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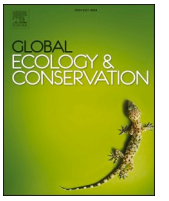

Original research article

Mowing increases the vulnerability of sand grassland restoration to secondary invasion despite the sensitivity of invasive species to drought

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ABSTRACT

Increased frequency and severity of droughts as a result of climate change coupled with invasions by alien species may have a significant impact on vegetation development and thus on ecological restoration efforts. We studied the impact of restorative mowing, time and drought severity on sand grassland restoration in Hungary. Using data spanning 1995–2019, we explored the dynamics of target, invasive and C4 species. Restoration interventions involved the removal of invasive *Robinia pseudoacacia* (1994/1995) and regular mowing (1995–2001) at three sites. Rising temperatures and more frequent summer droughts were measured at all sites based on long-term weather data (1995–2020) from the FORESEE-HUN v1.0 database. Target species were not significantly affected by drought, C4 species had higher proportions at higher drought severity, while invasive species generally had higher proportions at lower drought severity. Mowing was neutral to target species and had a positive impact on invasive and C4 species. Mowing amplified drought responses only for C4 species in the short term in August. Our results confirm that sand grassland vegetation is resistant to drought during restoration. Mowing was found to control targeted invasive *R. pseudoacacia* but is insufficient for accelerating the regeneration of sand grassland and can promote secondary invasion by herbaceous species, with long-lasting effects, despite the negative impact of droughts on invasive species. Our results also highlight the need to consider not only the length of the monitoring period, but also the frequency of data collection and its relationship to environmental changes, such as the expected frequency of droughts.

1. Introduction

Climate change has multiple impacts on biodiversity and this is expected to become even more pronounced (IPCC et al., 2022). Along with the global rise in temperature, extreme climate events, such as heat waves, precipitation excesses, storms and floods, and increased risk and duration of droughts are expected to become more frequent and more intense at the local scale (Spinoni et al., 2018). A recent study by Bede-Fazekas and Somodi (2024) pointed out that the inter-annual distribution of some climate patterns might shift

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by more than 2 months in many regions of the world (e.g. precipitation timing shifts in the temperate and Mediterranean region and both precipitation and temperature shifts in the tropical region) that may also affect the likelihood of species adaptation to climate change.

Ecosystems are generally resistant to episodes of infrequent drought events (Hoover et al., 2014; Lloret et al., 2012; Orbán et al., 2023), but prolonged or recurrent droughts or larger shifts in within year precipitation patterns are expected to increase the likelihood of permanent changes in species phenology, vegetation composition and ecosystem functioning (Bede-Fazekas and Somodi, 2024; Smith et al., 2024). For example, severe droughts can lead to significant mortality of dominant plant species that are less adapted to drought conditions (e.g. grasses), and can favor the growth and spread of drought-tolerant species (both invasive or native), leading to changes in dominance and potentially local species extinction. For example, in a semi-arid region of Arizona, Gitlin et al. (2006) found significant dieback of native cottonwood (*Populus fremontii*), especially in the presence of invasive tamarisk (*Tamariscus* sp.). Based on a mesocosm experiment, drought tolerant *Senecio inaequidens* is likely to profit from climate change compared to native species (Vetter et al., 2020). In Pannonian sand grasslands, serious dieback of dominant grass species occurred as a result of 2022 drought (Gyalus et al. unpubl.) and native annual and tap rooted forb species became dominant at least temporarily.

Climate change, and especially the increased frequency of local drought events also influence the regeneration of degraded sites. Ecosystems recovering from disturbance may be more sensitive to even minor changes in climate, while late successional states may be more resistant and resilient (Kröel-Dulay et al., 2015). Thus, the ability of an ecosystem to recover from disturbance is expected to significantly contribute to its vulnerability to climate change. Ecological restoration aims to accelerate the recovery of disturbed, degraded or destroyed ecosystems, and ecosystems under restoration are generally in an early successional stage and may be more vulnerable to the impacts of climate change (Choi et al., 2008; Lyons et al., 2023).

The spread of invasive species is another globally relevant driver of biodiversity loss (Roy et al., 2023), and represents a main threat for grassland ecosystems (Buisson et al., 2022). The removal of invasive alien species is becoming an important part of ecosystem restoration (Weidlich et al., 2020). After removal of invasive alien species, degraded native habitats do not always regenerate due to the dispersal limitation of target species (Török et al., 2018) and/or legacy effects (e.g. increased soil nitrogen and its impacts on biodiversity and ecosystem functioning) left by invasive alien species (Corbin and D'Antonio, 2012), and may be vulnerable to re-invasion or secondary invasion, i.e. invader-facilitated invasions (Pearson et al., 2016, 2018). For example, if nitrogen-fixing invasive alien species are removed, in more than 30 % of the cases other invasive species can colonize and spread, hampering the long-term results of restoration efforts (Nsikani et al., 2018). Revegetation efforts have been successful in increasing the biotic resistance of restored communities to invasive plants (Halassy et al., 2023). Other restoration interventions that disrupt vegetation cover or disturb soils, thereby increasing the resources available, may facilitate invasion (Kettenring and Adams, 2011). The presence of such disturbance factors combined with high propagule pressure of invasive species from the landscape can determine the need for different restoration approaches (Csákvári et al., 2021; Kröel-Dulay et al., 2019; Reis et al., 2022).

Little is known on the interaction of drought severity and disturbance on invasion and even less so in relation to restoration efforts. Invasion events are often facilitated by changes in the pattern of temperature and rainfall regimes resulting in an increased invasion risk under climate change (Walther et al., 2009). In particular, rising atmospheric CO_2 concentrations and temperatures may benefit C4 plants, as they tend to come from warmer and drier regions than their introduced range (Weber, 2017) and have therefore been "pre-adapted" to climate change (Sage and Kubien, 2003). However, local studies show that drought and water limitation can directly negatively affect invasive species, especially in semi-arid or arid environments (Har-Edom and Sternberg, 2010; Thomsen et al., 2006) and during the early stages of establishment (Orbán et al., 2021). Regarding the interplay between drought and disturbance, although more frequent or severe droughts can negatively affect the establishment of invasive species, disturbance can mitigate this direct effect (Orbán et al., 2021). Invasive alien species with rapid resource acquisition can indirectly benefit from drought events coupled with disturbance (Vetter et al., 2020), taking advantage of increased resource availability as a result of vegetation loss and rapid resource utilization (Diez et al., 2012; Manea et al., 2016).

The present study aims to investigate the long-term effects of experimental restoration treatments aimed at eradicating black locust (*Robinia pseudoacacia*) populations and restoring native sand grasslands in Hungary in the face of changing weather conditions, particularly drought severity. The study area is semi-arid with sandy soil of low water retention capacity (Kovács-Láng et al., 2000) and expected to experience more frequent heat waves and longer periods of summer drought in the future (Kiss et al., 2017). *R. pseudoacacia* is an N_2-fixing woody species that is expected to have soil legacy effects primarily due to increased soil nitrogen content and increased amounts of nitrogen returning from leaf litter, resulting in increased nitrogen mineralization rates, altered resource availability and soil microbial community (Corbin and D'Antonio, 2012). Mowing and hay removal was carried out as part of the treatments to prevent woody re-growth, so the treated areas are considered to be in an early successional stage and may therefore be more sensitive to drought and invasion than unmown control. The following hypotheses were put forward:

(1) Drought severity: Severe drought can have direct negative impacts on both target and invasive species, and neutral to positive impacts on C4 species (both native and invasive).
(2) Short-term impact of mowing: Areas under restorative mowing are likely to be more sensitive to drought than control areas where vegetation is only initially disturbed, and this is reflected in the stronger responses of target, invasive and C4 species to drought.
(3) Long-term impact of mowing: Sand grasslands are adapted to semi-arid conditions and should be resilient to drought also in restoration, but the interaction of drought and mowing can weaken this resilience and provide opportunities for alien invasion in the long term.

