

RESEARCH ARTICLE

To moo or to mow: Disentangling the effects of management on *Gladiolus imbricatus* in coastal meadows

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Abstract

1. Semi-natural grasslands are extremely species-rich, but when management ceases, they become overgrown and lose their exceptional biodiversity. During the twentieth century, most formerly mown or grazed grasslands in northern Europe were abandoned and subsequently encroached by tall herbs and shrubs. An indicator species of extensively managed semi-wet grasslands is *Gladiolus imbricatus*, a tall perennial herb, declining across its range in parallel with the loss of these habitats.
2. We investigated the response of *G. imbricatus* to different management regimes—mulching, mowing and grazing—in coastal meadows in southwest Estonia, which were restored in 2001 after more than a decade of abandonment. In addition, we assessed the effects of recent adjustments to these regimes introduced in 2021, specifically the timing of mowing and the intensity of grazing. We collected data from permanent plots from 2021 to 2025, recording the number of individuals at different life stages (juvenile and adult, with adults further subdivided into vegetative and generative), which we used as demographic indicators of population dynamics.
3. Cutting regimes (mulching and mowing) supported a higher abundance of *G. imbricatus*, whereas grazing at both tested intensities resulted in a population decline. Temporal fluctuations in population size between management regimes were driven by variations in juvenile numbers. Under mulching, the population increased from a stable population structure initially characterized by a juvenile-to-adult ratio greater than one to a dynamic structure with a ratio greater than eight. We did not find significant results by variation in mowing date. However, although not statistically significant, medium grazing intensity appeared more favourable than high intensity to maintain a stable population structure.
4. *Practical implications.* To promote a growing population of *G. imbricatus* in semi-natural wet grasslands, vegetation removal by mulching or mowing should be prioritized over grazing, which, if applied, should be implemented at lower intensities. We found no conclusive evidence regarding the optimal time to mow but advise conservation practitioners to actively select a mowing date under consideration of target species' requirements and desired conservation outcomes.

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KEYWORDS

Boreal Baltic coastal meadow, conservation, grazing intensity, life-stage distribution, mowing date, mulching, population structure, semi-natural grassland

1 | INTRODUCTION

Since humans began settling permanently approximately 11,700 years ago, semi-natural grasslands in the northern temperate zone have evolved through a mutualistic relationship between human activity and landscape (Carey, 2023). Over time, this interaction has created some of the most species-rich habitats outside of tropical rainforests (Chytrý et al., 2015; Dengler et al., 2020; Wilson et al., 2012). However, the abandonment of traditionally grazed and mown grasslands during the 20th century has led to widespread successional overgrowth and associated decline in plant species richness (Moora et al., 2007; Norderhaug et al., 2000; Willems, 2001). As a result, grassland-specific ecosystem services, such as feed supply, increased nutrient cycling, carbon sequestration and their aesthetics have diminished (Wehn et al., 2018). Within the European Union, agriculture—whether through intensification or abandonment—remains the primary pressure on most habitats, with grasslands being particularly affected (European Commission, 2020). The particular pressure of abandonment and consequent overgrowth is pronounced in semi-wet grasslands in the northern reaches of the Palaearctic, where cold temperatures and wet conditions complicate management (Dengler et al., 2020; Valkó et al., 2018). Furthermore, post-socialist societal transformation has made small-scale farming, which is common with extensive grassland management, uneconomical, thus accelerating the abandonment of these habitats (Biró et al., 2013).

Semi-natural grasslands have historically been managed by making hay and grazing livestock, both of which are essential for maintaining biodiversity and ecosystem functioning (Wehn et al., 2018). Traditional haymaking involves one to two cuts per growing season, with the first cut occurring around midsummer, when forage quality peaks (Boob et al., 2019). Modern restoration approaches adapt these practices to meet conservation goals. Two sward-cutting methods in conservation included mowing the sward and either removing the hay or leaving it in place; and mulching, where the sward is crushed into small pieces that are then left to decompose (Moog et al., 2002).

There are different approaches to the timing of cutting. In coastal meadow conservation, it is often delayed until after mid-July to avoid disturbing the breeding season of ground-nesting birds. Additionally, late-season cuts allow for seed maturation of typical meadow species (Canella et al., 2020). To restore and maintain plant diversity, a mowing regime with variable dates across years has been shown to yield positive results for plant species richness (Leng et al., 2011; Pihlgren, 2007). Livestock grazing in semi-natural northern grasslands typically involves cattle or sheep and is carried out at varying intensities. More intense grazing has been shown to decrease plant

species richness (Pihlgren, 2007), while low-to-medium intensity grazing has been beneficial for preserving it (Milne & Osoro, 1997; Olff & Ritchie, 1998). Although grazing is the most commonly used restoration method (Tälle et al., 2016), it is less suitable for tall bulbous herbs due to their susceptibility to trampling (Richter, 2012). All three types of extensive management—mowing, mulching and grazing—are generally suitable for grassland conservation, as they serve the main purpose of preventing overgrowth and thus maintaining sufficient light availability for meadow species to establish and persevere. This study examines habitat conditions through the state of populations of the rare *Gladiolus imbricatus*, a tall perennial herb threatened by lasting cessation of extensive grassland management (Kostrakiewicz-Gieratt, 2014, 2017; Moora et al., 2007). A more recent study by Kostrakiewicz-Gieratt et al. (2023) reported secondary succession as beneficial for the study species; however, this may be because their comparative extensively managed area consisted of post-cultural land, which did not represent a suitable habitat for *G. imbricatus*. Prior studies in Estonian semi-wet meadows have found evidence for the effectiveness of mowing (Kose et al., 2019; Moora et al., 2007) and mulching (Jõgar & Moora, 2008) the sward in increasing the abundance of the study species, compared with grazing or burning. Mechanisms underlying the greater effectiveness of cutting regimes relative to grazing include the species' sensitivity to grazing and trampling (Richter, 2012). Compared with cattle, sheep have been found to graze more selectively on *G. imbricatus*; therefore, their use in conservation has been discouraged (Kose et al., 2019; Moora et al., 2007). In addition, mulching regimes may provide benefits over conventional mowing by leaving cut biomass in situ as plant litter, which can increase soil moisture retention and nutrient availability, and may facilitate the germination of some meadow species.

