

RESEARCH ARTICLE

The role of drought, disturbance, and seed dispersal in dominance shifts in a temperate grassland

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Abstract

Aims: More intense and frequent droughts predicted for the future will heavily affect grasslands worldwide and, along with various other disturbances, possibly trigger major vegetation shifts. Therefore, documenting these changes and understanding the mechanisms behind them is essential. Our study aimed to investigate how dominant species in a semiarid grassland respond to a combination of small-scale experimental disturbances and naturally occurring droughts and uncover the underlying mechanisms.

Location: Central Hungary.

Methods: We conducted a small-scale disturbance experiment in a semiarid temperate grassland and followed recovery for 18 years, including severe drought events. In 1999, we established 16 sites, eight dominated by *Festuca vaginata* and another eight by *Stipa borysthenica*, the two dominant species of sand grasslands in the region. At each site, three permanent plots were marked that received either a cutting or digging treatment or remained as controls. We monitored the cover and density changes of *Festuca* and *Stipa* annually.

Results: In the early years following the disturbance, *Festuca* recovered at a similar rate under both disturbance treatments, while *Stipa* recovered faster in cut than in dug plots. When natural drought events caused major diebacks of both species, *Stipa* recovered very quickly and regained dominance in initially *Stipa*-dominated plots, and it also took over in initially *Festuca*-dominated control and cut plots. However, digging at *Festuca*-dominated sites delayed drought-induced *Stipa* colonisation and thus favoured *Festuca* recovery. We found that the poor performance of *Stipa* in dug plots was related to sharply reduced seedling establishment, which resulted from the low number of seeds captured by the bare soil surface after digging.

Conclusions: Our results demonstrate that recurring drought events may induce dominance shifts in temperate grasslands, but small-scale disturbances can modulate vegetation responses. Our findings emphasise the importance of post-disturbance regeneration patterns in drought-induced vegetation shifts and show that seed dispersal strategy may have a major effect on vegetation dynamics.

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KEYWORDS

climate change, dominance shift, drought, extreme events, long-term observation, recovery, seed dispersal, soil disturbance

1 | INTRODUCTION

Drought events have become more frequent and intense in recent decades (Dai, 2011, 2013; Stagge et al., 2017). This trend is expected to continue in the future in many regions, partly due to precipitation decrease and partly to increasing evaporative demand caused by higher temperatures (Lehner et al., 2006; Trenberth et al., 2014; Spinoni et al., 2018). According to the projections presented in the latest IPCC report (IPCC, 2021), in dry regions, droughts that occurred once in a decade before the 20th century will occur two to four times (depending on the extent of warming) every 10 years by the end of the 21st century. With this prospect in mind, it is essential to get a better understanding of how drought impacts natural ecosystems and what determines ecosystem resilience.

Droughts have a profound effect on vegetation that can manifest at different levels of organisation from physiological reactions of individual plants (Gutschick & BassiriRad, 2003; Milbau et al., 2005; Nippert et al., 2009; Hoover et al., 2014) through tissue dieback (Kreyling et al., 2008), productivity changes (Hoover et al., 2014), increased mortality (Breshears et al., 2005), altered population demography (Lloret et al., 2012), shifts in community composition (Evans et al., 2011), changes in dominant species or plant functional types (Suarez & Kitzberger, 2008), all the way to the regime and biome shifts (Allen & Breshears, 1998; Peñuelas & Boada, 2003; Scheffer et al., 2008; Beck et al., 2011). Substantial shifts in species composition, changes in dominant or functionally unique species and subsequent regime shifts are especially of concern, as they may transform the structure and functioning of ecosystems (Mueller et al., 2005; Peñuelas et al., 2013), and change ecosystems services (Anderegg et al., 2013).

Despite the obvious impact of extreme climatic events on vegetation dynamics, well-documented drought-induced dominance shifts are still rare, and few studies provide a mechanistic understanding of these transitions (Stampfli & Zeiter, 2004; Martínez-Vilalta & Lloret, 2016). Several studies highlight that multiple factors may interact with drought events. Therefore, the actual impact cannot be adequately predicted from the constituent species' autecological characteristics or from the communities' bioclimatic requirements alone. External modifying factors, such as microsite variability, can considerably modulate plant responses by influencing water availability. Biotic factors, such as species composition, community-level attributes and biotic interactions, may also influence the drought sensitivity of ecosystems (Martínez-Vilalta & Lloret, 2016; Felton & Smith, 2017).

Land use and the legacies of past disturbance events are important in explaining the variability of drought responses observed worldwide. Higher management intensity can lower ecosystem resilience to drought in some systems (see Vogel et al., 2012) but can also be unimportant in others (Auerswald et al., 2012). Non-climatic

disturbances during or before a drought can also modify ecosystems' resilience. A cross-European study found that sites previously impacted by fire, pest outbreaks, and mowing were more sensitive to simulated warming and drying than intact ecosystems, most likely because they were in an early successional stage and not in equilibrium with their environment (Kröel-Dulay et al., 2015).

The effect of drought events can be directly studied by experimental or observational approaches. Climate manipulation experiments, including regionally or globally coordinated efforts with shared protocols (e.g., Beier et al., 2004; Tielbörger et al., 2014; Smith et al., 2016), provide us with invaluable information on vegetation response to controlled levels of precipitation reduction. However, several reviews emphasise that most of these manipulation experiments failed to apply treatments extreme enough to induce significant plant dieback, mortality or regime shifts (Beier et al., 2012; Asbjornsen et al., 2018) and overall, experimental results have been shown to underestimate ecosystem response to drought (Kröel-Dulay et al., 2022). Observational studies on naturally occurring drought events can augment our knowledge, even if they are uncontrolled and depend on the stochastic occurrence and intensity of drought events. Yet, well-documented, long-term case studies uncovering the exact mechanism of drought-induced vegetation changes, especially dominance and regime shifts, are relatively scarce (e.g., Fischer et al., 2020), and even fewer studies investigate other non-climatic drivers simultaneously.

Our study combines a small-scale disturbance experiment with a subsequent long-term observation of grassland dynamics over 18 years that covered several drought periods in a semiarid grassland in central Hungary. Since our study system has two dominant perennial grass species (*Stipa borysthenica* Klovov ex Prokudin and *Festuca vaginata* Waldst. et Kit. ex Willd.) representing two genera that are widespread across the forest-steppe biome in Eurasia (Erdős et al., 2018), our initial disturbance experiment was stratified according to the dominant species. This design allowed us to evaluate the separate and combined effects of small-scale disturbance and drought and to answer the following research questions: (1) how do dominant grass species recover after different types of small-scale disturbances (cutting and digging); (2) how do dry years affect the two dominant species; and (3) do disturbances modify the effect of drought events?

