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REGULAR PAPER

Effects of fire disturbance on alpha and beta diversity and on beta diversity components of soil seed banks and aboveground vegetation

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Background and aims – Although an understanding of the effects of fire severity on diversity components of the soil seed bank (SSB) and aboveground vegetation (AGV) is important to inform conservation and restoration practices of biodiversity, the effects of fire severity on α- and β-diversity of SSB and AGV are poorly understood. While β-diversity is shaped by spatial turnover and nestedness, research on the effects of fire severity on these components of β-diversity is limited. We aimed to determine the effects of low and high fire severity on species richness and α- (within sample) and β- (among sample) diversity components on the relationship between the SSB and AGV. Since turnover and nestedness are components of β-diversity, we assessed their patterns of change after different fire intensities in the SSB and AGV.

Methods – Soil seed bank samples were collected from the same 180 sample points used for measurement of AGV in semi-arid *Quercus persica* woodlands. Additive partitioning diversity was used to divide total diversity into α-and β-diversity of the SSB and the AGV. Total β-diversity of the SSB and AGV was additively partitioned into spatial turnover and nestedness.

Key results – Fire severity had significant effects on α- and β-diversity of both the SSB and AGV. The highest and lowest richness and α- and β-diversity in both the SSB and AGV were found in low and high severity fire sites, respectively. Partitioning β-diversity of the SSB and the AGV into turnover and nestedness components revealed that spatial turnover was the main contributor to β-diversity. High fire severity significantly increased similarity between SSB and AGV.

Conclusions – Low, but not high, severity fire can increase species diversity in the AGV and SSB, and it has the potential to serve as a tool for management and restoration of semi-arid Mediterranean regions, thereby enhancing plant diversity and structural heterogeneity. However, high severity fire may lead to loss of many species in both the SSB and the AGV resulting in loss of biodiversity.

Key words – Additive partitioning, disturbance, nestedness, semi-arid, turnover, woodland.

INTRODUCTION

Since species diversity can change across different spatial or temporal scales, diversity patterns in a plant community or soil seed bank need to be analysed at different spatial and temporal scales (Crist et al. 2003). For example, it is known that low and moderate severity fires can increase species diversity and richness in a plant community by providing additional ecological niches and preventing competitive exclusion of rare species (Pourreza et al. 2014b). However, high severity fires can decrease species diversity, richness, and evenness of both the soil seed bank (SSB) and aboveground vegetation (AGV) (Pywell et al. 2002, Mamede & Araujó 2008). The challenge is how to analyse the effects of varying fire intensities on the SSB and AGV.

One way to analyse the pattern of plant distribution at different scales is to use diversity partitioning methods (additive or multiplicative). The idea of diversity partitioning originated with Whittaker (1960), who described alpha (α,

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within sample) and beta (β, among sample) diversity as components of the total diversity (gamma, γ) and linked them to a spatial scale. Although the effects of fire on SSB and AGV have been widely considered (Rawson et al. 2013, Pourreza et al. 2014b), little is known about the effects of fire severity on α and β components. Thus, although partitioning is extensively used for analysis of the diversity component in spatial-temporal scales, it is very rarely used in SSB and AGV studies (e.g. Elsey-Quirk & Leck 2015). Further 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). On the other hand, 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).

Although methods are available for looking at α- and β-diversity and the turnover and nestedness components of β-diversity, they have not been widely used to better understand the effects of varying fire intensities on SSB and AGV. Thus, our main objective was to use additive diversity partitioning to understand how plant species diversity of the SSB and AGV changes across three disturbance regimes (non-burned, low severity fire and high severity fire) in semi-arid woodlands in the Zagros region of western Iran. Based on information from previous studies on responses of vegetation to fire (e.g. Pourreza et al. 2014a, 2014b, Pywell et al. 2002, Mamede & Araujó 2008), we formulated and tested three hypotheses. (1) Total (γ) diversity for both SSB and AGV is the highest in areas with low severity fire due to formation of additional ecological niches and prevention of competition. (2) In both non-burned areas and areas with low severity fires, α-diversity components contribute less to γ-diversity than β-diversity components (for both SSB and AGV) because of high habitat heterogeneity. However, in areas with high severity fires β-diversity components contribute less to γ-diversity than α-diversity components because of high habitat homogeneity resulting from the localized loss of species from the SSB and AGV due to fire. (3) The turnover component of β-diversity contributes more to total diversity than does the nestedness component at non-burned sites and sites subject to low severity burns, but high severity burns increase the contribution of nestedness to total diversity due to localized loss of species from the SSB and AGV, respectively.