Gladiolus imbricatus (L.) (*Iridaceae*) is native to Central and Eastern Europe, ranging from Mediterranean regions to western Siberia, with Estonia marking its northern distribution limit (Meusel et al., 1965). It grows between 30 and 120 cm tall (Kose et al., 2019) and is the most winter-hardy species in the genus *Gladiolus*. This species is also known as the 'Turkish marsh gladiolus', reflecting its primary occurrence in wet habitats, such as coastal meadows. It prefers thick, soft, noncalcareous sandy loam. Well adapted to harsh conditions, such as regular inundation and cold climates, the mesophyte *G. imbricatus* is a perennial geophyte with bulbs as below-ground storage organs that can tolerate dry and wet conditions typical of periodically flooded coastal meadows. It can reproduce vegetatively through short tubers (1–2 cm in diameter); however, generative reproduction from seed was found to be more common (Moora et al., 2007). Generative individuals typically have two rosette leaves, one to three leaves on a single flowering stalk, and a one-sided inflorescence bearing 3–10 purple flowers for around 2 weeks. In southwest Estonia, flowering

occurs in late June to early July, with seed production peaking in the first half of August. Each flowering plant produces approximately 200–400 relatively heavy seeds (1.7 mg per seed; unpublished data from this experiment). Seed dispersal occurs through water (i.e. hydrochory) or animal movement (i.e. zoochory). Like most meadow species, high light availability is crucial for successful reproduction.

After a chilling period lasting several months, the life-cycle of *G. imbricatus* begins with hypogeal seed germination (Kose et al., 2019). The below-ground establishment of the cotyledon during this stage allows for rapid sprouting under favourable conditions. Both, individuals growing from seed and growing vegetatively from a daughter corm initially appear as one-leaved juveniles in their first year, develop into two-leaved vegetative plants in their second year, and can reach the generative, flowering stage in their third year. These three life stages are observable in the field, although their indicators may not always reflect the actual stage of an individual. For example, a one-leaved plant could be a juvenile or an older vegetative individual that has adapted to unfavourable conditions (Kose et al., 2021; Moora et al., 2007). Nevertheless, this classification remains the best, non-intrusive field method for estimating growth stage and was therefore adopted for classifying individuals in this study. The life-stage distribution resulting from this classification was proven successful in characterizing the condition of populations of *G. imbricatus* (Kostrakiewicz-Gierałt, 2017; Moora et al., 2007). Dynamic populations are dominated by juveniles, stable populations include all life stages in a balanced proportion, and regressive populations are dominated by adults (vegetative and generative individuals), indicating a delayed demographic response to unfavourable conditions (Moora et al., 2007; Rabotnov, 1985). Prior studies on population structure have found more dynamic populations associated with greater abundances of *G. imbricatus* in meadows at earlier successional stages (Kostrakiewicz-Gierałt, 2014, 2017), and in mown compared with grazed or unmanaged meadows (Kose et al., 2019; Moora et al., 2007).

Estonia, with its long Baltic coastline, shallow waters and cold-temperate climate, provides ideal conditions for the formation of Boreal Baltic coastal meadows (habitat code 1630)—a priority habitat listed in Annex I of the EU Habitat Directive 92/43/EEC (1992). Although the conservation status of Boreal Baltic Coastal Meadows in Estonia has improved over the last two decades (EU report habitat summary 2001–2018), the most recent assessment (2013–2018) still classified their overall status as 'Unfavourable–Inadequate' (European Union, 2018). To sustain this habitat, extensive management by grazing or cutting is crucial. This habitat type is limited to Estonia, Finland, Sweden and Latvia, making conservation their shared regional responsibility. Among these countries, Estonia contains the largest proportion of Boreal Baltic coastal meadows (140 km², or approximately 43% of the total area; Supporting Information S1; European Union, 2018), placing it in a key position to develop best practices in restoration and long-term monitoring. This study takes place in such coastal meadows in southwest Estonia that belong to the Natura 2000 network, and where extensive management was reintroduced in 2001 through an EU LIFE Project (2001).

The aim of this study was to compare the effects of different management regimes on the abundance of different life stages of *G. imbricatus*. To date, there is limited research on the life-cycle of tall bulbous herbs and their responses to different management regimes. Here, we examine both, long- and short-term management effects. Based on previous research, we hypothesized that (1) removal of swards once per season (i.e. mowing and mulching) supports higher abundance of *G. imbricatus* than continuous grazing, as suggested by earlier studies (Jõgar & Moora, 2008; Kose et al., 2019; Moora et al., 2007). (2) Mulching is more beneficial than mowing or grazing, according to an earlier study in an Estonian wet meadow (Jõgar & Moora, 2008). (3) Late-season mowing in the end of July, results in a higher abundance of *G. imbricatus* compared with early- and mid-season mowing in early and mid-July, given the seed ripening period of the species in August (Canella et al., 2020; Kose et al., 2019). (4) Lower grazing intensity leads to greater abundance of *G. imbricatus*, due to the plants' sensitivity to trampling and herbivory (Kostrakiewicz-Gierałt, 2017; Richter, 2012).