2. Methods

2.1. Study site and restoration interventions

The experiment took place at three locations: 'Fülöpháza', 'Izsák' and 'Bugac' within the (Kiskun LTER site network), Kiskunság, Hungary (Fig. 1). The region has a temperate climate that is influenced by both continental and sub-Mediterranean factors. Monthly average temperatures range from 1.8 °C in January to 21 °C in July, and the annual precipitation is between 500 and 550 mm (Kovács-Láng et al., 2000). The soil type is calcaric arenosol with > 90 % sand and < 1 % humus content.

The landscape is historically characterized by inland sand dunes covered by forest-steppe vegetation. Forest-steppes are natural, complex vegetation types consisting of both tree and herbaceous components, distributed in a mosaic pattern within the temperate zone. They are characterized by semi-humid to semi-arid climates, and had been formed due to additional abiotic and biotic factors, topography, soil, herbivory (Erdős et al., 2022). The herbaceous component of the forest-steppe is historically present as the result of the combination of climatic (semi-arid), edaphic (loose sand) and topographic (distance from water table) factors, grazing by wild ungulates and natural disturbances, e.g. fires. Natural grazing were replaced by domestic grazers in the past centuries, like the traditional grey Hungarian cattle (mostly on more clayey soils) and mostly sheep in sand grasslands, but especially open sand grasslands tolerate only very slight grazing (Ónodi et al., 2006).

Sand grasslands are endemic habitats of the Carpathian Basin hosting several endemic, protected (e.g. *Dianthus serotinus*, *Onosma areanria*, *Iris arenaria*) and strictly protected species (e.g. *Colchicum arenarium*, *Dianthus diutinus*, *Ephedra distachya*). Open sand grasslands are distributed at the driest locations on dune tops and dune slopes. They are characterized by less than 75 % total cover, primarily dominated by perennial C3 bunch grasses such as protected *Stipa borysthenica* and endemic *Festuca vaginata* with perennial dicots and annual species, lichens and mosses in-between tussocks.

Over the past two centuries 92 % of the sandy forest-steppe have been destroyed, fifty percent of which have been afforested by mainly *R. pseudoacacia* stands (Biró et al., 2013). The remaining open sand grasslands are the most common in the Danube Plain (9440 ha), and within this area they occupy large areas on the sand dunes of the Kiskunság (Molnár et al., 2008). Current threats include fragmentation, expansion of neighboring infrastructure, overgrazing and illegal technical sports. Moreover, the region is heavily infected by invasive alien plant species, such as herbaceous *Asclepias syriaca*, *Cenchrus incertus*, *Conyza canadensis, Tragus*

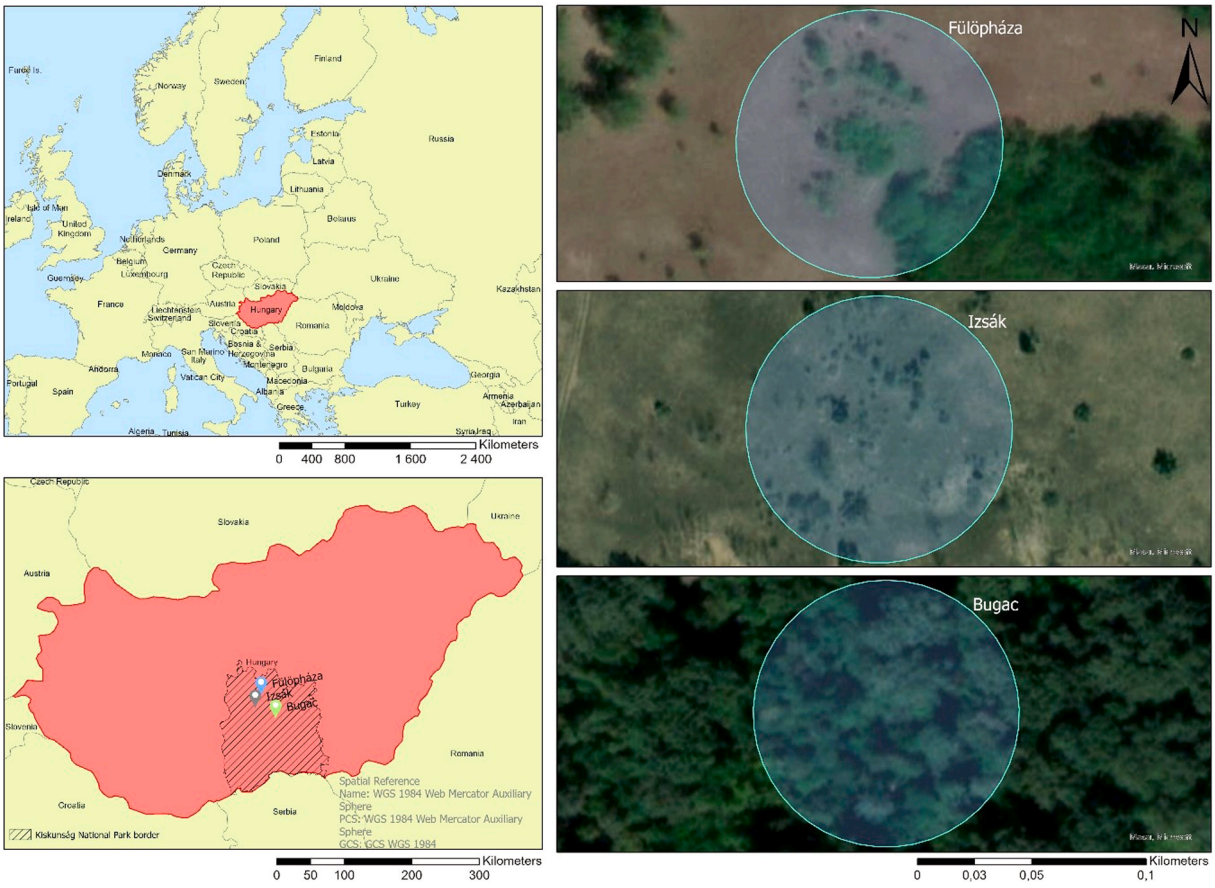

Fig. 1. The location of the three experimental sites in Kiskunság, Hungary, Europe using satellite images (ArcGIS Pro 3.0).

racemosus and woody *R. pseudoacacia* and *Ailanthus altissima* (Csecserits et al., 2016) that in case of disturbances can spread into the grasslands. Nomenclature follows Király et al., (2009).

R. pseudoacacia stands at the study sites were approximately 35 years old, situated on dune-top position. Each site had somewhat different landscape features: 'Izsák' site (0.4 ha) was the most open area, almost entirely surrounded by grasslands, 'Fülöpháza' site (1 ha) was a semi-open area surrounded by woodland and grasslands and 'Bugac' site (1.1 ha) was closed in a poplar (mostly exotic *Populus x canadensis*) and *R. pseudoacacia* plantation (Fig. 1). When the project began in the winter of 1994/95, *R. pseudoacacia* was harvested at all sites and the stumps were treated with herbicide (Garlon® 4E) to prevent re-sprouting. After clearing, a 30 m by 40 m area was selected at each site and divided into 12 plots of 10 m by 10 m, half of which were randomly designated as treated plots and half as controls. Treatment involved mowing and the removal of hay. Mowing was chosen out of necessity, as grazing was not a viable alternative at the time due to the lack of animals and human labor. Mowing began on the treatment plots in the first vegetation season in 1995. Plots were mowed twice a year, once in early June and once in September until 2001, when the treatments stopped.

