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PLANT ALPHA AND BETA DIVERSITY IN RELATION TO SPATIAL DISTRIBUTION PATTERNS IN DIFFERENT PLANT COMMUNITY TYPES

NAGHMEH PIROOZI[1], ASGHAR KOHANDEL[2]*, MOHAMMAD JAFARI[3],
ALI TAVILI[3] AND GHASEM MORTEZAII FARIZHENDI[2]

[1]Department of Range Management, Science and Research Branch, Islamic Azad University, Tehran, Iran
[2]Iranian Academic Center for Education, Culture & Research (ACECR), University of Tehran, Iran
[3]Department of Reclamation of Arid and Mountainous Regions, Faculty of Natural Resources, University of Tehran
[4]Department of Reclamation of Arid and Mountainous Regions, Faculty of Natural Resources, University of Tehran
[5]Department of Academic Center for Education, Culture & Research (ACECR), University of Tehran, Iran
[*]Corresponding author's email: asgharkohandel@yahoo.com

Abstract

While β-diversity is shaped by spatial turnover and nestedness, research on the effects of spatial patterns of plants on these components of β-diversity is limited. Therefore, to determine how spatial pattern in different vegetation types may be related to plant α- and β-diversity as well as turnover and nestedness components of β-diversity, we assessed plant spatial patterns in three communities dominated by shrubs, woody and trees species in the semi-arid regions of central parts of Zagros mountain, Iran. In order to determine the spatial patterns of dominant plant, the Morisita index was used. Additive partitioning diversity was used to partitioning the total diversity (γ-diversity) into α-and β-diversity and partitioning β-diversity into spatial turnover and nestedness. The observed Morisita indices indicated that dominant species in forest and shrubland were aggregated (I_d = 1.445; I_d = 1.258, respectively) while, in woodland regular patterns observed (I_d = 0.94). The positive and negative effects of aggregated patterns were related to increase and decrease of diversity within and among samples, respectively, that reflected the role of disturbances filters on vegetation heterogeneity. Partitioning β-diversity into its components revealed that spatial turnover was the main contributor to β-diversity that revealed the overall patterns of multiple-sites dissimilarity of our plant communities were driven by the spatial turnover (species replacement) component and not by the nestedness component. We demonstrated that disturbance types affected the importance and interactions within plants in these communities, and caused different spatial patterns of the plant taxa resulted in variation on diversity components and turnover.

Key words: Additive partitioning, Aggregation, Biodiversity, Heterogeneity, Iran.

Introduction

Plant heterogeneity plays a fundamental role in the stability and maintenance of ecological communities. The two broad functional roles of vegetation heterogeneity are temporal and spatial heterogeneity that destabilizes and stabilizes ecosystems, respectively (Lilleeng *et al*., 2016). The robustness of ecosystem to disturbances is related to spatial heterogeneity. In addition, it also provides important ecosystem functions (e.g. recolonization and dispersal) by increasing resources (Hovick *et al*., 2015). On the other hands, homogenization of plant communities has resulted in a decline of ecosystems function, services and biodiversity (Derner *et al*., 2009; Fuhlendorf *et al*., 2010; Hovick *et al*., 2015). So, measuring of the spatial heterogeneity in different communities is necessary to evaluate ecosystem stability and resilience (Elmqvist *et al*., 2003; Lilleeng *et al*., 2016). It is accepted increasing of the heterogeneity could result in increase of diversity (Benton *et al*., 2003; Fahrig *et al*., 2011; Lilleeng *et al*., 2016), but determine the level of heterogeneity that maintain and maximizes diversity remains, however, largely unknown, especially in different plant communities.

