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Recovery of a plant community in the central Anatolian steppe after small-scale disturbances

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Abstract How plant communities in Anatolian steppes recover after disturbances has remained unknown. To study the effects of small-scale disturbances on plant communities of the central Anatolian steppe, we established thirty-two plots 1 × 1 m in size in a natural steppe near Ankara (Turkey). The plots were subjected to mowing or hoeing treatments representing low- and high-intensity disturbance, respectively. Some plots were left untreated to serve as the control. The plots were sampled for three consecutive years to investigate changes in species occurrence, cover and biomass under various disturbance frequencies and intensities over time. The vegetation was able to recover within a few months, particularly in the growing season after mowing treatments, but the recovery level of the vegetation was lower after hoeing, especially when it was applied with high frequency. Species richness and cover of annual herbs increased with moderate disturbance frequencies in both disturbance types whereas perennial herbs were negatively affected by the hoeing disturbance, but not by the mowing disturbance. Both types of disturbance had a significant negative effect on plant aboveground biomass in the plots. The results partly support the intermediate disturbance hypothesis. High-level resilience to small-scale disturbances was observed, possibly due to adaptations of Anatolian steppe plants to natural and anthropogenic disturbances.

Keywords Central Anatolian steppe · Disturbance · Growth form · Recovery · Resilience · Vegetation

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Introduction

Grassy biomes of Earth are prone to various disturbances, including grazing and fire (Bond 2019). Many plants in these biomes are adapted to specific disturbance regimes operated in grasslands for thousands or millions of years (Coughenour 1985; Overbeck et al. 2005; Tavşanoğlu et al. 2015). These adaptations make grasslands resistant or resilient to various disturbances. Grasslands constitute an open vegetation state, and this stable vegetation state is mainly maintained by herbivory and fire (Dantas et al. 2016; Bond 2019). Recent observations suggest that the lack of a historical disturbance regime leads to the invasion of woody vegetation into grasslands (i.e. shrub or tree encroachment) in several grassy biomes (Van Auken 2009). Such invasions into open ecosystems may result in a state shift towards a closed, wooded stable state, which in turn leads to the loss of biodiversity (Ratajczak et al. 2012). Therefore, disturbance is necessary for the sustainability of grassy vegetation in some biomes, including tropical grasslands (O'Connor et al. 2020). On the other hand, some grassy ecosystems suffer a high level of human-caused disturbance driving changes in plant community composition and ecosystem function (Feng et al. 2009; MacDougall et al. 2013). For example, severe human-caused disturbances (e.g. overgrazing, agriculture, plantations) lead to the loss of species diversity in temperate grasslands and drive these ecosystems towards endangerment (Török et al. 2016; Carbutt et al. 2017).

Whereas natural disturbances create alternative vegetation states, as shown in tropical grassy ecosystems (Dantas et al. 2016), human-caused disturbances have strong influences on the plant species composition, plant functional traits and structure of grassland vegetation (MacDougall et al. 2013; Zhang et al. 2018). Most severe effects are observed in croplands, in which all natural vegetation is removed by tillage and in many cases is sprayed with pesticides to create a monoculture crop fields without any element of original grassland vegetation (McLaughlin and Mineau 1995). Vegetation recovery after field abandonment can be expected, but it may take several decades (Helm et al. 2019). On the other hand, the effect of grazing is relatively limited, but it results in long-term changes in vegetation structure and species composition (Carmel and Kadmon 1999). Many grassland ecosystems have evolved under natural grazing activities for millions of years (Mack and Thompson 1982; Strauss and Agrawal 1999). It is suggested that an intermediate level of grazing pressure can be helpful to sustain biodiversity in grassland ecosystems (Hobbs and Huenneke 1992; Yuan et al. 2016), and continuous mowing, which simulates grazing, can be a preferable disturbance regime for the conservation of threatened temperate grassland ecosystems (Smith et al. 2018).

The central Anatolian steppe is one of the ecoregion types of the grassland biome consisting of endemic-rich plant and animal communities extending between the northern and southern mountain ranges on the Anatolian Peninsula, Turkey (Vural and Adıgüzel 2006; Ambarlı et al. 2016). This ecoregion is found in the Irano-Anatolian province of the Irano-Turanian phytogeographical region (Zohary 1973) and is considered a global biodiversity hotspot (Mittermeier et al. 2004). The vegetation of the central Anatolian steppe is regarded as a unique grassland ecosystem important for the biodiversity in the Palaearctic biogeographic region (Ambarlı et al. 2016), harbouring approximately 2,000 plant species with 30% endemism (Kurt et al. 2006). However, at the same time, it is one of the most disturbed habitats among global biodiversity hotspots (Sloan et al. 2014), mainly by agricultural activities and domestic grazing (Şekercioğlu et al. 2011). Moreover, central Anatolia has a semi-arid climate with less than 500 mm annual rainfall, and climate change projections predict a much drier climate after the second half of the 21st century (Ergüner et al. 2019). Consequently, the region is thought to be prone to desertification in the near future (Camci-Çetin et al. 2007).

Effects of grazing on the vegetation of central Anatolia have long been reported by different authors, and it is known that tall grass-dominated vegetation was turned into subshrub-dominated rangelands because of grazing (Fırıncıoğlu et al. 2009). In addition, grazing affects this vegetation by decreasing total plant coverage (Fırıncıoğlu et al. 2009). The effect of resting rangelands for grazing management was also studied in central Anatolia (Alınoğlu 1971; Büyükburç 1983; Fırıncıoğlu et al. 2007).

