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Original Research Article

Long-term effect of different management regimes on the survival and population structure of *Gladiolus imbricatus* in Estonian coastal meadows

Marika Kose [a, *], Jaan Liira [b], Kadri Tali [a]

[a] *Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Chair of Biodiversity and Nature Tourism, Kreutzwaldi 5, Tartu, EE51006, Estonia*
[b] *University of Tartu, Institute of Ecology and Earth Sciences, Department of Botany, Lai 40, Tartu, EE51005, Estonia*

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ABSTRACT

Questions: How does the population structure of the threatened plant species *Gladiolus imbricatus* differ in the early and late stages of habitat restoration under different management regimes? What is the best management regime for the species?

Location: Luitemaa Nature Reserve in Southwest Estonia.

Methods: A long-term field experiment (2002–2004 and 2014–2016) studied the effect of four management regimes: (1) mowing in late July, (2) grazing by cattle, (3) grazing by sheep and (4) continuous lack of management (i.e. the control).

Results: In contrast to the highly positive short-term response to habitat restoration, in the long term, late-season mowing was the most favourable management type for *G. imbricatus*. The universal increase in juveniles across treatments during the early phase of the restoration project remained high only in mown plots. For the other treatments, after 10 years, the number of juveniles declined to the starting level or lower. Additionally, in contrast to the uniformly high number of premature and generative plants across treatments during the first two years of restoration, the number of premature plants in grazed sites declined. In particular, the frequency of premature and generative plants differed between the mowing and sheep grazing treatments in the long term. The success of generative reproduction was poor in the sheep-managed pasture, as all the shoots were grazed and none had any fruits or flowers.

Conclusions: While grazing is the most commonly subsidised restoration measure applied to coastal meadows, we recommend diversification of management types by promoting late-season mowing and reducing grazing intensity. In particular, sheep grazing must be avoided. The results of short-term evaluation of restoration methods can be misleading, and long-term monitoring must be a default evaluation task in biodiversity management support schemes.

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* Corresponding author.
E-mail addresses: marika.kose@emu.ee (M. Kose), jaan.liira@ut.ee (J. Liira), kadri.tali@emu.ee (K. Tali).

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1. Introduction

Most vegetation in Europe evolved under the constant influence of man. Species-rich grasslands are semi-natural heritage communities that developed under long-term traditional mowing and grazing (Austrheim et al., 1998; Eriksson et al., 2002; Joyce, 2014; Kull and Zobel, 1991) However, cessation of traditional land use measures (Kahmen and Poschlod, 2004; Pykälä et al., 2005; Valkó et al., 2018), intensified grazing (Bouchard et al., 2003; Dupré and Diekmann, 2009; Rosen, 1982) and fertilising (Jacquemyn et al., 2003; Myklestad and Sætersdal, 2004; Spiegelberger et al., 2006) have reduced the species richness of plant communities (Joyce, 2014) and diminished the provision of grassland-specific ecosystem services (Wehn et al., 2018b). This dramatic decline in semi-natural species-rich grasslands in Europe and the loss of habitat connectivity for the species that rely on these habitats have resulted in the extinction of local species (Harrison and Bruna, 1999; Waldén et al., 2017), thereby causing a decline in biodiversity at different trophic levels of semi-natural communities (Krauss et al., 2010).

Grassland abandonment, as a conservational problem, can be addressed as an opportunity for restoration (Valkó et al., 2016), but this leads to numerous challenges. Numerous authors have outlined that species diversity in heritage communities significantly depends on the management history—that is, the historical context—of the site (Gustavsson et al., 2011; Otsus et al., 2014; Purschke et al., 2014). This is also referred to as traditional ecological knowledge (Wehn et al., 2018b). Those aiming to conserve and perform restoration management for semi-natural communities must identify methods and economically viable practices that are appropriate for those activities (Rannap et al., 2017; Tälle et al., 2016; Valkó et al., 2018). Although the reintroduction of traditional management regimes is most appropriate for grassland restoration from an ecological perspective, it is not feasible in most cases (Valkó et al., 2018). Numerous authors have experimented to find contemporary replacements for traditional land use, evaluating their ecological and economical trade-offs (Bonari et al., 2017; Henning et al., 2017; Liira et al., 2009; Szépligeti et al., 2018). A meta-analysis of various experiments on benefits of grassland management by either grazing or mowing for biodiversity revealed that grazing has a more positive effect than mowing (Tälle et al., 2016). However, another meta-analysis of meadow mowing regimes indicated that the most effective mowing frequency depends on the productivity of the given site, but in general, less frequent mowing regimes yield better results for biodiversity (Tälle et al., 2018).

