

Article

Interaction of Management and Spontaneous Succession Suppresses the Impact of Harmful Native Dominant Species in a 20-Year-Long Experiment

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Abstract: Our study focused on the compositional changes of Pannonian semi-natural dry grasslands. The preservation of these valuable habitats requires regular management. Our mowing experiment aimed to study the suppression of the native dominant *Calamagrostis epigejos* L. Roth in mid-successional grasslands. Mowing was applied twice a year in eight permanent plots. The vegetation was sampled annually from 2001 to 2021. The impacts of mowing were tested using repeated-measures analysis of variance (ANOVA). After 10 years, the cover of *C. epigejos* in the mown plots decreased significantly, from an initial average cover of 56.6 to 5.6%. In 20 years, it declined to 1.3%. Surprisingly, in the control plots, it decreased also from 63.7 to 6.9%. Species richness was affected by mowing: significant differences between mown and control plots were detected from the eighth year of our experiment. However, species richness steadily increased in both treatment types from 15 to 36 in the mown plots and 18 to 25 in the control plots, indicating a combined effect of vegetation succession and treatment. Our results suggest that long-term in situ experiments and comprehensive botanical studies are necessary to provide a basis for multi-objective management and reliable utilization of grasslands.

Keywords: *Calamagrostis epigejos* L. Roth; conservation management; grassland expansion; invasion; land abandonment; long-term data; nature conservation; restoration treatment



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1. Introduction

The phenomenon of biological invasion has been a longstanding hot topic in ecology [1], especially due to its negative biological and socioeconomic effects [2,3]. The concept of invasive species can be interpreted in various ways, e.g., [4–7]. They are usually defined based on the geographical origin of species. The term ‘invasive species’ is restricted to alien (non-native) species [1,6,7]. However, in some cases, native species can behave similarly (spread rapidly, conquer new areas intensively and remain dominant in the new community), causing serious ecological and economic damages [4,5,8,9].

The evolution of natural grasslands is driven by natural disturbances, such as wild-fires, grazing by large herbivores, burrowing of small mammals, etc. [10]. Therefore, the characteristics of disturbance regimes are crucial for the structure and diversity of grasslands. Traditional grassland management in Central Europe (including extensive grazing, prescribed burning and mowing) produced moderate disturbances that were similar to the naturally occurring disturbances [11–14]. These traditional grassland management techniques maintained high alpha diversity within grasslands [13] and high gamma diversity at the regional scale [15–17]. This high diversity is now threatened by the expansion and

consequent negative impacts of certain native and non-native species. When comparing the impacts of alien and native species, previous studies suggested that native species have a weaker negative impact on ecosystems [18,19]. However, other studies found native species to have a similar or even larger impact than alien species [6,20]. As results are often contradictory and comparative studies are scarce, further research is necessary to clarify this question [9,20].

It is widely becoming accepted that explosive population growth, expansion and superdominance of certain native species, followed by the associated decrease in diversity, can be attributed to the recent climatic and land use changes that transformed disturbance regimes and environmental conditions [9,20]. Non-native invasive species can rapidly spread to overused and abandoned habitats. However, native species—especially tall grasses—are also capable of rapid and aggressive expansion in such habitats. *Deschampsia* [21], *Sesleria* [22], *Brachypodium* [23,24] and *Molinia* [25] are widespread dominant grass species in Europe, whose rapid expansion alters the availability of nutrients as well as spatial and temporal niche divisions. In some cases, the native dominants (such as *Calamagrostis epigejos*, *Cirsium oleraceum* and *Phalaris arundinacea*) had a stronger impact on species richness than exotic invasive species [6,26–28].

Calamagrostis epigejos (L.) Roth (see below *C. epigejos*) is a tall, perennial, clonal grass with a rapid growth rate [29–31], allowing it to spread successfully in previously managed, abandoned areas [32–34]. It is highly plastic both morphologically and physiologically [31]. Furthermore, it is exceptionally resistant to harmful environmental factors. With such traits, it is a perfect example of dominant species in post-industrial ecosystems [35,36] and a promising candidate for phytoremediation [30,37]. *C. epigejos* is common in Europe, occurring in natural grasslands [38], forests [39,40], river floodplains [41,42], and ruderal sites [43–46]. It can be found in various habitats [47], such as secondary habitats forming after deforestation or on abandoned agricultural fields [48,49].

Studies showed that human intervention often facilitates the spreading of *C. epigejos* by disturbing semi-natural vegetation [50]. Controlling its expansion is challenging; however, frequent mowing was shown to suppress it [42] successfully. Therefore, *C. epigejos* is nowadays investigated as a potential fodder plant for goats [51]. Other promising experiments aimed to suppress *C. epigejos* with semi-parasitic plants, e.g., *Rhinanthus* species [52].