α- and β-diversity, firstly introduced by Whittaker (1960), are two of the most key important indicators and are mostly considered in relation to measuring diversity (e.g. Rickert *et al.*, 2012; Zhang *et al*., 2014; Erfanzadeh *et al*., 2015). They play fundamental roles in ecological researches, however, the β-diversity indices are more than α-diversity (see review in Koleff *et al*., 2003; Anderson *et al*., 2011). There are two main approaches in order to quantitating of the α- and β-diversity [additive (γ = α + β; Lande, 1996) vs. multiplicative (γ = α × β; Whittaker, 1972)]. In this regards, additive diversity partition is more popular than multiplicative approach, because it expresses α- and β-diversity in the same unit and allow to direct compare of diversity components across spatial and temporal scales (Crist *et al*., 2003) that resulted in easily quantifying and interpretation (Zhang *et al*., 2014). On the other hand, it has been reported that β-diversity created by two different process, Turnover and Nestedness (Baselga, 2010). In this regard, Baselga (2010) has developed the method of additive partitioning to divide total dissimilarity (β-diversity) into turnover and nestedness components. Turnover refers to the replacement of some species by others, which may be the result of niche and dispersal processes, either contemporarily or historically (Angeler, 2013; Gutiérrez-Cánovas *et al*., 2013) while, nestedness accounts for the differences in composition when no species is replaced from one site to the other, which may be due to contemporary or historical processes such as selective extinction, selective colonization, or habitat nestedness (Dapporto *et al*., 2014; Si *et al*., 2015).

Plant distribution patterns (spatial patterns) is important property of plant community which has a key role in ecosystem stability (Mouro *et al*., 2007), competition patterns, reproduction and dispersal mods, evaluation of evenness in environmental variables (Dale, 2003; Measture *et al*., 2005) as well as plant diversity and heterogeneity (Haase, 1995). According to literature, attributes such as the number, relative abundance and identity (dominant) of species have the potential to influence these ecosystem features (Grime, 2001; Loreau *et al*., 2002; Measture *et al*., 2005). In addition, spatial patterns of plants need more attention when explaining observed patterns in ecosystem functioning and stability (Measture *et al*., 2005). Therefore, information of the spatial distribution of plants (especial dominant plant) is necessary for appreciate interpreting of diversity and heterogeneity. However, selecting the best methods (distance or quadratic) and indices remain a challenge that needs a special attention.

This study was applied on three vegetation types including: shrubland (dominated by *Astragalus gossypinus* Fischer.), woodland (dominated by *Amygdalus arabica* Oliv.), and forest (dominated by *Quercus brantii* Lindl.) in the semi-arid regions of central parts of Zagros mountain, Iran. In the present study, we attempted to address how was relation between plant diversity and heterogeneity with distribution patterns across three different plant community that were dominated by shrub, woody and tree species. In details, we tried to test the following questions:

(I) do shift in plant vegetation types lead to changes in diversity components (α- and β-diversity) and turnover? In other words, is there any significant difference among α- and β-diversity and turnover of shrubland, woodland and forest?

(II) Is there any relationship between spatial pattern of dominant species with diversity (α-diversity) and heterogeneity (β-diversity) in shrubland, woodland and forest. In detail, do the plant diversity components [α- and β-diversity] and turnover could reflect spatial patterns of different plant community?

(III) do the relative contribution of additive diversity components β-diversity differ among shrubland, woodland and forest communities?

Materials and Methods

Study area: The current study was carried out in the central part of Zagros mountain, Chaharmahal va Bakhtiari Province, Iran (extending between northern latitudes of 31° 31´ N and 31° 39´ N, and eastern longitudes of 50° 58´ E and 51° 03´ E), with an elevation of 1988 m above sea level (with minimum and maximum values of 1,846 and 2,131 m, respectively; Fig. 1). The average annual temperature and precipitation are measured as 17°C and 565 mm, respectively. The climate is arid-cold based on the Demarton climate classification, according to the updated world map of the Köppen-Geiger climate classification (Peel *et al*., 2007). Traditionally, the main land use in these areas has been livestock husbandry and rain-fed agriculture.