The effects of different herbivore species and breed-grazing strategies on grassland biodiversity were thoroughly analysed by Metera et al. (2010). The authors conclude that grazing species have different food preferences and suggest that mixed grazing systems may be a way to guarantee diversity and that local conditions should be considered instead of using blanket stocking rates, as suggested by agri-environment schemes (Metera et al., 2010). Different restoration experiments compared the re-introduction and replacement of old breeds by allowing sheep, goats (Benthien et al., 2018, 2016), cattle (Lyons et al., 2017; Oldén et al., 2016; Schaich et al., 2010) and horses (Köhler et al., 2016) to graze. These efforts yielded the expected results in terms of restoration. In Europe, it is a common practice to replace milk cattle with beef cattle, both equally contributed to semi-natural grassland management and restoration activities (Laurila et al., 2015).

Numerous works on bird and arthropod species have examined different management and restoration activities in wet and coastal meadows (Bruppacher et al., 2016; O'Neill et al., 2003; Verhulst et al., 2011). Compared to studies of animals, however, long-term and large-scale demographic studies of plants are scarce. A 32-year study of *Ophrys sphegoides* indicated that sheep grazing is more favourable for the species than cattle grazing (Hutchings, 2010), however, the study indicated that over half of the plants were browsed by livestock. Schrautzer et al., 2011Schrautzer et al., (2011) reported that mowing had a positive effect on *Dactylorhiza incarnata* populations, as there was an exponential increase in the number of flowering plants during the first 10 years of the experiment. Further, Lundberg et al. (2017) reported that several protected species in Norwegian dry coastal dunes had a positive reaction to mowing only after 10 years of annual efforts.

The coastal meadow restoration efforts in the Luitemaa Nature Reserve are not focused on maintaining the *G. imbricatus* population in particular, but on creating a habitat for rare shorebirds and natterjack toads. Our grassland management experiment studied a very important side effect of the grassland restoration process: the response of a rare grassland species to various types of maintenance. Since we have already observed the positive reaction of *G. imbricatus* to restoration activities during the first three years of management and its uniform reaction to all management types (Moora et al., 2007), here we examine whether the trend continues in the long term. We hypothesise that different management regimes have different effects on the structure of the *G. imbricatus* population and its survival during long-term restoration efforts.

2. Materials and methods

2.1. Study species

The sword lily *Gladiolus imbricatus (Iridaceae)* is a decorative tuberous clonal plant that is native to Central and Eastern Europe, the Mediterranean, Caucasia and West Siberia (Meusel et al., 1965). *G. imbricatus* grows up to 30–80(100) cm tall, and it forms bulb-like tubers that are 1–2 cm in length and tubercules for vegetative reproduction. Vegetative plants start as a single-leaf juveniles and then grow to become two-leaved premature plants. Generative plants have single slender stalks with 2 rosette leaves and 1–3 leaves on the flower stalk and 3–10 purple flowers within a one-sided inflorescence. In Estonia, flowering occurs in July, and relatively large seeds (1.8 mg) ripen during the first half of August. One plant can produce 200–400 seeds, and a chilling period of several months is needed for the seeds to germinate when temperatures increase in late spring (Rakosy-Tican et al., 2012). Prior studies reported that the success of establishment in reintroduction field

experiments can range from 60% (mowing and mulching) to 20% (burning and no management; Jõgar and Moora, 2008). Reaching the generative stage is rare and may be time-consuming. Seeds can survive in a seed bank, but the success of establishment after storage in a seed bank depends on the height of vegetation, availability of light and level of nearby disturbance. Significantly higher seed germination can be achieved by removing litter, bryophytes and the above-ground parts of plants; ensuring the availability of larger gaps in vegetation; and planting in open meadows (as compared to shaded areas covered by large tussock grasses and overgrown with willows; Kostrakiewicz-Gierałt, 2014a).

No specific literature is available on *G. imbricatus* dormancy patterns, but in their review of dormancy among perennial herbaceous plants Shefferson et al., 2018 Shefferson et al., (2018) found that rhizomatous species have the longest maximum dormancy values, while those with corms or bulbs have the shortest. In our special study, we observed only some hypogeal germination and no dormant bulbs (personal unpublished observation). *G. imbricatus* is plastic in its responses to the environment, as its productivity and traits depend on the light conditions and vegetation density.

The *G. imbricatus* species is categorised as threatened, red-listed or under protection across Europe (Kostrakiewicz-Gieralt et al., 2018) and has become locally extinct in numerous regions (Richter, 2012). In Estonia, *G. imbricatus* is under legal protection and is considered to be vulnerable (Kull et al., 2018), as its population is in decline (Kukk and Kull, 2005). *G. imbricatus* occurs in various habitats across Europe, from termophilous oak forests to wet meadows, including floodplains, coastal grasslands and marshes Kostrakiewicz-Gieralt, 2014b(Kostrakiewicz-Gieralt et al., 2018). In Estonia, the distribution of the species is restricted to a sub-region of Livland (the southern half of Estonia), forming a west—east belt from coastal meadows in the west to flooded meadows near the River Emajõgi in the east (Kukk and Kull, 2005). The species is threatened by the picking of flowering plants and changes in land use (i.e. abandonment and urbanisation of coastal areas). During the previous century, the abandonment of seashore and floodplain grasslands resulted in the encroachment of reeds and bushes. Grazing, which is the most traditional measure of grassland restoration, is unadvisable for the species (Krall et al., 2010; Richter, 2012). Thus, reintroduction has been recommended (Jõgar and Moora, 2008).