Long-term vegetation studies have been carried out in temperate climates [53], semi-arid steppe systems [54,55], and North American prairies [56]. However, long-term observations are rare, and studies documenting the effects of interventions carried out systematically over a long period of time are even rarer. The merit of our study is that we monitored the successional context by repeatedly observing permanent plots over a long period of time. We introduced mowing at regular times, which allowed us to analyze the interaction of time and treatment. Our aim was to study the mechanisms of suppression of *C. epigejos*. We carried out our field experiments in abandoned vineyards. At the end of the 20-year experiment, we evaluated the impact of mowing on the cover of *C. epigejos* and the occurrence of other species, as well as community-level species richness. We investigated the following questions:

- (1) Does mowing alter the competitiveness of *C. epigejos*? Can mowing reduce it, and if so, how long does it take?
- (2) How does mowing affect the performance of other subordinated species? Does mowing affect species richness?
- (3) How do mowing and time interact, and how does this interaction influence dry grassland composition over the long term?

2. Material and Methods

2.1. Study Area

The study area was located in the western region of the Cserhát mountain, in the Duna-Ipoly National Park, within the administrative borders of Vác and Rád (center coordinates: 47°45058.8700 N, 19°12051.5700 E, Supplementary Materials Figure S1). The climate of

the region is temperate. The annual precipitation is 520–590 mm, and the average annual temperature is 8–10 °C [57]. The area is covered by loess of different thicknesses. From the loess layer, parallel ridges emerge, one of which is the Bükkös hill (190 m above sea level). The study sites were located on the north-facing slope (3.3 ha) of this hill. The predominant semi-natural grassland vegetation of the area can be identified as *Salvia nemorosa*-*Festuca rupicola* Zólyomi ex Soó 1964 community [58], which corresponds to the Natura 2000 habitat type 6240 “sub-Pannonic steppic grasslands” [59]. In this extensively managed rural landscape, large areas were in agricultural use as vineyards, orchards and croplands for centuries. Due to socioeconomic reasons, these fields have been abandoned since the 1960s–1970s.

2.2. Experimental Design and Data Collecting

In our study, we focused on *C. epigejos*, a perennial, rhizomatous grass spreading vigorously and changing plant community composition. Our aim was to reduce the vegetative growing potential of *C. epigejos* with a systematic mowing treatment. We established eight pairs of 3 × 3 m large permanent plots, positioned randomly along the north slope of the Bükkös hill, and arranged a split-plot design of mown and control plots (Supplementary Materials Figure S1). Vegetation data were monitored in 2 × 2 m large permanent quadrats placed in the middle of each 3 × 3 m large plot, leaving a 2 m buffer zone between the paired (mown and control) quadrats. With the stratified random sampling design, we intended to represent the vegetation variability within the study area (two plots on the top of the hill, two plots along the foothill, two plots near shrubberies, and two plots in open grassland). In this way, we could get robust results about the effect of mowing. However, we did not aim to directly study the effect of these vegetation patch types on the results. The shrub and *Robinia pseudoacacia*-dominated patches were omitted, and patches with low cover of *C. epigejos* (less than 60%) were also disregarded.

There were two main considerations behind this experimental design: (1) to avoid forest edge effects and (2) to minimize the heterogeneity resulting from variable surfaces. The relatively small size of the experimental site allowed us to minimize heterogeneity in topography, vegetation, and land use, reduce site-based variation in priority effects and provide as similar initial conditions as possible.

Mowing was performed with a hand clipper to an approximate height of 5 cm in late spring (June) and in autumn (September) in all treated plots. Mowing treatments were repeated annually in the same months, during the most active aboveground growing phase. In each plot, we visually estimated and recorded the cover of every vascular plant species present with an accuracy of 1%. Below 1%, we used decimal precision. The plots were surveyed twice a year (in June and September) before management took place, with each plot being assessed for species composition and cover-abundance. Immediately after mowing the plots, the biomass was removed. Treatments and surveys were conducted twice every year between 2001 and 2021. The spring and autumn data of the given year were evaluated together based on the higher cover value for each species.

2.3. Statistical Analyses

The analyses were performed with R statistical software (version 4.0.5, R Core Team 2021) [60] using the packages “tidyverse”, “ggpubr”, and “rstatix”. The effects of mowing were tested by repeated-measures analysis of variance (ANOVA). For pair-wise comparisons, paired t-tests were conducted to compare the treatment to the controls and to compare all treatments to each other.