2.2. Weather parameter

Due to the lack of available weather stations close to the experimental sites (except for 'Fülöpháza' meteorological station from 2001), climate data was retrieved from the FORESEE-HUN v1.0 database that was released in September 2022 (Kern et al., 2024). This version of data only applies to Hungary, for an observational period of 1971–2021 at 0.1° x 0.1° resolution. Daily mean temperature as well as daily precipitation were used covering a period of 25 years, from 1995 to 2020 of the three sites. All years were treated as non-leap years. We calculated monthly mean temperature, total precipitation and the minimum of three-month climatic water balance for the growing season (April-September) for the study period (Orbán et al., 2023). Three month climatic water balance was calculated as the difference between the sum of precipitation (P) and the sum of potential evapotranspiration (PET) for three months intervals. PET was determined by using the Thornthwaite equation with the SPEI package (Beguería and Vicente-Serrano, 2023) in R studio (R version 4.1.2).

For each year, we plotted the minimum water balance value for 3-month-periods between April and September (Orbán et al., 2023). We used the percentile method and considered drought years all minimum three-month period PET values (further referred to as P-PET-3) that lie below the 15 percentiles of the 1971–2021 period. We also expressed drought severity potentially affecting the vegetation of the given sampling season in terms of minimum P-PET-3 values calculated over the three-month period corresponding to the sampling season: April-June for the June sampling and June-August for the August sampling. The lower the P-PET-3 value, the greater the severity of the drought.

2.2.1. Vegetation data

Vegetation sampling started in 1995 after the removal of *R. pseudoacacia* with samples taken twice a year in June and August. Sampling was continued yearly until 1999. In 'Bugac', sampling was stopped in 1999 due to the inaccessibility of the area, and it was only re-sampled in 2019. The other two sites ('Fülöpháza' and 'Izsák') were monitored regularly, but not yearly until 2009 (2002, 2003, 2005, 2007, 2009), and were resampled in 2017. Vegetation data were collected in three 2 m by 2 m subplots per treatment plot, which were permanently marked ($n = 18$ per treatment per site). Percentage cover of each vascular plant species was estimated per subplot. To minimize bias from different human estimates, monitoring were led by the same individuals throughout the study, each occasion was started with a joint estimate to ensure similar estimation methods, and proportion of the total cover (the cover of a species or group divided by the total estimated cover) was used in statistical analysis.

We listed species into two category types: 1. the role in restoration and 2. the carbon fixation pathway (Table S1). Based on their role in restoration, we distinguished target species that are the focus of restoration, including mostly specialist species of open sand grasslands and invasive species that could threaten the success of restoration efforts. The categorization of target and invasive species followed the lists established by Csecserits et al. (2011) and Balogh et al. (2004), respectively. Species were categorized according to their carbon fixation pathway (C3 and C4 species) based on the TRY Database (Kattge et al., 2020). This categorization was independent from the species' role in restoration, given the limited occurrence of C4 species. However, it is considered significant in the context of climate change, which may favor species with C4 pathways, including potentially invasive alien species. Dominant indigenous non-target C4 species were *Cynodon dactylon* and *Salsola kali*, exotic C4 species included *C. incertus* and *T. racemosus*. Only one C4 species was considered target: *Bothriochloa ischaemum*. We summarized data for each group per site per year per season (June, August separately) and calculated the proportion of the given group of the total vegetation cover. We did not include indigenous non-target and C3 species in the analysis that can be considered as neutral for the restoration of open sand grasslands.

2.3. Statistical analysis

We built separate Generalized Linear Mixed Models (GLMM) for each indicator group (target and invasive, plus C4 species) per season using Template Model Builder from the glmmTMB package (Brooks et al., 2017) applying ordered beta distribution models with logit link function. In all models, the proportion of the studied group (target, invasive or C4) was the response variable. We included treatment (0 or 1), time (continuous variable) and weather parameters (total precipitation, mean temperature and drought severity) as explanatory factors in our models. All weather parameters were centered. Because of high correlation (>0.7) assessed by Pearson correlation coefficient between weather parameters, only drought severity (P-PET-3 for the given period) was included in the models as explanatory factor. Multicollinearity between the remaining explanatory variables was checked with Variance Inflation Factor from the performance package (Lüdecke et al., 2021), but no further multicollinearity was found (VIF < 2). In order to account for

differences in location, site ID was also included in the models as fixed effect. Plot ID was added as random effects in each model. As we were interested in the interactive effect of treatment with time and also with P-PET-3, we included these interactions in our full models, then manually dropped the non-significant factors ($p < 0.05$) starting from the interactions to find the best models. The residuals were checked for all models using the DHARMa package (Hartig, 2022). Data over the years and P-PET-3 were plotted with the help of ggplot2 package in R (Wickham, 2016).

3. Results

3.1. Weather parameters

The mean daily temperature of the growing season (April-September) showed an increasing trend at all three sites (Fig. 2). Since 2015, average annual temperatures exceeded the long-term average (1995–2020) and did not fall below 21°C. Precipitation fluctuated between years, and showed no decreasing trend for the growing season. The year 2010 was notable for the amount of rainfall exceeding 600 mm. Based on the percentile test, the years 2000, 2003, 2012, 2013 and 2015 were all classified as drought years, with the lowest water balance found in 2012. In comparison, only one year could be considered as drought year based on the percentile tests for the period prior the experiment (1971–1995). For drought years, the driest period was always between June and August. The three sites had slightly different climates, best illustrated by the frequency of drought years (‘Fülöpháza’ 5, ‘Izsák’ 6, ‘Bugac’ 7 dry years).

3.2. The impact of treatment, elapsed time and drought severity on target species

We did not find any significant effect of mowing or drought severity (P-PET-3), but time and site significantly impacted the proportion of target species (Table 1).

The proportion of target species increased considerably with time already during the treatment period, but continued to increase after the cessation of mowing (Fig. 3).

Of the three sites, the ‘Bugac’ site had the lowest proportion of target species with a maximum of 4 %. The most important target species in ‘Bugac’ were *Poa angustifolia*, *Carex liparicarpos* and *Achillea collina*. ‘Fülöpháza’ had a moderate proportion of target species (with an increasing trend up to 13 % on the short term and 19 % in the long term). The most important target species being (besides the species already mentioned in ‘Bugac’) *S. borysthenica, Teucrium chamaedrys* and *Centaurea arenaria*. Izsák had the largest proportion of target species up to 40 % on average in the short and 50 % in the long term. The target species pool was similar to ‘Fülöpháza’ with additional dominant species like *Gypsophila paniculata*, *Euphorbia cyparissias* and *Verbascum lychnitis*.

3.3. The impact of treatment, elapsed time and drought severity on invasive species

In the case of invasive species, we found a significant impact of treatment in interaction with time in the short term in August and significant main effect in the long term (June, August). Drought severity (P-PET-3) had a significant impact on the proportion of invasive species as main factor, but not in interaction with treatment. Time also had a significant impact as main factor, and had a significant interactive effect with treatment in the short term in the August period. The site impact was generally significant (Table 2).

