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The effects of woody plant encroachment and wildfire on plant species richness and composition: temporal changes in a forest-steppe mosaic

Running title: Shrub encroachment and wildfire

Gábor Ónodi^{1*}, Miklós Kertész¹, Attila Lengyel¹, Ildikó Pándi², László Somay¹, Katalin Szitár¹, and György Kröel-Dulay¹

¹ Centre for Ecological Research, Institute of Ecology and Botany,
Alkotmány 2-4, H-2163 Vácrátót, Hungary

² Szent István University Gödöllő Botanical Garden,
Páter Károly 1, H-2100 Gödöllő, Hungary

* Correspondence: Gábor Ónodi

E-Mail: onodi.gabor@okologia.mta.hu

ORCID ID: <https://orcid.org/0000-0003-4308-7997>

E-Mail addresses of the further authors:

kertesz.miklos@okologia.mta.hu

lengyel.attila@okologia.mta.hu

pandi.ildiko@gmail.com

somay.laszlo@okologia.mta.hu

szitar.katalin@okologia.mta.hu

kroel-dulay.gyorgy@okologia.mta.hu

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40 Abstract

41

42 Questions

43 Woody plant encroachment and wildfire may both have major effects on species richness and composition, yet
44 studies that assess these two factors in combination are rare. We asked the following specific questions. (1) How
45 did juniper cover change over a decade in the study area? (2) What are the effects of juniper encroachment and
46 subsequent wildfire on plant species richness, and (3) on vegetation composition?

47

48 Location

49 Sand forest-steppe in Kiskunság, Central Hungary.

50

51 Methods

52 We studied a juniper encroached grassland hit by a wildfire. We assessed changes in plant species richness and
53 composition in burnt and unburnt grassland and juniper plots for eleven years following the wildfire. Yearly
54 vegetation sampling was performed in permanent quadrats of 1 m² and 25 m² using visual cover estimation.
55 Temporal changes of juniper cover, and species richness were evaluated with generalized linear mixed-effects
56 models. Compositional changes were analysed by non-metric multidimensional scaling and fidelity analysis.

57

58 Results

59 At the beginning of the study, the presence of individual juniper shrubs increased species richness, and did not
60 alter species composition. However, microsites covered by junipers were extremely species poor. Juniper growth
61 during the study period caused sharp decline in species richness at the edge of juniper shrubs and a shift in species
62 composition compared to grassland plots. Wildfire increased species richness both in grassland and juniper plots.
63 It caused only transient compositional responses in grasslands, but converted juniper habitats back to grassland
64 state.

65

66 Conclusions

67 We conclude that neither moderate juniper encroachment nor wildfire have negative effects on plant species
68 richness in the studied ecosystem. However, as juniper thickening may cause species loss and devastating fires,
69 conservation management should prevent the development of dense juniper stands.

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72 Keywords

73 forest-steppe, juniper, habitat management, post-fire recovery, semi-arid grassland, species composition, species
74 richness, wildfire, woody plant encroachment

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1. Introduction

Woody plant encroachment (WPE) causes transition of grassland and savanna ecosystems into woodlands in many parts of the world (García et al. 2014; Soliveres et al. 2014a). The most common way of this process is the spread of native woody plant species into adjacent grassy communities (Nackley et al. 2017). There are several causes of WPE including the effects of changing climate and land use. Increasing concentration of atmospheric CO₂ (D'Odorico et al. 2012), within-year shifts in soil moisture regime (Gremer et al. 2018), rising temperature (Huang et al. 2018), fire-suppression due to over-grazing (Gibbens et al. 2005), and the cessation of grazing or mowing (Debussche et al. 1999; Anthelme et al. 2007) have all been linked to WPE. Spread of woody species initiates structural and functional changes such as increasing productivity in grassland ecosystems (Nackley et al. 2017), but ecological consequences are not well known (Soliveres et al. 2014a). Increasing woody cover is expected to lead to higher extent of wildfires in temperate shrublands (Moritz et al. 2012) that may move the encroached ecosystems back to the grassland state (D'Odorico et al. 2012). However, grasslands have markedly different species composition and dynamics compared to neighbouring woody patches (Kertész et al. 2017). Therefore, studies that assess both WPE and wildfires in encroached ecosystems are necessary to understand properties of woody invasion in grassland communities, its complex ecological consequences, and the possibilities of grassland regeneration (Knapp et al. 2008).

WPE due to fire suppression affects species richness negatively in most North American grasslands (Ratajczak et al. 2012) in the course of both desertification (Báez & Collins 2008) and forest expansion (Briggs et al. 2002). On the contrary, forest regeneration after cessation of grazing in semi-arid and sub-humid areas does not always cause loss in species richness (Maestre et al. 2009). In this case, woody vegetation was decreased by former land use, and WPE may have neutral or positive effects on species richness depending on the state of the regeneration process after abandonment (Eldridge et al. 2011). Besides direction, the degree of WPE also has very different effects on plant species richness. Positive effects are expected up to intermediate degree (50% shrub cover) of encroachment (Soliveres et al. 2014b), as it is the case in savanna ecosystems in Ethiopia (Belay et al. 2013), where richness increased with shrub density. Variable WPE effects on species richness emphasize that studies should take account of former land use as well as species identity and the degree of woody plant expansion.

