

Effectiveness and limitations of fencing on the conservation of the grassland specialists in a semi-natural grassland degraded by increased large herbivores

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Abstract

Rare grassland herbs are increasingly threatened by increase in large herbivores. Exclosures that exclude large herbivores can be effective tools for the protection and conservation of grazed plant communities. However, installation of the exclosures in abandoned semi-natural grasslands has two aspects: protection of vegetation and elimination of disturbance by herbivores. We aimed to clarify the exclosures promote or hinder the conservation of grassland herbs in a semi-natural grassland. The field survey was conducted in a semi-natural grassland under grazing pressure by sika deer in central Japan. Fences were erected in 2010 and 2011. Plant species composition and species in flower were recorded from 2011 to 2022 inside and outside the fences. We compared the change of species composition with species composition data recorded in the same grassland patch in 1980s, before deer numbers increased, as reference. Within the fence erected in 2010, species composition was getting similar to the reference from 2011 to 2017, but regressed by 2022. Correspondingly, the cover of grassland herbs and the number of grassland herbs in flower first increased and then decreased. Tree species conversely increased from 2017 to 2022. Within the fence erected in 2011, the species composition was hardly getting similar to the reference, and grassland herb cover remained lower. Long-term fencing can lead to a decline in grassland herbs with an increase in competing shrubs though the grassland herbs temporarily increase within the fence erected earlier. Anthropogenic disturbance may be necessary for the conservation of grassland herbs in long-term fenced grassland communities.

Keywords Disturbance · Exclosure · Grazing pressure · Irreversible change · Permanent plot

Introduction

Grazing pressure is a major disturbance caused by increasing numbers of large herbivores in terrestrial ecosystems and can often decrease palatable plant species (Côté et al. 2004; Reid et al. 2010; Arcese et al. 2014; Schulze et al. 2014)

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and increase unpalatable species (Husheer et al. 2003; Royo et al. 2010). Changes of species composition and community structure in response to increased numbers of wild deer have been reported in North America, Europe, New Zealand, and Japan (Côté et al. 2004; Nuttle et al. 2013; Otsu et al. 2023). Under overabundant deer grazing, grazing pressure can reduce plant diversity and simplify species composition (Beguin et al. 2022; Nagaike 2023).

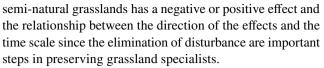
Semi-natural grasslands are among the most important habitats for biodiversity conservation; many grassland specialist plants are endangered species in Japan because of land abandonment and land use change (Koyanagi & Furukawa 2013). These grasslands are also where biodiversity loss due to grazing pressure by overabundant sika deer (*Cervus nippon* Temminck) is a concern (Otsu et al. 2017; Uchida et al. 2020). Responses to grazing differ among grassland herbs, non-grassland herbs, and trees (Otsu et al. 2017). The decrease in grassland herbs is particularly significant as the use of vegetation by sika deer increases (Otsu



et al. 2017). The increase in deer can promote the invasion of non-specialist plant species in plant communities (Boulanger et al. 2018). It is necessary to take measures to conserve rare grassland specialists and to evaluate the effectiveness of these measures.

Since it is not easy to the manage populations of large ungulates, exclosures are often installed as an emergency measure to protect vegetation against disturbance by overabundant deer. However, fences to exclude large herbivores have shown both a positive effect (Meier et al. 2017; Chollet et al. 2021) and no or negative effect (Collard et al. 2010; Wright et al. 2012; Nuttle et al. 2014; Johnstone et al. 2016; Knauer et al. 2023) on the conservation of plant diversity. Factors such as differences in the intensity of grazing pressure on vegetation by deer (Otsu et al. 2019) and in vegetation types (Virtanen et al. 2002) influence the effectiveness of fencing. However, the effect of the time since the elimination of grazing pressure on the change of species composition has not been adequately investigated. Some studies of long-term fencing in forest communities found that the response of vegetation varies with the years elapsed since the elimination of grazing pressure. Woodward et al. (2021) observed that herbaceous species, shrub species, and ferns increased within a decade or so after fencing was installed, but after 36 years, the understory of a temperate rain forest became dominated by shrubs. This suggests that short-term responses of species reflect functional traits related to the ability to avoid or tolerate herbivory (Woodward et al. 2021). Over the longer term, effects reflected changing competitive relationships among vegetation layers and other ecosystem dynamics. Eventually, long-term fencing can cause a shift from vegetation characterized by specialist to generalist species, with a long-term decline in species diversity (Virtanen et al. 2002; Perrin et al. 2011). It is important to estimate the effect of the time since fencing was installed on the plant community composition in order to take effective conservation and management measures.