2 | MATERIALS AND METHODS

2.1 | Study site

The study was carried out in southwest Estonia, in the coastal meadows of the Luitemaa nature reserve, a species-rich area that hosts up to 35 vascular plant species per m² and home to more than 250 vascular plant species (Moora et al., 2007). The meadow areas at the study site are edaphically homogeneous, providing ideal semi-wet and mesotrophic conditions for *Gladiolus imbricatus*. The soil consists of an approximately 10–15 cm thick humus layer over sandy loam. The plant community corresponds to the *Deschampsia-caricetum nigrae* type, with up to 26 vascular plants recorded on 0.25 m² during the study period. Dominant plant species include *Sesleria caerulea*, *Deschampsia caespitosa*, *Achillea millefolium* and *Centaurea jacea* (Kose et al., 2019). *G. imbricatus* is highly abundant and forms its largest population in Estonia—possibly the largest across its entire distribution range—with an estimated occurrence exceeding 1 million individuals (Kose et al., 2020).

The weather conditions during the flowering period of *G. imbricatus* from mid-June to mid-July varied. Temperatures were highest in 2021; then, 2022 and 2023 were still warmer, and only 2025 was colder than average, based on data from a weather station located roughly 7–10 km from the study sites. Precipitation was highest in the years 2023 and 2025, while 2021 and 2022 were comparatively dry (Supporting Information S1; Truhanov, 2025).

2.2 | Management history and experimental setup

Following abandonment in the 1990s, management in the Luitemaa coastal meadows was resumed between 2001 and 2004 and has been carried out annually ever since (Moora et al., 2007). The

experiment has been designed with and confirmed by the [Estonian Environmental Board](#), responsible for Natura 2000 area management in Estonia (grant number: 5-2/25/78). It has also been agreed with all other relevant institutions, land managers and landowners; therefore, no additional permit was needed. Data for this study were collected from 2021 to 2025, capturing both the long-term effects of the management regimes established since 2001 and the short-term response to recent management adjustments that were introduced in 2021. The latter have again been implemented in collaboration with the Estonian Environmental Board, in order to determine the optimal management regime for *G. imbricatus* in more detail.

The plots are situated within 3.2 km along the southwest Estonian coast, all less than 1 km from the coastline ([Figure 1](#)). The long-term management regimes were mulching (four plots), mowing (nine plots) and grazing (nine plots). Mulching has been carried out in late August since 2004 with the intention to prevent reed and shrub overgrowth. It was performed with a tractor that fragmented the

sward into small pieces, in contrast to mowing, which cut the vegetation into hay without fragmentation. After mulching, these pieces were left to decompose, thereby retaining nutrients and forming a litter layer on the soil surface that reduced temperature and moisture fluctuations in the upper soil layer (Zarzycki et al., 2024). Although mulching was stopped in one plot in 2021, that plot was still included in the analysis of long-term management regimes. Mowing has been conducted around 15 July since 2003. In 2021, the mown site was subdivided into three areas: mown around 1 July (early), around 15 July (mid) and around 1 August (late). The setup was unbalanced with respect to early mowing: only one plot was mown early, compared with four plots each in the mid- and late mowing regimes. Grazing was introduced in 2002 and applied during the vegetation period (May–September) at 50% intensity, corresponding to one livestock unit per hectare (Rannap, 2020). In 2021, the site was subdivided into two areas: one continued with 50% grazing intensity (medium), while the other was subjected to an increased grazing intensity of 75% (high).