3. Results

3.1. Effects of Mowing on the Cover of *C. epigejos*

C. epigejos was the dominant species in all plots at the beginning of the experiment, with a similar average cover. After the first mowing treatment (in September 2001), the average cover of *C. epigejos* decreased to 33.12% in mown plots, compared to 61.25% in

control plots ($p = 0.0025$) (Figure 1). After ten years of mowing, in 2011, the cover of *C. epigejos* in the mown plots decreased drastically from 56.63 to 5.63%. Contrary to our expectations, a considerable decrease was also observed in the control plots, from 63.75 to 33.38%. After 20 years of repeated treatment, in 2021, the average cover of *C. epigejos* dropped from the initial 56.63 to 1.35%. Likewise, the control plots also demonstrated a decline in average cover from the initial 63.75 to 6.88%. The total cover of all species did not change substantially. Consequently, the relative cover of *C. epigejos* decreased from 0.55 to 0.01 (Table 1).

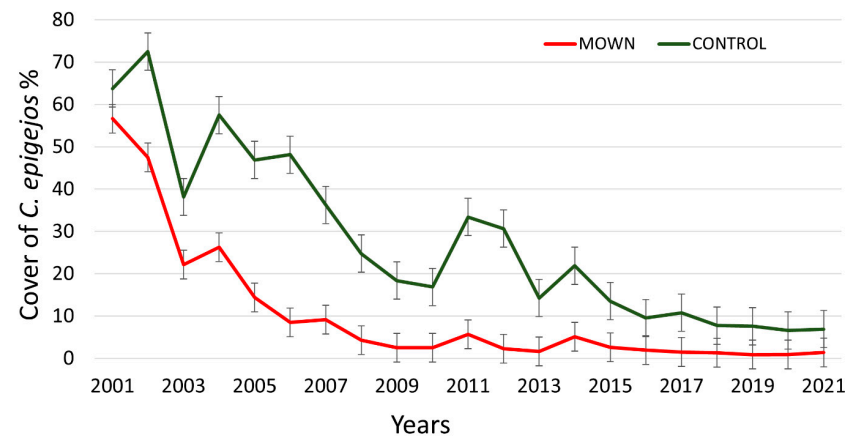


Figure 1. Average cover of *C. epigejos* in mown and control plots with standard errors during the study period.

Table 1. The average cover and standard error of different parameters of mown and control plots. “Total cover absolute” = cover of all vascular plant species; “Cover of CALEPI absolute” = the cover of *Calamagrostis epigejos*; “Cover of CALEPI relative” = the cover of *Calamagrostis epigejos* relative to the overall coverage; “the cover of subordinate species absolute and relative” = cover of all species except *Calamagrostis epigejos*, “Species richness” = the number of all vascular plant species. For each variable, the same letter shows if the temporal difference between means was not statistically significant.

	MOWN					
	2001 Mean ± SE		2011 Mean ± SE		2021 Mean ± SE	
Total cover absolute	103.38 ± 2.11	a	117.43 ± 4.11	b	99.83 ± 5.00	a
Cover of CALEPI absolute	56.63 ± 4.38	a	5.63 ± 2.18	b	1.35 ± 0.59	c
Cover of CALEPI relative	0.55 ± 0.04	a	0.05 ± 0.01	b	0.01 ± 0.01	c
Cover of subordinated species absolute	46.75 ± 4.79	a	111.8 ± 3.39	b	98.48 ± 5.27	b
Cover of subordinated species relative	0.45 ± 0.04	a	0.95 ± 0.02	b	0.99 ± 0.01	c
Species richness	14.88 ± 0.95	a	36.75 ± 1.38	b	36.13 ± 1.31	b

	CONTROL					
	2001 Mean ± SE		2011 Mean ± SE		2021 Mean ± SE	
Total cover absolute	115.70 ± 1.69	a	124.80 ± 5.69	a	113.05 ± 3.08	a
Cover of CALEPI absolute	63.75 ± 4.30	a	33.38 ± 7.27	b	6.88 ± 2.41	c
Cover of CALEPI relative	0.55 ± 0.04	a	0.26 ± 0.05	b	0.07 ± 0.03	c
Cover of subordinated species absolute	51.95 ± 4.61	a	91.43 ± 7.29	b	106.18 ± 5.68	b
Cover of subordinated species relative	0.45 ± 0.03	a	0.74 ± 0.05	b	0.93 ± 0.02	c
Species richness	18.25 ± 1.56	a	27.25 ± 1.88	b	25.50 ± 1.16	b

Results of the ANOVA indicated a significant interaction between years and treatment (Table 2). The results of the paired t-tests between the initial and subsequent years revealed a significant decrease in the cover of *C. epigejos* in the mown plots between each compared

year, except for the first year after treatment (Supplementary Materials Figure S2). Paired t-tests in certain years indicate that mown and control quadrats were very similar at the start of the experiment (Supplementary Materials Figure S3). During the years of treatment, differences emerged in the cover of *C. epigejos* between mown and control quadrats (Figure 1 and Supplementary Materials Figure S3).

