetic diversity. PD was calculated with the R package 'PICANTE'; Kembel et al. (2010). To quantify the Frich index, we built a functional space through a Principal Coordinate Analysis (PCoA), using a Euclidean trait matrix after standardizing traits (mean = 0, SD = 1) (Maire et al. 2015). We calculated the functional and phylogenetic MPD indices (FMPD and PMPD, respectively) based on existing algorithms (de Bello et al. 2016). These four indices integrate the main components of community structure enclosed by other related indices.

In order to account for trait coordination and to identify the major axes of trait variation, we run a Principal Component Analysis with the three CWM traits values (VH, SM and SLA) (Biotic_PCA). In addition, to reduce the number of variables characterizing the soil environment and their collinearity, other PCA was performed with the soil variables measured in this study (Soil_PCA). When necessary, variables were previously standardized and log-transformed to fulfil assumptions of normality (based on Kolmogorov-Smirnov) and homoscedasticity. We used an ANOVA analysis to check for differences on the distribution of the three types of habitats (Grassland, Shrubland, and Mixed) along the principal components analysis (PCA) in both biotic and soil PCAs. Post-hoc Tukey tests were performed to check the significance of differences between the least square means of each type of habitats. We also performed a one-way ANOVA to check for the variation of the diversity indices among habitats.

In order to evaluate shifts in the functional and phylogenetic structure distributions in response to edaphic factors, we used the generalized least-square model (GLS) controlling for the potential spatial correlation between soil variables associated with the type of habitat. We included a spatial autocorrelation structure using the cor-CAR1 function. We built one generalized least square regression model per community property; for each CWM trait and diversity index (respond variable) with the first and second Soil_PCA axes as predictors, using the gls function of the nlme package (Pinheiro et al. 2016). The variance explained by the GLS model was estimated by extracted the marginal R^2 value, which was calculated with the rsquared function in the 'piecewise SEM' package (Lefcheck 2016).

In addition, we used null models to check if the functional and phylogenetic diversity patterns were a trivial consequence of species richness variation. We randomized the traits combinations across species, while fixing the number of species of each plot (999 runs) and estimating the same functional and phylogenetic indices. For each index, we estimated the Standardized Effect Size (SES, = (observed difference - mean null difference) / SD null differences), in order to assess if the relationship observed between the functional and phylogenetic indices and the soil variables were significantly different from those obtained between randomized communities (null differences).

All the statistical analyses were performed using the R 3.1.3 software (R Development Core Team, 2014).

Results

Trait space distribution at community level was relatively well captured by the first two axes of the Biotic_PCA (Fig. 2). The first PCA axis accounted for 39.4% of overall variation and was related mostly with vegetation height. The second principal component, which explained 33.8% of the overall variance, was represented mainly by variations in SLA and SM. In addition, the first Soil_PCA axis (explaining 37.1% of the total variance) showed a high loading of soil nutrients (N, P, K, OM) and pH, while the second axis (which explained 22.1% of the variance) exhibited a high loading of pH at the top and K at the bottom (Fig. 3). The positions of the plots along the first and second Soil_PCA axes reflect the segregation of the different types of habitats (Fig. 3 and Table 1), while not significant differences were found among habitats for the Biotic_PCA (data not shown). Thus, shrublands were significantly segregated from the other habitats, showing the highest nutrient concentration. In contrast, the grasslands show significantly the lowest nutrient concentration (Fig. 3 and Table 1). Significant differences were also observed in the second axis, where the mixed ecosystem was segregated by its higher values of pH, while the shrubland was in the opposite end with higher values of K.