Because the majority of cultivated areas in Turkey are found in steppe ecosystems (Camci-Çetin et al. 2007), agricultural activities also affect steppe vegetation in central Anatolia. The conversion of central Anatolian steppe vegetation into monocultural crop fields is still the main threat to this ecosystem (WWF and McGinley 2008; Kürschner and Parolly 2012). For these reasons, untouched steppe vegetation can rarely be found in central Anatolia and is mostly restricted to steep slopes that cannot be used for agriculture or to some inaccessible places located far from human populations (WWF and McGinley 2008). Although many such threats linger over central Anatolian steppe vegetation, there is no protected area dedicated to steppe vegetation in Turkey, except the salty steppes around Lake Tuz designated a special protected area (Şekercioğlu et al. 2011). Therefore, the central Anatolian steppe is a vulnerable ecosystem with high biodiversity that is under severe human pressure. Despite all these threats and problems over the central Anatolian steppe plant communities, scientific research on the ecology of these ecosystems has rarely been done, and the lack of knowledge makes it impossible to make conservation decisions and implement protection measures (Ambarlı et al. 2016).

In some parts of the world, such as Europe, croplands which are formerly grassland ecosystems, have been abandoned, and an old-field succession process occurs. Ecological restoration of these old fields is a major concern for preserving biodiversity (Török et al. 2011). Field abandonment sets off secondary succession, a process whereby natural communities replace monoculture croplands over time (Cramer et al. 2008). This process often starts off with the arrival of more opportunistic (and transient) plant species on abandoned land, which are later joined and gradually replaced by more competitive and persistent species as successional time passes (Bonet 2004). Agricultural activities represent the most frequent disturbance by humans in the central Anatolian steppe. In theory, following crop field abandonment, one may expect natural steppe vegetation to replace the crop field community over successional time. However, lack of knowledge on old-field succession and successional strategies of individual plant species or functional groups in this habitat type hinders predictions about how a post-disturbance successional process may proceed in the central Anatolian steppe.

This study aims to reveal the regeneration responses of central Anatolian steppe plants and vegetation to different disturbance types and frequencies and to assess the recovery potential of central Anatolian steppe vegetation after small-scale disturbances. Considering the long-term disturbance history of the region, both of natural and of anthropogenic origin, we hypothesized that plant species of central Anatolia should regenerate quickly and well after small-scale disturbances are applied. Therefore, we expected a full recovery of vegetation after disturbances. To test this hypothesis, we performed a field experiment to observe the recovery of the plant community and vegetation by applying small-scale artificial disturbances of two intensities at three different frequencies in natural steppe vegetation in central Anatolia.

Materials and Methods

Study Site

The study was conducted for three consecutive years between 2012 and 2014 at a 1-ha site covered by natural steppe vegetation in a complex rural landscape in Lalahan district, Ankara, central Anatolia, Turkey (39°57′ N, 33°07′ E, 1,170 m a.s.l.), including crop fields, villages and wildlands covered with steppe vegetation. The study site was a 1-ha area composed of natural steppe vegetation without any clear sign of disturbance. Soil has developed over metamorphic or calcareous bedrock in the study area. The mean annual temperature is 11.9°C, and the total annual precipitation is about 391.9 mm (Ankara Meteorological Station data of 1927–2019, Turkish State Meteorological Service, www.mgm.gov.tr). These climatic conditions are consistent with the climate of steppe areas of central Anatolia, characterized by a semi-arid climate with cold winters and warm summers (Kurt et al. 2006; Fırıncıoğlu et al. 2009).

Experimental Design

In 2012, thirty-two quadrats 1 m^2 (1 × 1 m) in size, distributed regularly, were established within a 78 × 34-m plot at the centre of the study site. The quadrats were marked with metal pins and mapped by using a GPS to locate their position. A buffer zone, 0.5 m in length, was also extended from all four sides of the quadrats (Fig. S1 in the Electronic supplementary material) to avoid possible edge effects, and the vegetation in this zone was completely removed by hoeing.

We assigned each quadrat to a disturbance treatment (or control group) following an 8 × 4 Latin square design, in which each line includes at least one of the four different treatment groups (and control). We included two disturbance types (mowing and hoeing) and three disturbance frequency treatments (once, twice and three times disturbed) in the study. We also assigned eight untouched quadrats to serve as the control. Each disturbance type × frequency combination included four replicate quadrats. Consequently, the experimental design included twelve quadrats for the mowing treatment, twelve quadrats for the hoeing treatment and eight quadrats for the control.

Application of Disturbances

The disturbances were applied in June 2012 (to all disturbance quadrats), September 2012 (to quadrats disturbed twice and three times) and April 2013 (only to quadrats disturbed three times). Using this procedure, a gradient of disturbance frequency (i.e. disturbed once, twice and three times) was created. The mowing treatment was applied by using pruning shears to remove all aboveground plant material within the quadrat. The hoeing treatments were applied with a spud by grubbing down to 5 cm deep of the soil from the surface in the quadrat. We assumed that these treatments reflect the effects of grazing (and browsing) and agricultural ploughing, respectively, which are frequent anthropogenic disturbances observed in the central Anatolian steppe. We considered the mowing treatment a low-intensity disturbance simulating domestic grazing because removing only aboveground plant material mimics the effects of grazers and browsers. On the other hand, we considered the hoeing treatment a higher-intensity disturbance simulating agricultural ploughing because of the removal of both aboveground and underground organs of plants.

Field Sampling and Measurements

All the measurements in the field were performed within 1 × 1-m quadrats. Three main measurements were done within each quadrat: (1) plant species richness, (2) plant coverage, and (3) plant biomass. Species richness and coverage measurements were performed before applying any disturbance in disturbed quadrats and simultaneously in non-disturbed quadrats.

Plant species richness was estimated as the total number of vascular plant species within each plot at each sampling time. The nomenclature followed Davis (1965–1985), but taxonomic updates were obtained using Güner et al. (2012). Growth form classification was based on Davis (1965–1985) and field observations, and the regeneration strategy after the disturbance was determined based on field observations. To assess the regeneration strategy, we checked seedlings and resprouts in disturbance quadrats for each species.