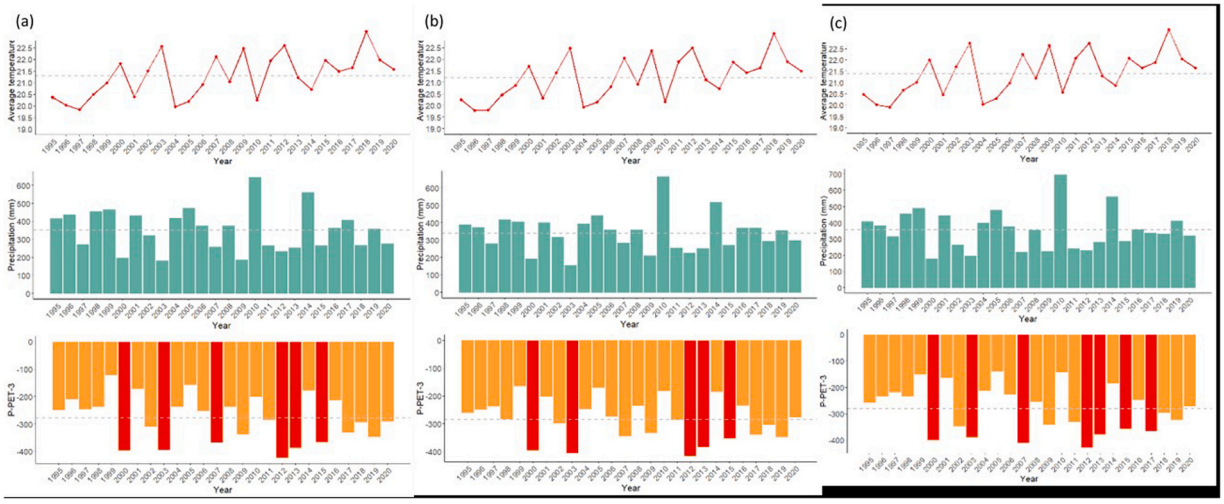

Fig. 2. Daily mean temperature (°C), daily sum precipitation (mm) and the minimum water balance of three-month growing seasons (P-PET-3). Data are derived for the April-September vegetation period, from 1995 to 2020 at ‘Izsák’ (a), ‘Fülöpháza’ (b), and ‘Bugac’ (c). Additionally, each graph includes the indication of the mean of the period 1995–2020 marked as dashed line. Red color signs drought years when P-PET-3 values are lower than the 15 percentile for the 1971–2021 period.

Table 1
Summary of the statistical results for target species for the two studied seasons (June and August) for the treatment application period (short term) (A) and in the long term (B).

	JUNE				AUGUST			
A. **When mowing still applied (1995–1999)**								
	Estimate	Std. Error	z value	Pr(>|z|)	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	−3.369	0.2547	−13.2288	0.0000	−2.691	0.238	−11.3077	0.0000
TIME	0.1939	0.0405	4.7893	0.0000	0.1714	0.0428	4.0024	0.0001
SITE (Fülöpháza)	1.3308	0.1835	7.2517	0.0000	0.4222	0.1815	2.3262	0.0200
SITE (Bugac)	2.0084	0.1882	10.6722	0.0000	1.682	0.181	9.295	0.0000
B. **In the long term (1995–2019)**								
(Intercept)	−3.5436	0.1873	−18.9174	0.0000	−2.9978	0.1642	−18.2575	0.0000
TIME	0.049	0.005	9.8815	0.0000	0.0512	0.0053	9.6329	0.0000
SITE (Fülöpháza)	1.6233	0.1637	9.9133	0.0000	0.8644	0.153	5.6489	0.0000
SITE (Bugac)	2.7375	0.1668	16.4128	0.0000	2.2813	0.1544	14.7753	0.0000

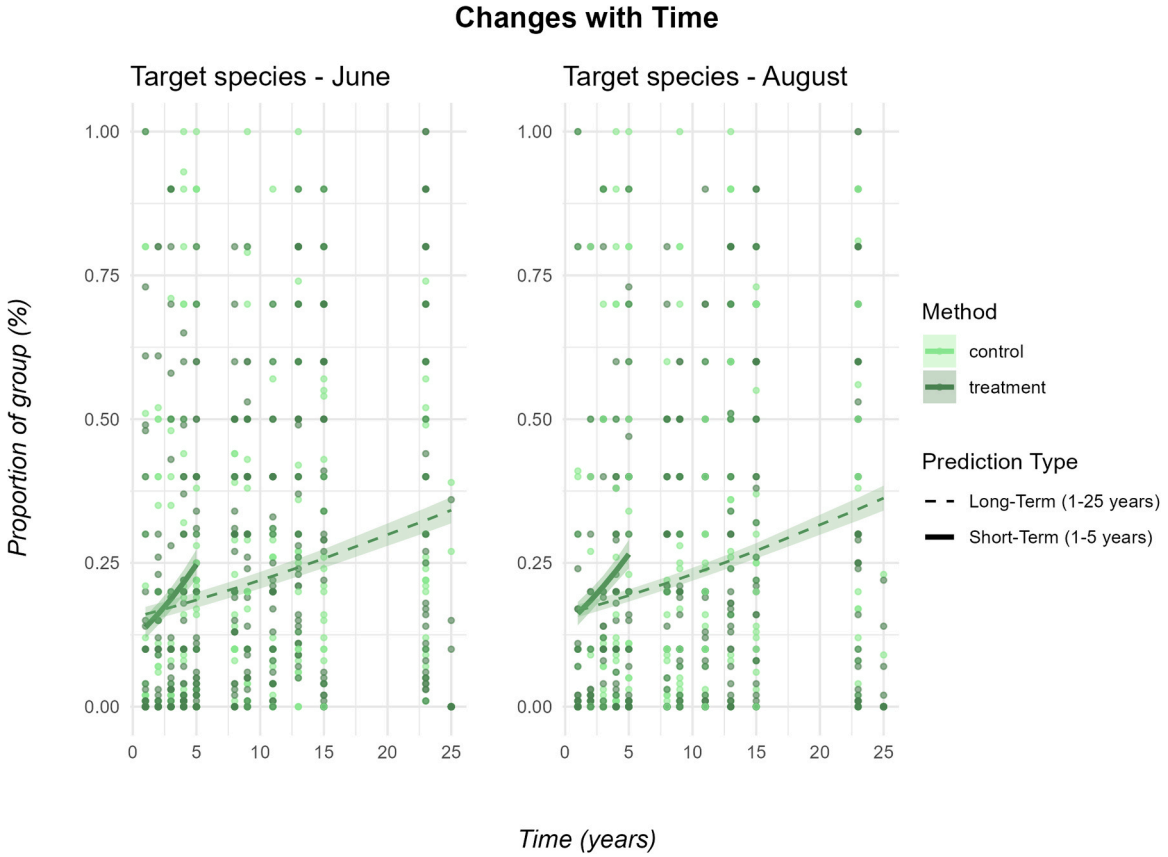

Fig. 3. Scatterplots of the proportion of target species with time and treatment. A) target species, June; B) target species, August. N = 54 per treatment per year. Darker colors indicate treatment plots, lighter colors control plots. Predicted regression lines with se are indicated for the treatment application period (short term: 1995–1999) and in the long term (1995–2019).

Mowing had a strong positive impact on invasive species in the short term in August, and was generally beneficial for invasive species compared to control (Fig. 4). Although mowing controlled *R. pseudo-acacia*, but instead secondary invasion by herbaceous species was prevalent in treatment plots. *R. pseudoacacia* could reinvade only control plots (15 %) in 'Bugac', where secondary invasion by *A. altissima* and *Celtis occidentalis* also occurred. In the other sites, there was no invasion by woody species, including *R. pseudoacacia*.

The proportion of invasive species generally increased with time up to ca. 40 % on average in the long term. Besides the woody species already mentioned, the dominant herbaceous species leading to this increase were *A. syriaca* and *C. canadensis*.

Higher proportion of invasive species was found at lower P-PET-3 values in the short term in June, however in August and in the long term, a strong positive correlation was found with increasing P-PET-3 (Fig. 5).

Table 2
Summary of the statistical results for invasive species for the two studied seasons (June and August) during the treatment application period (short term) A) and in the long term (B).