Determining the effect of the time since fencing was installed in semi-natural grasslands may be especially important. Maintaining the seral phase in succession, as in semi-natural grasslands, requires appropriate disturbance (Hansson & Folgefors 2000; Vassilev et al. 2011). Longterm elimination of disturbance could stagnate recovery through declines in disturbance-dependent species such as grassland specialists (Liu et al. 2019). In Europe, increased wild deer numbers contributed to increased plant species diversity in abandoned semi-natural grasslands (Schütz et al. 2003; Riesch et al. 2020). Therefore, in semi-natural grasslands that depend on intermediate disturbance, the longterm elimination of disturbance by fencing may reduce plant species diversity. Thus, disturbance management should both maintain the seral habitat and eliminate heavy grazing. Determining whether the elimination of disturbance in



To plan such management, recording the time-series change process of vegetation after fencing would be effective. The process should be measured against baseline data (i.e., data of vegetation that has not been subjected to overgrazing by large herbivores.) (Suding et al. 2011). To date, however, there are no recognized cases of long-term effects of fences based on baseline vegetation data in semi-natural grasslands.

This study aimed at comparing the response of vegetation within fenced areas in semi-natural grasslands disturbed by overabundant deer over the long term. We estimated the change of species composition relative to that before deer numbers increased. We also assessed the response of grassland species on the basis of flowering, which are sensitive to deer management (Nuzzo et al. 2017).

Materials & methods

Study site

The study site on Mt. Kushigata (2053 m a.s.l.; Yamanashi Prefecture, central Japan), in a cool-temperate zone, has an elevation of 2003 m. The mean annual precipitation at the nearest meteorological station (Oizumi, 867 m a.s.l., 2002–2011) was 1186 mm. The mean annual temperature was estimated as ~4.9 °C from the value of 11.7 °C at Oizumi on the assumption of a decrease of 0.6 °C with every increase of 100 m in elevation.

Patches of semi-natural grassland covering 5.5 ha were previously dominated by *Iris sanguinea* (Table S1). They were surrounded by *Larix kaempferi* plantations and fragmented natural forests dominated by subalpine coniferous stands containing *Abies veitchii* and *Tsuga diversifolia*. These semi-natural grasslands had been mown by the local populace (J. Imakiire, pers. comm., 2010), but by 2010 had been abandoned for more than 40 years (M. Ishihara, pers. comm., 2010). In this area, sika deer density in 2010 had been linearly increasing from 13.5 ind./km² in 2005 to 30.4 ind./km² and reached its highest level of 33.2 ind./km² in recent years in 2011 (Iijima et al. 2013; Iijima 2020). Thereafter, the mean density ± standard deviation of sika deer in the period 2011–2020 was 27.1 ± 6.6 ind./km² (Iijima et al. 2013; Iijima 2020).

Field survey

In the summer of 1981, the Science Club at Koma High School examined the vegetation in the same grassland patch



(Koma High School 1986). The club deployed 24 precisely measured 1-m×1-m quadrat plots in a grassland typically dominated by *I. sanguinea* and sampled the vegetation inside the frames by using phytosociological procedures (Braun-Blanquet 1964). Species identification was confirmed by Dr. Ohkubo of Yamanashi Gakuin Junior College. Deer distribution here had not been recorded in 1981 but was confirmed in 2003 (Biodiversity Center of Japan 2004). This grassland had already been abandoned in 1981 and may have been affected by the abandonment, but was still dominated by broadleaved herbs. Thus, we considered the species composition in 1981 to be representative of the vegetation before the beginning of increase in sika deer grazing.