2 | MATERIALS AND METHODS

2.1 | Study site

The study area is situated on the Danube-Tisza Interfluvium (central Hungary), in the Kiskunság National Park, near the village of Fülöpháza (46°52'N, 19°25'E, see Figure 1b). The landscape is



FIGURE 1 Location and study design. (a) The study area within Europe and (b) Hungary, and (c) the layout of the plots within sites

characterised by sand dunes covered by forest-steppe vegetation, including open and closed grasslands and forest patches. The soil consists primarily of sand (over 95%); it has a low humus content (below 1%) and a very low water-holding capacity (Kovács-Láng et al., 2000). The climate is moderately warm, with continental and submediterranean influences: mean annual temperature is 10.6°C and mean annual precipitation is 534.2 mm based on records from the period between 1936 and 2019.

The study site is located within the Fülöpháza Sand Dunes, which is part of the Kiskunság National Park. The area is grazed only by native wildlife (roe deer and European hare). We studied open sand grasslands which are characteristic of the driest habitats of Pannonic sand steppes, and represent a unique community endemic to the region (ŠeffEROVÁ StanOVÁ et al., 2008). These grasslands are dominated by two perennial bunchgrasses: *Festuca vaginata* is an endemic species that occurs in dry, calcareous sandy areas in the Pannonian biogeographic region, while *Stipa borysthenica* (a synonym of *Stipa sabulosa* (Pacz.) is widespread across the steppes of Eurasia, and it is close to its westernmost distribution limit in Hungary (taxonomic nomenclature follows Király et al., 2009). Both grass species form dense tussocks (Figure S1 in Appendix S2) and are capable of short-distance, phalanx-type clonal growth only (Csecserits, 2007). Since no other species from these two genera were present in plots during our study, we will only use the genus names to refer to them (unless the context requires otherwise).

The total vascular plant cover in this vegetation type is approximately 30%–35%. The two dominant grass species contribute most to this cover: during our study period, their combined cover was, on average, 61.3% (of the total cover, see Figure S2 in Appendix S2), which included years with large declines and increases up to above 90%. Stands dominated by *Festuca* or *Stipa* are distinct subtypes of open sand grasslands (Borhidi, 2003). Yet, the determinants of their dominance, particularly the role of disturbance events and weather fluctuations, are poorly understood. *Stipa* is generally considered more drought-resistant and is usually dominant in the most extreme habitats on dune tops and flats. Conversely, *Festuca* is dominant at slightly moister sites, for example, forest edges and north-facing dune sides. Also, *Festuca* is among the first species to colonise freshly exposed bare ground during succession (Fekete, 1992). In terms of palatability, we know that *Festuca vaginata* is often preferred to *Stipa*

borysthenica within this vegetation type, and recent study results show that it has a notably high crude protein, fat and fibre content (Fűrész et al., 2022). According to previous studies, apart from the dominant species, there is no remarkable difference between species richness of *Festuca*- and *Stipa*-dominated vegetation subtypes (Biró & Molnár, 1998). Accompanying species include perennial herbs (*Artemisia campestris* L., *Dianthus serotinus* Waldst., *Euphorbia seguieriana* Neck., *Fumana procumbens* Gren. & Godr.) and annuals, which temporarily become dominant after disturbance events (*Secale sylvestre* Host, *Salsola kali* L., *Polygonum arenarium* Waldst. & Kit, *Bassia laniflora* (S.G.Gmel.) A.J.Scott). A moss-lichen cryptogamic layer often covers the ground between grass tussocks. Growing season in the region starts in April and lasts until September. The vegetation has a productivity peak in May–June and a secondary, minor peak after the dry summer in September.

2.2 | Study design and data collection

Within the study area (approximately 1 km²), we selected eight sites dominated by *Festuca* (20%–30% cover) and another eight dominated by *Stipa* (20%–30% cover).

At the start of the study, three 1-m² plots were marked permanently at each site, located 1 m from each other (Figure 1c). These received three treatments in April 1999. One plot was dug to approximately 20 cm depth, and all vegetative plant material was removed (hereafter referred to as 'digging' treatment and 'dug' plots). In the second plot, above-ground biomass was cut at ground level in April and then repeatedly (four to six times depending on regrowth) until ca mid-summer, when no further regrowth was observed, and the plants were considered dead ('cut' plots). Live and standing dead plant materials were removed, but litter on the ground was not.

The two different disturbance treatments were chosen to represent two main categories of disturbances: those that involve soil perturbation (natural processes such as the burrowing of rabbits, foxes or badgers; or anthropogenic disturbances, such as construction work, maintenance and use of dirt roads, ploughing), and those that do not (e.g., overgrazing, high herbivore pressure caused by gradation). To make the treatments comparable in intensity, we ensured that all individual plants of the dominant species died



following digging and repeated cutting and that there was no vegetative regrowth.

From 1999 onwards, the number of individuals of the two dominant grass species (including tussocks and young plants, i.e., *Stipa* individuals that germinated in the spring but survived until autumn and *Festuca* individuals that germinated in autumn and survived until the following autumn) was recorded in late September or early October each year. In 1999, an early survey in April was also conducted, representing the state of vegetation after the 1998 growing season. *Stipa* density was not recorded in 2009 and 2010, and we are missing *Festuca* density data from all the sites for 2009 and from two sites for 2010. We visually estimated the percentage cover of *Festuca* and *Stipa* in late June or early July from 2001 to 2016. The cover was not recorded before 2001, but we drew the outlines of *Stipa* and *Festuca* tussocks on gridded maps each summer between 1999 and 2001. Since we found a high correlation between the estimated cover values based on drawings and the cover values from the field surveys for 2001 ($r_{\text{Pearson}} = 0.88$, $df = 14$, $p < 0.001$ for *Stipa*, and $r_{\text{Pearson}} = 0.95$, $df = 8$, $p < 0.001$ for *Festuca*), we calibrated the drawn cover values for 1999 and 2000 and merged them with our existing cover data set.

Since density data were recorded in late September or early October and cover data were recorded in June (following peak growth but before potential drought-induced dieback), we shifted cover data back by one year when plotting to match the two data sets, and also to show the drought-induced diebacks in the year of the drought (e.g., cover detected in June 2009 is presented for 2008). Note that mortality events occur during summer (after sampling in June or early July), so matching early summer cover with September density in the same year would lead to a mismatch between the two measures (e.g., high cover in June in 2003, but extremely low density in September). We consider the cover of *Festuca* and *Stipa* our primary response variable since it is a proxy for above-ground biomass. On the other hand, density can show whether an observed change in the cover is only due to the growth or shrinkage of individuals (no change in density) or to actual establishment or dieback, respectively.

In addition to the long-term vegetation survey in permanent plots, we also conducted a one-year experiment to assess the number of *Stipa* seeds after seed dispersal in the three treatment types. In April 2002, we established three 0.5*0.5 m plots at the eight *Stipa*-dominated sites and subjected them to the same treatments as in the permanent plots (control, cutting, digging). The number of *Stipa* seeds found in each plot was counted at the end of May, after seed dispersal, but before summer rains would further disperse propagules and trigger their movement into the soil.