2.2. The research area and description of the management experiment

In the restoration management planning and EU agri-environmental schemes, coastal grasslands are intended to be maintained as low-sward homogeneous permanent grasslands. Many grasslands managers use the opportunity for a short term contract for habitat restoration to begin with, but are then required to switch to the contract system of agri-environmental schemes. Grazing is the prescribed as the main management method by the agri-environmental support scheme, while restoration support schemes additionally allow the use of mowing, mulching and other methods as well. Grazing with different beef cattle is the main method of conservation management in coastal grasslands in Estonia. Sheep (mostly meat breeds) do not frequently graze in coastal grasslands due to wet conditions and numerous specific diseases. Moreover, large carnivores have become a threat to sheep as their populations have increased.

The research area is located in the Luitemaa Nature Reserve on the southwestern coast of Estonia (hereafter, Luitemaa; Fig. 1A, B, C). Luitemaa hosts approximately 800 ha of an EU priority habitat called the Boreal Baltic coastal meadow (92/43/EEC), which represents approximately 10% of the current area of this type of habitat in the country. The area is edaphically homogeneous and was established on an area that used to be at the bottom of the sea due to the post-glacial land uplift (0.1 mm per year). The sandy loam is covered by a humus layer 10—20 cm deep.

The plant community in the experimental sites belongs to the association of the *Deschampsio-caricetum nigrae* type (Krall et al., 1980), which is typical of coastal areas in Estonia. The prevailing species in the community are *Molinia caerulea* and *Sesleria caerulea*, with *Festuca rubra* occasionally co-dominating in more grazed areas. Historically, the lower parts of the meadow (i.e. those near the shoreline) have been used for grazing by a variety of domestic animals, including dairy cows, heifers, sheep and horses.

Historically, the lower part was separated from the higher parts of the meadow by different types of fences or was guarded by shepherds. The higher parts of the meadow were used for haymaking and late-summer grazing (Kasvandik et al., 2003). This management regime declined in the 1950s, and the entire area was abandoned from the 1970s to the 1990s (personal communications). All the experimental plots are situated in the upper zone of the meadow (0.5—1 m above sea level), which was mown and grazed in history (Fig. 1B). However, these upper areas continue to be flooded by brackish seawater, with floods ranging in frequency from once to several times a year.

In 2001, an intensive habitat restoration project focusing on rare birds and natterjack toads was commenced in the Boreal Baltic coastal meadow (1630*, Natura, 2000) with the support of the EU LIFE Nature programme (Kose et al., 2004). The restoration and management activities have continued and been extended by EUagri-environmental support and various other projects until the present. Farmers in this area chose different types of livestock for the restoration activities and introduced new adaptive management patterns in different parts of Luitemaa.

2.3. Experiment description and sampling

In 2002, within abandoned grasslands of the upper part of the coastal meadow, we identified distinct areas in which *G. imbricatus* populations had survived and specimens were abundant enough for analytical experiments (for details, see Moora et al., 2007). These locations were very scarce and scattered along 7 km of the coastline. We selected four different management regimes: 1) grazing by beef cattle, 2) grazing by sheep, 3) late July mowing and 4) the continuation of abandonment