In October 2010, the Minami-Alps City Government installed a 2-m fence enclosing an area of 60 m × 60 m to protect the vegetation from deer grazing. In October of the following year, the Yamanashi Forest Research Institute installed an adjacent fence enclosing an area of 20 m×25 m. Both exclosures were located on open and homogeneous land with a 20° slope and stood about 10 m beside the edge of the forest, enclosing similar topographical conditions (Fig. S1). We characterized the vegetation in three treatments: one of the three equal Sects. (20 m × 60 m) inside the fence installed in 2010 ("fence 2010"), inside the fence installed in 2011 ("fence 2011"), and outside both fences ("outside"). We deployed $10.1-m \times 1-m$ quadrat plots inside fence 2010, 12 in fence 2011, and 10 outside. In each treatment, the plots were placed every 2–5 m on one or two lines. All treatments lay within 30 m of the plots deployed in the Koma High School study.

We recorded the cover of species occurring in each plot in August of each year from 2011 to 2015, 2017, and 2022. Cover was evaluated on the Braun-Blanquet scale (Braun-Blanquet 1964). Species with buds, flowers, or fruits in each plot were also recorded. In this grassland patch, the flowering of plants has been confirmed from July to September. By recording the number of plant species with fruits, flowers or buds as of August, it is possible to cover the number of species that have reproduced within the plots.

Statistical analysis

We examined the effect of treatment on the change of plant species composition, the changes of cover in each species group, and the response of reproduction by a generalized additive model (GAM). Because the time intervals between survey years were not equal and the temporal trends of the three response variables were not linear, we included smooths in these models. For examining the change of plant species composition, we examined the differences in plant community composition among treatments. We calculated the Chao dissimilarity index (Chao et al. 2005) to compare the species composition in 1981 with compositions in

2011-2022 in each of the three areas. The Chao dissimilarity index was designed to consider unseen shared species by using (replicated) abundance-based sampling data (Chao et al. 2005) and was therefore considered appropriate for our datasets, which excluded species with a cover score of < 1 on the Braun-Blanquet scale, assumed as unseen rare species. We also examined the ordination diagrams to evaluate species composition in 1981 and from 2011 to 2022 by nonmetric multidimensional scaling (NMDS) using the Chao dissimilarity index to compare changes in species composition between treatments. The index was calculated by using the "vegan" package (Oksanen et al. 2018) in R v. 3.2.2 software (R Development Core Team). Next, we examined the temporal change of the Chao dissimilarity index in each treatment. We fitted a GAM with a beta error distribution and a logit link function to the index in each treatment. The GAM included smooths of an interaction term of year (2011–2022) and treatment (Fence 2010, Fence 2011, and outside) and an explanatory variable of treatment as below:

Dissimilarity index, $\sim \text{Beta}(p_i)$

$$logit(p_i) = \alpha + f(Year_i : Treatment_i) + \beta \times Treatment_i$$

where α is an intercept, f is a spline smoother for an interaction term of year and treatment, and β is a coefficient of treatment. The GAM was fitted by the "mgcv" package (xxxx) in R. We examined the statistical differences among treatments by Holm's multiple comparison test.

For examining the changes of cover in each species group, we categorized species identified in the plots into grassland herbs, non-grassland herbs, and trees. We examined the change in the cover of each species group and in the number of species in flower over time. Grassland herbs occurring in the study area were defined as those whose habitat was listed as "grassland" in Satake et al. (2002, 2006a, b). Non-grassland herbs were defined as all other herb species. Each of these species groups included species reported as unpalatable species for sika deer (Hashimoto et al. 2014). However, just prior to fencing, these unpalatable species were observed to decline due to grazing by increased deer, as were the palatable species. Therefore, the analysis did not take into account whether the target species were palatable or unpalatable species. We calculated the cumulative cover of each functional group, treatment, and year. We fitted a GAM with a beta error distribution and a logit link function by each species group. The response variable of the GAM was the cumulative cover of each species group and the linear predictor of the GAM was the same as that of dissimilarity index.