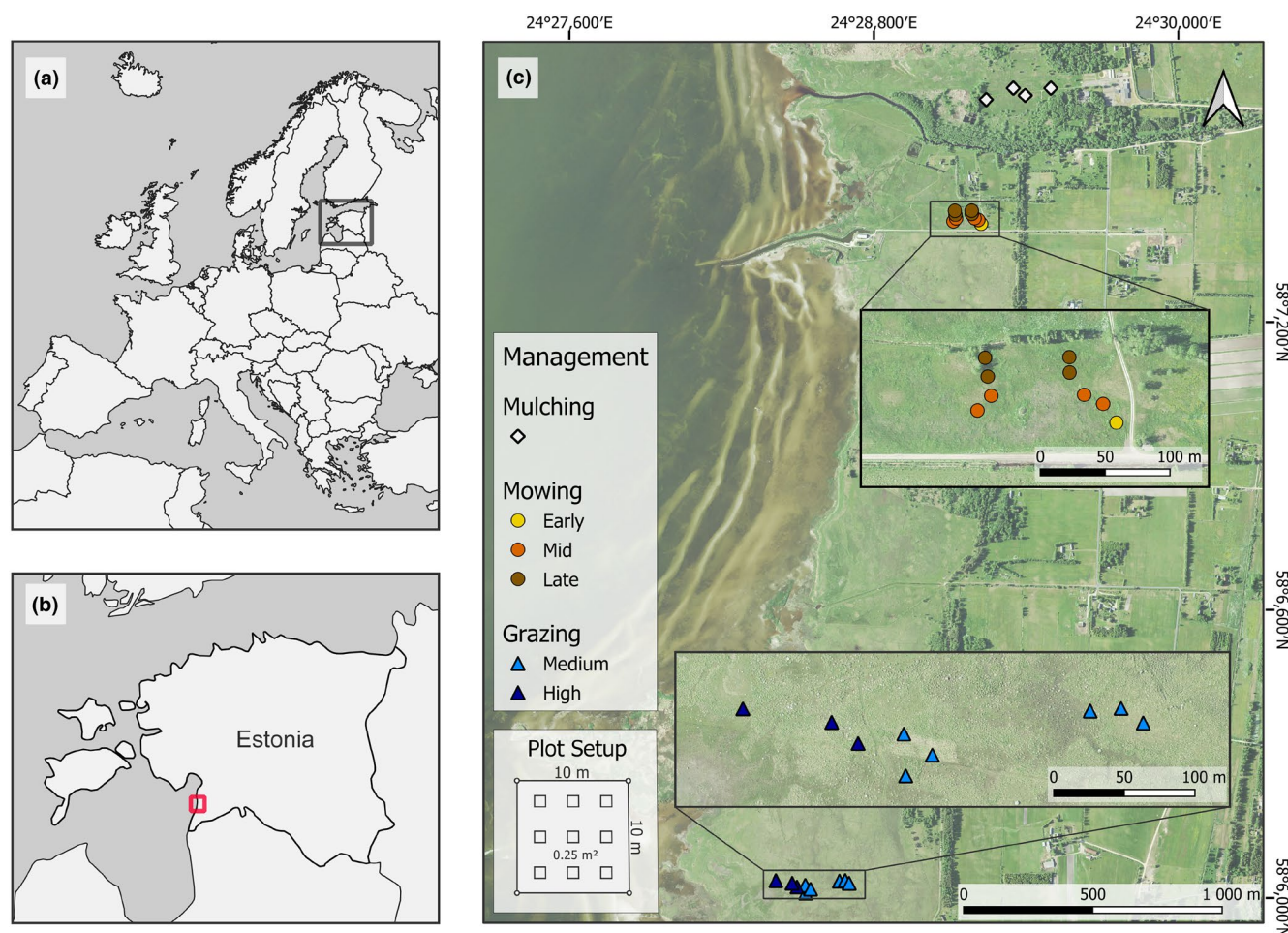


FIGURE 1 Map of the study site in southwest Estonia. (a) shows the location of Estonia within Europe, (b) the location of the study site within Estonia, and (c) the location of the plots along the coast. Four plots were situated in the mulched site, nine plots in the mown site—split into three mowing dates (early: one plot, mid: four plots, late: four plots) and nine plots in the grazed site—split into two grazing intensities (medium: six plots, high: three plots). The four corners of a plot are marked permanently; each plot is comprised of nine quadrats. Projected Coordinate System: Estonia 1997 National Grid. [Orthophoto 08/09.06.2023](#), Republic of Estonia Land and Spatial Development Board. Made with QGIS.

Fieldwork was carried out in early July from 2021 to 2023 and again in 2025, using a permanent plot setup. After initially marking the 10m×10m permanent plots in 2021, nine points were designated within each plot at distances of 1, 5 and 9 m from each corner. These nine points were treated as corners and data were collected in 50cm×50cm quadrats (see also Figure 1). In each quadrat, *G. imbricatus* was counted: 1 as leaved individuals were classified as juvenile, 2 as leaved individuals as vegetative and any shoot with flowers or visibly grazed flowers as generative (Kostrakiewicz-Gierałt, 2017; Moora et al., 2007). All vascular plant species found in each quadrat were listed. The total number of data points was 198 per year (22 plots×9 quadrats).

2.3 | Data analysis

All data were aggregated at the plot level to reduce the influence of outliers at the quadrat level. For each graph and year, we calculated the ratio of juvenile and adult individuals (vegetative and generative combined) and visualized this ratio across study years and management regimes. Ninety-five per cent confidence intervals were obtained by resampling with replacement 1000 times, also known as bootstrapping (Puth et al., 2015). Based on Moora et al. (2007) we decided to use a ratio of 1 as the threshold between dynamic/stable (juvenile:adult ratio ≥ 1) and regressive (ratio < 1) population structure. To test our four hypotheses, we fitted generalized linear mixed models (GLMMs) with negative binomial error distributions, appropriate for count data. The response variables were the count of juvenile, vegetative and generative individuals of *G. imbricatus*, as well as the total individual count per plot. To test the effect of long-term management regimes on the population of *G. imbricatus*, we used the following fixed effects: (1) management type with two levels (mowing and mulching [together hereafter 'meadow'] and grazing);

and (2) management type with three levels (mowing, mulching and grazing). To test the differences between short-term adjustments to the management regimes, we used (3) mowing date with three levels (early, mid and late); and (4) grazing intensity with two levels (medium, high). A significance threshold of $p < 0.05$ was applied.

All models included plot identity as a random effect to account for repeated measurements across years. In the final models, we included an interaction term between the management regime and study year to account for temporal variation in the treatments. Model fits were evaluated using a Type II Wald χ^2 test. For each model, we conducted post hoc multiple comparisons with the Dunn-Sidak correction to assess pairwise differences among management regimes and years. GLMMs were run using the lme4 version '1.1.32' R package (Bates et al., 2015). Model estimation was carried out using the R packages lmerTest version '3.1.3' (Kuznetsova et al., 2017) and emmeans version '1.8.8' (Lenth et al., 2018). Visualizations were created using the R packages ggplot2 version '3.1.4' (Wickham, 2016) and patchwork version '1.2.0' (Pedersen, 2024). All statistical analyses were performed using R software (R Core Team, 2023).