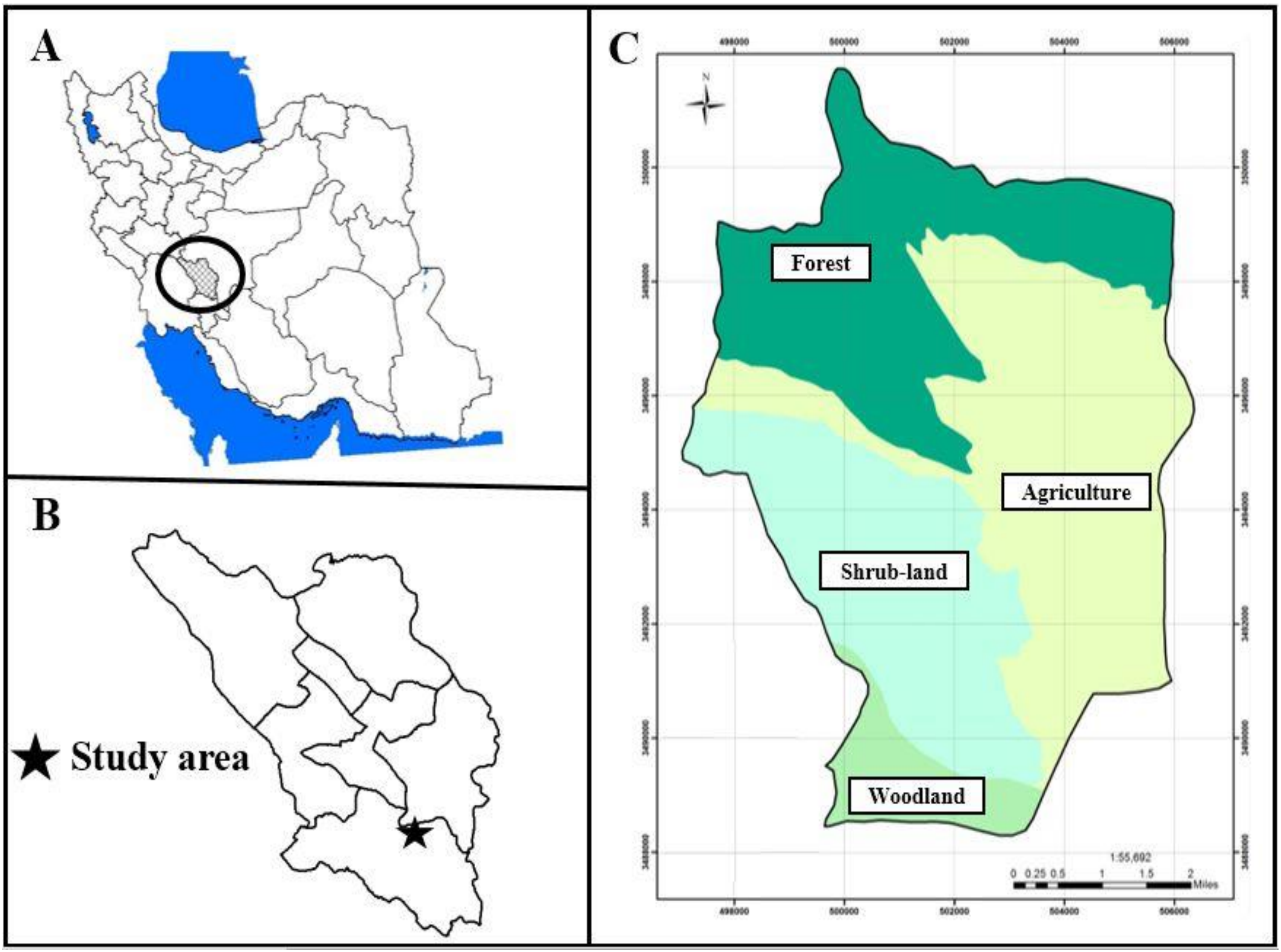

Fig. 1. Location of the study area, (a) in Iran, (b) in Charmahal va Bakhtiari Province and (c) location of vegetation types in the study area.