Wildfires act as immediate disturbance that affect plant species composition. They drastically decrease woody cover in the short term (Bond & Keeley 2005), but can also lead to invasion of bushes or trees in the longer term (Franzese et al. 2009). Fire severity has increased recently in ecosystems where frequency of wildfires was reduced by anthropogenic fire suppression and thus fuel accumulation was enhanced (Slingsby et al. 2020). Increasing fire frequencies are expected during the 21st century at mid to high latitudes, depending on the productivity in grassland and savanna communities (Moritz et al. 2012; Fusco et al. 2019). Juniper encroachment changes carbon cycle and increases productivity in US grasslands (Wang et al. 2018), thus it moves the grassland into a more fire-prone state. When these ecosystems are dominated by fire-sensitive species such as the non-resprouter Ashe or common junipers (*Juniperus ashei*, *Juniperus communis*) (Fuhlendorf et al. 1997; Marozas et al. 2007), wildfire may cause marked changes in plant species composition due to complete dieback of formerly abundant woody species and immediate decrease of shaded microhabitats (Ónodi et al. 2014; Kertész et al. 2017).

Wildfires often maintain high species richness in fire-adapted grassland and savanna ecosystems (Uys et al. 2004; Bond & Parr 2010; Slingsby et al. 2020). However, effects of wildfire events vary among communities depending on climate and plant species composition (Abella 2009). In prairie vegetation, effect size of wildfires increases with productivity (Knops 2006, Peterson & Reich 2008). Consequently, effects of WPE and wildfire may interact with each other, as the degree of encroachment decreases after fire, and the strength of wildfire effect depends on the amount of accumulated biomass, mainly on woody cover. Therefore, studying WPE and wildfire in combination may provide a better understanding of woody cover effects on vegetation structure and diversity. However, joint studies on WPE and wildfire effects are rare (but see Ansley & Castellano 2006; Ravi et al. 2009; Srinivasan 2011; Lipoma et al. 2016), and few studies to date have been conducted on long-term wildfire effects both in the presence and absence of native WPE (but see Ratajczak et al. 2017).

WPE can have the strongest impact on communities developed on sandy, nutrient-poor soils (Case & Staver 2017). In sandy region of the Great Hungarian Plain, common juniper (*Juniperus communis*) is one of the dominant woody species of semiarid juniper-poplar forest-steppe habitats. Negative effects of juniper thickening were reported in studies conducted in North America (Briggs et al. 2002; Van Auken 2009), and even in the case of common juniper in Europe (Rejmánek & Rosén 1988). By contrast, juniper shrubland is generally considered a habitat type of high conservation value in the European Union (Natura 2000 network code: 91N0). Indeed,

common juniper is often the target of conservation efforts in the region (Simon 1971), yet it is unclear whether it boosts or threatens species richness in this ecosystem. This question is increasingly important from a conservation perspective, because afforestation by black pine (*Pinus nigra*), decreased grazing pressure, and juniper encroachment increased fire severity during the last decades leading to marked changes in species composition (Ónodi et al. 2014; Kertész et al. 2017). All these issues underline the need for a better understanding of the role of juniper encroachment and subsequent wildfire in this ecosystem.

The objective of this study was to assess changes in plant species richness and composition in burnt and unburnt grassland and juniper plots over a decade following a wildfire. We asked the following specific questions:

1. What was the extent of juniper encroachment during the study period?
2. What are the effects of juniper encroachment and subsequent wildfire on plant species richness?
3. What are the effects of juniper encroachment and subsequent wildfire on vegetation composition?

2. Methods

2.1. Study area and site description

The study site is located in the Kéleshalom Nature Reserve (46°22' N, 19°20' E) in the southern part of the Kiskunság National Park, Hungary. The climate of the study area is continental with sub-Mediterranean influence (Zólyomi et al. 1997). Mean annual temperature is 10.4 °C, with a minimum of -1.9 °C in January and a maximum of 21.1 °C in July, while mean annual precipitation is 505 mm with a maximum in June (72.6 mm) (1961-1990; Kovács-Láng et al. 2000). The soil is nutrient poor Calcaric Arenosol (FAO-ISRIC-ISSS 1998) developed on Pleistocene calcareous sand deposit of the Danube River. The sand content of the soil is over 90% and humus content is below 1% (Szitár et al. 2014).