Since the two species' phalanx-type clonal growth only enables them to spread very slowly on the edges of their tussocks, their establishment on bare ground (i.e., their regeneration) depends on newly established individuals. Therefore to assess seedling establishment in different treatments, we used the main 1 m² experimental plots and counted the number of seedlings between 2000 and 2008. Since *Festuca* seeds germinate in early autumn

and start growing in early spring, these seedlings were counted in April. Based on our field observations, *Festuca*'s mortality during the first winter is probably negligible, as dead seedlings were rarely found during the early spring survey. Seedlings of *Stipa* appear at the start of the vegetation season; therefore, they were counted in May. The seed bank of both species is transient and according to previous studies, most seeds germinate in the first year (Csontos, 2001).

The climatic data used in our study came from two sources. A data set from a meteorological station in Kecskemét (~26 km from the site) covers the period between 1998 and 2000. Data from the Fülöpháza meteorological station on the eastern edge of the study area cover the years between 2001 and 2016. A high and significant correlation between the monthly measurements of these two stations (Pearson correlation, $r = 0.999$, $df = 225$, $p < 0.001$ for monthly mean temperature and $r = 0.866$, $df = 226$, $p < 0.001$ for monthly precipitation based on data between 2001 and 2019) supported the merging of the two data sets. Later this combined data set was used to calculate meteorological indices for the study period (see next section). For historical context and for evaluating the rarity of drought events during our study, a long-term meteorological data set from Kecskemét covering the period between 1901 and 2019 was used.

2.3 | Data handling and statistical analyses

We calculated the mean temperature and the total precipitation during the vegetation period (April–September) for both the historical data set and the data set covering the study period. We also calculated the climatic water balance (P-PET) as the potential evapotranspiration (PET) determined using the Thornthwaite equation (Thornthwaite, 1948) subtracted from the amount of precipitation (P). We determined P-PET for all three-month intervals within the vegetation period (April–June, May–July, June–August and July–September) and used the minimum values as a drought severity index in a given year. This three-month window was chosen because field experience showed that phytomass correlates best with the amount of precipitation in the two to three months before measurement (Ónodi et al., 2017). We used linear regression to test for trends in the growing season temperature, precipitation and drought severity. To assess drought severity in each year during the study period, we calculated the percentiles for each temperature, precipitation and P-PET value based on the historical data set.

We used a non-parametric Kendall-type correlation to explore the relationship between year-to-year cover and density changes and our chosen measure of drought. This analysis was only performed on the data from control plots, separately for the two species and dominance types. Specifically, we calculated the correlation between the previous year's three-month P-PET minimum and the change in cover values (the previous year's cover value subtracted from the given year's value) and the correlation



between the yearly change in density and three-month P-PET minimum in a given year.

The effect of treatments on the cover was modelled with mixed-effect models assuming a Gaussian error distribution (package *glmmTMB*, see Brooks et al., 2017). We ran separate models for the two species, one for *Festuca* in *Festuca*-dominated plots and another for *Stipa* in *Stipa*-dominated plots. The response variable was square-root-transformed. The assumptions of linear mixed models (normality and homogeneity of residuals) were checked for both models (see Appendix S3).

Density data were analysed using generalised linear mixed models (GLMMs) with a negative binomial error distribution and a canonical log-link function (package *glmmTMB*, see Brooks et al., 2017) using untransformed response data, separately for *Festuca* in *Festuca*-dominated plots, and for *Stipa* in *Stipa*-dominated plots. Since the first few years (1998–2001) in the dug and cut plots for both cover and density data contained a high number of zeros, to facilitate model conversion and post-hoc comparison, we added a dummy site to years where all sites within at least one treatment had only zeros. These dummy sites contained only values of 1 for both species and all treatments, and hence, did not increase the differences between treatments.

Similarly to the density data in the long-term data set, the effect of treatments on the number of *Festuca* and *Stipa* seedlings (from the survey between 2000 and 2008) was also modelled by two separate negative binomial GLMMs using untransformed response data. For all models above, treatment, year, and their interaction were used as fixed factors, and to account for temporal autocorrelation between observations at the same site, an autoregressive (ar1) correlation structure nested within the site was added to the models. Post-hoc analysis was done by calculating estimated marginal means with the *emmeans* package (Lenth, 2020) and using them to conduct a pairwise comparison of treatment groups within each year. The number of *Stipa* seeds in the short-term experiment was analysed using a generalised linear model with a negative binomial error distribution and a canonical log-link function (package *glmmTMB*, see Brooks et al., 2017). For all models above, diagnostics were done using the *DHARMa* package (Hartig, 2020). We used a simulation-based approach to create standardised residuals and then visually inspected their overall uniformity and whether they showed any pattern along predicted values. We also checked for overdispersion (see Appendix S3).

We performed a Kendall-type correlation test between the dominant species' cover and next year's seedling numbers in control plots to assess the effect of within-plot seed rain. Two tests were done separately for *Stipa* and *Festuca* (at *Stipa* and *Festuca*-dominated sites, respectively).

To evaluate species dominance (we defined 'dominant species' as the one with higher cover values) in plots under different initial dominance and different initial disturbance treatments, we calculated the ratio of *Stipa* cover and *Festuca* cover. We applied a logarithmic transformation to make the statistical distribution of the data symmetrical around 0 [overall transformation: $\ln(Stipa + 0.01)/(Festuca + 0.01)$]. We

then conducted a one-sample Wilcoxon signed-rank test separately for each year within each initial dominance type (*Festuca* or *Stipa*) and treatment (control, digging, cutting). We tested whether the cover ratio was significantly different from 0 (implying the dominance of one of the species) or not (implying co-dominance). In disturbed plots, these tests were not conducted in the first few years, in which more than two sites had zero cover values for *Festuca* and *Stipa*. These years included 1998–2000 for *Festuca*- and *Stipa*-dominated dug plots and 1998–1999 for *Festuca*- and *Stipa*-dominated cut plots. It must be noted that annual species (e.g., *Polygonum arenarium*, *Salsola kali*, *Conyza canadensis*) may temporarily become dominant in this system after major disturbance events, but their dominance is transient (usually lasts for a single year); hence we neglected them while evaluating the dynamics of dominant species.

All statistical analysis was done in R (version 4.0.3, R Core Team, 2020).

3 | RESULTS

3.1 | Meteorological data

No linear trend was detected for either of the climatic variables over the study period (vegetation season precipitation: $R^2 = 0.001$, $F_{1,16} = 0.010$, $p = 0.922$; vegetation season mean temperature: $R^2 = 0.033$, $F_{1,16} = 0.553$, $p = 0.468$; drought severity index: $R^2 = 0.004$, $F_{1,16} = 0.061$, $p = 0.809$). Values of the drought severity index (minimum three-month P-PET value within the growing season) were lowest in 2012, 2000, 2013, and 2003, signalling the years with the most severe moisture deficit (Figure 2). Comparison with the historical data revealed that conditions during the driest three months in these years occur roughly once every 10 years (they were all below the 12th percentile, see Table S1 in Appendix S1).

The Kendall-type correlation test revealed significant, positive correlations between changes in the cover/density and the previous year's three-month P-PET minimum values in all four cases (r_t values between 0.219 and 0.387, further details see Table S2 in Appendix S1).