Table 2. Results of repeated measures ANOVA of *C. epigejos* cover. Asteriks indicate statistical significance.

Treatment	F: 30.085	$p: 9.21 \times 10^{-4}$	$p < 0.01$ ***
Time	F: 39.559	$p: 1.21 \times 10^{-47}$	$p < 0.01$ ***
Treatment: Time	F: 05.493	$p: 3.68 \times 10^{-10}$	$p < 0.01$ ***

3.2. Impact of Mowing on the Species Composition and the Cover of Subordinated Species

In parallel with the recess of the initially dominant *C. epigejos*, subordinate species spread (Table 1). Such changes were most pronounced among grass species (Figure 2).

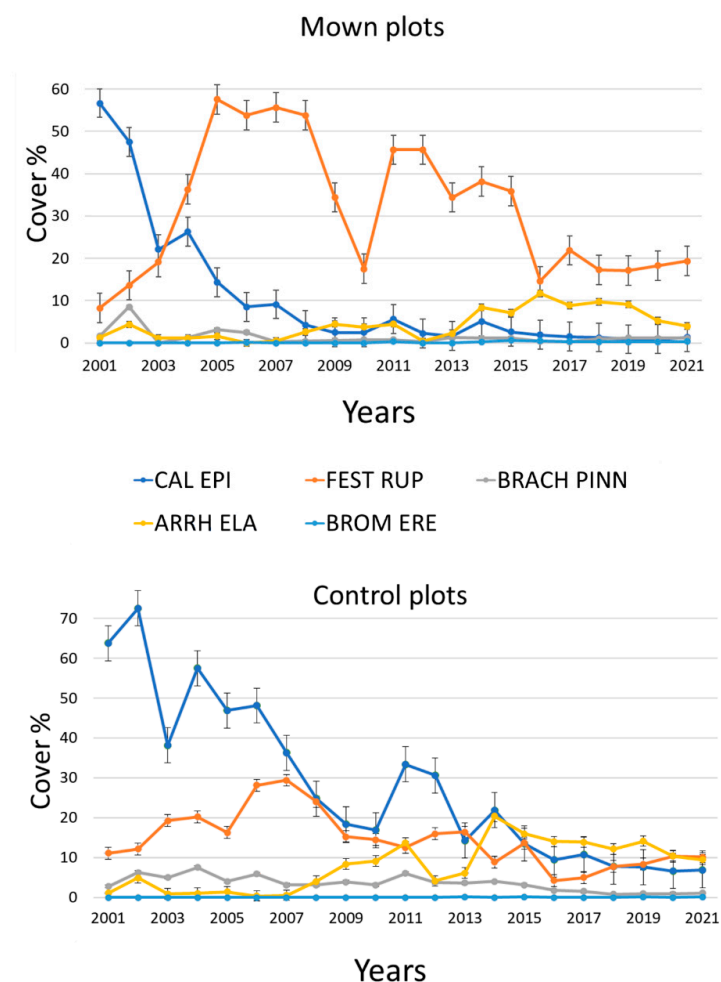


Figure 2. Changes in the cover of main grass species over time in treated and untreated plots. Abbreviations: CAL EPI = *Calamagrostis epigejos*, FEST RUP = *Festuca rupicola*, BRACH PINN = *Brachypodium pinnatum*, ARRH ELA = *Arrhenatherum elatius*, BROM ERE = *Bromus erectus*.

With the recession of *C. epigejos*, a window of opportunity appeared for other grass species. *Festuca rupicola* demonstrated a particularly spectacular expansion in the mown plots in 2004. In the control plots, the *C. epigejos*–*Festuca rupicola* switch occurred much later, in 2019, and the cover of *Arrhenatherum elatius* surpassed that of *Festuca rupicola*,

suggesting that in the absence of treatment, succession moved towards a more mesophyll state of hay meadow, with mowing, the cover of dry grasses increased. The species *Brachypodium pinnatum* and *Bromus erectus* were present in the study area, but they did not reach considerable abundance during the experiment (Figure 2). Both mowing and time had a significant effect on the cover of *Festuca rupicola*. Mowing treatment had the largest effect. The interaction of time and treatment was also significant (Table 3).

Table 3. Results of repeated measures ANOVA of *Festuca rupicola* cover. Asteriks indicate statistical significance.