The study area is covered by Pannonian sand forest-steppe vegetation mosaics embedded into a matrix of arable lands and plantation forests (Molnár et al. 2012). This semi-natural forest-steppe has a high nature conservation value due to its richness in endemic and rare species with restricted distribution. The vegetation mosaic is composed of open and closed sand grassland and juniper-poplar stands. Open sand grassland (*Festucetum vaginatae*, Natura 2000 category: 6260) is a Pannonian endemic community evolved under semi-arid conditions on coarse-textured calcareous sand soil (Kovács-Láng et al. 2000), and is co-dominated by perennial bunchgrasses *Festuca vaginata* and *Stipa pennata* subsp. *sabulosa* (for a list of characteristic species see Csecserits et al. 2011). Woody patches of the forest-steppe habitat complex are co-dominated by *Populus alba*, *Juniperus communis*, and *Crataegus monogyna* (*Junipero-Populetum albae*, Natura 2000 category: 91N0). Juniper encroachment started during the 19th century after a change in the grazing system from grey cattle to sheep (Biró et al. 2013). The native *J. communis* is an endozoochorous species, its seeds are usually spread by birds. Hereinafter, juniper encroachment means growth of juniper shrub individuals at the expense of grasslands.

At the end of July 2007, a wildfire went through 1000 ha of forest plantations and protected forest-steppe habitats in the area of Kiskunhalas, Kunfehértó, and Kéleshalom, south-central Hungary. The wildfire partially destroyed the study site, which is 63.4 ha in size. Common juniper does not resprout after fire as described in other studies (Ónodi et al. 2014; Kertész et al. 2017). Mosaic of burnt and unburnt grasslands and woody patches provided a natural experiment to study the effects of WPE, wildfire, as well as WPE and subsequent wildfire on plant species richness and composition.

2.2. Sampling design and data collection

In July 2008, one year after the wildfire, we established 18 blocks both in burnt and unburnt stands (36 blocks in total) for studying vegetation changes within the study site (Figure S1 in Appendix S1). Individual juniper specimens (18 burnt, i.e. killed, and 18 unburnt) were chosen in spatially mixed arrangement. Distance between adjacent blocks was a few tens of meters with an average of 45 meters.

Within each block, vegetation sampling was performed in two different spatial scales of permanent quadrats (Figure 1). We established two 5 m × 5 m plots, a few meters from each other. One of them was centred on a juniper specimen (burnt or unburnt) and the other was placed on a grassland patch without juniper. Hereinafter we refer to these positions of sampling quadrats as Juniper plot, and Grassland plot, respectively. Juniper plots included the whole juniper specimen, and also some grasslands around the juniper (Figure 1). Unburnt Grassland plots served as controls, where neither wildfire nor WPE took place. Unburnt Juniper plots and burnt Grassland plots allowed us to assess the separate effects of WPE and wildfire, respectively. Finally, burnt Juniper plots, when compared to unburnt Grassland plots, shows the effects of juniper encroachment (WPE) and subsequent wildfire.

Microplots of 1 m × 1 m were placed in the very centre of the Juniper and Grassland plots, and are referred to here as Central-Juniper microplot and Central-Grassland microplot (Figure 1), based on their position within the block. Within the Juniper plots, we established two additional microplots (1 m × 1 m) at the northern and southern edges of each juniper shrub (Northern-edge microplot and Southern-edge microplot) in order to cover the unique species composition of the four seemingly different microhabitats within each block (Erdős et al. 2019). These microplots were located to have approximately 30% juniper cover at the start of the study in 2008. Burnt junipers had no canopy in 2008, but unburnt branches made it possible to place these microplots in a way similar to that at unburnt junipers.

Between 2008 and 2018, the presence and visually estimated percentage cover of each vascular plant species were recorded in the permanent plots in each year (except for 2014). We sampled the plots twice a year to account for the different phenology of species. All species were sampled in early July, while we resampled summer annuals (annuals that germinate in spring grow mostly in the summer) in early October. Summer and fall recordings were combined, and a single maximum cover value was obtained for each species per plot per year. Nomenclature of plant species follows the online database of The Plant List (2010).

2.3. Statistical analyses

All calculations were performed in the R statistical environment (version 3.6.2., R Core Team 2019).

We assessed the temporal changes of juniper cover in unburnt Juniper plots, and in unburnt Central-Juniper, Northern-edge, and Southern-edge microplots by applying two separate generalized linear mixed-effects models assuming beta distribution with logit link function (*glmmTMB* package, Brooks et al. 2017). In the model for unburnt Juniper plots, we used the cover of juniper as the dependent variable, time as a continuous explanatory variable expressed in years, while block was used as a random factor. In the model for unburnt microplots, position was included as fixed factor, while microplot ID within block was used as nested random effect (Zuur et al. 2009). To conform the dependent variable to the beta distribution, we transformed juniper cover percentages using the following equation (Smithson, & Verkuilen, 2006):

$$y' = [y / 100 * (N - 1) + 1/2] / N,$$

where y is percentage cover of juniper, and N is the sample size. As a result, the transformed cover values ranged on (0; 1) interval. For pairwise differences in the temporal change of juniper cover in the microplots, we used Z tests.

We tested the main and interactive effect of wildfire, plot position within block, and time (sampling years as a continuous variable) on plant species richness by using all sampling quadrats. Juniper was not counted to species richness, as it served as selection criteria for plot and microplot types. We analysed total species richness, because the number of non-native species were negligible in both burnt and unburnt plots. We applied two generalized linear mixed-effect models with Poisson distribution (*lme4* package, Bates et al. 2014) for plots and microplots separately. Block and plot ID nested within block were used as random effects for the analyses of plots and microplots, respectively.