3 | RESULTS

3.1 | Population structure in managements and years

Over the course of the study, the population structure of *G. imbricatus* under long-term grazing at both, medium and high intensities shifted from a stable state (juvenile:adult ratio > 1) to a regressive state (ratio ≤ 1 , Figure 2a). This shift was accompanied by a continuous decline in population size, most strongly between 2022 and 2023 (−70.7%, Supporting Information S3). Under long-term mowing, the population structure was generally stable and

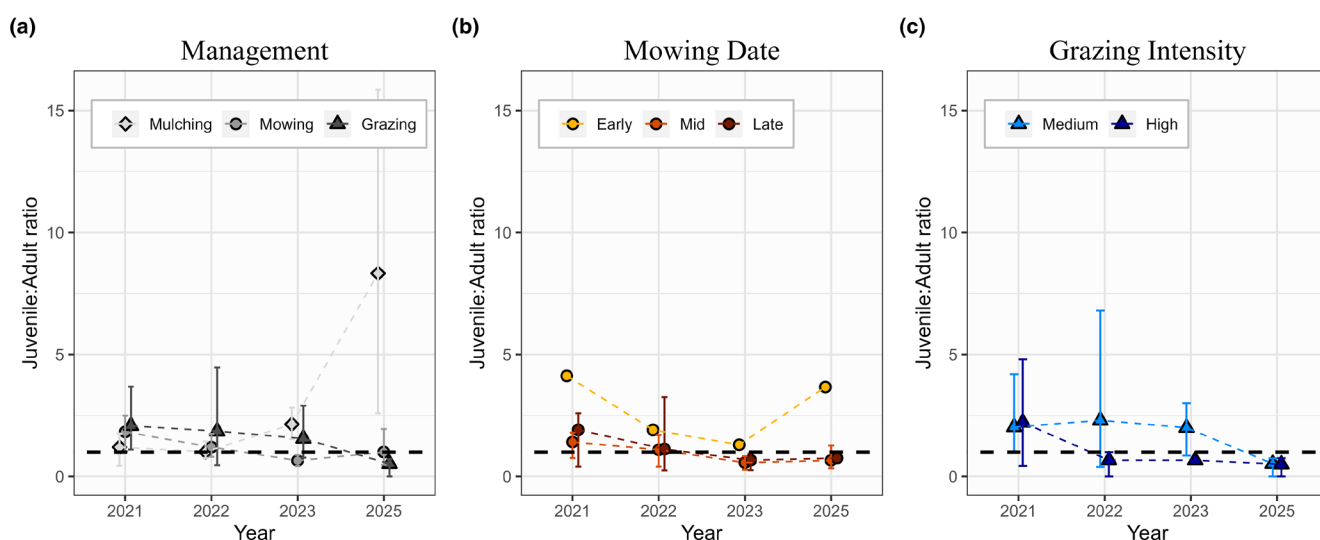


FIGURE 2 Juvenile-to-adult ratio of *Gladiolus imbricatus* individuals per management and year between (a) overall management regime, (b) mowing date and (c) grazing intensity. The dotted line at $y = 1$ marks the transition from a stable state (> 1) to a regressive state (≤ 1) of the population. Error bars represent the 95% CI.

fluctuated around 1, while in contrast, the population under mulching treatment developed from a stable to a highly dynamic structure (ratio $\gg 1$, [Figure 2a](#)). Although total counts increased in mulched plots, they declined in both, mown and grazed plots ([Supporting Information S3](#)). Notably, in 2022, the total count of *G. imbricatus* more than halved across all mowing dates (-54.1% ; [Supporting Information S3](#)). The short-term introduction of different mowing dates showed a diverging response: Early-mown plots differed from mid- and late-mown plots, in that the latter two dates exhibited a slightly regressive population from 2023 onward, while the number of juveniles in the early-mown plots noticeably increased in 2025, maintaining a stable—potentially dynamic—population ([Figure 2b](#)). Finally, plots subjected to medium grazing intensity maintained a stable population until 2023, whereas under high grazing intensity, the population became regressive already in 2022 ([Figure 2c](#)).

3.2 | Response to long-term management

Long-term management, implemented since 2001, either as meadow or through grazing, had a significant effect on the total count of *G. imbricatus* (p -value <0.001 and $R^2=0.57$; see [Table 1-1](#)). Across all study years, the meadow plots exhibited significantly higher total counts of *G. imbricatus* than the grazed plots. Furthermore, while the count of *G. imbricatus* decreased in grazed plots during the study period, it increased in meadow plots ([Supporting Information S4](#)).

When meadow management was further differentiated into mulching and mowing, the difference between the three management regimes was also significant, especially in the later years of

data collection (2023 and 2025; p -value <0.001 and $R^2=0.63$; see [Table 1-2](#); [Figure 3a](#)). Under mulching, increasing total counts were primarily driven by juveniles, whereas the number of vegetative and generative individuals remained relatively stable ([Supporting Information S3](#)). In contrast, the mowing treatment showed a drastic decline in total numbers in 2022, mainly attributable to decreases in juvenile and generative individuals, whereas the total count of vegetative individuals remained relatively constant ([Supporting Information S4](#)). In the grazing treatment, counts for all stages decreased continuously from 2021 to 2025.

3.3 | Response to short-term management modifications

Within the mown site, the variation in mowing date did not have a statistically significant effect on the total count of *G. imbricatus* (p -value $=0.46$; see [Table 1-3](#) and [Figure 3b](#)). The only near-significant interaction between mowing date and year was observed for the count of generative individuals (p -value $=0.057$; [Supporting Information S4](#)). Overall, early- and mid-mowing tended to result in higher total counts than late mowing, although patterns differed between life stages and years ([Supporting Information S4](#)).