	JUNE				AUGUST			
A. **When mowing still applied (1995–1999)**								
	Estimate	Std. Error	z value	Pr(>|z|)	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	−1.8453	0.1582	−11.6663	0.0000	−0.0991	0.163	−0.6076	0.5435
TIME	0.1166	0.0371	3.138	0.0017				
P-PET−3	−0.2769	0.0603	−4.5898	0.0000	0.283	0.0677	4.1838	0.0000
SITE (Fülöpháza)	−0.4161	0.1162	−3.5817	0.0003	−1.4376	0.1233	−11.6571	0.0000
SITE (Izsák)	0.938	0.1248	7.5141	0.0000	−0.9064	0.1402	−6.4656	0.0000
Control:TIME					0.0349	0.0484	0.7194	0.4719
Mowed:TIME					0.1323	0.0476	2.7815	0.0054
B. **In the long term (1995–2019)**								
(Intercept)	−1.4261	0.0959	−14.8735	0.0000	−0.3123	0.0882	−3.5412	0.0004
TREATMENT	0.2023	0.0692	2.9247	0.0034	0.3189	0.0709	4.4977	0.0000
TIME	0.0352	0.0051	6.9047	0.0000	0.0166	0.0057	2.9117	0.0036
P-PET−3	0.1172	0.04	2.9277	0.0034	0.3759	0.0389	9.6532	0.0000
SITE (Fülöpháza)	−0.3723	0.0906	−4.1106	0.0000	−1.0607	0.0888	−11.9439	0.0000
SITE (Izsák)	0.2025	0.0956	2.1192	0.0341	−0.9609	0.0955	−10.0642	0.0000

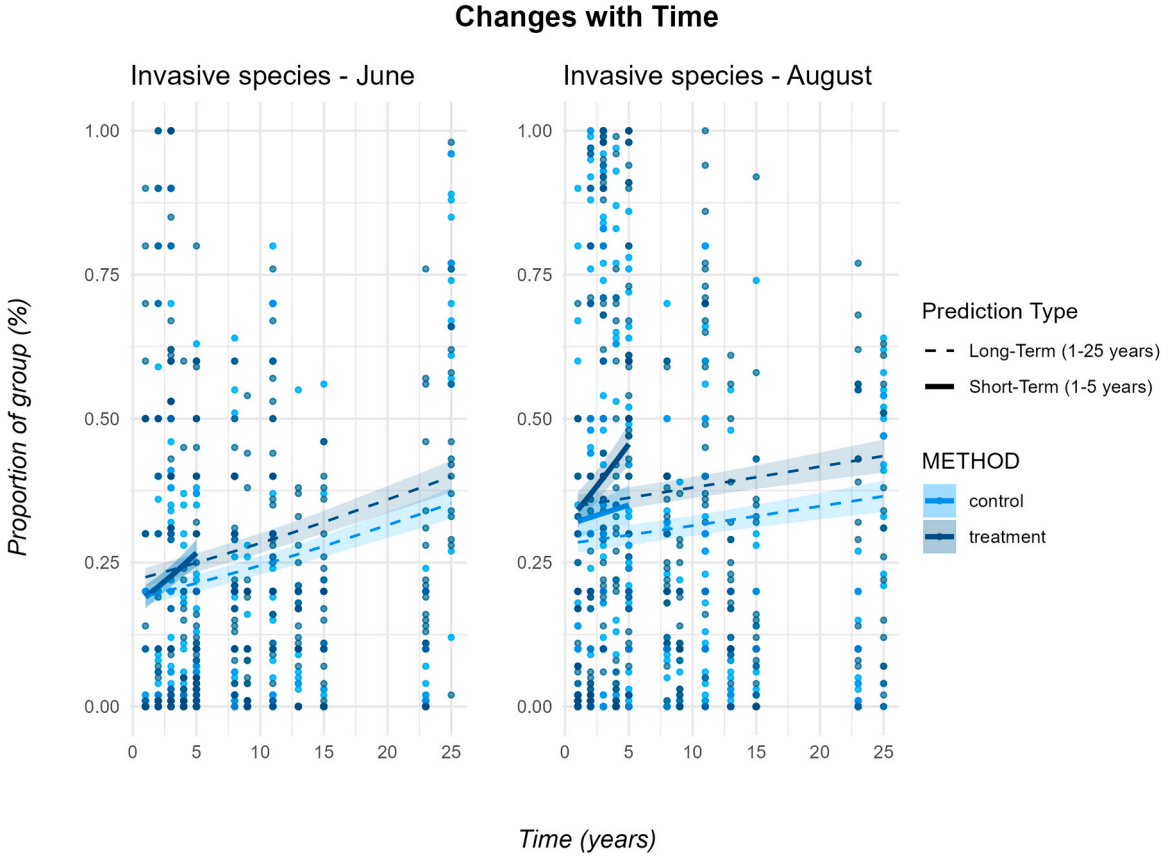

Fig. 4. Scatterplots of the proportion of invasive species with time and treatment. A) invasive species, June; B) invasive species August. N = 54 per treatment per year. Darker colors indicate treatment plots, lighter colors control plots. Predicted regression lines with se are indicated for the treatment application period (short term: 1995–1999) and in the long term (1995–2019).

The highest proportion of invasive species was found in 'Bugac', where target species were limited. The proportion of invasive species was 11 % in the short term on average in June and 50 % on average in August. Considering the long-term, the proportion of invasive species reached almost 60 % in June. The proportion of invasive species was moderate in 'Fülöpháza' and increased in time up to 15 % and 20 % in June and in August, respectively. After a temporary increase in midterm (2002–2005), mainly due to annual species and temporary reinvasion by *R. pseudoacacia*, the proportion of invasive species decreased below 3 % in 'Izsák', and only

A. syriaca and *C. canadensis* persisted at this site.

3.4. The impact of treatment, elapsed time and drought severity on C4 species

The proportion of C4 species was significantly affected by treatment in interaction with time in the short term in August, and by treatment and time as main factors in the long term. Drought severity (P-PET-3) significantly affected the proportion of C4 species as main factor for all study periods, except in the short term in August where it exerted its impact in interaction with treatment. Site had a general significant impact (Table 3.)

The proportion of C4 species increased in treatment plots and decreased in control plots with time in the short term. In the long term, the proportion of C4 species decreased in both treatments, but was significantly higher in treated plots (Fig. 6).

We found generally higher proportions of C4 species at lower values of P-PET-3, and their proportion was significantly higher with lower P-PET-3 in treatment plots in the short term in August than in control plots where their proportion was stable (Fig. 7).

There was only a limited proportion of C4 species in 'Bugac', less than 1 % in June and 8 % in August. The dominant species were invasive *Amarathus* sp. and native *Setaria viridis.* In 'Fülöpháza', average proportion of C4 species was 15 % in June and 35 % in August. The proportion of C4 species was similar in June and August in 'Izsák' (18 %). In both sites, mid-successional stages had higher proportions of C4 species. Native *C. dactylon*, *S. kali* and *Kochia laniflora* were dominant, but two invasive species also occurred: *C. incertus* and *T. racemosus*.

4. Discussion

We found that daily mean surface temperatures increased at all three sites during the study period. Although there was no decreasing trend in daily precipitation, the minimum of three-month climatic water balance for the growing season (April-September) was persistently low, with drought years becoming frequent in the study period (1995–2020). Target species were not significantly affected by drought, C4 had higher proportions at higher drought severity, while invasive species tended to have higher proportions at lower drought severity. Mowing was generally neutral to target species, had a positive impact on invasive species and on C4 species.