For species richness analyses, the full models were subjected to backward variable selection by AIC (Akaike 1978). To allow comparison of the nested models, we applied maximum likelihood (ML) fitting, and the final models were then refitted using restricted maximum likelihood (REML) method, and were evaluated by Wald tests. For species richness data in the microplots, we compared the least squares means of factor levels of quadrat position and wildfire using post-hoc contrasts (*lsmeans* package, Lenth 2016). For this purpose, we tested the

pairwise differences in temporal change between the unburnt grassland (as control) and the other seven groups of microplots according to combinations of factor levels of wildfire and position.

We analysed the species compositional differences between the Juniper and Grassland plots and the first and last year of the sampling period (2008 and 2018) in burnt and unburnt stands. Non-metric multidimensional scaling using Bray-Curtis dissimilarity index was implemented to visualize compositional changes among the plots using convex hulls. For this analysis, we used the metaMDS and the ordihull functions (*vegan* package, Oksanen et al. 2019). Differences in species composition between factor levels (burnt vs. unburnt, grassland vs. juniper encroached, and 2008 vs. 2018) were tested with multivariate analysis of variance (PERMANOVA, Anderson 2001) using the adonis function (999 random permutations) of the *vegan* package. To determine compositional overlap between groups, a post-hoc multilevel pairwise analysis was performed (*pairwiseAdonis* package with *p*-value adjustment, Arbizu 2017). To determine which species prefer Juniper vs. Grassland plots, we calculated fidelity values based on species abundance data using the phi coefficient (Chytrý et al. 2002).

3. Results

3.1. Juniper cover

In the 5 m × 5 m Juniper plots, the cover of *J. communis* increased through time (Figure 2a, Table 1). Mean cover values were 43.8% (SD: ± 18.6%) in 2008 and 61.0% (± 20.4%) in 2018.

In the 1 m × 1 m microplots, temporal changes depended on quadrat position (Figure 2b, Table 1). Juniper cover decreased through time in Central-Juniper microplots, while increased at the edges of the shrubs, more in Southern-edge than in Northern-edge microplots ($Z = -3.19$, $P = 0.001$). By the end of the study, juniper cover in the edge microplots reached the values characteristic of Central-Juniper microplots where mean cover was 80.6% (± 15.4%).

3.2. Species richness

In the 5 m × 5 m plots, species richness was higher in burnt (22.4 ; SD: ± 4.11) compared to unburnt (20.3 ± 4.19), and in Juniper (22.9 ± 4.41) compared to Grassland plots (19.8 ± 3.50), while we found a slight decreasing trend over time (Figure 3a,b, Table 2).

In the 1 m × 1 m microplots, we found different temporal trends of species richness depending on combinations of wildfire and position (Figure 3c,d, Table 2). Richness increased more both in burnt Central-Juniper microplots ($Z = 7.462$, $P < 0.001$) and in burnt Southern-edge microplots ($Z = 2.808$, $P = 0.005$) compared to the unburnt grasslands. Species richness decreased considerably through time in unburnt edge microplots (Northern-edge $Z = -5.104$, $P < 0.001$, Southern-edge $Z = -5.633$, $P < 0.001$) compared to the unburnt grasslands. Unburnt Central-Juniper microplots had the lowest species richness throughout the study period.

3.3. Species composition

We found significant compositional differences (Figure 4) in 25 out of 28 pairwise comparisons between groups of the eight wildfire * position * time combinations. In 2008 (Figure 4a), the difference between unburnt Grassland and unburnt Juniper plots was not significant ($F = 3.57$, $P_{adj} = 0.084$). However, this difference became significant after ten years of WPE in 2018 ($F = 9.10$, $P_{adj} = 0.028$; Figure 4b). Temporal changes of composition between 2008 and 2018 were non-significant only in the unburnt Grassland group ($F = 2.87$, $P_{adj} = 0.252$). In 2018 (Figure 4b), the composition of the burnt Juniper group did not differ from the burnt Grassland group ($F = 2.08$, $P_{adj} = 0.700$), in contrast to the beginning of the study.

In unburnt blocks, the number of species showing positive fidelity towards Juniper plots (having a live juniper shrub in the middle) increased (5 species in 2008 and 10 species in 2018), while the number of species associated

with Grassland plots decreased through time (10 species in 2008 and 4 species in 2018; Table S1 in Appendix S2). In burnt blocks, the number of species associated with Juniper plots (having a dead juniper shrub in the middle) did not change (10 species in both years), while the number of species associated with Grassland plots decreased through time (7 species in 2008 and 3 species in 2018; Table S1 in Appendix S2).

4. Discussion

4.1. Changes in juniper cover

We detected a gradual juniper encroachment during the study period: in unburnt Juniper plots, juniper cover exceeded 60% on average, while both in Northern-edge, and in Southern-edge microplots, cover values increased to 80% by the end of the study. This degree of encroachment shifted the edge microplots into shrub-dominated microhabitats, similar to Central-Juniper microplots. In the meantime, juniper cover in the Central-Juniper microplots showed a slight decrease, most likely related to an aging and opening up of dense juniper canopies. No juniper reestablishment took place in any of the sampling plots.