3.2 | The effect of digging and cutting on initially dominant species

At the initially *Stipa*-dominated sites, *Stipa* regenerated rapidly in the cut plots and showed cover values similar to those in the control plots by 2003 (Figure 3a). Dug plots had considerably lower values in the post-treatment years than cut plots and only caught up with the other treatments after the 2003 drought event, by 2005. After this year, no treatment effect was detected, but the droughts in 2012 and 2013 were associated with substantial declines irrespective of treatments. The difference in *Stipa* recovery between cut and dug plots is even more pronounced when looking at density (Figure 3b).

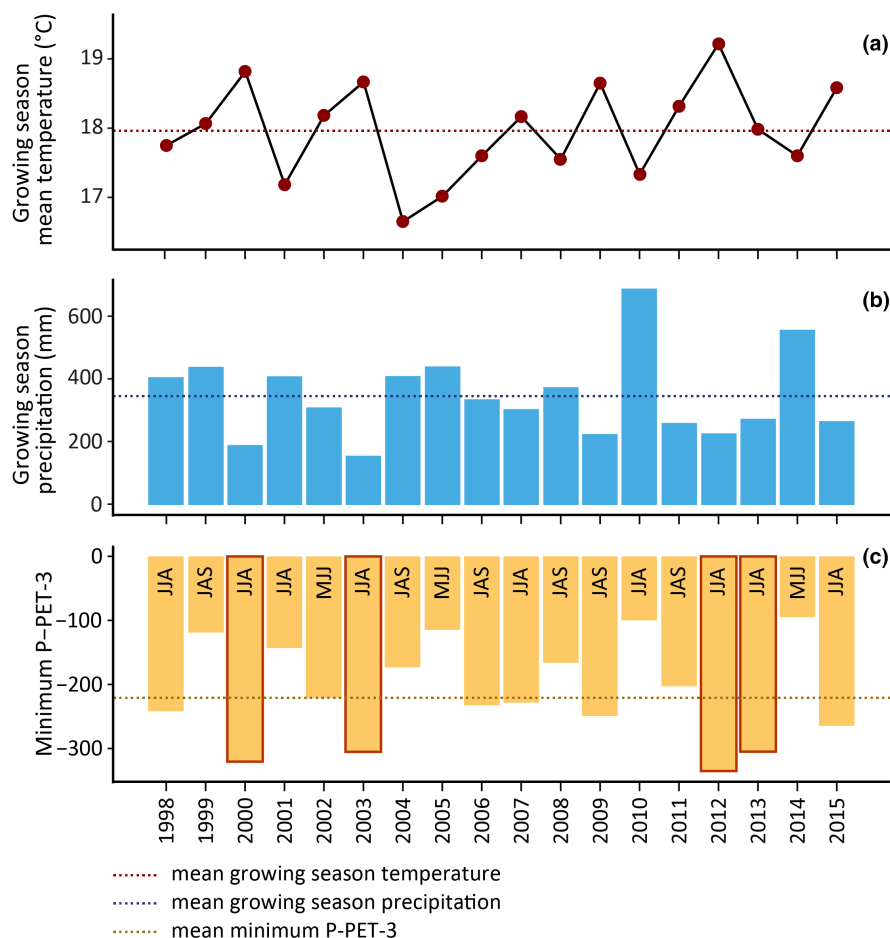


FIGURE 2 Meteorological conditions during the study period. (a) Growing season (April–September) mean temperature; (b) growing season precipitation; and (c) drought severity index (minimum three-month P-PET values for the growing season within a given year). Dotted lines mark the mean values of (a–c) over the study period. The four years with the most intense dry spells in the growing season (with minimum P-PET-3 values below the 12th percentile in the long-term data set) are marked with a red outline. Letter combinations in the bars mark the three months with minimal P-PET values (MJJ = May, June, July; JJA = June, July, August; JAS = July, August, September).

Stipa density in cut plots recovered to values similar to that in the control plots by 2001, while in dug plots only by 2007. (For further details, see: Appendix S1).

At the initially *Festuca*-dominated sites, the recovery of *Festuca* cover was similar in the cut and dug plots in the early years following the disturbances until 2003 (Figure 4a). In 2000 and 2003, extreme drought caused severe *Festuca* diebacks. Following these drought events, *Festuca* cover was higher in dug plots compared to cut plots. Changes in *Festuca* density (Figure 4b) were generally similar to those of *Festuca* cover (Figure 4a), with the only notable difference that the drought years of 2012 and 2013 negated the positive effect in the dug plots, resulting in similar numbers in the three treatments.

3.3 | Changes in species dominance

In initially *Stipa*-dominated control plots, *Stipa* was negatively affected by the drought years of 2000, 2003, 2012, and 2013, but it recovered and was able to maintain its dominance after each of

these events (Figure 5a). In initially *Stipa*-dominated disturbed plots, *Stipa* became the dominant grass species very quickly after the disturbances, by 2000 in the cut plots and by 2001 in the dug plots (Figure 5b,c), and it maintained its dominance throughout the study period, with year-to-year fluctuations similar to what we observed in the control treatment. *Festuca* generally maintained low (mostly <5%) cover values throughout the observation period. There was some minor increase in its cover between 2008 and 2011 (1%–3%) in all treatments due to better weather conditions, but it was interrupted by the dry years of 2012 and 2013. For the last two years of the data set, there was a steady increase in both species' abundance but no change in the dominant species.

In initially *Festuca*-dominated control plots, *Festuca* was very heavily affected and lost its dominant status during the drought years of 2000 and 2003 (Figure 5d). *Festuca* and *Stipa* co-dominated these control plots until 2011, but in the drought years of 2012 and 2013, *Festuca* cover decreased again, and *Stipa* became dominant. Similarly, in cut plots, *Festuca* could not regain dominance after the disturbance (except for a single year in 2009), and the repeated