Plant coverage was estimated as the percentage cover of individual plant species and total vegetation. To estimate the coverage in each quadrat, we used the point-intercept method. First, we established three transects parallel to each other and the lines of the quadrat and checked the point at each 10 cm (in total 10 points) along each transect if any plant tissue touches the point or not (Fig. S1 in the Electronic supplementary material). In this way, in total, we sampled thirty points in each quadrat. Then, we calculated the coverage of each plant species in a quadrat by multiplying the ratio of the presence points to the total number of points by 100.

In June 2013, the plant material in each quadrat (including control and previously disturbed ones) was taken as a biomass sample for all quadrats. For biomass sampling, the plant material was collected separately, considering the growth form of each species, as annual herbs, perennial herbs and woody plants. For some dominant species, biomass samples were also collected separately. The plant material collected from the field was separated into small pieces and heated in the oven for 48 hours at 80°C. During this procedure, each sample was placed in a separate aluminium container. Just after the treatment, the samples were weighed using an electronic scale to determine their dry weight. The values obtained with these measurements were used as the biomass of individual plant species or growth forms.

An additional sampling was also performed in all quadrats one year after the biomass sampling was conducted in June 2014. This extra sampling allowed us to evaluate the recovery potential of the vegetation in the lack of disturbance for a relatively long period.

Data Analysis

To analyse the effect of disturbance type and frequency on species richness, coverage and aboveground biomass, we performed mixed model analyses. In these analyses, we also included the sampling period (not for aboveground biomass; see below) and growth form in the models as fixed factors to elucidate the effect of sampling time in different seasons and the differences between different growth forms. The quadrat was the only random factor in analyses. To analyse the species richness, we used a generalized linear mixed model (GLMM) assuming a Poisson error distribution due to the data comprised of integers. We preferred to use a Poisson error distribution for this analysis rather than a negative binomial distribution because mean values were equal to variances (i.e. low overdispersion). Because the coverage and biomass data had a continuous structure, we used a general linear mixed model (LMM) for the analysis. Shapiro–Wilk tests were performed to check the normality, and if needed (in the case of biomass data and coverage data of some sampling periods), data were square-root transformed for a better approximation to the normal distribution before the analyses. For the analysis of the aboveground biomass, we did not use the sampling period as a fixed factor because we performed biomass sampling only once in the study. All mixed model analyses were performed using the analysis of deviance by comparing a null model including only the random factor (quadrat) with models including both the random factor and relevant fixed factors. Model residuals were checked for the presence of trends and outliers after each analysis.

Besides the overall models explained above, we performed additional mixed model analyses to reveal whether the disturbance type and various disturbance frequencies significantly affect species richness and coverage at each specific sampling period. In these analyses, we compared species richness and coverage in treatment quadrats with the controls. This analysis, again, was performed at only one sampling period for aboveground biomass. In these analyses, the statistical significance was set at $P < 0.01$ to reduce the possibility of Type-I errors, because of the high number of tests performed.

Non-metric multidimensional scaling (NMDS) was used to visualize the differences in species composition across treatments, and permutational multivariate analysis of variance (permANOVA) was used to test this hypothesis statistically, based on 999 permutations of a Bray–Curtis dissimilarity matrix of the presence/absence of taxa in quadrats.

Mixed model and permANOVA analyses were performed by using the packages 'lme4' (Bates et al. 2015) and 'vegan' (Oksanen et al. 2018), respectively. R^2 values were extracted from mixed models using the 'r.squaredGLMM' function of the 'MuMIn' package (Bartoń 2020). Graphics were drawn using the 'ggplot2' package (Wickham 2016). All analyses were performed in R version 4.1.1. (R Core Team 2021).

Results

In total, 116 vascular plant taxa were collected from quadrats throughout the experiment period between 2012 and 2014. Among these taxa, 62 were annual herbs, 41 were perennial herbs, nine were woody plants, and four were biennial herbs. Among biennial herbs, perennial herbs and woody plants in the study site, resprouting after the disturbance was recorded in nineteen species (35% of those taxa; Table S1 in the Electronic supplementary material). However, except annual species, which can all be regarded as having a seeding strategy, we obtained direct observational evidence of seeding strategy (i.e. seedling recruitment) in only two taxa of other growth forms: *Alyssum sibiricum* Willd. and *Malabaila secacul* (Mill.) Boiss. Although 103 taxa were detected both in control and disturbed quadrats, thirteen taxa (11 are annual herbs) were observed only in disturbed quadrats (Table S2 in the Electronic supplementary material).

Disturbance type, frequency and their interaction explained a limited portion of the variability in species richness (less than 3%, Table 1) and coverage (less than 7%, Table 1). On the other hand, their interactions with the sampling period made them the most explanatory factors included in the study both for species richness (explained deviance > 20%, Table 1) and coverage (explained deviance > 44%, Table 1). This result indicates the importance of the season and time after disturbance for the recovery dynamics of the vegetation under study. Indeed, the effect of season was more apparent when analyses were performed separately for different sampling periods (Tables 2, 3). The general effect of both mowing and hoeing disturbances on species richness and coverage was negative (i.e. decrease in comparison to the controls), but most of these decreases were statistically insignificant (Tables 2, 3). The most severe effects were observed in the first sampling period in September 2012 (3 months after the disturbance was applied) and in three times disturbed quadrats in some of the sampling periods throughout the study (Tables 2, 3).