4.2. Effects of juniper encroachment and wildfire on species richness

4.2.1. Juniper encroachment effects on species richness

In the 5 m × 5 m plots, we found a small but significant increase in species richness in Juniper plots compared to Grassland plots irrespective of wildfire and time. This is especially remarkable, given that juniper occupies about half of the study plots and has a dramatic negative effect on species richness in those overgrown microsites. The positive juniper effect on species richness is consistent with juniper invasion studies in North America, where native juniper thickening in grasslands decreased native species richness only after a threshold of shrub cover was reached (Taft & Kron 2014). At the same time, most studies dealing with juniper encroachment emphasize the negative effects at high juniper cover (Rejmánek & Rosén 1988; Briggs et al. 2002; Van Auken 2009). Our study was conducted in a moderately encroached forest-steppe with individual juniper shrubs that grew through time. Similar to our results, Maestre et al. (2009) found more vascular plant species in the shrub-dominated than in uninvaded plots in a regenerating Mediterranean woodland. In agreement with the findings of Koyama et al. (2015), our results also suggest that juniper shrubs increase microhabitat diversity and thus provide favourable conditions for different species. According to Soliveres et al. (2014a) species richness peaks at intermediate WPE in arid climatic conditions, and this might be the case in more humid ecosystems as well (Tölgyesi et al. 2018). Our results show an example of positive WPE effects in species richness at an intermediate level of juniper encroachment in a semi-arid forest-steppe.

In unburnt microplots, juniper encroachment had a clear negative effect on species richness. We documented a gradual decrease in richness in unburnt Northern-edge and Southern-edge microplots through time, while the lowest richness values were observed in unburnt Central-Juniper microplots throughout the study period. We suggest that the main reason for the decrease in species richness is the competitive effect of juniper shrubs, namely physical space occupation and shading. Studies conducted on juniper encroachment in North America have provided evidence that species richness increases with distance from trunk (Briggs et al. 2002; Linneman & Palmer 2006; Els et al. 2010), and shade tolerant species preferred the northern plots (Linneman & Palmer 2006), while C4 species preferred more sunny conditions (Gehring & Bragg 1992). In this present study, we documented the transformation of unburnt edge microplots into woody habitats irrespective of their relative position due to growth of juniper shrubs. Our results reveal that besides facilitation found in shrub scale, competition by woody species (Scholes & Archer 1997) may also affect the same grassland patches and exclude many species within a decade. In line with Yoshihara et al. (2010), we emphasize that the detection of positive or negative effects of woody cover on plant species richness may depend on the spatial scale used in a given study.

4.2.2. Wildfire effects on species richness

Wildfire had positive effects on species richness in the 5 m × 5 m plots irrespective of the presence of juniper. At finer scale (1 m × 1 m), effects were positive or neutral depending on the position of the microplots relative to the juniper shrub. Different positions also represented a likely increase in wildfire intensity from Central-Grassland through edge up to Central Juniper microplots associated with an increasing amount of fuel. Low intensity fire in grasslands may explain why the temporal trend of species richness did not differ between burnt and unburnt Grassland microplots where most of the perennial species can resprout after wildfire (Knops 2006; Ónodi et al. 2008). By contrast, an increase of species richness through time was found in burnt Southern-edge and Central-Juniper microplots. In the latter case, the number of plant species started from extremely low values characteristic of the unburnt centres of juniper shrubs and increased steeply during the first three years until it reached the value typical of grasslands. Positive effects of the studied wildfire found in our study are in line with other studies conducted in fire-adapted ecosystems where wildfires maintain species rich communities (Slingsby et al. 2020). Indeed, controlled fires of low severity are sometimes applied to increase biodiversity in juniper encroached landscapes (Twidwell et al. 2013).

Post-fire recovery depends on legacies of persisting plant tissues or seeds, and propagules arriving from the surrounding habitats (Abella 2009). We suggest that both of these pathways of plant recolonisation played considerable role in the higher richness in burnt plots compared to unburnt Grassland plots by the first year after the wildfire. Lipoma et al. (2016) found regeneration from persisting plant organs to be the most important factor during early stage of recovery. However, regeneration from newly arriving propagules must have been the dominant pathway in the Central-Juniper microplots in our study, where soil had burnt deeply, and richness was likely very low before wildfire.

4.3. Compositional changes during juniper encroachment and after wildfire

Compositional dissimilarity between unburnt Grassland and unburnt Juniper plots was not significant in the first year of our study when Juniper shrubs covered only 40% of the study plots. However, eleven years of further juniper thickening (growth of juniper specimens) led to different plant species composition of these woody and grassland habitats in the unburnt landscape. Our results support considerable and long lasting effects of juniper encroachment on species composition during the transformation of grasslands into woodlands (Gehring & Bragg 1992; Linneman & Palmer 2006; Ganguli et al. 2008). Furthermore, native shrub invasion have been reported to induce substantial compositional changes in several ecosystems, such as in South-Western Australian heathlands (Shackelford et al. 2015), in South American savanna wetlands (Barbosa da Silva et al. 2016), in Indian montane grasslands (Srinivasan 2011), and also in European dry grasslands (Maestre et al. 2009; Görzen et al. 2019). We also showed that the expansion of juniper patches led to an increase in the number of plant species associated with Juniper plots.