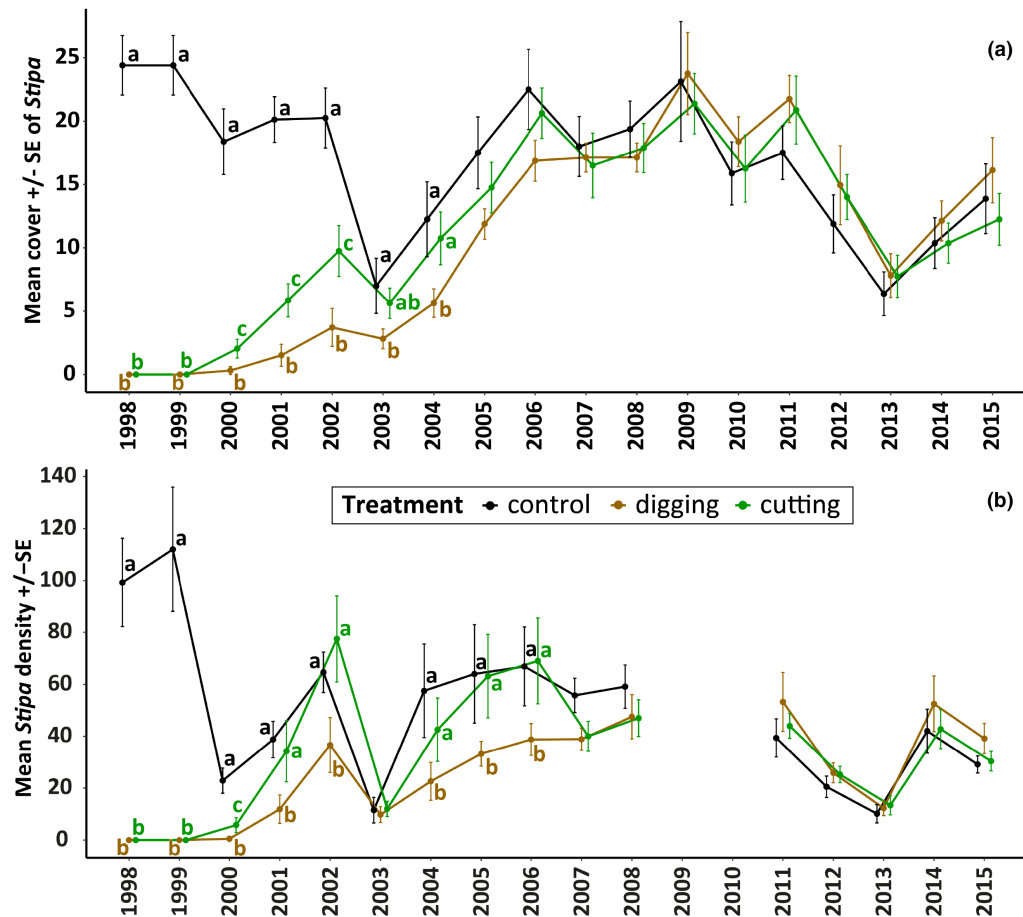


FIGURE 3 (a) Cover estimates (mean \pm SE) and (b) density (mean \pm SE) of *Stipa* at *Stipa*-dominated sites over the study period. Cover values presented for 1998 and 1999 were estimated from field notes with accurately drawn maps. Different letters mark significant differences between treatments in a given year (Tukey post-hoc tests; $\alpha=0.05$). For both subplots, the sample size was $n=8$ within each year, except for the missing density values in 2009 and 2010.

droughts in 2003, 2012 and 2013 eventually led to continuous *Stipa* dominance (Figure 5e). By contrast, in dug plots *Festuca* was able to quickly regain its dominant status (by 2001), and again after the drought of 2003, and maintained it until 2007. Although the droughts in 2012 and 2013 led to a *Festuca* decline, *Stipa* could not take over dominance completely (Figure 5f).

3.4 | *Stipa* and *Festuca* seedling density

According to our observations, seedling establishment was the main process of occupying the bare ground, and vegetative growth from outside the plots did not play a role due to the slow rate of clonal spread these species can exhibit.

The seedling numbers showed great interannual variation for both species. Despite this variation, we found significant differences between treatments at the initially *Stipa*-dominated sites. Cut plots had more *Stipa* seedlings than control plots in 2000, while dug plots had only a few seedlings in the first few years after disturbance (2000–2002 in Figure 6a). Digging significantly

lowered seedling numbers until 2006, except for the extreme dry 2003 when seedling numbers were uniformly low in all treatments (Figure 6a).

In the initially *Festuca*-dominated plots, there was no difference in the number of *Festuca* seedlings among treatments in the first four years (2000–2003, see Figure 6b). Afterwards, however, in 2004, 2006 and 2008, dug plots had more *Festuca* seedlings than cut and control plots. (For more details on model outputs, see Appendix S1.) The correlation between species cover and next year's seedling density was only significant for *Festuca* ($N=72$, $r_c=0.3072$, $p<0.001$ for *Festuca*, $N=72$, $r_c=0.084$, $p=0.300$ for *Stipa*).

3.5 | Number of *Stipa* seeds

In the additional experiment conducted in *Stipa*-dominated stands in 2002, cut and control plots had similarly high numbers of *Stipa* seeds (511.0 ± 58.1 SE and 358.5 ± 27.0 SE, respectively), while dug plots had very few seeds (4.5 ± 2.1 SE, for details see Figure S3 in Appendix S2).

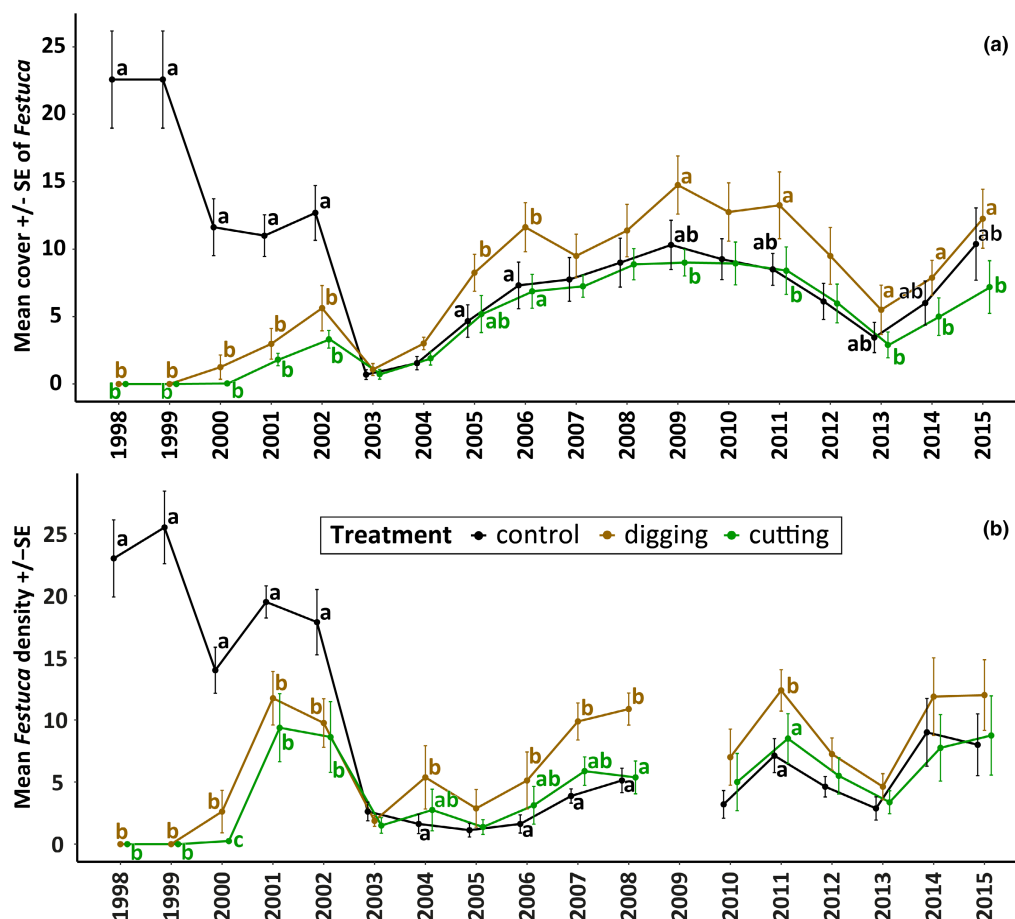


FIGURE 4 (a) Cover estimates (mean \pm SE) and (b) density (mean \pm SE) of *Festuca* at *Festuca*-dominated sites over the study period. Cover values presented for 1998 and 1999 were estimated from field notes with accurately drawn maps. Different letters mark significant differences between treatments in a given year (Tukey post-hoc tests; $\alpha=0.05$). For both subplots, the sample size was $n=8$ within each year, except for the missing density values in 2009 and partially missing values in 2010 ($n=6$).