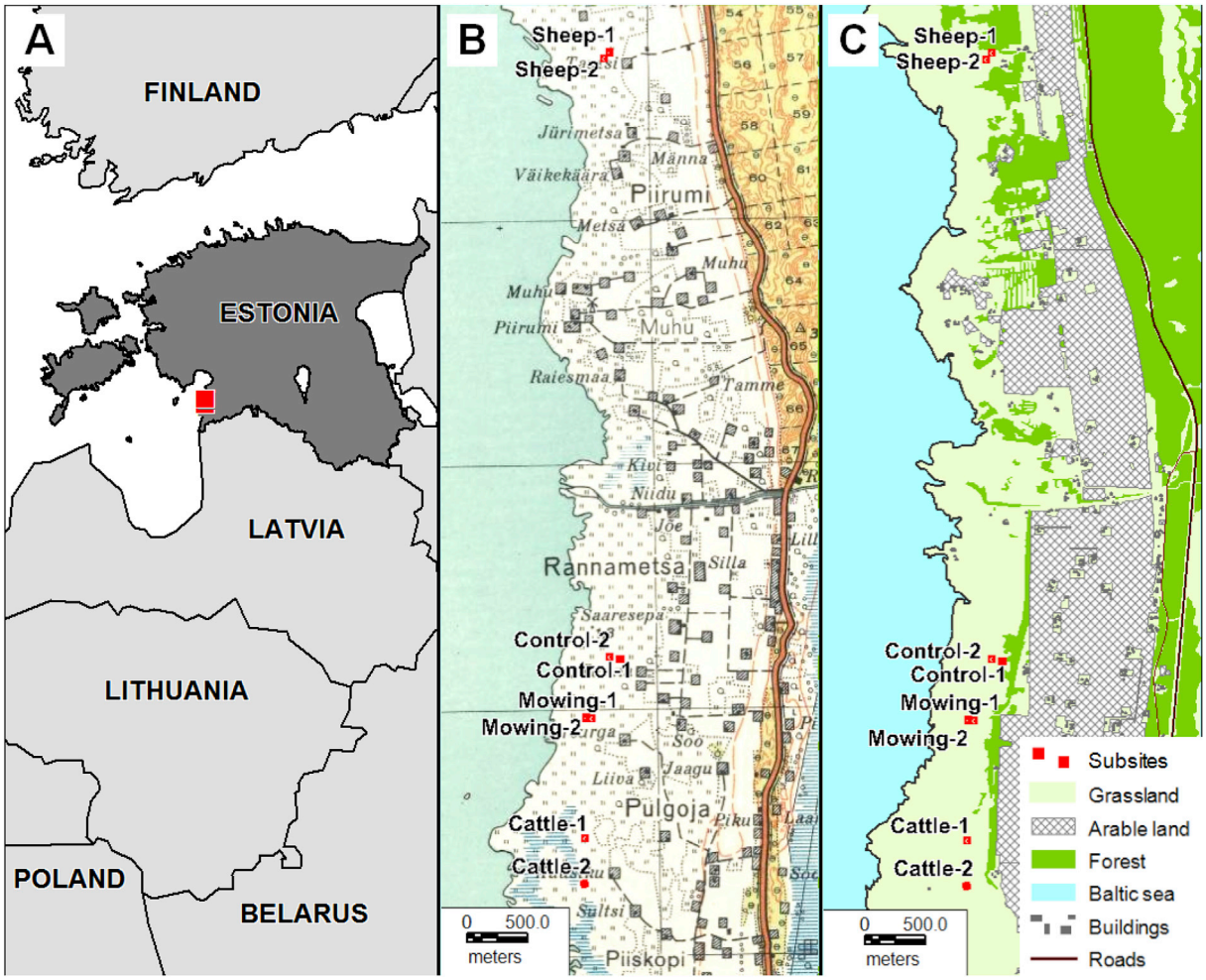

Fig. 1. The location at which *G. imbricatus* was researched in the Luitemaa Nature Reserve in southwestern Estonia (A). The distribution of study sites on a map from 1938 (B) and a contemporary land use map (C). Source for maps: the WMS-service of the Estonian Land Board.

(as the control). Each treatment was repeated at two subsites within a larger site given the same treatment. The treatments were partly spatially clustered because of the scarcity of *G. imbricatus* populations and the low management stability of the land owners at that time. The clustering, however, probably has only some negative effects on the representativeness of the study, as (1) the base environmental conditions are similar throughout the coastline examined in the experiment and, (2) after some years, management intensity became different between subsites given the same treatment because of heterogeneous behaviour of grazing animals.

The grass is mown after the 15th of July each year, dried and then collected. Thereafter, the areas are exposed to occasional grazing by beef cattle as part of a larger paddock. Grazing in both treatments was not intensive as legislation has set the limit of average grazing pressure up to 0.8−1.2 livestock units (LU) per hectare throughout the vegetation period from early May until late September (Lotman, 2011). Further, a paddock system was utilised to regulate grazing intensity and guarantee food availability for livestock. All grazed and mown areas are fenced permanently year-round except the shoreline, where fences are removed in the winter for safety reasons. The abandoned portion of the meadow, which has remained unused since the 1980s, was used as the control for the current study. The abandoned areas are slowly becoming overgrown with *Alnus glutinosa*; *Salix ssp.*; and tall herbs such as *Filipendula ulmaria, Molinia caerulea, Carex disticha, Selinum carvifolia, Angelica palustris* and *Angelica archangelica*. During the research period, the control areas and nearby sites remained open.

In 2002, two 20 × 20 m subsites were randomly located within each site. Ten 1-square metre plots were randomly placed in these subsites each year. Within these plots, *G. imbricatus* specimens were counted at three ontogenetic stages: 1) juveniles (i.e. one-leaved seedlings and vegetative juveniles; Fig. 3), 2) premature plants (i.e. two-leaved or vegetative adults) and 3) generative (i.e. flowering) plants. The plant coverage, species composition (i.e. presence and cover), maximum height and upper height limit of leaves were reported for each plot. Measurement was done during the second half of July, when the plants were fully flowering and mowing had not yet begun. Sampling was performed annually from 2002 to 2004 and then

the sample was re-surveyed annually from 2014 to 2016. From 2005 to 2013, no plants were measured, but coastal meadow management was performed in the same manner.