MATERIALS AND METHODS

Study area

The study area covers 153 ha in Bankol, Ilam Province, Western Iran (fig. 1). Mean annual rainfall is 560 mm, and

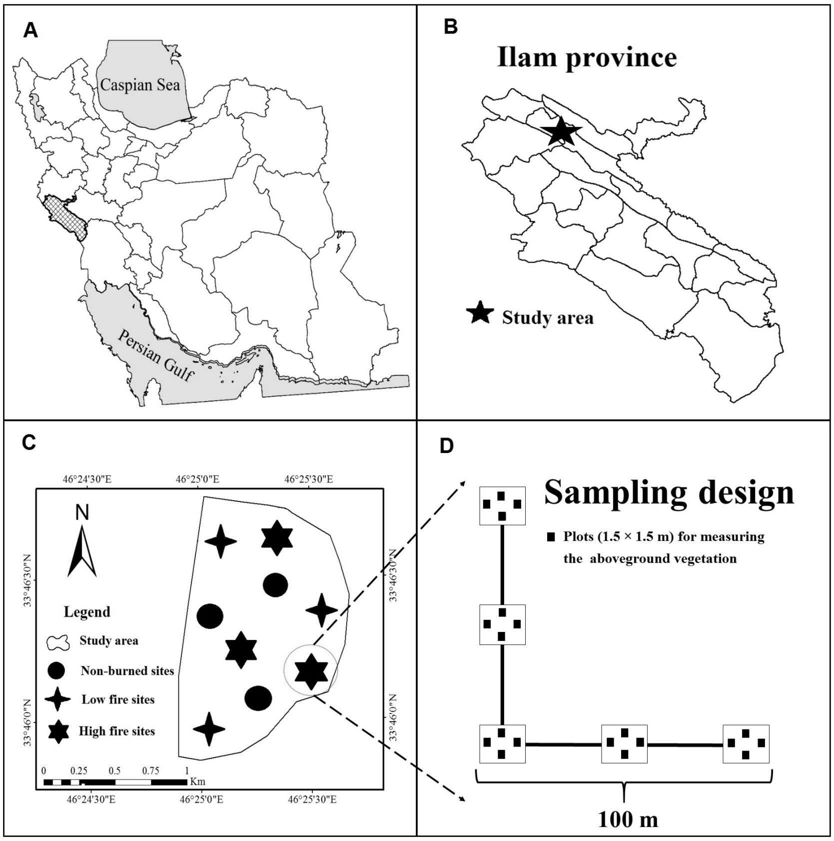

Figure 1 – Location of the study area in: A, Western Iran; B, Ilam Province; and C, selection of low and high fire and control areas in Bankol region. D, the sampling design (in each of the nine sample sites, the two perpendicular transects of 100 m were established).

Table 1 – **Classification of fire severities based on visible indicators.**

Fire severity	Visible indicators
Non-burned	No evidence of fire, litter accumulation, soil surface covered by litter, high cover of herbaceous, sprouts survived
Low severity burns	No obvious evidence of fire (only the scorched collar of burned grasses and annual plants), no litter, high cover of herbaceous, sprouts survived
High severity burns	Obvious evidence of fire, litter consumed, soil surface bare or covered by ash, low cover of herbaceous cover, sprouts consumed or dead (not survival)

mean maximum and minimum annual temperatures are 18 °C and 6 °C, respectively. Overall, the environmental conditions correspond to a Mediterranean climate. The study area is homogenous in terms of physiographic conditions and is characterized by a generally flat topography. The dominant tree species in this region is oak (*Quercus persica* Jaub. & Spach), and it occurs in more than 90 % of the study area. The dominant understorey species are species such as *Bromus tectorum* L. and *Medicago rigidula* (L.) All. (see electronic appendix). The soil is classified as a clay loam Typic Humixerept. Fire is an important ecological factor in the Zagros region (Pourreza et al. 2014a, 2014b, Heydari et al. 2016) that usually is of non-prescribed origin and mostly occurs during summer (especially July and August).

Several fire events, mainly of human origin and sometimes naturally have occurred in these woodlands in recent decades. In our study area, there are not records of a serious fire in the recent decade until September 2013, when a fire occurred. The origin of this fire is not known, but the forest ranger suggested that it might be due to sunlight shining into a glass bottle abandoned on the forest floor (non-prescribed origin).

Sampling

The study area was subjected to a fire of varying severity during September 2013 (after seed dispersal of most species), after which we delimited each burned area by considering all areas surrounded by non-burned woodland. The burned areas were scattered as separate burned patches. Fire severity was determined in each burned patch by using a classification system based on visible indicators such as litter depth, sprout consumption and mortality, ash cover, and vegetation reestablishment (table 1). According to this procedure, we identified two levels of fire severity: low and high severity, and non-burned was the control.