4 | DISCUSSION

4.1 | The recovery of dominant species after disturbance treatments

Stipa recovered more slowly in dug compared to cut plots. Our data on seed dispersal revealed that the low number of *Stipa* seeds on the bare surface of dug plots limits seedling numbers, which may constrain recovery for several years. Since *Stipa borysthenica* and *Festuca vaginata* are characterised by a transient seedbank, their yearly recruitment depends almost entirely on the given year's seed rain and subsequent establishment (Török et al., 2018). Therefore, we assume that the role of regeneration from seeds buried in previous years was negligible during our study.

The markedly higher *Stipa* seed numbers, seedling numbers and the associated faster *Stipa* regeneration in the cut compared to dug plots are most likely related to the presence of litter and cryptogamic crust on the soil surface. Even though *Stipa* seeds are much heavier than those of *Festuca* (thousand-seed weights: 15.28 g for *Stipa*; and 0.56–0.64 g for *Festuca*, Csontos et al., 2013), they are also characterised by 30–45 cm long, feathery awns (Király et al., 2009),

which have evolved to utilise the wind and animal fur as a means of dispersal (anemochorous and epizoochorous dispersal strategy, see Csontos et al., 2002). The lack of correlation between within-plot *Stipa* cover and the subsequent year's seedling numbers indicates that these seeds are not settling locally but are indeed redistributed over the landscape. As a downside to being able to travel long distances, the propagules need some kind of seed trap to anchor themselves to; therefore, soil surface roughness is of great importance in the establishment of *Stipa*.

Several studies have already shown the importance of soil surface roughness in seed trapping, but our study highlights the role of this mechanism in driving differential vegetation responses following different types of disturbance. In other semiarid grasslands, where vegetation patches are interspersed with areas of bare ground, seeds were also found in much lower numbers on bare soil compared to shrubby, grassy or littery surfaces, even when the seed rain was similar (Aguiar & Sala, 1997), and graminoid seeds were shown to accumulate at wind-protected microsites (Bertiller, 1992). Also, Van Tooren (1988) observed that bryophyte patches act as seed traps in chalk grasslands in the Netherlands. In special cases, cryptogamic crusts may have the opposite effect: in some desert

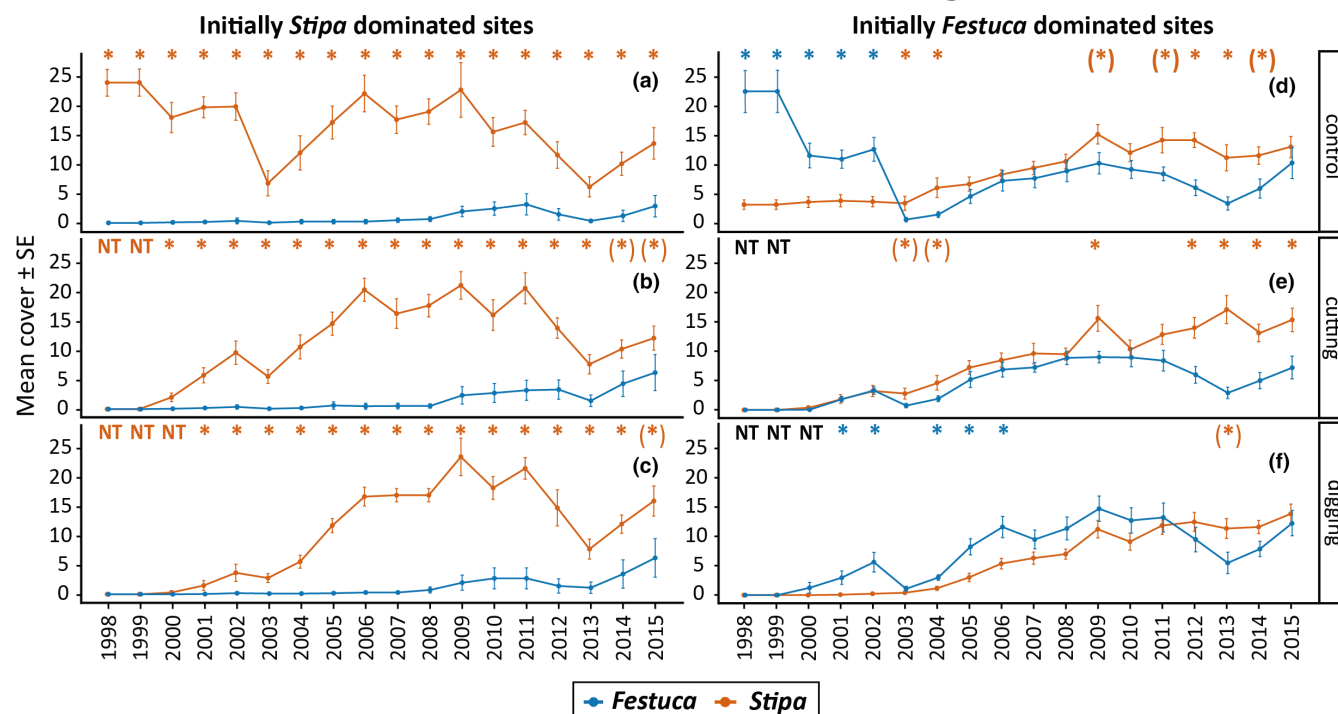


FIGURE 5 Comparison of the cover (mean \pm SE) of dominant species in plots with initial (a–c) *Stipa* and (d–f) *Festuca* dominance. Marks above each year denote the results of one-sample Wilcoxon signed-rank tests performed on the logarithm of the *Stipa*:*Festuca* ratio, separately for each year within a dominance and treatment group. *p*-Values under 0.05 are marked with *, and marginally significant values (0.05–0.1) are marked with (*). The colour of the asterisks corresponds to the dominant species. Tests were not performed in years marked with “NT” (not tested).