In the last years of the experiment, vegetation in the managed plots was lower than in the abandoned plots (Fig. 2). However, there are significant variations in treatments between years (Table A.2, Figs. A1 and A2). The maximum height of vegetation reflects the higher peaks of flowering shoots in the plots (Fig. 2A and A2). It varies significantly over time (Table A.2), although it is significantly higher in abandoned plots. The average height of vegetation and the upper height of leaves in

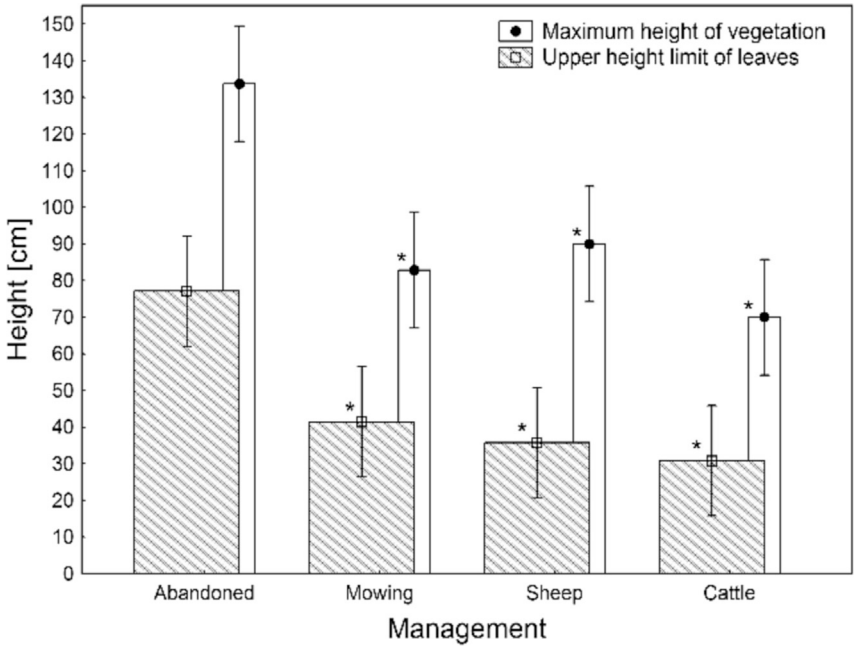

Fig. 2. Mean vegetation height over three years under four types of management (more details in Table A.2 Fig. A1). Whiskers denote a 95% confidence interval of means. Asterisks denote significant differences from the abandonment treatment according to Tukey post-hoc multiple pair-wise comparison tests.

Fig. 3. Juvenile and premature stages of *G. imbricatus*. The one-leaf stages formed a pooled group of juveniles (I A: seedlings; I B: one year or more, I C: two years or more) and II represented two-leaved premature or vegetative adults. Photo by Märt Kose.

grassland plants follow the same pattern (Figs. 2 and A1). Additionally, the plots grazed by sheep and cattle have significantly lower average vegetation than abandoned areas (Table A.2). The species richness of plots also contrasted between treatments (Table A.2, Fig. A3). Specifically, the abandoned subsites had the lowest species richness and the mown subsites had the highest species richness.

In 2016, an additional study was carried out. Some parameters of *G. imbricatus* specimens were measured for comparison with the vegetation parameters (i.e. height of rosette leaves, number of flowers). Up to 20 specimens were collected per treatment when the number of specimens within the given age group was available (Fig. 5).

In 2019, juvenile and premature plants were excavated from three 20 × 20 cm plots for each treatment to estimate the potential age of plants according to the morphology of bulbs/tubers. One-leaved specimens were distributed quite evenly in terms of the three developmental stages of tubers: seedlings, second-year plants and older plants (Fig. A4, Table A.3). One-leaved *G. imbricatus* specimens were all regarded as juveniles, even though they were different ages (Fig. 3). The proportion of juveniles of each bulb stage was similar for all treatments (Fig. A4, Table A.3).

2.4. Data analysis

Plot-level data were pooled at the subsite level, as sampling plots were located randomly within the subsite each year. The effect of treatments, successive years, ontogenetic stages and their interactions were evaluated based on the log-transformed count of individuals and a general linear mixed model. In the model, subplots were defined as random factors. The post-hoc pair-wise differences among specific management regimes were estimated using the Tukey HSD multiple comparison test. Another analogously structured model was run using logit-transformed frequency data regarding the ontogenetic stages of specimens in various plots within a subsite. The SAS 9.3 MIXED procedure was used for both analyses (SAS Institute Inc.). The model-based least-square means were back-transformed to real-life estimates, with 95% confidence interval ranges.