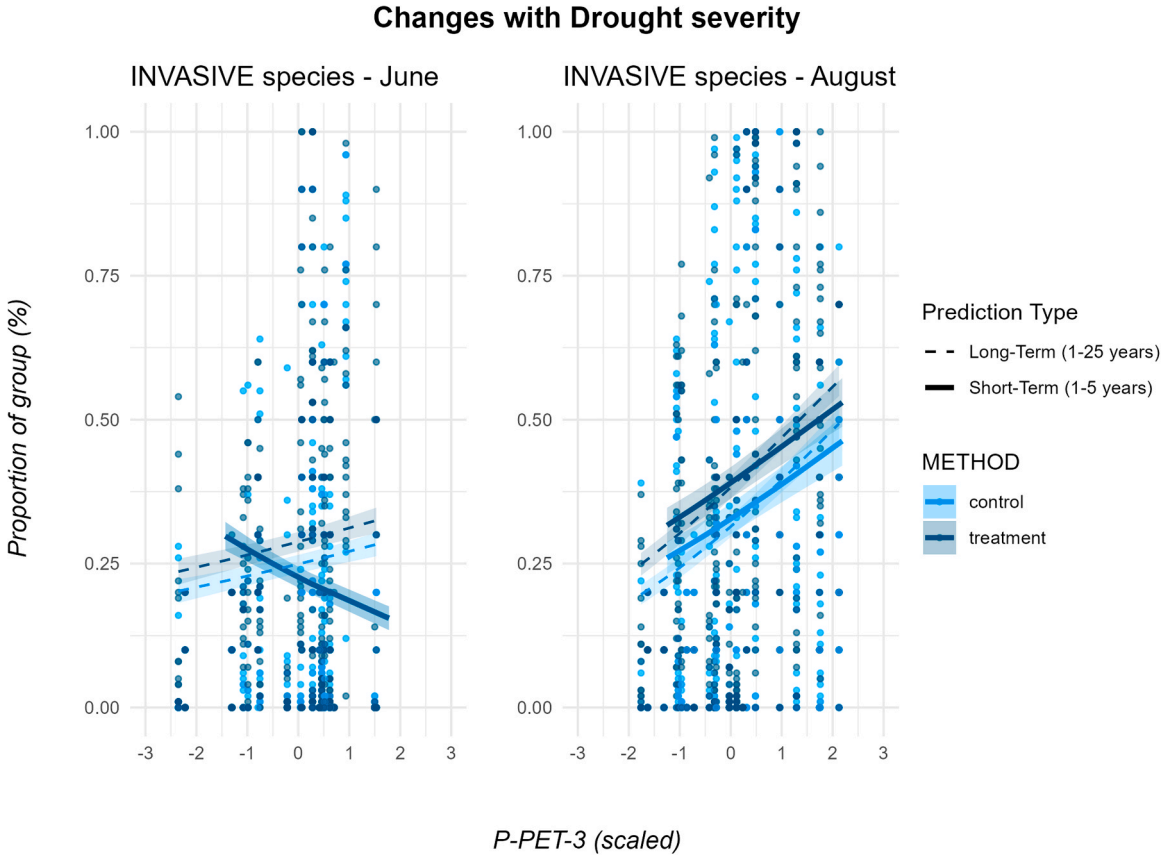

Fig. 5. Scatterplots of the proportion of invasive species with drought severity (P-PET-3) and treatment. A) invasive species, June; B) invasive species, August. N = 54 per treatment per year. Predicted regression lines with se are indicated for the treatment application period (short term: 1995–1999) and in the long term (1995–2019).

Table 3
Summary of the statistical results for C4 species for the two studied seasons (June and August) during the treatment application period (short term) (A) and in the long term (B).

	JUNE				AUGUST			
A. **When mowing still applied (1995–1999)**								
	Estimate	Std. Error	z value	Pr(>|z|)	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	−3.9679	0.3469	−11.4373	0.0000	−1.4552	0.1988	−7.3218	0.0000
TIME	−0.1129	0.0537	−2.1026	0.0355				
P-PET−3	−0.189	0.0702	−2.6928	0.0071				
SITE (Fülöpháza)	3.0452	0.3041	10.0146	0.0000	1.5835	0.1463	10.8199	0.0000
SITE (Izsák)	3.1825	0.307	10.366	0.0000	0.7412	0.1498	4.9477	0.0000
TREATMENT:TIME	0.2045	0.0438	4.6707	0.0000				
Control:TIME					−0.0872	0.0493	−1.7685	0.0770
Mowed:TIME					0.118	0.0476	2.4807	0.0131
Control:P-PET−3					−0.0043	0.0889	−0.0486	0.9612
Mowed:P-PET−3					−0.2214	0.0804	−2.7542	0.0059
B. **In the long term (1995–2019)**								
(Intercept)	−4.2018	0.2593	−16.2058	0.0000	−1.7994	0.1331	−13.519	0.0000
TREATMENT	0.7857	0.1423	5.523	0.0000	0.6393	0.0752	8.4968	0.0000
TIME	−0.0166	0.0066	−2.5219	0.0117	−0.0558	0.0065	−8.5436	0.0000
P-PET−3	−0.1627	0.0414	−3.9278	0.0001	−0.2223	0.0398	−5.5886	0.0000
SITE (Fülöpháza)	2.6129	0.2277	11.4769	0.0000	1.6589	0.1271	13.0486	0.0000
SITE (Izsák)	2.8287	0.2282	12.3974	0.0000	1.0725	0.1256	8.5385	0.0000

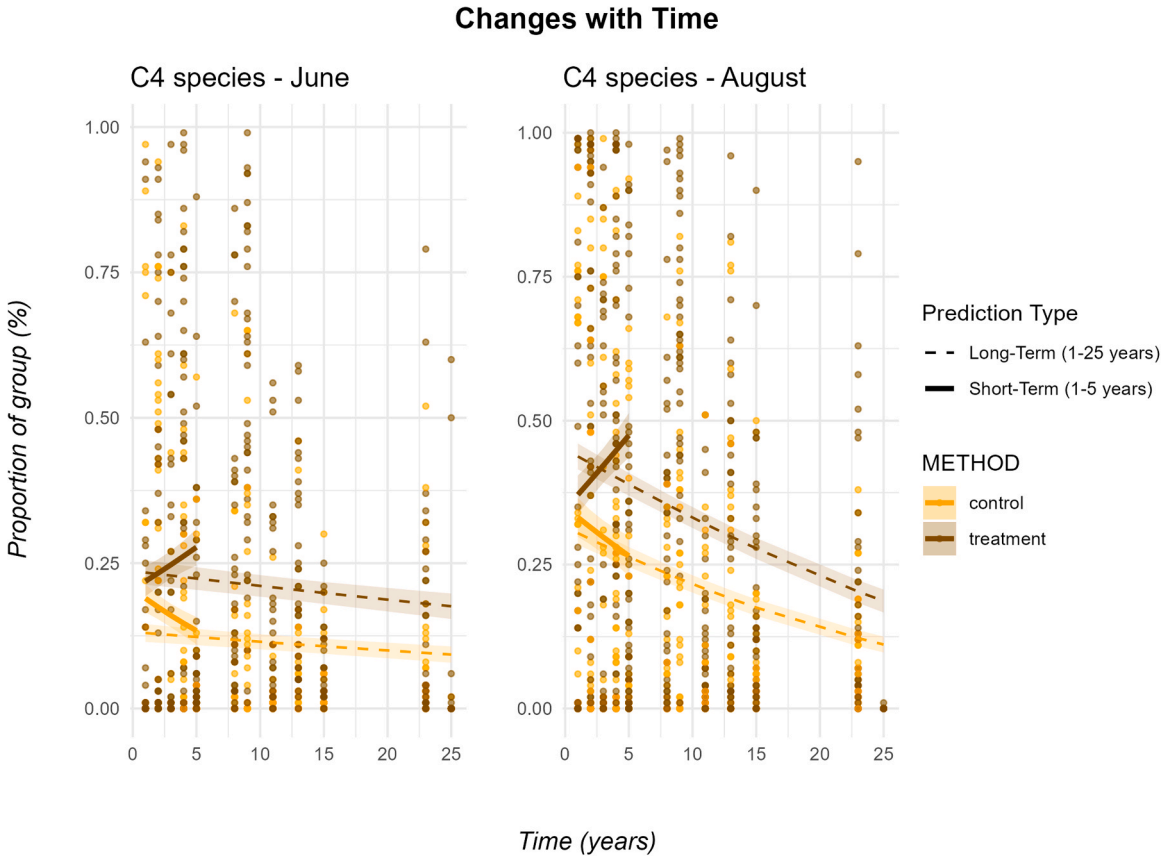

Fig. 6. Scatterplots of the proportion of C4 species with time and treatment. A) C4 species, June; B) C4 species, August. N = 54 per treatment per year. Darker colors indicate treatment plots, lighter colors control plots. Predicted regression lines with se are indicated for the treatment application period (short term: 1995–1999) and in the long term (1995–2019).