Soil seed bank (SSB)

A sampling site was located in each of three randomly-selected low severity burned patches and three high severity burned patches, and in each of three comparable non-burned control areas between these patches. Two perpendicular transects of about 100 m in length were established in each of the nine sample sites (patches).

For each of the nine sample sites, five sample points were located along two perpendicular transects (two sample points along each transect and one where the transects met). Around each of the 45 sample points, four plots were randomly established for collecting soil samples for seed bank analysis (180 samples). Soil samples were collected in November 2013. For each of the 180 samples, soil was collected from a 20 cm × 20 cm area to a depth of 10 cm. The litter layer was included in each soil sample, because it may have contained seeds. Samples were bagged and refrigerated at 3–4 °C for 3 months to cold-stratify the seeds (Heydari et al. 2013).

The seedling emergence method (in greenhouse at 20–25 °C and natural light conditions) was used to determine the number of viable seeds in the soil. Each sample was wet-sieved (0.2 mm) and the retained material spread in a layer (< 1 cm deep) on 3 cm of sterilized sand in a plastic tray (45 cm × 45 cm × 5 cm). Fifteen trays containing only sterilized sand were placed among the sample trays to test for contamination by local seeds. No seedlings appeared in these control trays during the course of the germination test. Seed trays were kept continuously moist by daily watering, and the position of each was changed every two weeks to avoid differences in light exposure. Every week, all seed trays were checked for seedlings. Newly emerged seedlings were identified, counted and removed from the trays. Soil samples were maintained and checked for emerging seedlings for nine months. During this period, soil samples were stirred four times to bring any non-germinated seeds to the surface to increase the possibility of exposing them to light and thus promoting germination. Plant growth form namely annual forb, annual grass, biennial forb, perennial forb, and perennial grass, and plant life form (according to the Raunkiaer 1934 classification scheme) was determined for each species found in the soil samples.

Aboveground vegetation (AGV) sampling

At each of the 45 sample points, four plots (1.5 m × 1.5 m) were randomly established for measuring the aboveground vegetation during the period of peak vegetative growth (i.e. May and June 2014). In each plot, we recorded the frequency and the percentage cover of each plant species, which was identified using available literature (Ghahreman 2000).

Partitioning diversity

We used additive partitioning to calculate and compare diversity components (α- and β-diversity) of both the SSB and AGV at local spatial scales across the different fire severities. This analysis was done for total data coming from the three treatments as well as for the SSB and AGV separately. Total SSB and AGV diversity in our study was partitioned according to the indices described in each treatment (See also Crist et al. 2003):

$$\gamma = \alpha_{1\,(\text{within plots})} + \beta_{1\,(\text{among plots})}$$

where γ is the total diversity (for SSB and AGV), α_1 is an average number of species within plots (α-diversity at the small scale) and β_1 is the average β-diversity (variation) at plot level. This procedure was repeated separately for calculating of α- and β-diversity of both the SSB and AGV for each fire severity. In this regard, we first considered the number of species in each plot as α-diversity, while the total species in each treatment was the total regional diversity (species richness or γ-diversity). β-diversity was calculated as the difference between γ- and α-diversity ($\beta = \gamma - \alpha$) for each plot.

Data analysis

α- and β-diversity components of both SSB and AGV were calculated for diversity components within and among plots for the three treatments according to the additive partitioning method. These analyses were performed using R version 3.1.3 (R Core Team 2015) and the “vegan” package (Oksanen et al. 2015) was used for calculating the species richness index. For calculation of the floristic similarity between SSB and AGV, Sørensen’s index of similarity (Sørensen 1948) was used:

Sørensen similarity $= 2w/(2w+A+B)$,

where A is the number of species found only aboveground (AGV), B is the number of species found only belowground (SSB), and w is the number of species found in both the SSB and AGV. The diversity component of SSB and AGV was analysed by nested ANOVA to determine the effects of fire severity on SSB and AGV diversity. This analysis was done according to the three hierarchical patterns of our data (Erfanzadeh et al. 2016), since there were three treatments (control, and low and high fire severity) and three sites/patches (each patch sampled by five quadrats) in each treatment. Prior to analysis of variance, normality and homogeneity of the data were tested using the Kolmogorov-Smirnov test 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 version 3.1.3 (R Core Team 2015).

Finally, we additively partitioned β-diversity 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 (Baselga 2010). This analysis was performed using the “betapart” package (Baselga & Orme 2012) within R version 3.1.3 (R Core Team 2015).