Contrary to the observed response of the plant community to the disturbance for the species richness and coverage, the aboveground biomass was negatively affected in the cases of most disturbance types and frequencies. The variability in aboveground biomass data is explained well by both the disturbance

Table 1 Results of statistical analyses (analysis of deviance) for the effects of the disturbance type and frequency, sampling period, and growth form on species richness (GLMM), coverage (LMM) and aboveground biomass (LMM). *Dev.* is explained deviance [%] and the statistical significance of fixed factors is shown in the R^2 columns (** $P<0.01$, *** $P<0.001$, **** $P<0.0001$)

Factor	Richness		Cover		Biomass	
	Dev.	R^2	Dev.	R^2	Dev.	R^2
Type (T)	1.6	0.100 ***	4.6	0.083 **	7.4	0.321 **
Frequency (F)	2.5	0.155 ****	4.0	0.072 **	12.0	0.457 ***
Sampling period (S)	15.2	0.607 ****	23.2	0.351 ****	–	–
Growth form (GF)	32.7	0.800 ****	8.2	0.260 ****	3.0	0.141 ***
T × F	2.9	0.179 ****	6.6	0.114 **	16.7	0.546 ****
T × S	20.8	0.730 ****	49.2	0.586 ****	–	–
T × GF	34.2	0.808 ****	10.8	0.323 ****	10.6	0.398 ****
F × S	23.2	0.725 ****	44.2	0.538 ****	–	–
F × GF	33.4	0.809 ****	10.2	0.306 ****	12.6	0.444 ****
GF × S	41.1	0.821 ****	18.1	0.480 ****	–	–
T × F × GF	35.2	0.823 ****	12.0	0.347 ****	15.8	0.493 ****
T × F × S	26.4	0.768 ****	66.2	0.664 ****	–	–
T × GF × S	44.8	0.859 ****	25.1	0.578 ****	–	–
F × GF × S	45.1	0.856 ****	24.7	0.563 ****	–	–
T × F × GF × S	47.9	0.991 ****	30.2	0.612 ****	–	–

Table 2 Statistical comparison of species richness (GLMM), coverage (LMM) and aboveground biomass (LMM) in disturbance type treatments with those in controls at each sampling period. The statistical significance was set at $P<0.01$ due to the high number of tests performed and is given in bold

Sampling period	Mowing			Hoeing		
	Estimate	*SE*	*P*	Estimate	*SE*	*P*
Species richness						
Sep. 2012	−0.63	0.2	**< 0.001**	−1.24	0.2	**< 0.001**
Apr. 2013	−0.03	0.1	0.784	−0.12	0.1	0.285
Jun. 2013	−0.20	0.1	0.078	−0.31	0.1	**0.006**
Jun. 2014	−0.04	0.1	0.699	−0.08	0.1	0.512
Coverage						
Sep. 2012	−4.56	0.5	**< 0.001**	−6.20	0.5	**< 0.001**
Apr. 2013	−0.44	0.6	0.490	−1.40	0.6	0.033
Jun. 2013	0.87	11.7	0.941	−16.3	11.7	0.174
Jun. 2014	−13.0	15.7	0.418	−16.6	15.7	0.302
Aboveground biomass						
Jun. 2013	−3.64	1.5	0.027	−5.82	1.5	**0.001**

type and frequency, and especially by their interaction (Table 1). The aboveground biomass decreased more with the hoeing disturbance, and three times disturbed quadrats than in the mowing disturbance and once and twice disturbed ones, respectively, compared to the controls (Table 2, Table 3). These results indicate that species richness and coverage recovered better than aboveground biomass after most disturbance type and frequency treatments except for the triple disturbance treatment. Indeed, NMDS of species-presence data differentiated three times hoed quadrats from the others (Fig. 1), although the permutational multivariate analysis of variance did not confirm this result ($F=1.2$, $R^2=0.26$, $P=0.118$), possibly because of the small size of the dataset. However, the NMDS graph also suggests that differences in species composition in quadrats are independent of the type and frequency of disturbance, except for three times hoed quadrats.

Growth form was the main contributor to the variability in the species richness data (explained deviance $>32\%$, Table 1). However, it explained relatively less variance in cover and aboveground biomass (explained deviance $<9\%$, Table 1). This

Table 3 Statistical comparison of species richness (GLMM), coverage (LMM) and aboveground biomass (LMM) in disturbance frequency treatments with those in controls at each sampling period. The statistical significance was set at $P <$ 0.01 due to the high number of tests performed and is given in bold

Sampling period	Once			Twice			Three times		
	Estimate	*SE*	*P*	Estimate	*SE*	*P*	Estimate	*SE*	*P*
Species richness									
Sep. 2012	−1.15	0.2	**< 0.001**	−0.79	0.2	**< 0.001**	−0.77	0.2	**< 0.001**
Apr. 2013	−0.04	0.1	0.743	−0.11	0.1	0.393	−0.18	0.1	0.176
Jun. 2013	−0.08	0.1	0.476	−0.10	0.1	0.377	−0.67	0.1	**< 0.001**
Jun. 2014	0.08	0.1	0.544	0.00	0.1	0.980	−0.30	0.1	0.028
Coverage									
Sep. 2012	−5.67	0.7	**< 0.001**	−5.15	0.7	**< 0.001**	−5.31	0.7	**< 0.001**
Apr. 2013	−0.51	0.7	0.470	−0.67	0.7	0.342	−1.58	0.7	0.031
Jun. 2013	4.34	10.3	0.676	6.01	10.3	0.564	−33.6	10.3	**0.003**
Jun. 2014	6.08	14.6	0.680	−10.2	14.6	0.493	−39.3	14.6	0.013
Aboveground biomass									
Jun. 2013	−3.42	1.5	0.033	−3.24	1.5	0.042	−7.53	1.5	**< 0.001**