Sampling procedure: Within each vegetation types, firstly, several sites were visually selected (each site up to 10 ha). Then, sites that differed in soil patterns and geomorphologic conditions were removed. Finally, in each vegetation types, four smaller key-areas were selected for sampling of vegetation characteristics at the peak of growing season, from June to July. The key-areas were representative of the entire area in that location (Head & Child, 1994). Inside each key-area, 10 plots were systematically established, comprising a total of 40 plots in each vegetation types. In addition, by using the minimum area method (Kent & Coker, 1996; Barbour *et al*., 1999), sample plots were taken for tree species each one having a size of 10*10 m^2 as well as sample sizes of 4*4 m^2, and 1*1 m^2 for wood and shrub species, respectively. Within each plot, the number, percent, and name of all trees, wood and shrub species were counted and recorded.

Distribution patterns: As a measure of dominance plant distribution patterns in each community, Morisita index (I_d) was used (Krebs, 2000). The results of Morisita index can be interpreted as the probability that two individuals randomly drawn from the observed population belong to the same sample compared with the expected probability from a population with a random dispersion (Crist *et al.*, 2003). Therefore, it is expressed as a likelihood ratio that when I_d values >1 indicate spatial aggregation of individuals and when I_d values <1 indicate a regular dispersion pattern (Hurlbert, 1990), while $I_d = 1$ indicate a random dispersion pattern. This analysis was performed in Ecological Methodology software version 6.0.

Partitioning diversity: In this study, in order to calculating of diversity components within and among sample, additive partitioning diversity methods was used (Lande, 1996). According to this method, total diversity partitioned within and among sample (Lande, 1996; Crist *et al*., 2003). In current study, additive partitioning analysis was applied for all data gathered from the three vegetation types. Total diversity in each vegetation types was partitioned based on the additive partitioning methods (for more detail see Crist *et al*., 2003): $\gamma = \alpha_{1\ (\text{within plots})} + \beta_{1\ (\text{among plots})}$; where, γ is the total diversity in each vegetation types, α_1 denotes an average number of species within plots (α-diversity at the small scale), and β_1 is an average β-diversity (variations) at plots level. In this regard, firstly, the number of species in each plot was counted as α-diversity. It needs to be clarified that the total species in each key-area of different plant types were calculated as the total regional diversity (species richness or γ-diversity). Finally, β-diversity was calculated by difference between γ- and α-diversity ($\beta = \gamma - \alpha$) for each plot.

β-diversity was additively partitioned into the two components of spatial turnover and nestedness, using the method suggested by Baselga (2010). Thus, total multiple dissimilarity derived from the Sørensen coefficient of dissimilarity was decomposed into components of spatial turnover and nestedness. This analysis was performed using the "betapart" package (Baselga & Orme, 2012) within the R version 3.3.1 (R Core Team, 2016).

Statistical analysis: Comparison of α- and β-diversity components in different plant community were analyzed by Nested-ANOVA. This analysis was used according to the available hierarchical patterns of data (Erfanzadeh *et al*., 2016) because there were three vegetation types including forest, woodland, and shrubland, and there were four key-areas in each community. Prior to data analysis, normality and homogeneity of the data were tested using the Kolmogorov-Smirnov and Levene's test, respectively. The log-transformed function was used when normality assumptions were not met. Tukey's honestly significant difference (HSD) was used for pairwise comparisons, whenever appropriate ($p<0.05$). All analyses were performed in the R 3.3.1 statistical software (R Core Team, 2016).

Results

The observed means of the Morisita indices showed that dominant species in forest (*Quercus brantii*) and shrubland (*Astragalus gossypinus*) were aggregated (I_d = 1.445, I_d = 1.258, respectively) while, in the dominant species of woodland (*Amygdalus Arabica*) regular patterns observed (I_d = 0.94). In addition, the level of aggregation in the forest was more than those found in the shrubland (Table 1).