RESULTS

We recorded a total of 46 plant species in thirteen families, and more than half of the species belonged to the Asteraceae (fourteen species), Apiaceae (six species), and Euphorbiaceae (five species). Annual and perennial forbs (50 % and 37 %, respectively) were the main growth forms in AGV and SSB (67 % and 20 %, respectively; electronic appendix 1). Biennial forbs only occurred in the AVG (4 %; electronic appendix).

The effect of fire and fire severity on SSB and AGV differed with plant growth form. In the SSB, annual forbs accounted for 80 % of all species in the non-burned plots, compared to 69 % and 17 % in plots subjected to low and high fire severity, respectively, while annual grasses increased 10 %, 12 % and 49 % in the control, low and high fire severity, respectively. On the other hand, percent composition of annuals in AGV did not differ between fire treatments. The percentage of biennial and perennial forbs also did not differ significantly between plots subjected to the different fire treatments (fig. 2). The percentage of perennial grasses was higher in the high fire than the low fire and control sam-

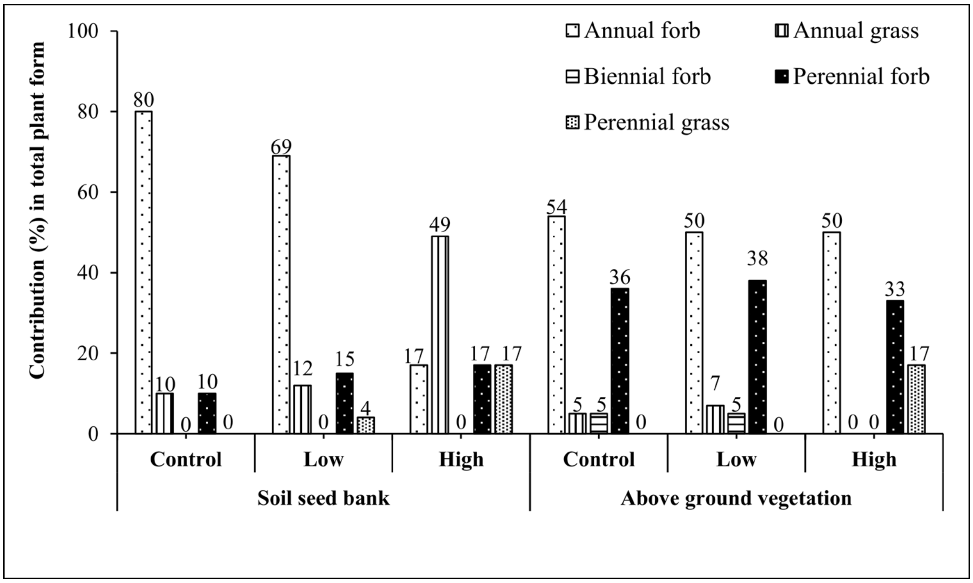

Figure 2 – Effect of fire severity on contribution of different plant growth forms in the soil seed bank and the aboveground vegetation. In each treatment (control, low and high fire severity), the contribution of each plant growth form (annual forb, annual grass, biennial forb, perennial forb, and perennial grass) is shown as a percentage. The numbers on the bars indicate the contribution (%) of each plant growth form.

Table 2 – **The percentage of species according to life forms in soil seed bank (SSB) and aboveground vegetation (AGV) under different fire severities.**

Biological type	Whole data		Soil seed bank			Above ground vegetation		
	SSB	AGV	Control	Low	High	Control	Low	High
Chamaephytes	3	2	0	4	0	0	2	0
Cryptophytes	0	2	0	0	0	3	2	0
Hemicryptophytes	37	52	29	31	67	51	50	67
Therophytes	60	44	71	65	33	46	46	33
Sum	100	100	100	100	100	100	100	100

ples for both the SSB and AGV (fig. 2). Therophytes (annuals) and hemicryptophytes (perennials with buds in/on the soil surface) were the most frequent life forms in the SSB (60 % and 36 %, respectively) and AVG (44 % and 52 %, respectively). The proportions of therophytes and hemicryptophytes in the SSB differed between the control and high fire severity areas. Therophytes and hemicryptophytes in the SSB accounted for 71 % and 29 %, respectively, of the species in the control and 33 % and 67 %, respectively, of those in the high fire severity areas (table 2). *Helianthemum salicifolium* (L.) Mill. was the only chamaephyte (perennial with buds slightly above the soil surface) observed in the low fire samples of the SSB and AGV, while *Allium stamineum* Boiss. was the only geophyte (buds below the soil surface) in the control and low fire samples of the SSB and AGV (electronic appendix).