We found only a weak evidence that areas under restorative mowing can be more sensitive to drought, namely C4 species showed a stronger response to drought in mown plots in the short term in August. Our results confirm that sand grassland species are resilient to drought even during restoration treatments, but mowing in our case was beneficial for alien invasions, which have long-lasting effects

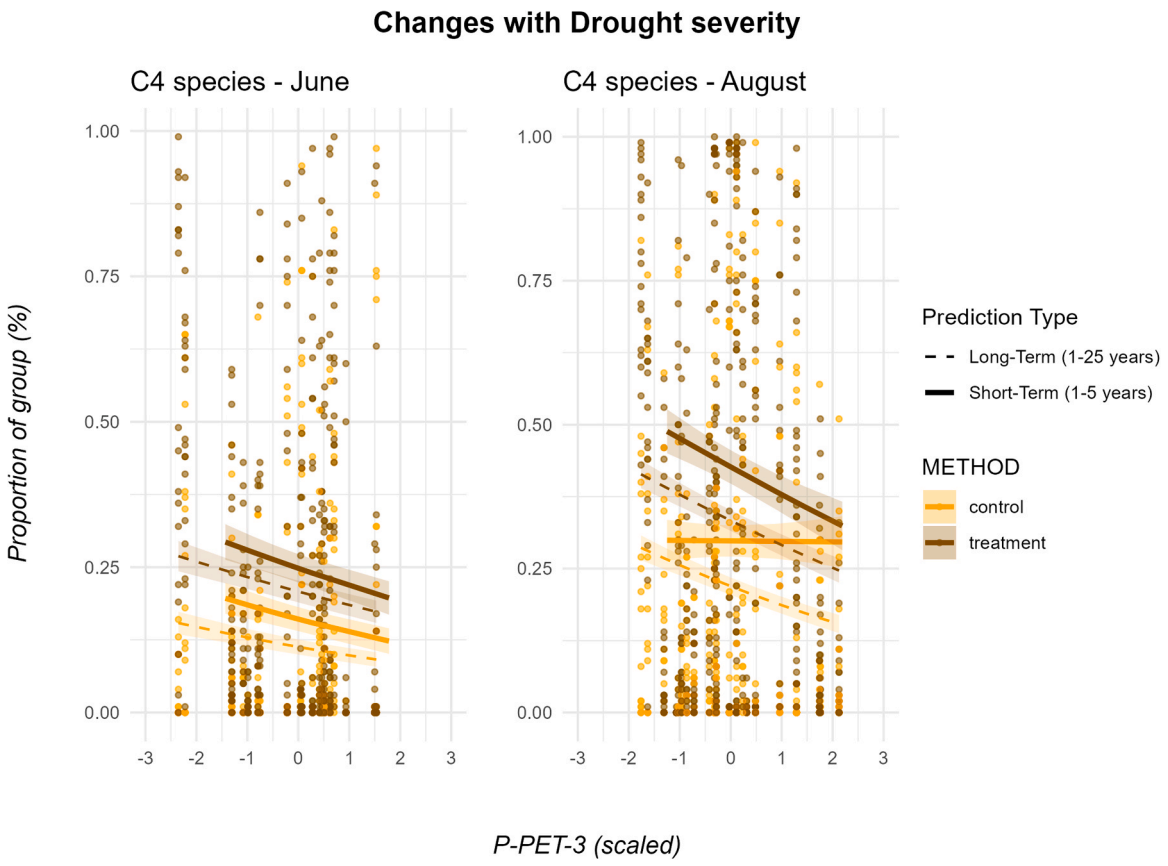

Fig. 7. Scatterplots of the proportion of C4 species with drought severity (P-PET-3) and treatment. A) C4 species, June; B) C4 species, August. N = 54 per treatment per year. Darker colors indicate treatment plots, lighter colors control plots. Predicted regression lines with se are indicated for the treatment application period (short term: 1995–1999) and in the long term (1995–2019).

even after mowing is stopped.

4.1. Changes in long-term weather parameters

Our weather data showed that the summer months (June to August) are particularly dry, with low water balance values. Temperatures have risen without any trends in rainfall that have led to more frequent droughts in the study area over the past few years. These results are consistent with previous findings that the Great Plain is the most drought-affected area in Hungary (Blanka et al., 2013). Kiss et al. (2017) predicted an increase in temperatures, especially in the summer months, and a shift of the driest months to July and August, which is in line with the global projections of Bede-Fazekas and Somodi (2024), who consider this region as a hotspot for expected precipitation shifts. In addition to the changing climatic conditions, the drying of the Hungarian Great Plain is further aggravated by the loss of soil water retention capacity and the decline in groundwater levels (Pinke et al., 2020). These shifts, and the increased severity and frequency of droughts, might have profound effects on vegetation (Inouye, 2022; Zhang et al., 2019) and on the success of restoration interventions (Choi et al., 2008, Lyons et al., 2023).

4.2. Response of indicator groups to drought severity

Although the direct effects of drought could not be determined in our study because the observation years and drought years did not overlap, and because of the ongoing changes in the succession, some trends could be identified. We found evidence that open sand grassland species and the process of recovery of the open sand grassland community in cleared *R. pseudoacacia* plantations were resilient to drought. In some years, particularly in drought years, a decrease in the proportion of target species was visible, but overall drought severity did not have a significant impact on target species. Sand grassland species are adapted to semi-arid conditions, drought, variations of water availability, and short-term water shortage (Hoover et al., 2014). Shallow-rooted grasses (e.g., *Festuca vaginata* and *Koeleria glauca*) are less resistant, but still resilient to drought and heat waves: severe drought causes aboveground shoots to die, as experienced lately in 2022 (Gyalus et al., unpubl.), but after rainfall, they can regenerate from belowground buds. Deep-rooted species, especially perennial herbs, are more resistant to drought and can quickly colonize surfaces left free by grasses.

Sand grasslands also harbor annual species that can survive drought in the form of seeds and utilize spring or winter precipitation for germination and growth. Based on previous results (Török and Lohász, 2004), mainly summer annuals were correlated with drought at our sites, but they are considered neutral for sand grassland restoration in this study. Instead, among the target species, deep-rooted biennial and perennial forbs (e.g. *C. arenaria, G. paniculata* and *V. lychnitis*) increased in cover, rather than perennial grasses.

Invasive species were primarily negatively affected by drought, similar to previous results (Har-Edom and Sternberg, 2010; Thomsen et al., 2006). The dominant species in our case were perennial common milkweed (*A. syriaca*) and a facultative winter annual Canadian horseweed (*C. canadensis*). Both species can tolerate a wide range of environmental conditions, including dry climates. *A. syriaca* was shown to be sensitive to drought in the early life stage (Orbán et al., 2021) and reacts with drying of the shoot apices in the adult stage, but is resistant and resilient to drought (and other negative effects) due to its underground bud bank (Follak et al., 2021). *C. canadensis* was found to be negatively affected by reduced water availability along a gradient from mesic Mediterranean to arid regions in Israel (Or-Leyl and Sternberg, 2010). In a local rain exclusion experiment, severe drought was found to increase mortality of *C. canadensis* individuals, but surviving individuals can respond positively to drought, which contributes to the invasive success of the species in such a changing climate (Mojzes et al., 2020).