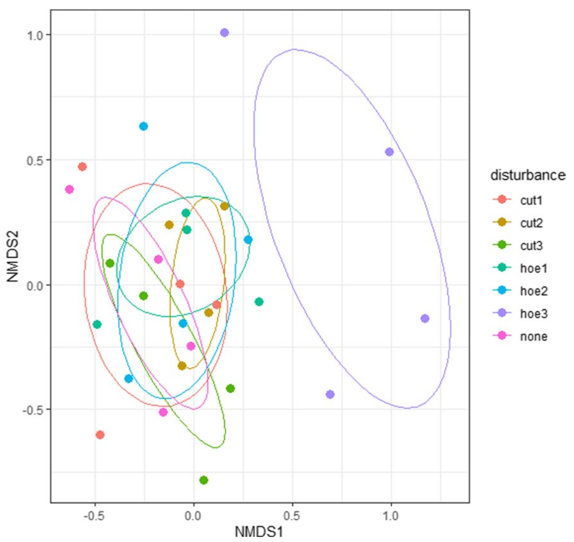

Fig. 1 NMDS ordination graph of taxa presence across disturbance treatments (stress value: 22.6). Each point represents the plant species composition of 1 × 1-m quadrat. Confidence ellipses (threshold: 0.50) are also shown for each treatment. About the legend, 'cut' is for mowing disturbances; 'hoe' is for hoeing disturbances; 1, 2, and 3 are for disturbance frequency; 'none' is denotes control quadrats.

result means that the recovery trends of different growth forms were more different when species richness, rather than cover and biomass, was considered. Indeed, species richness of annual and perennial herbs followed different trends throughout the study period. Annual species richness exhibited seasonal fluctuation, as the increase and decrease in control and disturbed plots at the same specific sampling times suggest, but such a fluctuation in species richness was not observed in perennial herbs (Fig. 2). Both growth forms showed apparent recovery in species richness in the mowing treatments, but recovery in disturbed quadrats was low for perennial herbs. For perennial herbs, the more frequent the disturbance, the lower the species richness at the end of the study period (Fig. 2). On the other hand, the species richness of annual herbs increased significantly after the single and double hoeing treatments compared to the control, both in June 2013 and June 2014. Moreover, although three times hoed quadrats had significantly lower species richness than the controls in June 2013, complete recovery was achieved by June 2014 compared to the controls (Fig. 2).

In both the mowing and hoeing treatments, the cover of the annual herbs was decreased in September 2012 and increased in June 2013. Whereas the cover of annual herbs in the mowing treatments seems to be decreased at the end of the study (2014) compared to the previous year, it was still greater in the hoeing treatments than the values at the beginning of the study, with the exception of the quadrat disturbed three times (Fig. 3). However, a different pattern was observed for perennial herbs. Although there were no differences between the coverage of perennial herbs at the beginning and end of the study in the mowing treatment, the coverage of perennial herbs decreased dramatically at the end of the study in the hoeing treatments compared to the beginning of the study (Fig. 3).

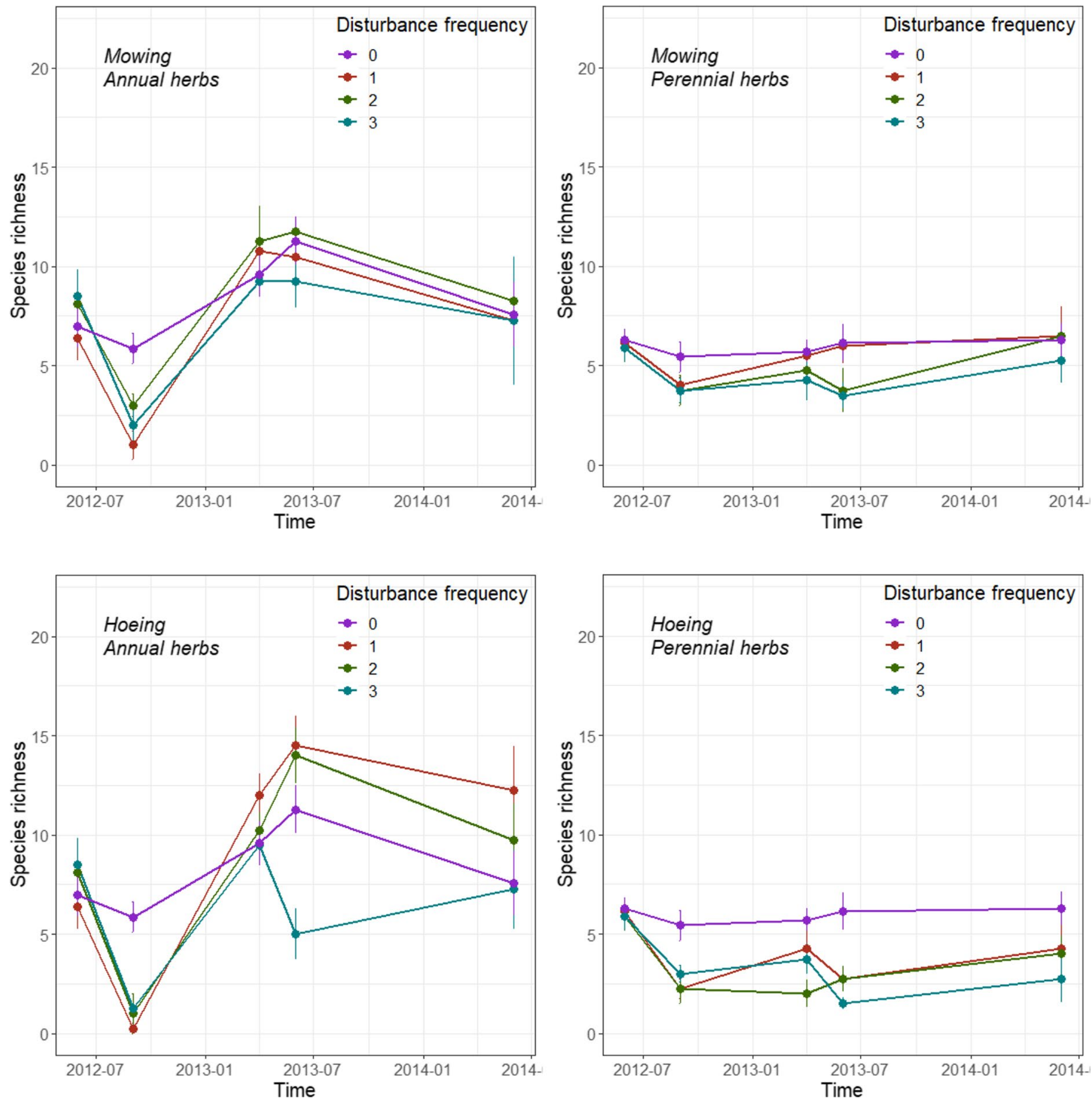

Fig. 2 Species richness of annual and perennial herbs throughout the study period under different disturbance treatments. Points represent mean values of quadrats, and error bars are the standard error of the mean.