The results of nested-ANOVA showed that diversity within and among samples (α- and β-diversity, respectively) significantly differ among plant communities (main effect: F = 57.12, $p<0.0001$ and F = 86.92, $p<0.0001$, α- and β-diversity, respectively, Table 2). Moreover, key-area within plant types had significant effects on beta diversity (F = 0.12.66, P = 0.0004) while no significant effects were observed on alpha diversity (F = 0.43, P = 0.51).

According to the results, by shift plant community form shrubland to woodland, α-diversity (average diversity within plots) significantly increased (from 9.45±0.63 to 13.43±1.26, mean ± SE in shrubland and woodland, respectively, Fig. 2), while there was no significant difference between α-diversity in forest (9.5±0.81) and shrubland (Fig. 2).

In addition, the results showed that β-diversity of woodland (8.83±1.39) was significantly (*p*-value <0.001) lower than those of the shrubland (12.55±0.91) and forest (13.5±0.72), however there was no significant (*p*-value >0.05) difference between β-diversity of shrubland and forest (Fig. 2).

Partitioning of β-diversity into spatial turnover and nestedness components revealed that the former accounted for a greater percentage of the β-diversity in forest (0.84) than the woodland (0.64) and shrubland (0.82), indicating that turnover was more important than nestedness (Fig. 3). The contribution of turnover component of β-diversity was always four time more than nestedness in all plant communities. In other words, the contribution of turnover in forest, woodland and shrubland were 0.85, 0.82, and 0.83 percent to total β-diversity (Fig. 3).

Table 1. Distribution patterns of dominant plant spices in three plant community based Morisita index.

	Forest	Woodland	Shrubland
Dominant species	*Quercus brantii*	*Amygdalus arabica*	*Astragalus gossypinus*
I_d	1.445	0.940	1.258
Distribution pattern	Aggregated	Regular	Aggregated

I_d values >1 indicate spatial aggregation; I_d values <1 indicate a regular dispersion pattern; I_d = 1 indicate a random dispersion pattern

Table 2. Results of nested ANOVA for comparing diversity components (α- and β-diversity) subject to different plant types.

Diversity	Source	DF	SS	MS	F	*P*-value
α-diversity	Type	2	296.4613	296.4613	57.12444	<0.0001
	Key-area	3	2.242667	2.242667	0.432134	0.51
	Residuals	157	814.7898	5.189744		
	Total	162	1113.494			
β-diversity	Type	2	671.6113	671.6113	86.92099	<0.0001
	Key-area	3	97.79267	97.79267	12.65648	0.0004
	Residuals	157	1213.09	7.726687		
	Total	162	1982.494			

α-diversity: average diversity within plots in each plant types; β-diversity: average diversity among plots in each plant types

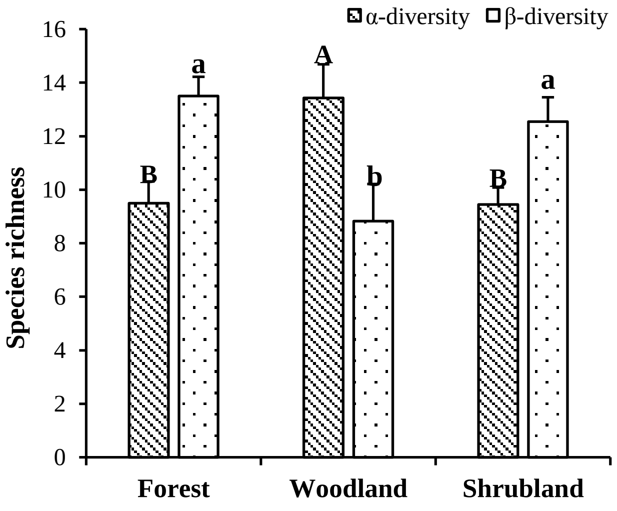

Fig. 2. The amount of α- and β-diversity in different plant types. Mean values ± standard errors are shown; different alphabetic letters indicate significant differences (p<0.05).