Wildfire had an immediate effect on plant species composition, thus burnt Grassland and burnt Juniper plots differed from unburnt plots and from each other already one year after the wildfire. However, both burnt and unburnt grassland plots were similar in composition after a decade of significant temporal changes. Similar to our results, Knops et al. (2006) found that burning itself has only short-term impacts on vegetation composition in grassland ecosystem of low productivity. Furthermore, we emphasize that the majority of species associated with burnt plots (either to Juniper or to Grassland plots; Table S1 in Appendix S2) are characteristic species of the studied natural habitat (Cseceserits et al. 2011). After eleven years of grassland regeneration, many grassland specialist species established also in burnt Juniper plots resulting in a decreased number of species associated with burnt Grassland plots.

Overall, our results indicate that shrub encroachment influenced vegetation composition more than wildfire (see also Görzen et al. 2019). The grassland recovery in burnt juniper plots following the wildfire was surprisingly fast and took place within the timeframe of our study. The fact that former presence of solitary juniper shrubs did not affect vegetation composition eleven years after the wildfire shows the high regeneration potential of the studied grasslands. This regeneration potential is considered a feature of the sand grasslands of the region (Erdős et al. 2015). In contrast, Gehring and Bragg (1992) concluded that regeneration of prairie ecosystem in Eastern Nebraska is unlikely even after removal of juniper shrubs. Likewise, Abella (2009) found many studies in a literature review where only little convergence occurred between composition of burnt and unburnt sites at decadal time scales, and post-fire regeneration depended on the sprouting abilities of the woody species. Therefore, besides high

regeneration potential of the studied open sand grasslands, their fast recovery is most likely related to the inability of common juniper to resprout, which allows grassland recolonization in formerly encroached patches.

4.4. Management implications

We found that sand grasslands regenerate fast after wildfire, not only in former grassland patches (Ónodi et al. 2008; Ónodi et al. 2014), but also in formerly encroached patches. However, our present study also showed that no management intervention is needed as long as juniper cover is low, which enhanced plant species richness. In fact, moderate juniper cover has also been found to increase the stability of grasslands due to reduced drought sensitivity in the studied forest-steppe ecosystem (Ónodi et al. 2014; Kertész et al. 2017). Furthermore, juniper patches were shown to be an important element of the forest-steppe vegetation mosaic of high habitat heterogeneity and conservation value (Erdős et al. 2018). In many cases, poplar species also appear in this vegetation mosaic further increasing habitat heterogeneity.

On the other hand, in cases when juniper becomes dense, and thus increases both fire danger and the extent of species poor habitat patches, a management intervention may be needed. Although prescribed burning has been found to be an effective conservaton management tool against WPE (D’Odorico et al. 2012), it may be difficult to apply in the study region, because dense juniper stands are embedded in a complex landscape that contain settlements and very flammable pine plantations. Alternatively, mechanical shrub removal has been reported to be an appropriate management tool (Lett & Knapp 2005). However, we emphasize that mechanical thinning have to be applied with care, because the studied ecosystem is sensitive to surface perturbation, which may facilitate the spread of invasive species (Szitár et al. 2014).

Overall, our results demonstrate that a low or intermediate level of juniper encroachment does not have negative diversity effects and that the development of dense stands should be avoided, but a careful cost-benefit analysis and feasibility analysis would be needed to decide if prescribed burning, mechanical shrub removal, or a mixture of the two could best help to reach this target state.

4.5. Conclusions

Both moderate level of juniper encroachment and wildfire were found to increase species richness in the studied forest-steppe community. At the same time, high juniper density negatively affected richness in the understory vegetation. Long-term observations provided further evidence for the negative effects of juniper on species richness at the edges of the shrubs. By contrast, we found fast increase in species richness after wildfire killed the junipers. In grassland sites, wildfire caused only transient change in species composition, but in burnt juniper plots it shifted vegetation composition towards the grassland state, while juniper thickening resulted in a considerable shift in composition. Collectively, these results suggest that neither moderate juniper encroachment nor wildfire have negative effects on plant species richness in the studied ecosystem, but in order to avoid species loss and devastating fires conservation management should prevent high juniper density.

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Author contributions

G.K-D. conceived the study. All authors contributed to data collection. K.S., A.L. and G.Ó. performed statistical analyses. G.Ó. led the writing of the manuscript, with major input from K.S., M.K., A.L and G.K-D. All authors discussed the results and commented on the manuscript.

418 Data availability statement

419 The data that support the findings of this study are available in the supplementary material of this article (Appendix
420 S3).