Plant species in the high fire samples of both the SSB and AVG were very similar, and some species appeared in both the SSB and AGV of the low fire samples but not those of the control. The highest and lowest richness in the SSB and AGV were found in low (27 and 42 species) and high (6 and 6 species) severity fire areas, respectively. Diversity partitioning indicated that α-diversity (within plots) was the largest contributor to total diversity for both the SSB and AGV, and it was two times greater than β-diversity in the whole data set. However, in high fire severity plots α-diversity and β-diversity in AGV were about equal (fig. 3).

The fire severity had significant effects on α-diversity and β-diversity of both the SSB and AGV (table 3). The results of pairwise comparison of means (HSD) showed that the relative contribution of α- and β-diversity to total diversity of the SSB differed significantly between treatments. The contribution of α- and β-diversity was significantly lower in plots subject to high severity burns, compared with the other treatments (fig. 4A & B). For the AGV, the highest and lowest α- and β-diversity occurred in low and high fire severity areas, respectively; however, there was no significant different between α- and β-diversity in control and low fire severity areas (fig. 4C & D). In addition, the proportion of β-diversity with respect to α-diversity was higher in the AGV than in the SSB, regardless of treatment.

Sørensen's index of similarity between the SSB and AGV was significantly greater for areas subject to high severity burn than for areas subject to low severity burn or no burning (control), and there was no difference between the last two (fig. 5). Partitioning of β-diversity into spatial turnover and nestedness components revealed that the former accounted for a greater percentage of the β-diversity in AGV than the

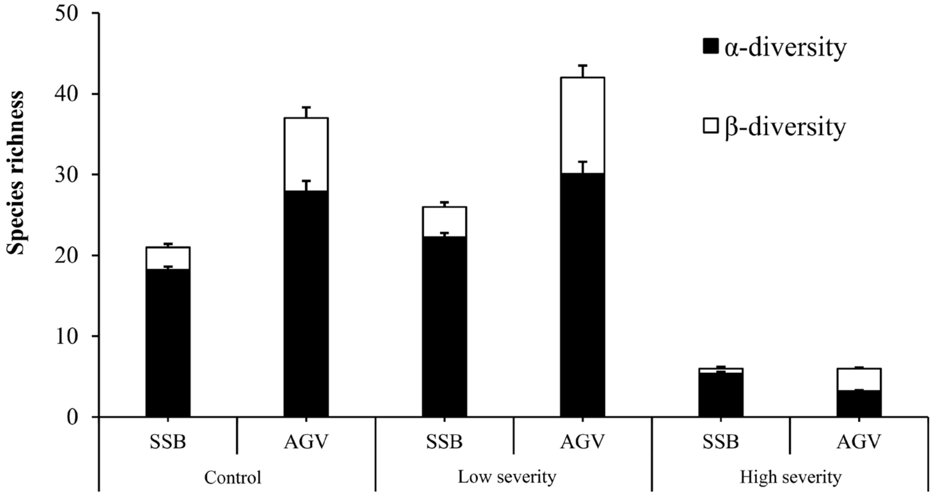

Figure 3 – Mean (± SE) of diversity components (α-diversity vs. β-diversity) of SSB and AGV under different conditions: control and low and high fire severity. SSB, soil seed bank; AGV, aboveground vegetation.

Table 3 – **Results of nested ANOVA for comparing diversity components (α- and β-diversity) between AGV and SSB between our treatments (different fire severity including control, low, and high fire severity sites) and sites (in each treatment: 3 stands including 5 quadrats).**
AGV, aboveground vegetation; SSB, soil seed bank; DF, degrees of freedom; SS, sum of squares; MS, Mean Squares, F, F-ratio; P-value, significance value.

	Diversity component	Source	DF	SS	MS	F	P-value
AGV	Alpha	Treatment	2	4224.53	4224.53	88.29	< 0.001
		Site	2	709.63	709.63	14.83	0.0003
		Residuals	42	2009.61	47.85		
		Total	46	6943.778			
	Beta	Treatment	2	396.03	396.03	15.16	0.0003
		Site	2	193.57	193.57	7.408	0.009
		Residuals	42	1097.51	26.13		
		Total	46	1687.11			
SSB	Alpha	Treatment	2	1228.8	1228.8	69.67	< 0.0001
		Site	2	415.14	415.14	23.54	< 0.0001
		Residuals	42	740.86	17.64		
		Total	46	2384.8			
	Beta	Treatment	2	36.3	36.3	10.19	0.002
		Site	2	18.94	18.94	5.319	0.026
		Residuals	42	149.56	3.56		
		Total	46	204.8			

latter, indicating that turnover was more important than nestedness in the AGV (fig. 6A). Thus, in the AGV, the contribution of turnover increased and that of nestedness decreased from the non-burned to the high fire severity areas (fig. 6A).