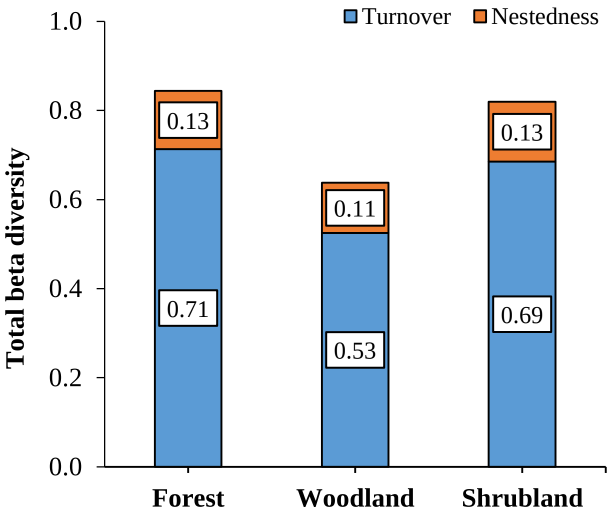

Fig. 3. The contribution of β-diversity components (turnover and nestedness) in forest, woodland and shrubland communities.

Discussion

The random spatial pattern of plants is rarely in natural plant communities and often plants spaced closer or farther away from one another than would be expected by chance (Stoll & Prati, 2001; Maestre *et al.*, 2005; Rayburn *et al.*, 2011). However, the causes, consequences and impacts of these patterns remain important topics in plant ecology (Raventós *et al.*, 2010). It has been demonstrated that there are several processes that generate plant spatial patterns such as plant-plant interactions (Phillips & MacMahon, 1981; Skarpe, 1991; Valiente-Banuet *et al.*, 2006), environmental heterogeneity (Schenk *et al.*, 2003; Perry *et al.*, 2009), seed dispersal (Schurr *et al.*, 2004), and disturbance (Rebollo *et al.*, 2002; Bisigato *et al.*, 2005; Rayburn & Monaco, 2011).

Morisita indices results indicated an aggregated distribution for dominant species in forest (*Quercus brantii*) and shrubland (*Astragalus gossypinus*). Similar results have been founded out in other studies for *Q. brantii* (Zabiholahii *et al.*, 2012) and *A. gossypinus* (Vahidi *et al.*, 2017) in Iran. However, distribution pattern of dominant species in woodland (*Amygdalus arabica*) was according to regular pattern. Spatial pattern of seed origin plant (reproduction by seed) is correlated with seed dispersal mods (Calviño-Cancela, 2002). Another reason for aggregated pattern in *Q. brantii* may be due to its heavy seed weight (6.13-19.9 gr, Alvaninejad *et al.*, 2010). In addition, the positive relationship between seed weight and seed germination of oak tree has been reported in Iran (Alvaninejad *et al.*, 2010) and other place (e.g. in red oak (Kormanik *et al.*, 1988); *Q. ilex* (Gomez, 2004)).

On the other hand, *A. gossypinus* is perennial shrub which play key role in nitrogen fixating. In addition, it is facilitats growth condition for its seed and other plants form (e.g. herbal grass and forb; see Jankju, 2013). Another explain for aggregated spatial pattern of Astragalus is high amount of moisture under their canopy cover (Maestre & Cortina, 2004; Gomez-Aparicio, 2009). Therefore, we thought that better condition (in soil properties and moisture) under Astragalus canopy cover resulted in aggregated patterns for shrubs communities dominated by *A. gossypinus*. On the other hand, disturbance by animal grazing is also recognized as significant mechanism that plays a critical role in spatial pattern formation (Adler *et al*., 2001; Seifan & Kadmon, 2006; Rayburn & Monaco, 2011). In this regards, Heydari *et al*., (2017b) reported that human activities and grazing were the main disturbance source in Zagros mountain of Iran. Finally, the regular pattern was observed for dominant species in woodland (*A. arabica*). The intense competition between plants for limited resources (Kenkel, 1988; Stoll & Bergius, 2005; Rayburn & Monaco, 2011) and negative plant-plant interactions (e.g. allelopathic; see in Gómez-Aparicio *et al*., 2004) is the potential mechanism for this patterns. The allelopathic effects for the genus of *Amygdalus* was reported by Zhang *et al*., (2012).