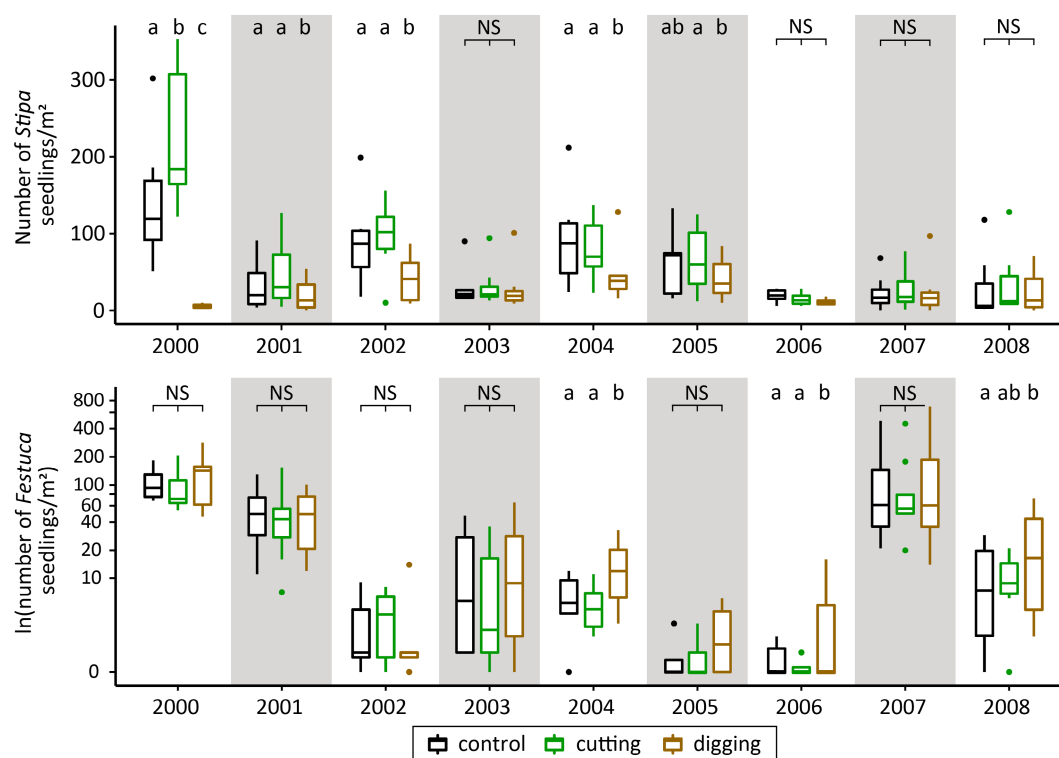


FIGURE 6 The number of (a) *Stipa* seedlings in initially *Stipa*-dominated plots and (b) *Festuca* seedlings in initially *Festuca*-dominated plots under different treatments between 2000 and 2008. (Note that *Festuca* seedling numbers are plotted on a ln-scale.) Different letters mark significant differences between treatments for a given year (Tukey post-hoc tests; $\alpha=0.05$).



ecosystems, where crusts consist primarily of a cyanobacterial layer and are characterised by a very smooth surface, seeds simply do not get trapped by anything on the ground (Prasse & Bornkamm, 2000). However, the cryptogamic layer at our site consists mainly of lichens and mosses, which results in a rough surface that operates as a seed trap (Lhotsky et al., 2008). This cryptogamic layer at our study site regenerates relatively slowly (Ónodi et al., 2014), which may explain the multi-year reduction in *Stipa* establishment and, in turn, the compositional differences between the treatments, even years after the initial disturbance. Overall, previous studies on the importance of soil surface roughness support our observations that the species-specific seed dispersal strategy interacts with seed entrapment after disturbance and may significantly impact establishment and vegetation composition.

In contrast to *Stipa*, *Festuca* responded similarly to the digging and cutting treatments for several years after the disturbance. A diverging trend from 2004, and higher *Festuca* cover and density in the dug plots, is most likely related to the reduced *Stipa* cover and density (Figure 5) and reduced competition compared to cut and control plots. Although we did not record *Festuca* seed numbers in different treatments, the similar *Festuca* recovery rate in cut and dug plots nicely corresponds with the similar rate of seedling emergence (Figure 6b) and provides further evidence that seedling establishment rate may strongly determine vegetation trajectory and may serve as a measure of regeneration potential. The fact that *Festuca* seeds are tiny and have no appendages may explain the insensitivity of the species to surface roughness, as smaller seeds have been reported to experience much less horizontal redistribution than the ones with a larger area and/or appendages (Chambers, 2000). This also aligns with previous observations stating that primary succession on the bare ground of sand dunes always starts with *Festuca* and not with *Stipa* (Fekete, 1992; Biró & Molnár, 1998).

4.2 | The effects of repeated droughts on species dominance

As expected, the immediate effects of drought were negative for both *Stipa* and *Festuca*. In the long run, however, *Stipa* recovered fully in initially *Stipa*-dominated control plots, while *Festuca* did not. Moreover, *Stipa* showed a steady increase across the time series and eventually became dominant in initially *Festuca*-dominated plots as well. Since there was no documented change in management and herbivore pressure during this period, nor was there any shift in the disturbance regime of the protected area, and since we can exclude legacies from previous disturbances as livestock grazing had been abandoned 30 years before the start of the study, it is highly likely that this dominance shift occurred as a consequence of frequently recurring droughts. Our case being an observational study, we cannot compare it to a climatic control treatment, but the repeated pattern we see with each dry year (*Festuca* numbers fall, it regenerates slowly, and then *Stipa* takes over after 2003 or 2012–2013) make the causal link between droughts and dominance shifts more likely.

A drought-induced dominance shift may happen due to differential sensitivity to drought and/or differences in subsequent regeneration, both of which are key drivers in drought-induced community change (McAuliffe & Hamerlynck, 2010; Martínez-Vilalta & Lloret, 2016). In our case, both of these processes may play a role. On the one hand, larger changes in cover values indicate that *Festuca* was more sensitive to the dry periods of 2000 and 2003 when cover decreased by 48% and 94%, respectively and dropped below 1% cover in absolute terms. In comparison, the *Stipa* cover only decreased by 25% and 65% in 2000 and 2003, respectively. The supposedly higher drought tolerance of *Stipa* could be a consequence of its deeper root system: the species' primary rooting zone is between 10 and 40 cm, while *Festuca* has a shallower root system of 5–30 cm (Simon & Batanouny, 1971; Kalapos, 1994). Interestingly, another phenomenon related to the drought response of *Stipa* might also play a role in the 2012–2013 dominance shifts: the dry periods at this point seem to affect *Stipa* to a smaller degree at the previously *Festuca*-dominated sites (there is even a minor increase in the cutting treatment) than in the initially *Stipa*-dominated plots. A possible explanation might be that density-dependent processes, for example intraspecific competition, are more intense at the initially *Stipa*-dominated sites.

In the case of regeneration capacity, the difference between the two species is much more evident. After the severe droughts in 2000 and 2003, *Stipa* rapidly recovered its cover to pre-event values (by 2006), while *Festuca* was unable to recover during the study period (2016). This lack of *Festuca* recovery resulted in co-dominance between the two species in initially *Festuca*-dominated plots (Figure 5d) and, ultimately, a shift towards *Stipa* dominance. The stronger regeneration capacity of *Stipa* was also observed after other types of disturbance: following wildfires in a forest-steppe habitat with similar species composition, *Stipa* was observed to recover its cover effectively and reached a dominant status in the vegetation, while *Festuca* cover showed a very slow increase (2%–3% in 10 years; Ónodi, G., unpublished data).