3. Results

3.1. Population number and structure

The mixed model results show very complex dynamics in terms of population size (Table 1). *G. imbricatus* juveniles increased in number during the starting phase of the restoration project for all treatments, particularly in mown plots (Fig. 4A). The abundance of juveniles in mown areas remained relatively high in the long term, even though the numbers reported from 2014 to 2016 were slightly lower than the peak observed in the third year of the experiment. For the other treatments, however, after 10 years, the number of juveniles declined to the starting level or below. This was the case for the unmanaged areas in 2015 and the sheep management plots in 2016 (Fig. 4A).

Further, the abundance of vegetative and generative shoots did not vary significantly between the treatments during the first two years of restoration (i.e. 2002 and 2003; Fig. 4B–C). However, in 2004, the number of premature shoots had declined in grazed plots and differed significantly from the estimates in the mown areas. Moreover, the numbers of premature and generative specimens were not statistically different from the numbers in the starting year across treatments, even though they did decrease under both grazing treatments. The unmanaged plots showed the most stable populations of premature and generative specimens.

The generative reproduction in the sheep-managed pasture was very poor (Fig. 5), as all the shoots were bitten and none had flowers or fruits (Table A.4, Fig. A5). In 2016, the height of *G. imbricatus* vegetative leaves (i.e. rosette leaves) was comparatively measured and found to be significantly higher during all ontogenetic stages in abandoned plots than in plots given other treatments (Fig. 5, Table A1). The leaf height of juveniles corresponds to the upper height of leaves of grasses in the plots (Fig. 2).

Table 1
Results of the mixed models in terms of the abundance and frequency of *G. imbricatus* at the subsites.

Effect	Abundance (log-transformed)			Frequency (logit-transformed)		
	df	F-statistic	P	df	F-statistic	P
Treatment	3;1120	19.78	<0.0001	3;40	11.82	<0.0001
Stage	2;1120	224.81	<0.0001	2; 40	55.07	<0.0001
Treatment*Stage	6;1120	5.90	<0.0001	6; 40	9.31	<0.0001
Year	4;20	5.30	0.0045	4; 20	3.44	0.0271
Treatment*Year	12;1120	3.04	0.0003	12; 40	3.40	0.0018
Stage*Year	8;1120	17.98	<0.0001	8;40	8.16	<0.0001
Treatment*Stage*Year	24;1120	1.16	0.267	24;40	1.98	0.0271
Covariance parameters	Estimate	Z-statistic	P	Estimate	Z-statistic	P
Random: SubSite(Treatment; Year)	0.012	2.170	0.015	0.0293	2.06	0.0197
Repeated: Year. Subject: SubSite(Treatment)	0.003	0.710	0.4771	0.0034	0.40	0.6917
Residual	0.112	0.005	<0.0001	0.0312	4.47	<0.0001

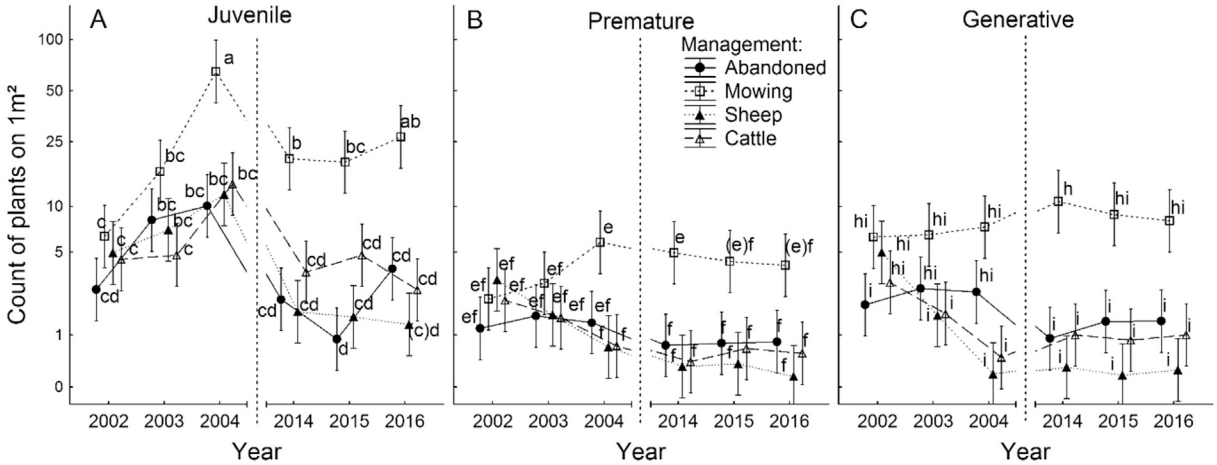

Fig. 4. Abundance response of *G. imbricatus* in different ontogenetic stages (i.e. juvenile, vegetative and generative) to different management regimes from 2002 to 2004 and 2014–2016. Y-axis is log-transformed, Statistically significant differences in abundance ($p < 0.05$) revealed by Tukey tests are indicated with different letters within the same age group. Whiskers denote a 95% confidence interval of means. Vertical dotted lines denote the survey gap from 2005 to 2013.