For the SSB, the turnover component of β-diversity in control and low fire severity sites was similar to that for the AGV (i.e. 77 % and 78 % for control and low fire severity SSB, respectively). However, in high fire severity the nestedness and turnover components of β-diversity of SSB were 60 % and 40 %, respectively (fig. 6B). In other words, high fire severity increased the contribution of nestedness and decreased that of turnover.

DISCUSSION

Our study is one of the first to assess α- and β-diversity components of SSB and AGV in relation to fire severity. Previous studies have focused mainly on the effects of fire and its

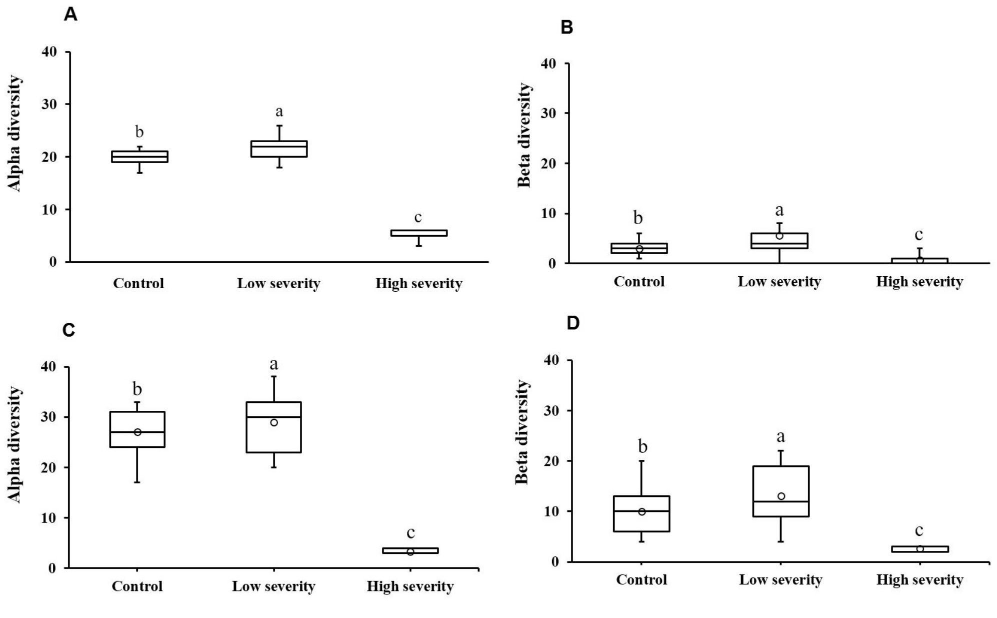

Figure 4 – Diversity components under different treatments: control, low and high fire severity. A, α-diversity in SSB; B, β-diversity in SSB; C, α-diversity in AGV; D, β-diversity in AGV. Different letters on each box-plot indicate significant differences ($P < 0.05$). SSB, soil seed bank; AGV, aboveground vegetation.

severity on the SSB and AGV without considering diversity components (Snyman & van Wyk 2005, Esposito el al. 2006, Rawson et al. 2013, Naghipour et al. 2015). Using three fire intensities as the disturbance treatments, we have revealed that the diversity partitioning method can provide insight into the dynamics of the effects of fire on the diversity of the SSB and AGV.

Therophytes and hemicryptophytes were the predominant life forms in both the SSB and AGV (whole data; table 2). The high frequency of these two life forms is not surprising because they are well adapted to harsh environments (i.e. arid and semi-arid regions) (Heydari et al. 2016). Further, therophytes and hemicryptophytes are the most common life forms in many semi-arid areas of Iran (Heydari et al. 2013), which generally are closely related to the Mediterranean climate conditions that characterize the Zagros region.

In our study, the relative contributions of α and β diversity to total observed regional diversity (γ-diversity) were consistent among all the treatments for the SSB. These results indicate a similar effect of different fire intensities on diversity components, and diversity within plots (α-diversity) made the highest contribution to the total diversity in all cases (table 1). High local habitat homogeneity may explain this pattern of diversity components of the SSB that created a great evenness within our sample units. This result is in contrast with that of Elsey-Quirk & Leck (2015) who reported a trend of increasing richness in the seed bank with an increase in spatial scales. We think our contrasting results are due to the fact that we did not consider the spatial patterns of the SSB and AGV in our study (i.e. our study was done at one scale). When species abundance was included, seed bank diversity was largely accounted for at the smallest scale, and vegetation diversity was largely accounted for locally, i.e. within- and/or between-plots (Elsey-Quirk & Leck 2015). Thus, it appears that widespread and common species contributed to relatively high small-scale diversity (Crist et al. 2003, Sasaki et al. 2012).