Generally, there are two main frameworks in order to partitioning beta diversity into its components including: turnover and nestedness (BAS; Baselga, 2010) and turnover and richness-difference (POD; Podani & Schmera, 2011). The different forms of indices are based on the same functional numerators and are complementary (Heydari *et al*., 2017a), and they can help researchers regard to understand different aspects of ecosystem functioning (Legendre 2014). However, both of these frameworks are valid and useable (Heydari *et al*., 2017a), but BAS is more frequently used than POD Indeed, Baselga & Leprieur (2015) showed that the turnover components of the BAS framework are independent of differences in richness, while the parallel component in the POD framework is not. Therefore, in our study we used the BAS framework to separate the contribution of β-diversity components.

β-diversity in the forest and shrubland were higher than those found in the woodland. It has been demonstrated that β-diversity increased with the degree of aggregation (e.g. Xu *et al*., 2015). Therefore, we think increase the level of community patchiness (aggregated or clumped) could resulted in decreasing of β-diversity. In addition, β-deviation could reflect the level at which spatial patterns of species deviate from a random distribution (Myers *et al*., 2013) therefore, more aggregated spatial patterns resulted in higher values of β-deviation. The results of spatial patterns in forest and shrubland that were aggregated compared to regular patterns in woodland, confirmed the results of β-diversity in our plant community. On the contrast to β-diversity, α-diversity was higher in woodland compared with in the forest and shrubland. Generally, α-diversity is defined as mean diversity (number of species in this study) observed within sample units in each scales (Crist *et al*., 2003). There are many researches that reported positive correlation between richness and evenness (e.g. Zhang *et al*., 2012). However, regarding empirical studies of the relationship between species diversity and evenness contrasting findings have also been reported including positively correlation (Hill, 1973), strongly negatively (Stirling & Wilsey, 2001) or independently (Wilsey *et al*., 2005) associated in plant communities. In the current study, we found a positive relation between α-diversity and spatial patterns of dominant species, because it was higher under woodland (regular pattern) than forest and shrubland (aggregated pattern).

The results of additive partitioning of β-diversity into its components (turnover and nestedness) showed that turnover had a greater contribution than nestedness. These results are similar to those reported by other researchers (i.e. Kouba *et al*., 2014; Boschilia *et al*., 2015; Lorenzón *et al*., 2016). The higher contribution of turnover than nestedness to β-diversity indicates that assemblages in species-poor plots are not a subset of assemblages of species-rich plots. In other words, from one site to another, the number of new species that replaces other species (turnover) is higher than that of species that appear without replacing other species (nestedness). As a result, the overall patterns of multiple-sites dissimilarity of our plant communities are driven by the spatial turnover (species replacement) component and not by the nestedness component.

Conclusion

The main findings of the present study were that different plant community types (shrubland, woodland, and forest) within the same landscape had different patterns in α- and β-diversity that reflected communities with aggregated patterns had high heterogeneity while, diversity within samples was higher under the regular pattern. In addition, we find that turnover is the main contributor of β-diversity than nestedness that highlighted the importance of species replacement. We conclude that there is low level for distribution in woodland due to low β-diversity and turnover comparing with forest and shrubland. Human activities and livestock grazing are main causes of degradation in forest and shrubland, respectively (Heydari *et al*., 2017b). However, the observed trend in α- and β-diversity were consistent in plant communities with different spatial patterns.

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