For examining the response of reproduction, we calculated the number of species in flower (including buds or fruits) in each species group. We fitted a GAM with a



Poisson error distribution and a log link function by each species group. The response variable of the GAM was the number of species in flower per treatment and the linear predictor of the GAM was the same as that of dissimilarity index. We could not fit a GAM for a species group of "trees" because the number of flowering species or trees was too small.

Results

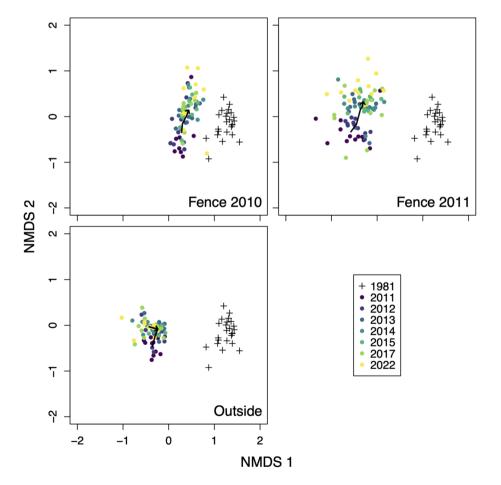
Past and recent plant communities

We found 84 plant species (57 grassland herbs, 20 non-grassland herbs, and 7 tree species) in all plots during 2011–2022 (Appendix S1). In 1981, only 24 species were identified (Appendix S1), and the plant community was characterized by the dominance of grassland herbs such as *I. sanguinea, Serratula coronata* var. *insularis, Geranium eriostemon* var. *reinii*, and *Veronicastrum sibiricum*. Within fence 2010, *Brachypodium sylvaticum*, a non-grassland herb, was the most dominant species in 2011 but linearly decreased, while *Rubus microphyllus* var. *subcrataegifolius*, a shrub, and *S. coronata* var. *insularis*, a grassland herb,

Fig. 1 Non-metric multidimensional scaling (NMDS) ordination of all sample plots in a two-dimensional space. Bold arrows in each figure indicate changes of mean scores of NMDS by each treatment from 2011 to 2022 increased. Grassland herbs such as *I. sanguinea* and *Carex nanella* initially increased and then declined. Within fence 2011 also, *B. sylvaticum* decreased. Conversely, non-grassland herbs such as *Fragaria nipponica* and *C. nanella* and shrubs such as *R. microphyllus* var. *subcrataegifolius* and *Rosa luciae* var. *fujisanensis* increased. In addition, *Betula ermanii*, a tall tree species, occurred only within fence 2011. Outside, *Achnatherum extremiorientale*, a grassland herb, gradually decreased while *F. nipponica* increased.

Change of plant species composition relative to that of 1981

Outside the fence, non-metric multidimensional scaling (NMDS) showed that the species composition did not approach that of 1981 over time; rather, it slowly diverged over time (Fig. 1). The dissimilarity index also changed little by 2022 (Fig. 2). However, that inside fence 2010 tended to decrease until 2017, and since then, that has increased in the opposite direction (Figs. 1, 2, Fig. S2). The variance in species composition within treatments also increased by 2017 (Fig. 2, Fig. S2). The dissimilarity index of fence 2010 was significantly lower than those of fence 2011 and outside (Table 1).





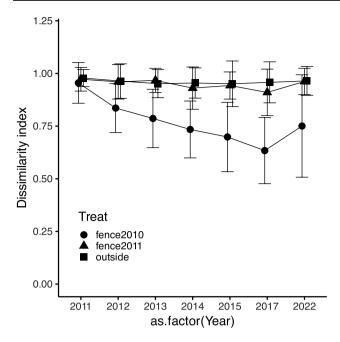


Fig. 2 Changes in dissimilarity index between the species composition in 1981 and those during the survey period by treatment and year. Error bars indicate SD. The dissimilarity index of 0 or 1 means respectively; 0: the species composition is completely identical to that of 1981, 1: the species composition is completely different from that of 1981