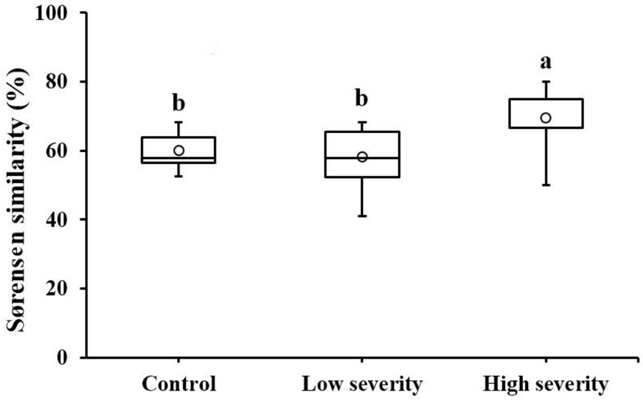

Figure 5 – Sørensen's index of similarity between soil seed bank and aboveground vegetation in different conditions: control and low and high fire severity. Different letters on the box-plot indicate significant differences (P < 0.05).

Analyses of the relative contributions of α- and β-diversity to total regional diversity of AGV demonstrated that α-diversity had a higher contribution in non-burned and low severity fire (75 and 72 % of total regional diversity, respectively) areas than β-diversity. On the other hand, in high severity fire areas α- and β-diversities were very similar (close to 50 %). Thus, different fire intensities can change the relative contribution of diversity components. For example, low severity fire can reduce competition by removing aboveground vegetation (Kinloch & Friedel 2005), resulting in an increase of species establishment and increased α-diversity. However, by knowing that β-diversity is the result of environmental heterogeneity in space and time (Loreau 2000), we can conclude that due to direct and unequal heating of the AGV in a high severity fire (Tyler 1995) local habitat heterogeneity increased, resulting in an increase in β-diversity. Since there was a higher contribution of α-diversity to total regional diversity (γ-diversity) than β-diversity, we conclude that our sampling units had uniqueness of composition. In other words, uniqueness of composition leads to an increase in contribution of α-diversity to total regional diversity as well as turnover in total dissimilarity (β-diversity).

There was a high degree of similarity between the SSB and AGV in all our treatments, and the highest similarity was in the areas with high severity fire (67 %). However, in other studies, disturbance increased similarity between SSB and AGV (Ungar & Woodell 1996, Ma et al. 2010), decreased similarity (Tessema et al. 2012, Erfanzadeh et al.

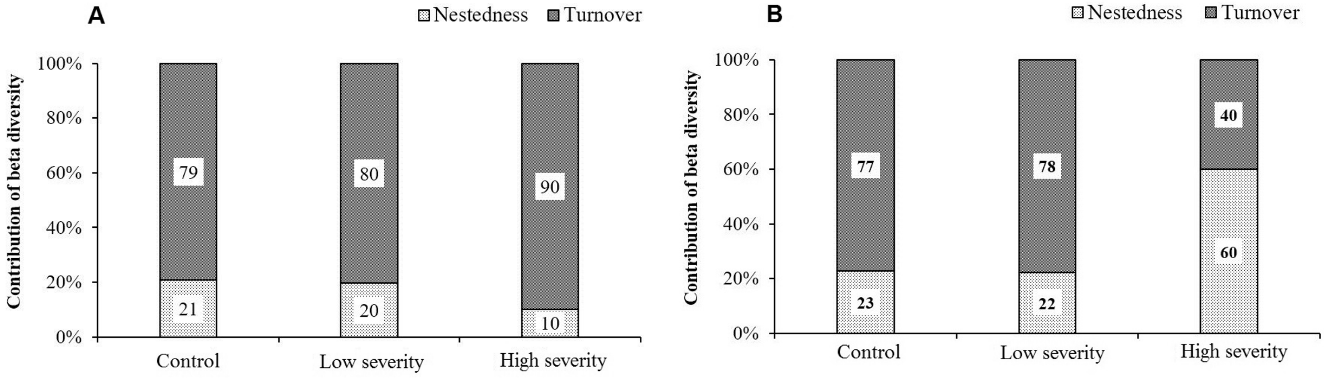

Figure 6 – The contribution of β-diversity components (turnover and nestedness) in A, AGV and B, SSB in relation to fire severity. SSB, soil seed bank; AGV, aboveground vegetation.