Treatment	F: 65.412	$p: 8.50 \times 10^{-5}$	$p < 0.01$ ***
Time	F: 18.923	$p: 2.01 \times 10^{-30}$	$p < 0.01$ ***
Treatment: Time	F: 08.675	$p: 3.46 \times 10^{-16}$	$p < 0.01$ ***

In the first third of the experiment, until about 2008, the cover of *Festuca rupicola* continuously increased in the mown plots. Compared to the initial value, this is significant between 2003 and 2009. In 2010, it dropped, and thus there was no significant difference, while between 2011 and 2015, the cover increased significantly again. However, from 2015, the cover of *Festuca rupicola* continuously decreased (Supplementary Materials Figure S4). In 2001, the most abundant species was *C. epigejos*, demonstrating the highest cover in all plots. Its rank decreased, and after 20 years, it was not even among the 10 most abundant species. The previously dominant *C. epigejos* was replaced by *Festuca rupicola* in 2005 and by *Dorycnium herbaceum* in 2010. A similar trend was observed in the control plots: a slight increase, decrease or stagnation—however, with smaller average cover values. There was no significant difference in either year in the *Festuca rupicola* cover compared to the initial stage in 2001 (Supplementary Materials Figure S5). Even without mowing, *C. epigejos* was suppressed due to the encroachment of shrubs: *Cornus sanguinea* became the third most abundant species. *Crataegus monogyna* and other shrubs, such as *Rosa canina*, *Acer campestre*, and *Ligustrum vulgare*, also demonstrated increasing cover and frequency in the plots (Supplementary Materials Figure S6).

3.3. Impact of Mowing on Plant Species Richness

The initial average species richness was 14.88 species per 4 m². After 10 years of regular mowing, the species richness increased to 36.75 and to 36.13 species per 4 m² by 2021. This difference—with the exception of three years—proved to be significant compared to the initial value. In the control plots, the average species richness also increased during the 20 years of observations from 18.25 to 25.50. Table 1 shows this difference was not significant. Paired t-tests in certain years indicated that species richness differences between mown and control quadrats became significant after 8 years (Supplementary Materials Figure S7).

Results of the ANOVA revealed that species richness was significantly affected by both treatment and time (Table 4). Time was the most important factor ($F = 25.629$ $p = 3.89 \times 10^{-37}$) in this case. Despite the fluctuations (Figure 3), the species richness steadily increased in mown and control plots.

Table 4. Results of repeated measures ANOVA of species richness. Asteriks indicate statistical significance.

Treatment	F: 20.634	$p: 3.00 \times 10^{-3}$	$p < 0.01$ ***
Time	F: 25.629	$p: 3.89 \times 10^{-37}$	$p < 0.01$ ***
Treatment: Time	F: 07.114	$p: 2.36 \times 10^{-13}$	$p < 0.01$ ***

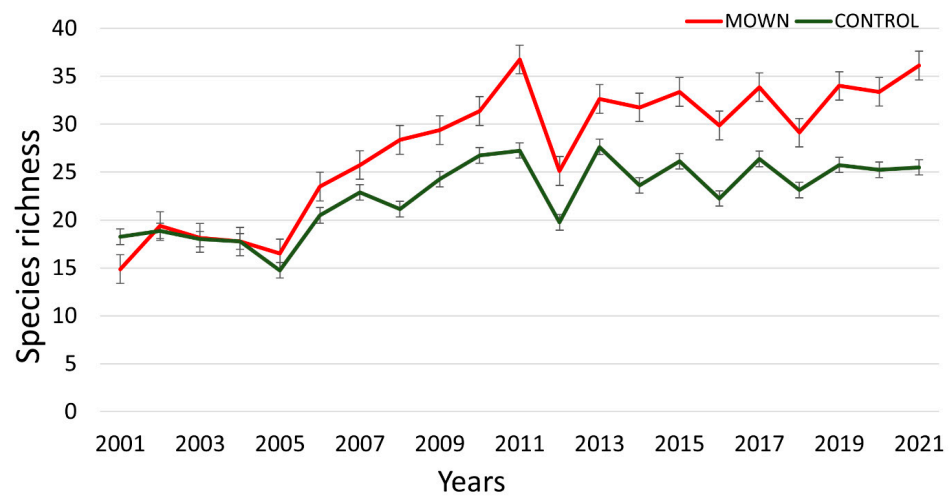


Figure 3. Average species richness in mown and control plots with standard errors during the study period.