421

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603

604 Tables and legends

605 Table 1

606 Results of generalised linear mixed models of *J. communis* cover in the unburnt Juniper plots, and in the unburnt
607 microplots

Explanatory variables	<i>DF</i>	Chi-square	<i>P</i>
5 m × 5 m plots			
time	1	94.55	<0.001
1 m × 1 m microplots			
position	2	265.40	<0.001
time	1	24.71	<0.001
position * time	2	169.26	<0.001

608 *DF* shows degrees of freedom, Chi-square and *P* are the test statistic and the probability of type III error of the
609 Wald test

610

611 Table 2

612 Results of generalized linear mixed models after backward variable selection of total plant species richness in the
613 sampling plots

Explanatory variables	<i>DF</i>	Chi-square	<i>P</i>
5 m × 5 m plots			
wildfire	1	9.75	0.002
position	1	58.26	<0.001
time	1	6.07	0.014
wildfire * position	1	2.83	0.093
wildfire * time	1	2.21	0.137
position * time	1	3.11	0.078
1 m × 1 m microplots			
wildfire	1	80.55	<0.001
position	3	327.16	<0.001
time	1	91.94	<0.001
wildfire * position	3	515.72	<0.001
wildfire * time	1	96.08	<0.001
position * time	3	58.76	<0.001
wildfire * position * time	3	39.01	<0.001

614 *DF* shows degrees of freedom, Chi-square and *P* are the test statistic and probability of type III error. In the case
615 of 5 m × 5 m plots, model selection excluded the three-way interaction of explanatory variables

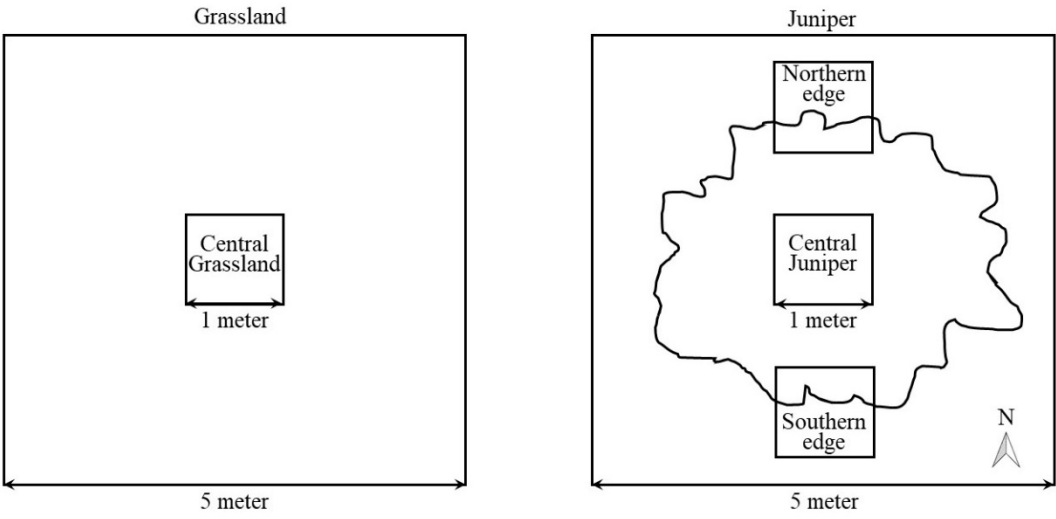


Figure 1 Sampling design: arrangement of sampling plots in a block established either in burnt or in unburnt patches. The edge of burnt or living juniper shrub is marked within the Juniper plot. 18 burnt and 18 unburnt blocks of the same design were set up and monitored for the study

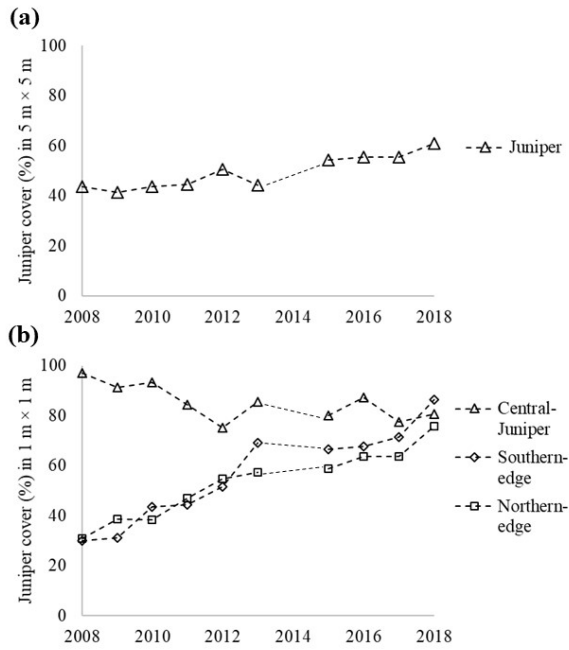


Figure 2 Changes in the canopy cover of *J. communis* (a) in the unburnt Juniper plots, and (b) in the unburnt microplots