Similarly, the interaction between the grazing intensity and the year did not have a statistically significant effect on the count of *G. imbricatus* at any stage (p -value $=0.43$; see [Table 1-4](#)). However, the overall pattern across all years and stages indicated higher counts in plots subjected to medium grazing intensity than in plots with high grazing intensity ([Figure 3c](#), [Supporting Information S4](#)).

Model	Explanatory variables	df	χ^2	p -value	R^2
1	Long-term management regimes				
	Management (meadow/grazing)	1	16.52	<0.001	0.57
	Year	3	9.57	0.023	
	Management:year	3	27.21	<0.001	
2	Management (mulching/mowing/grazing)	2	21.52	<0.001	0.63
	Year	3	10.89	0.048	
	Management:year	6	47.96	<0.001	
3	Short-term management adjustments				
	Mowing date (early/mid/late)	2	2.79	0.25	0.38
	Year	3	8.06	0.045	
	Mowing date:year	6	5.70	0.46	
4	Grazing intensity (medium/high)	1	1.57	0.21	0.61
	Year	3	58.48	<0.001	
	Grazing intensity:year	3	2.76	0.43	

TABLE 1 Effect of different management regimes and their interaction with the sampling year on the total count of *Gladiolus imbricatus*, based on four models (GLMMs).

Note: The sampling years were 2021, 2022, 2023 and 2025. Significant p -values are marked in bold.

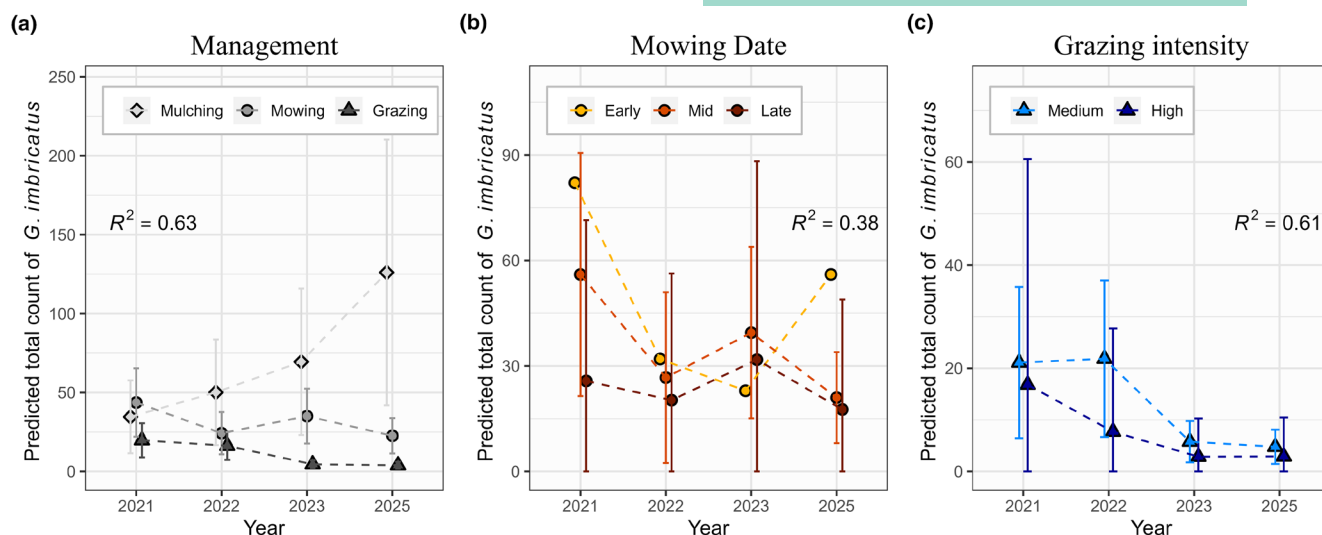


FIGURE 3 Predicted response of the count of *Gladiolus imbricatus* to different managements: (a) management regimes established since 2001 and (b, c) management adjustments since 2021. (a) Difference between mulched, mown and grazed plots; (b) differences between mowing dates (early, mid and late); (c) difference between grazing intensities (medium and high). Based on GLMMs with an interaction between management and year. Error bars represent the 95% CI.

4 | DISCUSSION

4.1 | Population structure in managements and years

Both, the overall abundance of *G. imbricatus* and the population structure varied between study years (Figure 2). These temporal differences may have been influenced by interannual variations in weather conditions. Interestingly, the mulching and mowing management regimes responded differently to the change from a warm and dry flowering period in 2021 to a cold and even drier one in 2022 (Supporting Information S2). The differences between managements in *G. imbricatus* abundance from 2021 to 2022 (decrease in the mown plots [−54.1%] and little change in the grazed plots [−3.7%] and mulched plots [+11.0%]; Supporting Information S3) cannot be explained by our data, because they may be site- or management-specific, or a combination of both.

Changes in population structure under long-term management regimes (i.e. a transition from stable to dynamic under mulching, or from stable to regressive under grazing) were expectedly driven by changes in juvenile abundance. Similarly, Kostrakiewicz-Gierałt et al. (2023) found that for *G. imbricatus* only the juvenile numbers, and not the adult numbers, differed significantly between sites. As a note of caution for the interpretation of abundance in our study species, Kubíková and Zeidler (2011) pointed out that dormancy periods that are typical of geophytes are also common with *G. imbricatus*.

4.2 | Response to long-term management

According to hypothesis (1), both mulching and mowing resulted in a higher abundance of *G. imbricatus* than grazing across all study years.

This pattern aligns with earlier observations in the Luitemaa coastal meadows, where long-term grazing (>10 years since restoration) negatively affected *G. imbricatus* compared with mowing (Kose et al., 2019).