2016), or had no significant effect on similarity (Naghipour et al. 2015). We think the high similarity in the high severity treatment is due to low species richness in this treatment. In other words, high fire severity could eliminate many of the plant species that are sensitive to fire and only those that are fire tolerant remain in the AGV. Then, fire tolerant species become the main contributors to the SSB, thus resulting in high similarity between the AGV and SSB. In addition, an increase in similarity of plant composition (due to increased homogeneity) could lead to a large decrease of β-diversity, and our results (fig. 3) support this conclusion, i.e. the contribution of α- and β-diversity to total regional diversity in SSB (γ-diversity) were 90 % and 10 %, respectively.

Another finding of our research is that diversity components and total richness of the SSB and AGV in low severity fire were greater than in the non-burned or high severity fire areas. Low fire severity can have several direct and/or indirect effects on the post-burn flush of seedlings by (1) direct heating of the seed bank that could affect dormancy break and seed germination (Tyler 1995) or by production of smoke that could promote germination (Baskin & Baskin 2014); and (2) removing aboveground vegetation that leads to a reduction in competition (Kinloch & Friedel 2005), thereby allowing seedlings greater access to light and water (Snyman 2004) and reducing allelopathic influences (Keeley et al. 1985).

The intermediate disturbance hypothesis model (IDH model) states that plant diversity should be highest at intermediate levels of disturbance (Connell 1978), while the dynamic equilibrium model (DEM) says that moderate disturbance intensity, e.g. fire or grazing) (Mackey & Currie 2001) should have positive effects on diversity in high-productivity systems and negative effects in low productivity systems. In this regard, our results support the IDH model, because diversity components and total richness were highest in areas subjected to low fire severity. Therefore, we concluded that low fire severity can be used as a management tool to enhance plant diversity and structural heterogeneity, especial in the arid and semi-arid oak woodlands of Western Iran. In this regard, Erfanzadeh et al. (2015) argued that low disturbance (i.e. grazing) intensity is likely to be an important tool for conservation of plant diversity.

There are two main frameworks for partitioning beta diversity: turnover/replacement and nestedness (BAS; Baselga 2010) and turnover/replacement and richness-difference (POD; Podani & Schmera 2011). The different forms of indices are based on the same functional numerators and are complementary, and they can help researchers understand different aspects of ecosystem functioning (Legendre 2014). However, both of these frameworks are valid and useable, but BAS is more frequently used than POD. Further, 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 the turnover and nestedness components of β diversity.

The results of additive partitioning of β-diversity into its components (turnover and nestedness) showed that turnover had a greater contribution than nestedness (except for high fire severity in SSB). These results are similar to those reported by other researchers (i.e. Kouba et al. 2014, Boschilia et al. 2016, 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 SSB and AGV are driven by the spatial turnover (species replacement) component and not by the nestedness component.

One of the main results of our research was that high fire severity had different effects on the contributions of turnover and nestedness in the SSB and AGV. That is, high fire severity increased the contribution of turnover components of β-diversity in AGV compared with non-burned and low fire severity, while high fire severity increased the nestedness contribution by more than half (60 % and 40 % for nestedness and turnover, respectively) in SSB. We conclude that, due to species loss in high fire severity in SSB (only six species remained), some species that remained after fire were a subset of other plots (five of this six species appeared in all sampling units), resulting in nested patterns (i.e. elimination or addition of species between plots; Baselga 2010). However, in the AGV substitution of species between plots leads to an increase contribution of spatial turnover to total multiple dissimilarity (β-diversity). Fire can change environmental conditions, thus the ecological niches for some species may no longer be available, causing the species to disappear. However, new species that are adapted to the new conditions could become established, resulting in species replacement that leads to a greater increase in the contribution of turnover than nestedness.

CONCLUSIONS

We found that total regional diversity of the SSB and AGV (γ-diversity) was more related to within sample diversity (α-diversity) than to among sample diversity (β-diversity). In addition, partitioning β-diversity of the SSB and AGV into turnover and nestedness components revealed that spatial turnover was the main contributor to β-diversity in the semi-arid Mediterranean woodlands of western Iran. High fire severity increased the contribution of nestedness and decreased that of turnover. That is, after high fire severity some species are removed and new ones have not replaced them. On the other hand, low severity fire can increase plant and seed bank diversity and has the potential to serve as a tool for management and restoration of semi-arid Mediterranean regions and thus enhance plant diversity and structural heterogeneity. However, high severity fire may lead to loss of many species in both the SSB and the AGV resulting in loss of biodiversity.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consists of a list of species according to family, growth form, and life form in the soil seed bank (SSB) and aboveground vegetation (AGV).

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