Woody plants were negatively affected by the mowing and hoeing disturbances more than annual and perennial herbs. Both coverage and species richness of woody plants decreased in frequently disturbed quadrats, and no woody plants survived or re-established in three times hoed quadrats by the end of the study (Fig. S2 in the Electronic supplementary material). However, in once and twice disturbed quadrats, recovery seemed to be partially successful for woody plants at the end of the study (Fig. S2 in the Electronic supplementary material).

Woody plant biomass was the most severely affected by both mowing and hoeing disturbance treatments (Fig. 4). By contrast, annual plant biomass increased in once and twice disturbed quadrats, both mowed or hoed, compared to the control

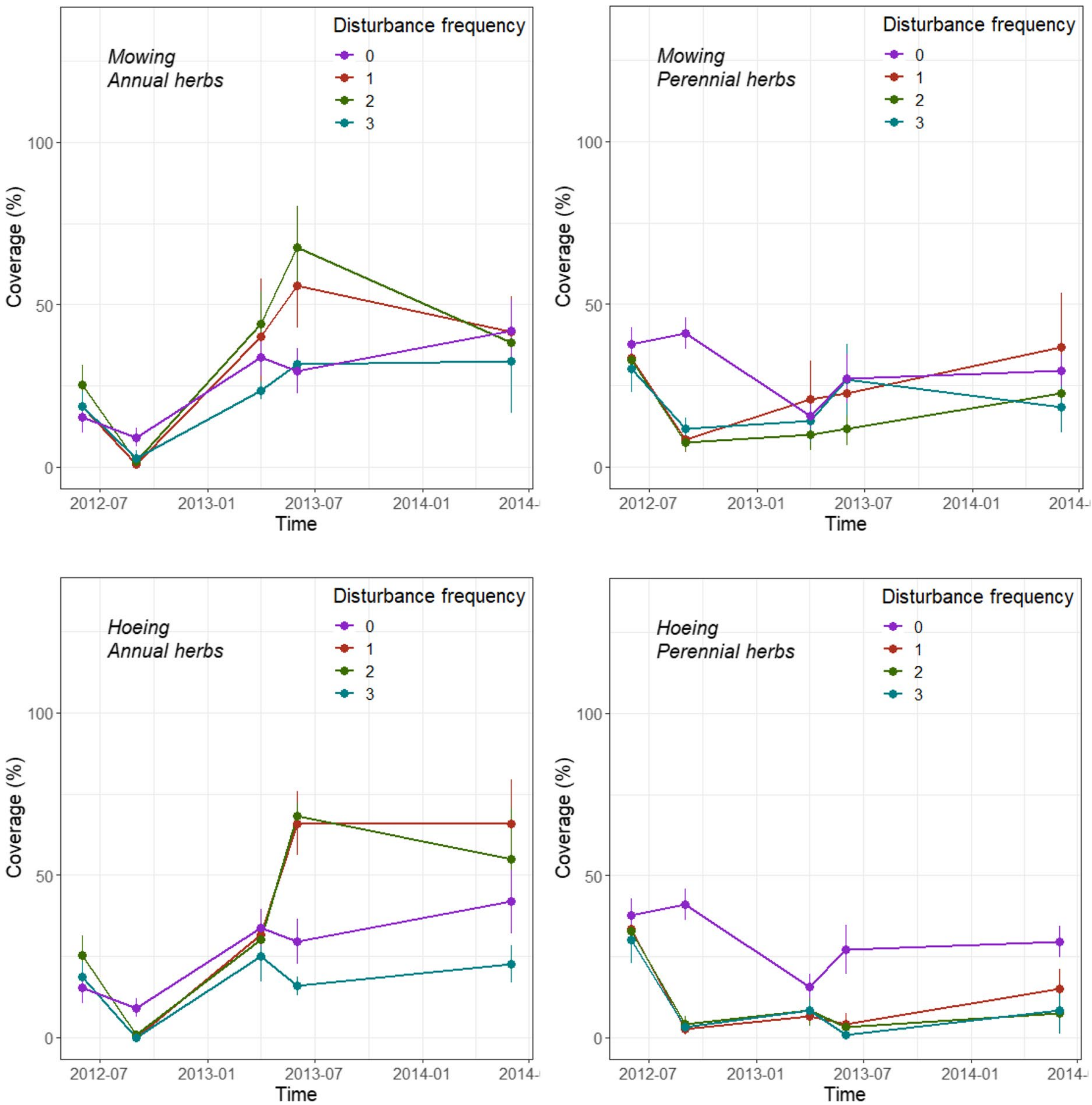

Fig. 3 Coverage [%] of annual and perennial herbs throughout the study period under different disturbance treatments. Points represent mean values of quadrats, and error bars are the standard error of the mean.

(Fig. 4). However, three times disturbed quadrats had lower biomass of annual herbs, especially in the hoeing treatment, compared to the control. Perennial herbs were in-between woody plants and annual herbs, in which biomass was negatively affected by the disturbance treatments, but a partial recovery was achieved in once and twice disturbed quadrats (Fig. 4).