There are various explanatory approaches to this result, all related to plant traits which relate to life stages and height. Stammel et al. (2003) reported that forbs with stems—such as *G. imbricatus*—occur in higher abundance in meadows than in pastures. Furthermore, grazing-tolerant species tend to be of short stature (Díaz et al., 2001), while flowering individuals of *G. imbricatus* typically reach heights above 60 cm and are therefore highly susceptible to grazing (Kostrakiewicz-Gierałt, 2017; Richter, 2012). In contrast to continuous grazing during the growing season, both mowing and mulching are one-time disturbances, allowing for either regrowth or seed maturation, depending on the timing. Additionally, an extensive meta-analysis by Díaz et al. (2007) on the impacts of grazing on plant traits found an overall negative response. This effect was largely attributed to the mechanical impact of the sharp hooves of livestock, which can cause substantial damage to herbaceous vegetation, especially bulbous and erect plants—such as *G. imbricatus* (Richter, 2012). A reduction in generative reproduction may lead to reduced genetic diversity over time for certain meadow species as suggested by Tsunamoto et al. (2025) for the rhizomatous *Calystegia soldanella*.

One of the most surprising results was the large abundance of *G. imbricatus* under mulching in 2023 and 2025 (Figure 3a), supporting hypothesis (2). Several factors may contribute to this observed pattern, some of which are not strictly linked to the management regime itself (e.g. hay removal and timing of the cut). First, mulching has previously been shown to promote the abundance of *G. imbricatus* more effectively than mowing (Moora et al., 2007). Second, by default, in the mowing treatment, the hay

was removed, while in all four mulched plots the crushed sward was left in place. The remaining mulch layer may have been thin enough to avoid light limitation for seedling establishment, while simultaneously contributing nutrients to the topsoil. An unpublished experiment of germinating *G. imbricatus* from seed supports the argument that leaving the plant litter in situ, as in the mulched plots, would benefit germination. Seeds covered with around 1 cm of garden soil had a germination success 20 times higher than those without additional cover. Third, the timing of removal of the sward differed between treatments: Mowing occurred between 1 July and 31, while mulching was carried out in late August. Because late cuts support seed ripening in *G. imbricatus* (Moora et al., 2007), the later cutting date in the mulched plots may be more important in explaining the observed increase in abundance than the cutting method itself. Finally, a site-specific difference between the mown and mulched sites may also have contributed to the contrasting responses, although such differences could not be detected by the design of the present study. Despite the promising response of *G. imbricatus* to mulching, it is important to note that several studies reported a decrease in plant species richness under mulching compared with mowing (Hensgen et al., 2016; Pavlů et al., 2016). Furthermore, high local abundance can lead to increased intraspecific competition, which according to a recent meta-study in predominantly grassland ecosystems exceeds inter-specific competition (Adler et al., 2018).

4.3 | Response to short-term management modifications

When interpreting short-term responses to management adjustments introduced in 2021, caution is advised due to the time it takes for plant communities to adjust. Consequently, we did not detect statistically significant effects of mowing date or grazing intensity on the abundance of *G. imbricatus* (Table 1-3 and -4).

Regarding mowing date, we found no evidence to support hypothesis (3) that late mowing would benefit the abundance of *G. imbricatus* over earlier mowing. Previous studies in Luitemaa coastal meadows reported a positive effect of mowing on the abundance of *G. imbricatus*, with their mowing date chosen in late July to align with the expected seed ripening (Kose et al., 2019; Moora et al., 2007). However, as discussed above, mowing at the end of July may still be too early to ensure the dispersal of fully ripened seeds (Moora et al., 2007). In our study, only early mowing showed a dynamic population structure throughout the study years (Figure 2b). This result could be explained by the reflowering mechanism, promoted by early mowing and a competitive advantage of *G. imbricatus* over surrounding meadow vegetation, which has been observed in another Estonian meadow. While mown in early June, we observed *G. imbricatus* standing tall above the surrounding vegetation in early July (personal observation, 2024 and 2025). The idea that mowing could be most beneficial when applied early or very late in the season is further supported by the gradual decrease in juvenile numbers

under mid- and late mowing treatments, but not under early mowing or late-season mulching (Figure 2a,b).

Early mowing may also provide socio-economic benefits, as early hay generally has higher nutritional value, making it more valuable to farmers (Boob et al., 2019). In Romanian mountain hay meadows, late mowing has been shown to support more flowering herbs at the beginning of the season, while also observing reflowering after early mowing (Johansen et al., 2019). In the Luitemaa nature reserve, mowing is generally restricted to dates after July 15 to protect the breeding sites of rare bird species. However, our findings suggest that a heterogeneous mowing schedule, including occasional early mowing, might be beneficial for both farmers and *G. imbricatus* populations, but only long-term monitoring can give conclusive results.

Although hypothesis (4) was not statistically supported, a consistent pattern suggests that medium grazing intensity was more beneficial than high intensity for the abundance of *G. imbricatus*. The earlier decline under high compared with medium grazing intensity indicates that high grazing intensity—following its introduction in 2021—had an immediate negative effect on the abundance and population structure of *G. imbricatus*, while under medium intensity the study species maintained a stable population structure for longer (Figure 2c). This trend is consistent with the documented sensitivity of *G. imbricatus* to grazing, related to the sensitivity of erect, bulbous and highly palatable plants, and based on previous experiments (Kose et al., 2019; Moora et al., 2007; Richter, 2012). Moreover, evidence exists that higher grazing intensity reduces reproductive capacity in vascular plants more strongly than medium intensity (Pihlgren, 2007).