Table 1 Estimated coefficients and p-values of GAMs about the dissimilarity index

A		В	Coefficient of B (A is a reference category)	3
Fence 2010	vs	Fence 2011	1.467	< 0.001
Fence 2010	vs	Outside	1.334	< 0.001
Fence 2011	vs	Outside	- 0.132	< 0.001

Changes of cover in each species group

For grassland herbs, the cover of fence 2010 increased until 2014, and then slightly decrease (Figs. 3&S3). The temporal trend of the cover of fence 2011 was similar as fence 2010 (Figs. 3&S3). Grassland herb cover of fence 2010 was significantly higher than fence 2011 and outside (Table 2). For non-grassland herbs, the cover of fence 2010 decreased (Figs. 3&S4). In contrast, the covers of fence 2011 and outside were relatively stable (Figs. 3&S4). Nongrassland herb cover of outside was significantly higher than fence 2010 and fence 2011 (Table 2). For trees, the covers of all treatments were low during study period, but those of fence 2010 and fence 2011 increased in 2022 (Figs. 3&S5). The differences of covers among treatments were not significant (Table 2).

Response of reproduction

For grassland herbs, the number of species in flower of fence 2010 increased until 2015 and slightly decreased after that (Figs. 4&S6). The number of species in flower of fence 2010 was significantly higher than those of fence 2011 and outside (Table 3). For non-grassland herbs, the temporal trends of number of species in flower differed among treatment. Those of fence 2010, fence 2011, and outside were decreased, stable, and increased, respectively (Figs. 4&S7). The number of species in flower of fence 2010 was significantly higher than those of fence 2011 and outside (Table 3).

Discussion

Effect of exclusion of grazing pressure

At this study site, multiple environmental changes, such as management abandonment and climate change, may have affected changes in species composition in parallel with deer grazing pressure even after 1981. However, the study site is the most heavily deer-influenced grassland site in central Japan (Otsu et al. 2017), and the increase in grassland herbs, palatable species for deer, following the installation of fence 2010. This suggests that deer grazing pressure were the most likely factor driving vegetation change at the study site with high deer densities. Nuttle et al. (2013) showed that browsing by deer in recent years has had a greater impact on change of forest species composition than the cessation of fire disturbance and closure of forest canopy. Based on these results, the following section discusses the impact of the exclusion of deer impacts on changes in plant species composition.

Within the fences, the response of the plant community to the exclusion of disturbance by deer varied with the time scale. Grassland herbs such as I. sanguinea and S. coronata var. insularis in particular showed an increasing trend in the first 8 years, and this change led to an increased similarity to the 1981 species composition (Fig. 3). By 13 years, however, they decreased with an increase in shrubs such as R. microphyllus var. subcrataegifolius and R. luciae var. fujisanensis, which were not abundant before the increase in deer, with a resultant reduced degree of similarity of grassland herb species composition (Fig. 3). This increase in tree species after about 10 years was also seen within fence 2011. Within fence 2010, the more resilient grassland herbs that remained as underground rhizomes reappeared over time, but tree species gradually replaced them (Fig. 3). Studies in temperate forest understories found that a community that was dominated by grasses for several decades after fencing transitioned to being dominated by shrubs after 30 years (Perrin et al. 2011; Woodward et al. 2021). Since



Fig. 3 Changes in mean cover of each species group by treatment and year. Error bars indicate SD