3.4. Impact of the Interaction between Treatment and Time

The temporal pattern of *C. epigejos* cover revealed a combined effect of succession and mowing treatment (Figure 4, Table 2). The ratio of *C. epigejos* abundance between mown and control plots declined strongly during the first five years, and then the ratio fluctuated around 0.3 in subsequent years. Similar patterns were observed in the case of species richness (Figure 5, Table 4). The ratio of species richness between mown and control plots demonstrated a continuously increasing trend over time (Figure 5). However, the rate of increase was different in different periods. The ratio of species richness between mown and control plots increased from 2001 to 2008. After seven years, it changed into a slow, continuous growth.

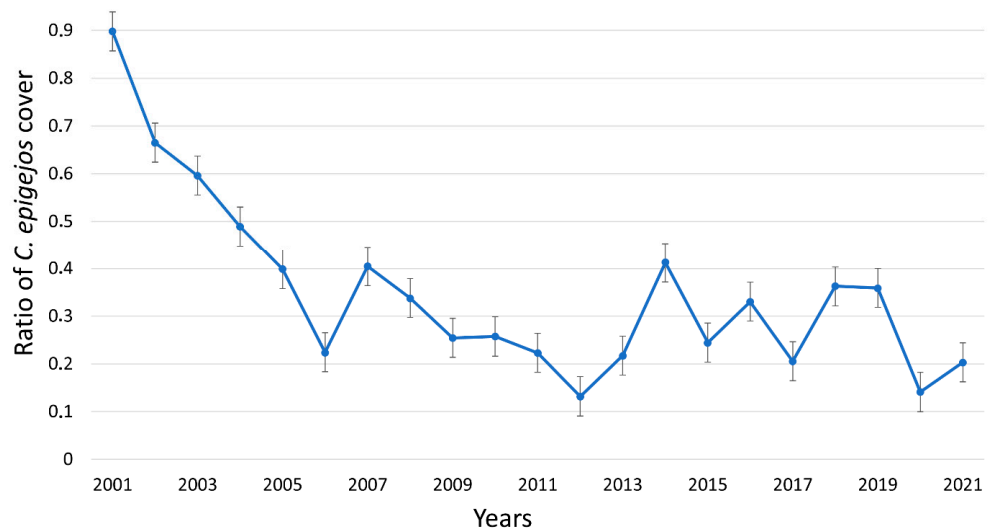


Figure 4. Ratio of *C. epigejos* cover between mown and control plots with standard errors over the study period.

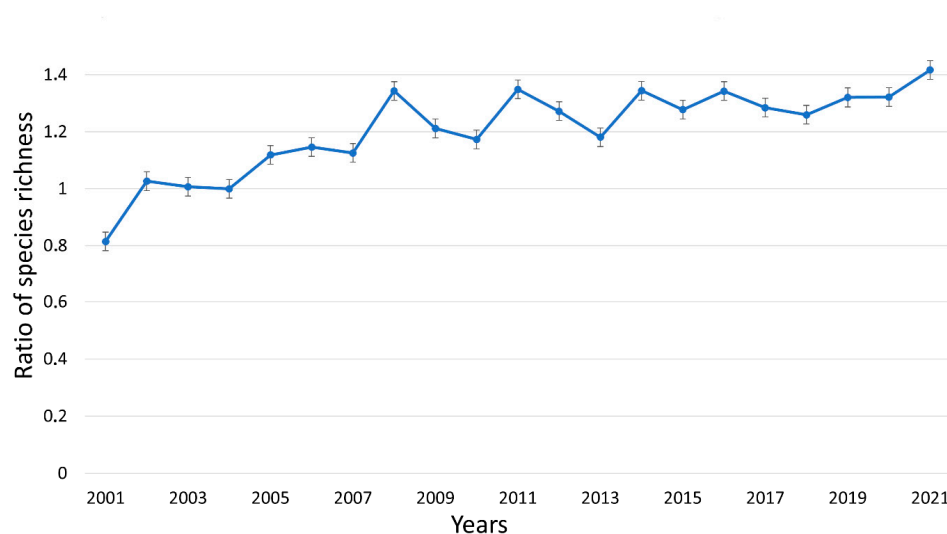


Figure 5. Ratio of species richness between mown and control plots with standard errors over the study period.

4. Discussion

In our 20-year experiment, we found a significant impact of mowing on the abundance and dominance of *C. epigejos*, along with considerable changes in species richness and composition.