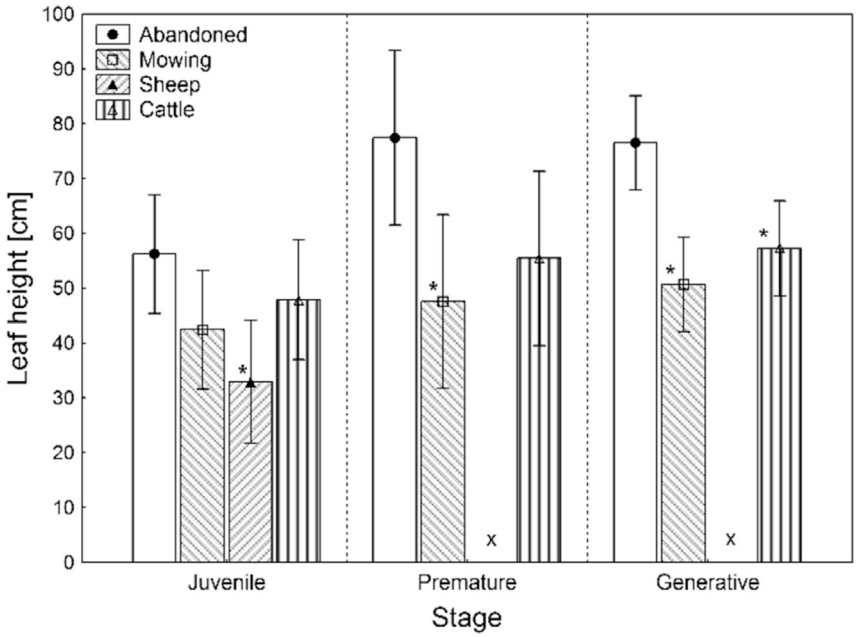

Fig. 5. The height of *G. imbricatus* vegetative leaves (i.e. rosette leaves; $n_{max} = 20$) during all ontogenetic stages in different management plots in 2016. Statistically significant differences in mean height between the abandoned treatment and other treatments revealing by Tukey multiple comparison tests are indicated by asterisks within the same age group. Whiskers denote a 95% confidence interval of means. X denotes missing ungrazed specimens in the given age group (only applicable to the sheep treatment).

The proportion of browsed *G. imbricatus* shoots of different ontogenetic stages in grazed plots differed significantly across years (Table A.4, Fig. A5). In 2014, the proportion of browsed shoots in all plots grazed by cattle was higher than that in sheep pastures, while in 2015 and 2016, the opposite was true. The average browsing rate of juveniles was 45–50% for cattle and 15–40% for sheep. The average browsing rate for generative shoots was 70–100% in both treatments. The most significant difference was observed in 2016 for browsing of premature shoots, with an average of 5% for sheep and almost 100% for cattle.

3.2. Population performance—frequency

There was a gradual decline in population frequency within the subsites (across 1 × 1 m plots) under all grazing treatments (Fig. 6, Table 1, right) as well as in abandoned plots in certain years. A particular difference in the occurrence frequency dynamics of premature and generative plants was observed between the mowing and sheep grazing treatments in the long