In line with our expectations, drought had only minor impact on C4 species. C4 species showed some minor peaks, usually coupled with dry years. However, opposite to our expectations, C4 species generally decreased in the long term. Only a few C4 species was considered target species or harmful (invasive) species for restoration, and instead common C4 species such as Bermuda grass (*C. dactylon*) and common saltwort (*S. kali*) were more abundant. The invasive C4 species were annuals (*Amaranthus* sp., *C. incertus*, *T. racemosus*) that generally occur in disturbed areas in the region and our results suggest that they do not compromise the outcome of restoration efforts. Recent perennial C4 grass invaders, such as sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), represent a new threat to Eurasian dry grasslands (Kröel-Dulay et al., 2024; Török et al., 2021). Given the evidence suggesting that this species is a potential transformer species, i.e. species that can significantly affect the composition, structure and functioning of the ecosystem (Török et al., 2021; Hábenczyus et al., 2022), and able to colonize not only areas disturbed by humans but also semi-natural areas with low vegetation cover (Kröel-Dulay et al., 2024), it is considered a new challenge for grassland restoration in the region, especially in the light of climate change.

4.3. The interaction of mowing and drought

Mowing as treatment increased the susceptibility of the developing sand grassland to drought to only a minor extent, regarding C4 species that have a subordinate role in sand grasslands. Ecosystems undergoing restoration are generally in an early successional stage and, as such, might be more vulnerable to the impacts of climate change, such as severe drought (Choi et al., 2008; Kröel-Dulay et al., 2015). Earlier results of our experiment also indicated that significant changes correlated with drought mostly in treatment plots (Török and Lohász, 2004). Mowing kept the vegetation short, with a significant amount of bare soil, and in the absence of mowing, a dense shrub or even woody vegetation established. Despite this strong impact on vegetation structure, mowing did not influence the response of target or invasive species to drought in our study. This can be partly due to the limited size of treatment areas (10 m x 10 m), as the presence of shrubs and trees in control plots and the proximity of forest edges at two sites could mitigate the effects of droughts. Forest edges were found to moderate the local microclimate in this region (Süle et al., 2020). This also means that, in the light of climate change, the sustainability of grassland restoration measures could be increased by restoring woody patches together with open systems, or even going further, by restoring transitional ecosystems such as forest steppes (Halassy et al., 2020). Although not in interaction, both mowing and drought favored invasive species early during restoration. This rapidly increasing trend in the proportion of invasive species is in line with our expectations and with earlier findings that invasive species can rapidly utilize resources after disturbance and drought and are often indirectly supported by climate change (Diez et al., 2012; Manea et al., 2016; Walther et al., 2009).

4.4. Long-term impact of mowing on the restoration of open sand grassland

Our results confirm that mowing with hay removal can be used to control *R. pseudoacacia* plantations and through this help the regeneration towards targeted open sand grasslands. Mowing successfully prevented reinvasion by *R. pseudoacacia* and secondary invasion by other woody species (like *A. altissima* and *C. occidentalis*) and this impact lasted in the long term even after the cessation of treatments. Mowing controlled woody invasive species, but allowed the establishment of herbaceous invasive species. Once established, the presence of invasive species can disrupt the recovery process of plant communities after drought (Vetter et al., 2020). In our case, this was exacerbated by the soil legacies left after the removal of the targeted invasive species, which in our case meant increased soil nitrogen in the upper soil layer (0–10 cm) compared to open sand grasslands and the presence of nitrogen rich litter (Halassy, 2004) that probably facilitated secondary invasion (Kettenring and Adams, 2011, Nsikani et al., 2018, Pearson et al., 2016, 2018). The lower proportion of invasive species in control is primarily due to the establishment of shrub cover in control plots that shaded out invasive species, and also to the overall decline of invasive species in the 'Izsák' site (Reis et al., 2021). The probability of invasion decreased with the proportion of target species and increased by high propagule pressure of invasive species in the landscape (Reis et al., 2022) and the proximity of non-native tree plantations that host various, mostly perennial invasive species in the region (Csecserits et al., 2016).

Although at the site level mowing was beneficial for the establishment of grassland species where dispersal of target species was possible, as the area was predominantly open and surrounded by grasslands in the immediate vicinity ('Izsák' and 'Fülöpháza') (Reis et al., 2021), our study did not confirm an overall positive impact when the three sites were analyzed together. This is partly due to the

impact of the 'Bugac' site where establishment of target species was limited due to limited dispersal opportunities in the forested landscape. Instead of specialist species, mowing favored generalist species. Open sand grasslands are not adapted to mowing, and can tolerate only light grazing. In particular, the matrix species *F. vaginata* is negatively affected by heavy grazing or mowing, which opens the vegetation to the establishment of subordinate species (Ónodi et al., 2006; Török and Lohász, 2004). Furthermore, the regeneration potential of sand grasslands on neighboring land is considered moderate to low (Csákvári et al., 2021), and grasslands regenerating on disturbed land are often accompanied by stable populations of alien invasive species (Csecserits et al., 2011). This is mainly due to the dispersal limitation of specialist species, which can be successfully overcome by the introduction of native species (Reis et al., 2022).

4.4.1. Limitations of the study

Unfortunately, the experimental design and the limited number of sites did not allow for a clear separation of the effects of mowing, drought and landscape context. Mowing stopped in 2001, followed by a severe drought in 2003 and monitoring frequency after the cessation of mowing did not overlap with additional drought years. The three sites under study showed significant differences in all studied aspects. The most open landscape has not only allowed the spread of target species, but has also had the lowest pressure of invasive species (Reis et al., 2022). In fact, environmental conditions, landscape and historical factors often act in parallel on landscape and community processes (de Blois et al., 2001) and cannot be easily separated in field studies (e.g. Smith et al., 2024), much less in restoration studies, where site selection is based primarily on the possibility of restoration, lowering the reproducibility and generalizability of the results (Lyons et al., 2023). Our results also highlight the need to consider not only the length of the monitoring period, but also the frequency of data collection and its relationship to environmental changes, such as the expected frequency of natural hazards, e.g. drought events and heat waves.

5. Conclusion

The study adds to the complex interplay between drought, invasion and restorative mowing in shaping the effectiveness of grassland restoration. Based on our results, target grassland species exhibit greater resistance and resilience to drought than the currently present invasive species. Restorative mowing successfully prevents the reinvasion by *R. pseudoacacia*, but not secondary invasion by herbaceous species. Open sand grasslands are naturally resilient to disturbances and can regenerate under various conditions in natural landscapes (Csákvári et al., 2021), but their vulnerability to invasion increases in fragmented landscapes where the matrix hosts hot-spots of invasive species (Csecserits et al., 2016). This underscores the need for further research to develop adaptive restoration strategies that account for alien invasion and its long-term implications for ecosystem resilience. A whole-ecosystem approach is critical for restoration, emphasizing functional diversity, below-ground ecosystem components and landscape context to ensure resilience to both climate change and invasion (Buisson et al., 2022; Lloret et al., 2012).

Author contributions

M.H., E.Cs. conceived and designed the study together and contributed to the data collection. E.K., M.H. carried out part the analyses and wrote the first version of the manuscript. K.T. conceived the design and ensured funding of the restoration implementation and monitoring, and contributed as consultant during the finalization of the manuscript. M.H. finalized the manuscript with substantial contribution of all authors.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03588.

Data availability

Long-term vegetation data is available at Kiskun Restoration Experiments, KISKUN LTER – Hungary. Any other relevant data are available from the corresponding author upon reasonable request.

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