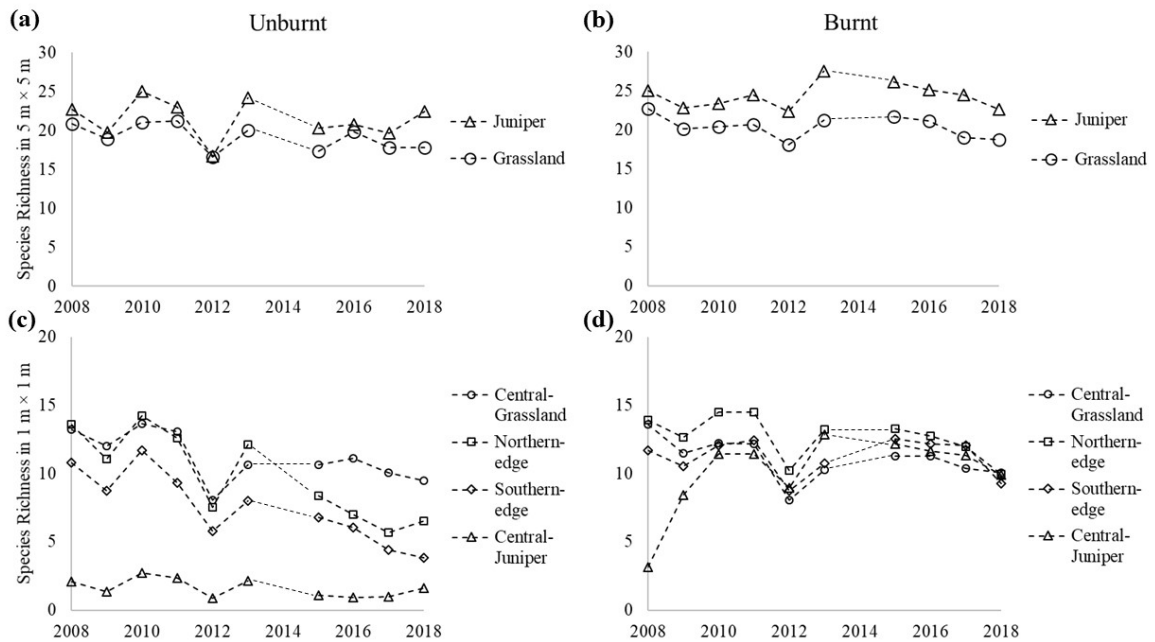


Figure 3 Changes in species richness in burnt and unburnt plots during the study period (2008-2018). Subplots (a) and (b) show results for 5 m x 5 m plots, while (c) and (d) are for 1 m x 1 m microplots

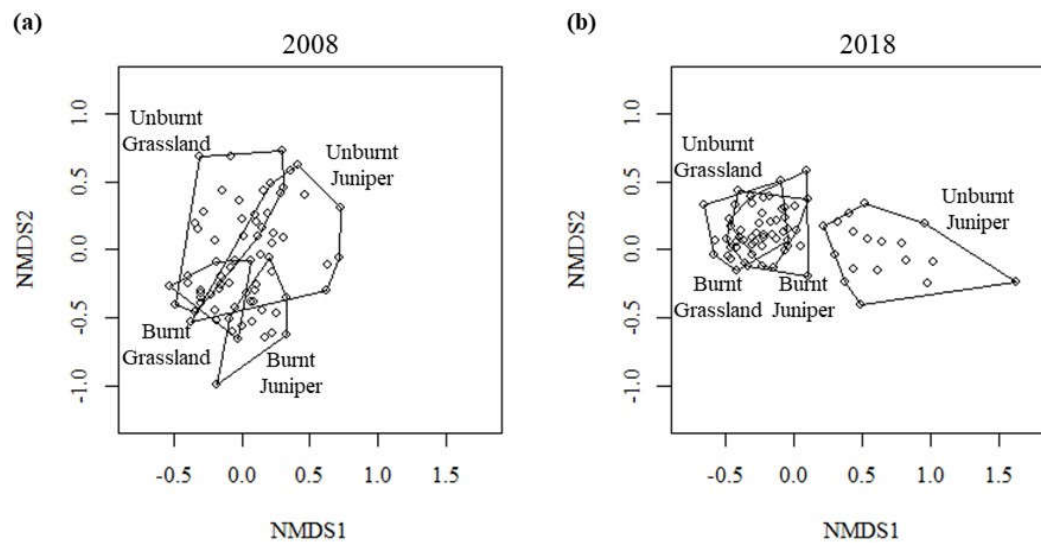


Figure 4 Ordination diagram of Non-metric Multidimensional Scaling (final stress = 0.294) of 5 m \times 5 m plots (Bray-Curtis dissimilarity). For better visualization, the results of the analysis are presented in two subplots: (a) plots in 2008, and (b) plots in 2018. Convex hulls show groups of fire * position combinations

637 Supporting Information

638

639 Additional supporting information may be found online in the Supporting Information section at the end of the
640 article.

641

642 Appendix S1 Map of the study area

643 Appendix S2 List of diagnostic plant species

644 Appendix S3 Original data tables