Among the most dominant species at the study site, two resprouter Poaceae members *Festuca valesiaca* Schleich. ex Gaudin and *Koeleria macrantha* (Ledeb.) P.Schult. responded well to the mowing disturbance, even in some cases increased their coverage compared to the control (Fig. S3, S4 in the Electronic supplementary material). However, both species were negatively affected by hoeing, and hoeing resulted in the

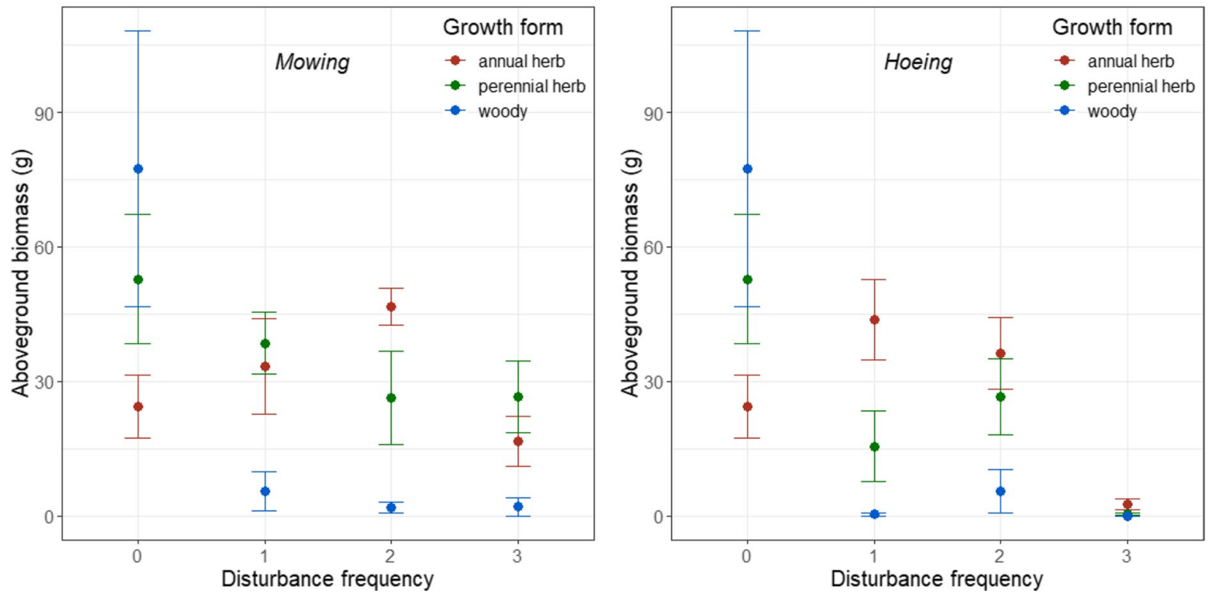

Fig. 4 Aboveground biomass [g] of annual herbs, perennial herbs, and woody plants throughout the study under different disturbance treatments. Points represent mean values of quadrats, and error bars are the standard error of the mean.

complete exclusion of *K. macrantha* from the study quadrats (Fig. S3, S4 in the Electronic supplementary material). *Thymus sipyleus* Boiss, a non-resprouter woody species, was also completely excluded from the disturbed quadrats, be it by cutting or hoeing (Fig. S5 in the Electronic supplementary material). Although there is seasonal variation in the cover of *Trigonella fischeriana* Ser., an annual herb, this species seems to be less affected by disturbances, as a negative effect was only observed in quadrats disturbed three times by cutting or hoeing (Fig. S6 in the Electronic supplementary material). Moreover, *T. fischeriana* had greater coverage in once and twice disturbed quadrats in June 2013 in comparison to the control (Fig. S6 in the Electronic supplementary material).

Discussion

High-level resilience to small-scale disturbances was observed in the vegetation under study. In general, the regeneration response to the low-intense disturbance (i.e. mowing treatment) was rapid and successful compared to the higher-intensity disturbance (i.e. hoeing treatment). Annual herbs were positively affected by disturbance at an intermediate frequency, and even in the highest frequency, full recovery was achieved one year after the last disturbance. The resprouting ability of perennial herbs promoted their recovery, especially after the mowing treatments. Woody plants were the most affected group by any disturbance.

Our study has some limitations because of the spatial scale we studied, especially when interpreting the effects of disturbance on vegetation at larger scales. The spatial scale of disturbance in grasslands may be an essential predictor of plant community response to disturbance (Coffin and Lauenroth 1988; Collins 2000). Furthermore, the proximity of quadrats to each other and the similar microhabitat structure of the study site may also limit us to drawing general conclusions across the central Anatolian steppe. Another limitation of our study is the relatively imprecise estimation of plant coverage caused by the restricted number of sample points in transects within quadrats, which may overlook the coverage of rarer species. As a fourth limitation, the effect of our mowing treatment on subshrubs may not reflect the situation in real-world grazing systems. In our study, we assumed that the mowing treatment mimicked the grazing (and browsing) effect in grasslands, but a decrease in subshrubs is not expected in natural conditions under various grazing regimes. In mixed grasslands vegetated by grasses, forbs and subshrubs, therefore, a selective cut treatment would be better to simulate the grazing effect on the plant community, especially on subshrubs which grazers do not strongly prefer. On the other hand, our results concerning the effect of the hoeing treatment on all growth forms and the mowing treatment on perennial and annual herbs are expected to be similar to the regeneration response of these groups to anthropogenic disturbances (i.e. agricultural ploughing and grazing, respectively) in the natural environment. As a first attempt to understand the response of central Anatolian steppe plants to such disturbances, however, our study still brings important insights on the dynamics of plant communities in this unique ecosystem despite these limitations. Therefore, more detailed studies at larger scales should be performed to increase our understanding of post-disturbance recovery dynamics in the central Anatolian steppe.