The main drawback of this study is the limited number of plots per management, resulting from time-consuming data collection. In addition, the requirement for consistent long-term management further restricted the number of suitable study sites. We therefore selected only sites with a known history and where land managers had collaborated since restoration in 2001 to ensure data quality. We could not account for variability among sites independent of their management, meaning that differences in management are partly confounded by location-specific variation. In the flat landscape, all plots are located within 1 km of the shoreline and within 3.2 km of each other. However, their histories differ in terms of abandonment duration and management type. For better comparability, measurements of nutrient content and other soil parameters would be useful. Despite these limitations, the results revealed substantial differences in the response of *G. imbricatus* to long-term management regimes, whereas the effects of their adjustments introduced in 2021 were less pronounced. Therefore, continuing the experimental setup and long-term data collection is strongly recommended to capture delayed responses to different mowing dates and grazing intensities. The quadrat size of 50 cm × 50 cm was relatively small for capturing the abundance of *G. imbricatus* and may be increased to 1 m × 1 m in subsequent study years. Finally, the implementation of the intended management regimes depended on cooperation with landowners and was therefore subject to occasional deviations from the plan. Although the overall management remained consistent,

certain plots were excluded from the analysis due to inconsistencies in management application.

5 | CONCLUSIONS

This study adds on to a still limited number of investigations on bulbous species in semi-natural grasslands. It confirmed cutting as superior over grazing for the abundance of *G. imbricatus* under long-term established management regimes in coastal meadows. In addition, we detected a higher abundance under mulching compared with mowing. This effect is potentially driven by in situ remains of plant litter and by the later date of the cut under the mulching regime compared with removed hay and earlier cutting dates under the mowing regime. Furthermore, we analysed the short-term adjustments in mowing date and grazing intensity to the overall management regimes in order to better understand implications of the exact application of the overall management regimes. Although mowing date did not significantly affect overall abundance, variation in population structure suggests that its role remains ecologically important. Both early- and late-season mowing may deliver benefits linked to flowering phenology, reflowering capacity and seed maturation. Additional factors to consider are hay quality and the bird breeding season. Regarding grazing, our results support the commonly held expectation that moderate intensity is more favourable than high intensity due to the species' grazing sensitivity.

A key methodological contribution of this study is the demonstrated value of incorporating population stage structure of *G. imbricatus* when assessing population performance. This approach presents a more nuanced understanding of population dynamics than abundance measures alone and therefore should be considered in future monitoring of rare perennial plant species. We strongly plead for the continuation of data collection in this study to further capture delayed and cumulative management effects. Future research should expand similar experimental approaches across a wider range of grassland types to improve the generalizability of findings. Finally, advancing our understanding of the life-cycle and ecological requirements of rare bulbous species, such as *G. imbricatus*, will be essential for optimizing conservation strategies and improving the efficiency of field-based studies.

AUTHOR CONTRIBUTIONS

Marika Kose and Lauri Laanisto conceived the ideas and designed the methodology. Marika Kose and many others collected the data. Xenia Uffrecht and Nicola Pavanetto analysed the data. Xenia Uffrecht led the writing of the manuscript. All authors critically contributed to the drafts and gave their final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have declared that there are no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are available under the following DOI: <https://doi.org/10.15159/eds.dt.26.03> (Uffrecht et al., 2026).

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SUPPORTING INFORMATION

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

Table S1. Baltic Boreal Coastal Meadow (EU habitat directive code 1630) area across countries, BOR—Boreal, CON—Continental (European Union, 2018).

Figure S1. Simple moving average (SMA) of 30 days of (a) the daily average temperature and (b) the daily sum of precipitation in the ve study years during theowering period of *Gladiolus imbricatus*, measured at and compared with the average (2013 until 2025) at the

weather station in Häädemeeste (Longitude 24.458048, Latitude 58.036709) (Truhanov, 2025).

Figure S2. Count of the total number of individuals of *Gladiolus imbricatus* by life stage; per management and year. (a) Difference between mulched, mown and grazed plots (since 2001); (b) differences between early, mid- and late mowing (since 2021); (c) difference between medium and high grazing intensity (since 2021).

Table S2. Change of the total count of *Gladiolus imbricatus* between study years, by management.

Figure S3. Predicted response of the count of *Gladiolus imbricatus* to the long-term management regimes (meadow, grazing) by growth stage: (a) total; (b) juvenile; (c) premature; (d) generative. Based on GLMMs with an interaction between the management and sampling year. Error bars represent the 95% CI.

Figure S4. Predicted response of the count of *Gladiolus imbricatus* to the long-term management regimes (mulching, mowing, grazing) by growth stage: (a) total; (b) juvenile; (c) premature; (d) generative. Based on GLMMs with an interaction between the management and sampling year. Error bars represent the 95% CI.

Figure S5. Predicted response of the count of *Gladiolus imbricatus* to short-term management modification of mowing date (early = July 1, mid = July 15, late = July 31) by growth stage: (a) total; (b) juvenile; (c) premature; (d) generative. Based on GLMMs with an interaction between the management and sampling year. Error bars represent the 95% CI.

Figure S6. Predicted response of the count of *Gladiolus imbricatus* to the short-term management modification of grazing intensity (medium = 50%, high = 75%) by growth stage: (a) total; (b) juvenile; (c) premature; (d) generative. Based on GLMMs with an interaction between the management and sampling year. Error bars represent the 95% CI.

Table S3. Results of GLMMs-effect of different managements, and their interaction with the sampling year on the count of *Gladiolus imbricatus* at different stages (total, juvenile, premature and generative). The sampling years were 2021, 2022, 2023 and 2025. Error bars represent the 95% CI.

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