The PCA of soil environmental factors showed a first main axis associated with soil fertility, while the second axis represent a trade-off between pH and soil K, and both axes, from which plots segregate, were the most important factors associated with diversity variation (Fig. 4 and appendix S1). Also, Box plot show the variation of species richness and phylogenetic indices among habitats. The line inside the box represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles, and filled symbols show outliers. Different letters denote significant differences between habitats (Tukey's test). In this regard, the higher soil nutrient concentration (first Soil_PCA axis) and pH (second Soil_PCA axis) were significant and positive related with species and functional richness and Faith's phylogenetic distance, while not significant results were obtained for any functional trait at community level (SLA_{CWM} , VH_{CWM} and SM_{CWM} , data not shown) or for the functional and phylogenetic mean pairwise distance (appendix S1). Nevertheless, the results of this significant relationship were not consistent when applying the null model (SES). Therefore, the null model suggests that changes in functional richness and Faith's phylogenetic distance were the reflection of the variations in species richness (Appendix S2).

Discussion

Our results report several insights on the relationship between vegetation structure, soil nutrient concentration and land use in Damavand Mountain. The LHS strategy scheme assumes a certain degree of independence between these functional traits along three main dimensions (Westoby et al. 1998; Laughlin et al., 2010; Reich, 2014). Yet, our approach to this scheme focused on the community level does not uphold it. Our results show that trait distribution was relatively well capture by the first two axes of a principal component analysis (PCA) on which community trait values converge: one axis shows the

positive covariation between SLA and plant height; while the positive covariation between SLA and seed mass could be loaded on separate axes. Surprisingly, community-level trait composition was poorly captured by the habitat or soil variables. This result suggests that species with opposing trait values co-exist in the same habitat, which is unexpected. Similar results under different grazing regimes were obtained in arid environments (Vesk et al. 2004) or fertility gradients (Rusch et al. 2009), contrasting with others (Laliberté et al. 2012; Vaieretti et al. 2018). The discrepancy with our expectations could be due to the fact that we deliberately chose similar climatic conditions, to focus on grazing disturbance and soil nutrient availability. Arid conditions promote specific adaptations to the imposed climatic constraints, leading to relatively small differences in terms of functional syndromes (Reu et al. 2011; Bruelheide et al. 2018; de la Riva et al. 2018), and thus, despite some diversification of strategies exist (see Jacobsen et al. 2008), they are limited within the range of viable traits that allow plants to persist in this arid environment (de la Riva et al. 2016). Hence, aridity may limit the success of species that are not physiologically able to tolerate such water scarcity, reducing the range of functional traits. We acknowledge that our study is observational and, therefore, we cannot demonstrate if the results are a consequence of water deficit or of pre-existing patterns in the species assemblage, such as land use history. However, the fact that there were no different community trait syndromes among habitats, suggests that the climatic filtering act as dominant structuring processes of community trait composition, promoting strong trait convergence independently of the habitat (Gross et al., 2013; Bruelheide et al., 2018); while the local variation in environmental filters tends to alter species composition rather than functional composition, which has been previously observed in areas with relatively long disturbance history (Cingolani et al. 2005; Conti and Diaz. 2013).

Our results showed that soils from shrublands have higher nutrient concentration than grasslands. Trapping by livestock can lead to congestion and changes in levels of infiltration, bulk density and reduced destructive activities (Li et al., 2011b; Yu and Jia, 2014). Moreover, under long-term pressure of grazing, some energy and nutrients are transmitted to the diet (Li et al., 2011b; Lu et al., 2015), while shrublands can collect a large amount of soil organic matter due to the increase of litter on the soil surface by the lowering of bed decomposition (Nieder and Benbi, 2008). This could be the consequence of the reduction segregation of the nutrient concentration among habitats. Overall, it seems that the phylogenetic and functional patterns responded more to the taxonomic richness variations than to trait-based assembly processes. These results are consistent with other studies in grazing areas where variations of functional diversity were related with species diversity (Niu et al. 2015; Simova et al., 2015; Salgado-Luarte et al., 2019). However, we observed an overall low covariation between species richness and functional and phylogenetic mean pairwise dissimilarity. This implies that the mechanisms that support the coexistence of the species not necessarily support the functional or phylogenetic differentiation among those species (de Bello et al., 2006), and thus, while aridity could more strongly constrain the overall functional and/or phylogenetic dissimilarity among species, competition for available resources could induce a niche differentiation among plants reaching the higher species richness in more productive plots (Turner 2008; Ceulemans et al. 2017). This pattern is especially

common on resource-poor environment, where an increased availability of limiting resource may provide niche opportunities for coexisting plant species (Huston 1979, Willems et al. 1993; Turner 2008).