Despite intensifying climate change, human impact and recently increased detection efforts, well-documented examples of drought-induced regime shifts are still relatively scarce. Even when observed, attribution of shifts to climatic drivers is hard either due to multiple possible causal factors or, in the case of observational studies, due to a lack of control conditions for comparison (Martínez-Vilalta & Lloret, 2016). However, a continued effort to detect and describe them is crucial since they may have important consequences scaling up to the community and ecosystem level. Several studies have shown that dominance shifts may have cascading effects that affect populations at higher trophic levels (e.g., may impact seed-eating herbivores and their predators, see Brown et al., 1997; Mueller et al., 2005). From a human perspective, it is even more alarming that dominance shifts may alter numerous ecosystem services (Anderegg et al., 2013). In a Mongolian steppe, in a similar climatic setting to our study site, Chen et al. (2013) described a drought-induced dominance shift between two *Stipa* species which affected above-ground productivity and forage quality. Reduced palatability and pasture



quality due to dominance shifts are also a cause for concern in other dry ecosystems, such as the Sahel area (Bremner & Cissé, 1977). Moreover, dominance shifts in the context of ongoing climate change may represent the first step towards a much larger shift in vegetation composition (e.g., in our case, from open perennial grassland to drought-tolerant vegetation dominated by annual species) and may therefore serve as an effective early warning sign.

One of the ways in which a dominance change from *Festuca* to *Stipa* may have a considerable impact relates to decomposition and, consequently, carbon and nutrient cycling. In a recent study, Seres et al. (2022) found that leaf and root litter from *Festuca vaginata* is decomposed by the local microbial community at a faster rate than the respective plant parts from *Stipa borysthenica*. In the case of leaves, this is due to higher lignin and lower N content in *Stipa*, making the litter from this species harder to break down.

A change in the abundance of the dominant grasses will possibly also directly affect ecosystem services such as forage provision. Endemic herbivores, the European hare (*Lepus europaeus* Pallas, 1778) and European rabbit (*Oryctolagus cuniculus* (Linnaeus, 1758)), were both found to consume large amounts of *Festuca* in these grasslands, while *Stipa* was rarely or not at all consumed (Katona et al., 2004). Similarly, livestock also has a preference for *Festuca*. In the broader context of sand grasslands in Hungary, different *Festuca* species generally provide the highest quality fodder (according to herder's accounts, see Biró & Molnár, 1998). Specifically, within our studied vegetation type, *Festuca vaginata* has been considered superior to *Stipa borysthenica* by shepherds, as the latter is often avoided by both sheep and cattle (Biró & Molnár, 1998; Molnár et al., 2020). Interestingly, thousands of kilometres away, ethnobotanical studies in the Mongolian steppe also found that traditional herders consider *Festuca* species the best grass for fodder (Gantuya et al., 2019).

Since various species from the *Stipa* and *Festuca* genera occupy vast areas in the Eurasian steppe and forest-steppe biome (Erdős et al., 2018), our results may be relevant for large areas, as climate change-induced shifts in the proportions of these dominant species may bring about change on a large geographical scale.

4.3 | The modifying effect of disturbance on dominance shift

We found that digging (i.e., soil disturbance) delayed drought-induced dominance shifts in our system by preventing the establishment of *Stipa* seedlings. Disturbance events have been widely reported to modify vegetation response to climate change, but this modifying effect may range from accelerating change to buffering against it. Several studies attest to the negative effect of disturbance on ecosystem resilience. In a multisite climate manipulation experiment in European shrublands, only sites disturbed (by fire or herbivore outbreak) experienced significant compositional shifts in response to experimental warming and drying (Kröel-Dulay et al., 2015). Under mild disturbances, species-specific sensitivity to different disturbance types becomes more important and may result

in dominance shifts between species, as documented in response to drought and defoliation for two *Stipa* species in a Mongolian steppe (Chen et al., 2013). Moreover, the combination of disturbance and drought can also facilitate ecosystem-level changes, as observed in a Californian mixed forest, where wildfires opened windows of opportunity for colonising shrub and graminoid species that increased abundance only when the fire was followed by dry years (Young et al., 2019).

On the other hand, disturbance may also attenuate climate-induced changes, similar to what we found for digging in sand grasslands. In an arctic ecosystem, grazing by large herbivores was observed to buffer against warming-induced shrub expansion into a low-shrub tundra (Post & Pedersen, 2008). Management decisions may also modify ecosystems' climate sensitivity, which may happen in both directions. De Frenne et al. (2011) found that dense forest canopies dampened the thermophilisation of the ground layer vegetation of temperate forests by cooling the forest floor, while opening up the forest canopy may speed up thermophilisation compared to current levels. Overall, these examples and our results highlight that disturbances may considerably modify ecosystem responses to changing climate, so we should include these in risk assessments and, potentially, in management planning.

Soil disturbance (digging) in our grasslands only delayed but did not entirely prevent *Stipa* colonisation, and repeated droughts led to a gradual increase in *Stipa*. In the short term, such interactions between small-scale disturbances and drought-induced changes mean that communities' responses to climate change will not be uniform across the landscape. With larger disturbance events (e.g., wildfires, land-use change), effects can also be greater and last longer. The simultaneous presence of several types of disturbances at a given place, combined with other factors that vary across the landscape and affect sensitivity to climate change, such as topography (Godfree et al., 2011) and successional state (Kröel-Dulay et al., 2015), will create a heterogeneous pattern of change across the landscape. Therefore, it is crucial to consider these factors modifying community resistance and resilience when studying possible future vegetation transitions.

5 | CONCLUSIONS

Our study provides further evidence that more frequent droughts in the near future may induce changes in vegetation composition, including dominance shifts, which may have far-reaching consequences for ecosystems (e.g., effects on forage provision in our case). Furthermore, our results show that even small-scale disturbances, which are part of the current disturbance regime, may substantially modify the response of dominant species to drought. On a larger scale, these processes will bring about heterogeneity in vegetation response and result in a non-uniform change across the landscape. As indicated by the interaction between disturbance and drought-induced changes in our study, basic mechanisms, such as seed dispersal, distribution, and entrapment, may have a major and species-specific effect on



regeneration after drought and can scale up to influence dominance shifts. This underlines the importance of studying these early stages of regeneration when assessing vegetation changes.

AUTHOR CONTRIBUTIONS

György Kröel-Dulay conceived the research questions, design and field methodology and collected the data; Gábor Ónodi compiled the meteorological data set and contributed to its analysis and interpretation; Ildikó Orbán analysed the data; György Kröel-Dulay, Gábor Ónodi and Ildikó Orbán interpreted the results and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data used in this study are available on Figshare, via the following identifier: <https://doi.org/10.6084/m9.figshare.23308634>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Output tables of statistical tests.

Appendix S2. Supplementary figures.

Appendix S3. Model diagnostics and validation for the statistical models presented in the article.

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