4.1. Long-Term Management Needs to Suppress Native, Dominant Grasses

In our experiment, mowing twice a year for several consecutive years effectively reduced the cover of *C. epigejos*, similar to the 28-year-long treatment in the experiment of Wahlman and Milberg [61]. The first significant reduction occurred in the second year of treatment. A similar ‘two-year-delay’ effect was reported by Rebele and Lehmann [30] from sandy landfill habitat. A similar study, but conducted on a wet meadow, found a significant difference in *C. epigejos* cover between mown and control plots from the fifth year of the experiment conducted by Blonska et al. [42]. Such slow response to mowing has also been reported in Poland [62] and could be attributed to the nutrient reserves accumulated in the rhizomes [63,64]. Our results—consistent with the results of Kavanova and Glaser [65]—suggest that mowing twice a year for two or more years is likely enough to deplete underground storage organs and produce a negative nutrient framework for this dominant species. Although the effect of treatment was already visible in the third year, reliable results require the long-term application of regular treatments [66–69]. Frequent mowing contributed to *C. epigejos* losing its dominant role. Numerous previous studies have reported decreasing dominance and increasing diversity as a result of mowing [33,70]. Suppression of the dominant species is often accompanied by a positive change in the sward structure, increasing microhabitat diversity and increasing the species pool. Regular mowing also increases the forage value of a given grassland: it is important to highlight that this treatment is valuable not only in light of nature conservation but also from an economic point of view [55,71,72].

4.2. How Does the Mowing Treatment Affect the Performance of Other Subordinated Species and the Temporal Development of Species Richness?

In the mown plots, a rapid rearrangement of the species dominance rank order was observed. Changes also took place in the control plots, but slower and to a much smaller extent. The importance of long-term monitoring was highlighted by the fact that *Dorycnium herbaceum* became dominant only after 15 years. Such a shift from *C. epigejos* to *Festuca rupicola*, followed by *Dorycnium herbaceum* in response to disturbance, has been previously reported by Sierka and Kopczynska [73]. In parallel with the suppression of the dominant

grass species, we observed the spreading of subordinated species. Notably, a compelling increase in the absolute cover of other (subordinate) species occurred in the control plots as well. This primarily happened due to the progress of shrub encroachment. Analyzing the change of relative cover (ratio to total cover) revealed that the subordinated species were relatively more abundant in the mown plots. Instead of *C. epigejos*, *Festuca rupicola* became the dominant species. *Arrhenatherum elatior*, *Brachypodium pinnatum* and *Poa angustifolia* were among the common, dominant grassland species. *Festuca rupicola* was dominant in the mown area until 2015 when *Dorycnium herbaceum* became more abundant. *Teucrium chamaedrys* and *Cytisus austriacus* (representatives of woody semi-dwarf shrubs) were also present in notable numbers. The frequency of *Arrhenatherum elatior* increased during the study period, and over time it became the second most abundant species (except in 2014). Among other accompanying species, *Galium mollugo* was abundant in the control plots. *Coronilla varia* and *Peucedanum alsaticum* were also abundant species and common taxa in the control plots. In mown plots, other tall species were also represented in noteworthy proportions (e.g., *Centaurea spinulosa*, *Origanum vulgare*, *Achillea collina*).

The shift from broad-leaved grass species to narrow-leaved, drought-tolerant ones can be explained by the gradual drying of the habitat as a result of mowing. The shorter sward allowed more sunlight to reach the soil surface. Furthermore, the amount of stubble also decreased due to intensive mowing [69]. These conditions have been reported to promote the germination of less competitive plant species [74]. The replacement of narrow-leaved grass with a *Fabaceae* species could have taken place due to the decreasing soil nutrient content [75,76]. In certain cases, *C. epigejos* can be replaced by *Brachypodium pinnatum* [77]. Many studies reported that less demanding species have an advantage in the later stages of succession [78,79]. In our experiment, species richness was found to be significantly higher in mown plots compared to untreated plots. Initially, the plots contained 15 plant species per 4 m² on average. In concert with previous studies [80], species richness more than doubled by 2021. The species richness differed slightly, even initially, but it was not visually obvious when we selected the plots. According to the first survey measurements, seven control plots had slightly higher initial species richness. The species richness started to slowly grow in the mown quadrats in 2003, and by 2005, the species richness of control plots only exceeded that of mown plots in two cases. Those were located in the higher part of the hills, close to the forest.

Mowing dry grasslands twice a year increased the number of plant species present. This result is consistent with other studies, e.g., [81], and suggests that grassland vegetation has adapted to the traditional forms of land use. Other experiments showed that moderate disturbance increased species richness [82]. Improving diversity and species richness is a critical part of restoring community function after abandonment and is vital in reducing the risk of invasion. In summary, successful management should aim to balance the trade-off between the reduction of invader density with increasing abundance of other species [83,84]. Several studies have shown that the absence of mowing leads to the accumulation of dry biomass and shading of the soil surface, thus preventing germination and causing the decline of many species [85]. Therefore, regular removal of biomass contributes to maintaining the diversity of grasslands and has a positive, long-term effect on suppressing native or indigenous invaders [16,25,72,81]. Studies have already suggested that traditional land use practices often prove to be the most suitable tools for maintaining biological diversity [86,87].