Overall, our research shows how some deterministic processes influenced functional and phylogenetic changes related with species richness in the semi-arid ecosystem from Damavand Mountain. However, the different traits and dimensions used show some correlations, and this, together with the lack of certain traits, which may be relevant to estimate a wide range of the functional niche occupation (e.g. belowground traits or leaf nutrients), could be limiting our assessments. Therefore, further studies based on meaningful syndromes or strategies should provide stronger tests of the underlying mechanisms causing community changes under different grazing regimes, which could be considerable importance in the effort to conserve taxonomic, functional and phylogenetic richness of these arid communities from west Asia.

Conclusions

In this study, we tried to discern the assemblage patterns of the semi-arid plant communities from Iran along natural nutrient gradient on three habitats. The functional and phylogenetic structures were mainly driven by soil nutrient availability, while the habitats, associated with three different grazing regimes, did not (apparently) exert any significant role. In fact, changes in the community functional and phylogenetic structure upon nutrient gradient can be explained by the variation of the species richness, while not differences were observed for the functional composition. Despite our observations also provide a significant understanding of the plant community assembly in these semi-arid communities from Damavand Mountain, long-term monitoring and higher number of functional dimensions are needed in future research. Our results show that the community-level trait composition was poorly captured by the habitat or soil variables. Soils from shrublands have higher nutrient concentration than grasslands, but this pattern has little effect over the functional or phylogenetic structure which tended to increase with nutrient content independently of grazing regimen. Also, suggest that the arid conditions of the region promote specific adaptations to the imposed climatic constraints, leading to relatively small differences in terms of functional syndromes, while the local variation in nutrient content tends to alter species composition rather than functional composition. Understanding the resistance of arid plant communities to global change is one of the most pressing issues to implement successful management measures. The results of this research can be used in major projects or implementation projects, because the functional and phylogenetic changes may help us to understand ecological processes, such as succession patterns and sustainability of communities. For instance, the species diversity and the soil characteristics seem to be a relevant driver of community structure and highlight the importance of considering the effects of ecological legacy on management plans. In this regard, favouring the expansion of shrubs patches on grasslands may promote communities with a higher nutrient concentration and species diversity, which could attenuate the potential impact of global change on these rangelands communities.

Declarations

Acknowledgement

The corresponding author would like to express his sincere gratitude to the Faculty of Natural Resource, Agricultural of Sciences and Natural Resources University, Sari for providing the facilities to do this research during a research project.

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Tables

Table 1.

Results of one-way ANOVA among habitats with the Soil PCA scores (see Fig. 3) for the three main axes. Abbreviations: Shr, Shrubland; Gra, Grassland; Mix, Mixed habitat.

Response variable	Df	F	p	Post-hoc
PC1	2	360.85	< 0.001	Shr>Mix>Gra
PC2	2	73.02	< 0.001	Mix>Gra>Shr
PC3	2	2.73	0.06	

Figures

Figure 1

(A and B) The location of the study area in Iran and Mazandaran province, (C) The southern hillsides of Damavand Mountain of rangelands

Figure 2

Principal components analysis (PCA) showing the trait distribution at community level (Community Weighted Means; CWM).

Figure 3

Principal components analysis (PCA) showing the soil variables per plot.

Figure 4

Relationship between the diversity indices at community level and the first and second PCA axes of the soil variables. The straight line corresponds to the estimated response of the diversity to soil variables by the GLS models.

Figure 5

Box plot show the variation of species richness and phylogenetic indices among habitats. The line inside the box represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles, and filled symbols show outliers. Different letters denote significant differences between habitats (Tukey's test).

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