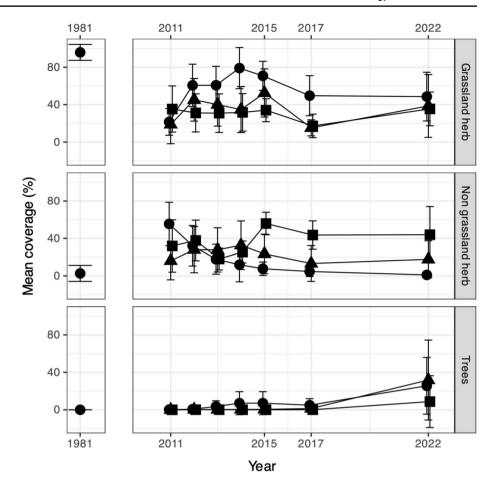


Table 2 Estimated coefficients and p-values of GAMs about the cumulative cover

	A		В	Coefficient of B (A is a reference category)	Adjusted <i>P</i> value
grassland herb	Fence 2010	vs	Fence 2011	- 1.026	< 0.001
	Fence 2010	vs	Outside	- 1.164	< 0.001
	Fence 2011	vs	Outside	- 0.138	n.s
Non grassland herb	Fence 2010	vs	Fence 2011	0.033	n.s
	Fence 2010	vs	Outside	0.955	< 0.001
	Fence 2011	vs	Outside	0.923	< 0.001
Trees	Fence 2010	vs	Fence 2011	- 0.199	n.s
	Fence 2010	vs	Outside	- 0.426	n.s
	Fence 2011	vs	Outside	- 0.227	n.s

we found an increase in tree species after only 13 years, our results show that grassland communities may transition to tree-dominated communities faster than expected because of their higher productivity than forest understories. The increase in shrubs and other competing species caused a decline in grassland herbs. *Rubus* spp. in particular showed a marked increase. Cessation of grazing pressure by large herbivores can promote the encroachment of tree species in grasslands (Su et al. 2015; Snell et al. 2022). Similarly,

Rubus fruticosus agg. showed by far the strongest and widest recovery within exclosures in forest understories (Boulanger et al. 2018). There are many reports of increases in Rubus spp. in North America and Europe following the removal or reduction of disturbance by deer (e.g., Collard et al. 2010; Perrin et al. 2011), as seen here. Van Uytvanck and Hoffmann (2009) showed that thickets of these brambles suppressed species of the herbaceous layer owing to competition for light. The increase in the cover of competing species



Fig. 4 Changes in mean number of species in flower in each species group by treatment and year. Error bars indicate SD

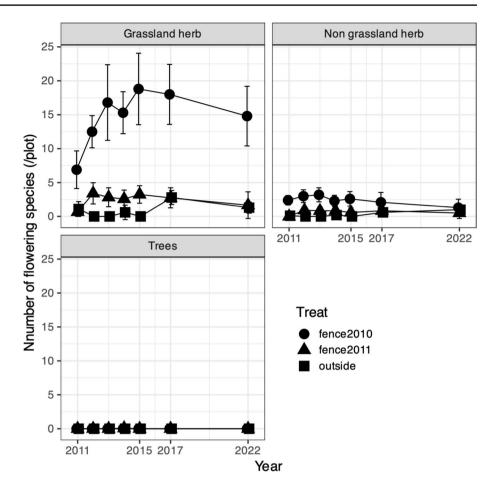


Table 3 Estimated coefficients and p-values of GAMs about the number of species in flower. A GAM for a species group of "trees" was not fitted because the number of flowering species of trees was too small

	A		В	Coefficient of B (A is a reference category)	Adjusted P value
Grassland herb	Fence 2010	VS	Fence 2011	- 1.026	< 0.001
	Fence 2010	VS	Outside	- 1.164	< 0.05
	Fence 2011	VS	Outside	- 0.138	n.s.
Non grassland herb	Fence 2010	VS	Fence 2011	0.033	< 0.01
	Fence 2010	VS	Outside	0.955	< 0.001
	Fence 2011	VS	Outside	0.923	n.s.

such as brambles may inhibit the recovery of grassland herbs (Pápay et al. 2020). Liu et al. (2019) noted the need for moderate disturbance for the retention of plant species diversity in long-term fenced grassland communities. Our results also emphasize that long-term removal of disturbance may inhibit the conservation of grassland specialists. Selective grazing by deer, which is observed from the low deer density stage (Tanentzap et al. 2012), causes an increase and dominance of unpalatable species and species tolerant to grazing, with a decrease in palatable species in plant communities (Côté et al. 2004). In Japan, declining grassland specialists has been observed as a result of an increase in the number of sika deer. On the other hand, annual mowing uniformly removes

the above-ground parts of plant species, thereby inhibiting the establishment of woody species, and can maintain the diversity of grassland specialists (Milberg & Tälle 2023). Management such as mowing may be needed even within exclosures for the conservation of grassland species.