Our results throughout the experiment reflect the temporal variability of central Anatolian steppe vegetation. Because of the semi-arid climate of the region, and since there are distinct dry and wet periods throughout the year (Kürschner and Parolly 2012), steppe vegetation shows a difference in species richness in different periods during the year, as in other grasslands in the world (e.g. Lavorel et al. 1994). For example, in our experimental site, coverage and species richness of plant community decreased significantly in September 2012 after the first disturbance treatments were applied in June 2012. This decrease occurred because the time period between the first and second disturbance treatments coincided with the hot and dry period in the region. After the cold winter and rainy spring periods, however, species richness obviously increased in April 2013. Therefore, the time of the disturbance is critical for an immediate recovery in the vegetation in the central Anatolian steppe.

Disturbance may increase the sensitivity of grassland plant communities to invasions (Hobbs and Huenneke 1992) and their vulnerability to ecosystem collapse (MacDougall et al. 2013). Our results suggest that annual species gain an advantage over other growth forms as disturbance intensity and frequency increase in the central Anatolian steppe. Promoting the richness and cover of annual herbs by disturbance is a widely known phenomenon (Stearns 1976; Grime 1977). Annual species exclusively depend on seed germination to complete their life cycle (Rees and Long 1992). In many cases, a persistent seed bank is a necessity for the dominance of annual herbs after disturbance in grasslands (Merou et al. 2013). Tavşanoğlu et al. (2015) even showed that seeds of several species are resistant to fire disturbance in the central Anatolian steppe. Another way in which annuals are favoured by disturbance is that they utilize their dispersal advantage when establishing patches in disturbed habitats. Disturbances may also promote invasion by non-native annuals, and there are records that the presence of annual plant cover inhibits regeneration by native perennials (Hobbs and Atkins 1991). We found eleven annual taxa only in disturbed quadrats but not in the controls throughout the study period. Among these taxa, nine identified at the species level have widespread geographic distribution, especially *Microthlaspi perfoliatum* (L.) F.K.Mey. and *Medicago rigidula* (L.) All. can be considered as cosmopolitan species. Although invasive or cosmopolitan species can reduce or increase species richness by colonizing a disturbed habitat (Hobbs and Huenneke 1992; McIntyre et al. 1995), in our case, they contributed to the increase in the species richness of annual herbs in our quadrats. The availability of bare ground can explain the appearance of those species after the disturbances created new vegetation gaps in the quadrats (Burke and Grime 1996). It is known that dominant species creating canopy closure with fast recovery after disturbances prevent plant invasions by decreasing the possibilities for resource patches (Armesto and Pickett 1985). The lack of such a dominant species in our study site may also decrease the resistance the plant community to invasion, especially after hoeing disturbance. Our results support the intermediate disturbance hypothesis (Connell 1978) for annual species, as species richness and coverage of annual herbs were higher at intermediate disturbance frequencies than the highest frequency and the control quadrats for both the mowing and hoeing disturbances. Indeed, several studies support the notion that disturbances improve diversity in grasslands (Lavorel et al. 1994; Yuan et al. 2016).

Besides the establishment of annual species via germination, resprouting of perennial species seems to be another key strategy to cope with disturbances in the central Anatolian steppe. We recorded resprouting after disturbance for several species first time for this vegetation in this study. As a result of their resprouting ability, perennial herbs were less affected by mowing treatments in terms of species richness, coverage and biomass. Therefore, they were able to recover independently of the disturbance frequency. However, the hoeing disturbance was more severe for perennial herbs, which resulted in a decrease in species richness, primarily because of the damage created in the belowground storage organs of plants (such as rhizomes) by hoeing. Resprouting is a fundamental trait of perennial plants in grazer-shaped ecosystems (McIntyre et al. 1999; Pausas and Lavorel 2003). It is well known that the central Anatolian Steppe has also been subjected to natural and domestic grazing activity for thousands of years since the last glacial period (Tavşanoğlu 2017). Accordingly, the perennial species in this region should have been adapted to grazing disturbance or selected during the community assembly process that filters specific plant traits such as resprouting after disturbance (Pausas and Keeley 2014). Similarly, domestic grazing has limited effects on North American grasslands, grazed for millennia by bison and other wild ungulates (Hart 2001), and on eastern Mediterranean grasslands of Israel (Sternberg et al. 2000). *Festuca valesiaca* is the most remarkable example for such perennial herbs, in which coverage significantly increases in areas subjected to grazing (Fırıncıoğlu et al. 2007, 2008, 2009, 2010). Some woody species, including *T. sipyleus*, were disappeared from quadrats in both disturbance treatments. In contrast to this result, Fırıncıoğlu et al. (2009) reported that the cover of *T. sipyleus* increases after grazing in the central Anatolian steppe. We found that *T. sipyleus* is not able to resprout after being cut at soil surface. Because this species is a woody subshrub that does not have belowground storage organs, such a difference in the results may arise because grazing activity may have less impact on foliage and buds aboveground. Identifying bud banks in species is essential to understand their response to disturbances such as grazing, browsing and fire (Pausas and Paula 2020).

In summary, high-level resilience to small-scale disturbances was observed in the vegetation studied. We conclude that this recovery potential is due to adaptations of central Anatolian steppe plants to natural and anthropogenic disturbances observed over thousands of years, especially the resprouting ability in perennial herbs as a recovery strategy against grazing.

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Author Contributions Çağatay Tavşanoğlu conceptualized and designed the study. All authors contributed to data collection in the field. Özlem Özüdoğru performed the laboratory work. Barış Özüdoğru identified plant taxa in the herbarium. Özlem Özüdoğru and Barış Özüdoğru prepared laboratory and field data for further analyses. Çağatay Tavşanoğlu analysed the data. Özlem Özüdoğru and Barış Özüdoğru wrote the first draft of the manuscript. All authors critically contributed to and approved the final version of the manuscript.

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