4.3. Interaction between Management and Spontaneous Succession

Literature rarely mentions the interaction of management and successional dynamics [88]. In our long-term study, we had the opportunity to explore the interaction between spontaneous grassland regeneration and regular mowing. Our analysis indicated a significant interaction between mowing and time for all examined variables. Our opinion about the harmful impact of dominant species and the effectiveness of mowing changed with time during the two decades of the experiment. The negative impact of *C. epigejos* on

species richness was stronger in the first 5–10 years of the experiment, and the mowing also had a stronger effect during this period. This raises the question of whether continuous mowing was necessary or should have been applied only in the first period of the experiment. Studies that applied only single or short-term treatment for removing unwanted dominant species indicated that these treatments are insufficient due to secondary invasions because other unwanted species spread in the freshly opened, treated areas [89]. Further experiments comparing the effects of treatments applied for different time intervals are necessary to clarify this question. In our control plots, *C. epigejos* abundance declined spontaneously after 15 years. However, after the decline of *C. epigejos*, the species richness remained significantly lower in control plots (species richness in control plots was only 70% of that mown plots).

Most previous studies assessing the impact of invasive and native dominant species compared the diversity of vegetation patches based on single, static surveys [2,3,5–7]. Our study highlighted that a single assessment might produce misleading results. We conclude that long-term studies with permanent plots are necessary for reliable impact assessments. *C. epigejos* is an example of native dominant species with harmful effects similar to the impact of invasive alien species. However, there are many other dominant native species that do not have harmful effects and do not expand aggressively. Although the terms used to distinguish alien and native species with aggressive behavior (*invasive* for aliens and *expansive* for natives) might be effective in large-scale studies [7], they are less appropriate in fine-scale studies of plant community organization. Native dominants maintain high diversity in many undisturbed, natural plant communities [11]. Nonetheless, many dominant species are transients in disturbed successional habitats, replacing each other without suppressing the immigration of other species. Further experiments, observations and efforts are necessary for establishing the appropriate scientific terms which could distinguish native dominant species with different impacts. In this respect, Bartha et al. [49] found significant differences between the impacts of native and alien dominant species. Others [20,90] found no functional differences between native dominant and invasive alien species. Warren [91] suggested that species-specific traits and behaviors should be considered instead of their origin when establishing and interpreting the abovementioned terms. The interpretation of our results is limited by the location of our field study: the experiment was carried out in mid-successional, abandoned vineyards. Thus, we cannot fully extrapolate our results to other types of environments or other successional stages.

5. Conclusions

Regular removal of biomass contributes to maintaining the diversity of grasslands. Furthermore, it enhances the long-term suppression of native dominants or indigenous invaders. Our study indicates that traditional land use practices are often the most suitable tools for maintaining biological diversity, validating previous studies with a similar conclusion.

- Over five years of conservation management (mowing twice a year) applied continuously was necessary for the effective suppression of an expanding native dominant species (*C. epigejos*).
- We found evidence that *C. epigejos* declined spontaneously in later successional stages. Although *C. epigejos* declined spontaneously, its period of dominance was three times longer (15 years) without management.
- Species richness increased faster during succession when plots were mowed two times per year, and after 20 years of management, species richness was 40% higher in the mown plots.
- The temporal perspective is crucial for proper assessment of the impact of harmful species (both aliens and natives).
- Long-term (20 years) in situ experiments and comprehensive botanical studies are necessary to provide a solid scientific basis for multi-objective management regimes and to achieve effective utilization of grasslands.

- Appropriate support programs and special agro-environmental management programs are necessary in order to maintain the diversity of grasslands, especially in the case of used and later abandoned agricultural lands.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/land12010149/s1>. Supplementary Materials Figure S1. Map of the study site. Supplementary Materials Figure S2. Average cover of *C. epigejos* in mown plots. Supplementary Materials Figure S3. Temporal change of *p*-values expressing the probability of the null hypothesis: that the cover of *C. epigejos* in a particular year does not differ between the mown plot and the control plot. Supplementary Materials Figure S4. Average cover of *Festuca rupicola* in mown plots during the mowing regime. Supplementary Materials Figure S5 Average cover of *Festuca rupicola* in control plots during the mowing regime. Supplementary Materials Figure S6. Species ranks based on their cover between 2001 and 2021 in mown and control plots. Supplementary Materials Figure S7. Temporal change of *p*-values expressing the probability of the null hypothesis: that species richness in a particular year does not differ between the mown plot and the control plot.

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Nomenclature

For species nomenclature, we used Vascular plants of Hungary: ferns—flowering plants [92].

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