Effect of delay of exclusion of grazing pressure

The 1-year delay in fence installation between 2010 and 2011 made a difference to the trajectory of species composition change: grassland herb cover was lower and tree and non-grassland herb species cover was higher within fence 2011 than within fence 2010. Encroachment of *B. ermanii*,



a tall tree species, may facilitate an irreversible change in the grassland community, because shading by tall trees suppresses grassland herbs (Kennedy et al. 2006; Pápay et al. 2020). Tanentzap et al. (2012) identified potential factors responsible for delaying the recovery of plant communities following the reduction of deer populations: (i) the slow growth rate of plants relative to the amount of biomass consumed by herbivores; (ii) depletion of seed sources of deerpreferred plants; (iii) formation of alternative vegetation types under high deer browsing; (iv) preferential browsing of forage even at low deer densities; (v) variation in browse damage of deer-preferred species with plant community composition (e.g. associational resistance or susceptibility); (vi) suppression of trophic cascades (suppression of the change due to fluctuations in other animal populations associated with changes in deer densities); and (vii) changes in abiotic conditions associated with other ecological processes. Here, factors i to iv may have led to divergence points in the plant community composition. The density of sika deer at the study site was still as high as 30.4 ind./km² in 2010 and 33.2 ind./km² (Iijima et al. 2013; Iijima 2020). In addition, sika deer in semi-natural grasslands in Japan generally tend to highly prefer grassland herbs, which are particularly prone to disappear at sites with high deer impact (Otsu et al. 2017). Therefore, it is possible that grassland herbs outside the fence were also preferentially grazed during 2010, damaging the population to a level where recovery was delayed; that is, the high grazing pressure may have removed enough above-ground stems to limit the seed supply. This difference in the trajectory of the change may be due in part to the characteristics of the study site, which is an isolated small patch of grassland. Thus, the settlement of a rather large fence in 2010 in the grassland may have further increased grazing pressure outside the fence thereafter. Furthermore, in grassland patches surrounded by forest, as at our study site, the encroachment of tree species from the surrounding forests is more likely to follow the sluggish recovery of grassland herbs. Historic grazing can alter herbaceous composition and reduced above- and belowground biomass production below the threshold level required for competitive exclusion of tree species (Brown & Archer 1999). Then, once the new shrubland vegetation has become established, it becomes even more difficult for grassland herbs to recover, creating a negative spiral. This result emphasizes that fences should be installed as early as possible when the aim is to conserve plant species composition. However, it cannot be ruled out that these results may have been partially influenced by the specificity of the study site being a small grassland patch and the spatial heterogeneity of the species composition that survived within the ground. It will be necessary to add more survey sites and conduct additional experiments to clarify the mechanisms that cause recovery to be delayed.



Conclusion

The responses of semi-natural grassland communities after exclusion of deer differed between short- and long-term time scales. Within fence installed in 2010, The species composition recovered as the cover of grassland species increased for at least eight years after the installation of the fence. However, the recovery trend regressed after that as the covers of competing woody species increased. Within fence installed in 2011, grassland species recovered more slowly. Even if grassland herbs temporarily recover within the fence erected earlier, long-term fencing can lead to a decline in the grassland herbs as competing tree species increase. Anthropogenic disturbance, such as mowing, may be necessary for conservation of grassland herbs in long-term fenced grassland communities.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11258-025-01504-2.

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Author contributions All authors contributed to the study conception and design. T.N. and C.O. conceived the research idea; T.N., C.O., and N.S. collected data; H.I. and C.O. performed statistical analyses; C.O., with contributions from T.N., H.I., and N.S., wrote the paper; all authors discussed the results and commented on the manuscript.

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Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Conflict of interest The authors declare no competing interests.

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