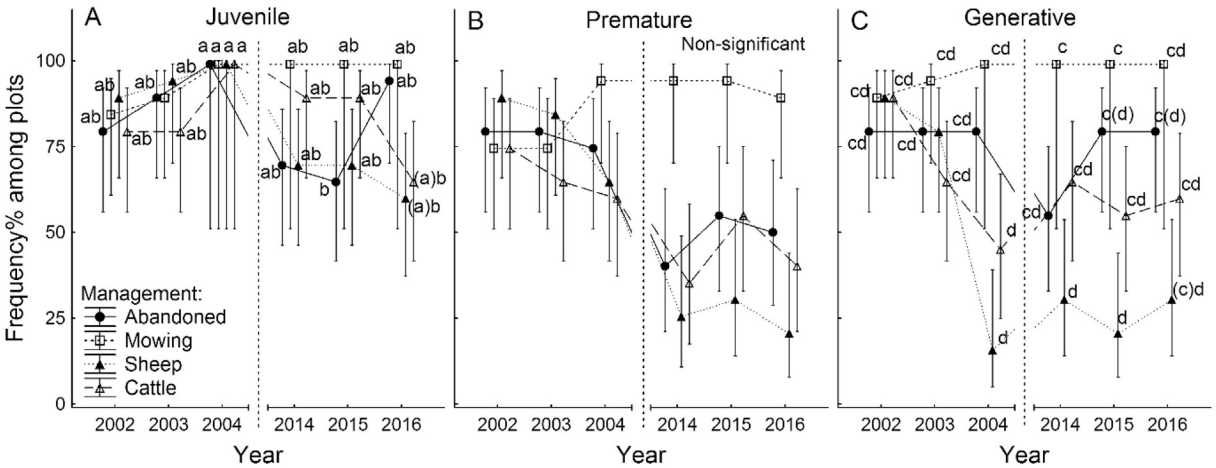

Fig. 6. Occurrence frequency (%) of *G. imbricatus* plants in plots under each management regime, presented by development stage (i.e. juvenile, premature and generative). Letters indicate the groups, which were significantly different ($p < 0.05$) according to the Tukey tests. Whiskers denote a 95% confidence interval of means. Vertical dotted lines denote the survey gap from 2005 to 2013.

term, although analogous trends were observed for juvenile plants (Fig. 6C). Less evident but similar trends were also observed for cattle grazing plots. The same trend was reported for premature plants, but the differences are not statistically significant (Fig. 6B).

4. Discussion

In 2002, when restoration activities began, all areas chosen for the experimental management regimes had a similar number and frequency of *G. imbricatus* specimens at each development stage. The mowing treatment resulted in a tenfold increase in the number of juveniles between 2002 and 2004, which was much more than the number reported in other years. The significant increase in the number of juveniles in mown plots in 2003 and 2004 may indicate that management disturbances had a positive effect on seed recruitment from the seed bank or new seeds from more abundant generative specimens. The increase was probably induced by the increased availability of establishment microsites and improved light conditions for germination, as reported by Kostrakiewicz-Gierałt (2014a) and Kostrakiewicz-Gieralt (2014b). The regeneration intensity in mown plots declined but stabilised after 10 years and was still at a higher level than before the restoration began. This short-term positive reaction was confirmed in an additional observation from nearby site in 2019, where long-term management of combined grazing and mowing led to the formation of tall-sedge areas with only a few *G. imbricatus* specimens, but the change in management to end-milling cutting in autumn 2018 led to a boost in juveniles (both, from bulbs and seedlings, as estimated from excavated specimens) and flowering shoots in 2019 (personal observation). An analogous short-term reaction of *G. imbricatus* to mowing was observed by (Kubíková and Zeidler, 2011) in the Na Bystrem meadow in Moravia.

The dynamics of premature and flowering shoots were different from those of juveniles. In abandoned areas and both types of grazed areas, the number of specimens of both stages began to decline after the second year of the experiment. By 2004, the frequency of flowering shoots decreased from almost 100% to 20% in the plots grazed by sheep. Further, in abandoned areas, the number of flowering individuals declined in a similar way to the grazing treatments, but the plants were more evenly distributed in the abandoned areas than in grazed areas. *G. imbricatus* is a phenotypically plastic plant, as it can adjust leaf length to rising competition with taller herb-layer vegetation during abandonment and in the early stage of encroachment of its habitats (Hänel and Müller, 2006; Kostrakiewicz-Gieralt, 2014b; Richter, 2012). Indeed, in the last year of the survey, the rosette leaves of generative *G. imbricatus* specimens were much taller in the long-term abandoned sites than in other treatments, indicating the plants' phenotypical plasticity to long-term encroachment. The average height of vegetation or the upper limit of leaves of vegetation was significantly lower in grazed plots. However, this was the case in all areas, indicating that the areas reflected annual environmental conditions in similar ways. The average height of the rosette leaves of *G. imbricatus* corresponds to the pattern of average grass leaf level across management regimes. The results confirm the conclusions of earlier studies regarding the abandonment effect on *G. imbricatus* (Hänel and Müller, 2006; Kostrakiewicz-Gieralt, 2014b; Kubíková and Zeidler, 2011; Richter, 2012): that plants become less abundant but flowering shoots elongate in response to competition for light and pollinators and, consequently, *G. imbricatus* populations survive meadow abandonment and overgrowth for a rather long time.

In contrast to positive trends in short-term counts, the re-survey of sites from 2012 to 2016 revealed that the population of *G. imbricatus* declined in grazed areas and continued to flourish only in mown plots. The contrast between the long-term and

short-term observations supports the objective assessment, which suggested that the goals of ecological restoration can be achieved only after 10 years of treatment (Joyce, 2014; Koch et al., 2017; Lundberg et al., 2017). Lundberg et al. (2017) observed that, over 16 years of mowing treatment, the increase in the target species became significant only after year 10. These results warn against prematurely making conclusions regarding the degree of success in the early stages of restoration.

Different restoration measures applied to *G. imbricatus* led to different population performances after 15 years of management. Mowing is the most—and only truly—favourable management regime for *G. imbricatus*, as suggested by several other recent studies (Bonari et al., 2017; Tälle et al., 2018). However, mowing should be moved to later in the season, just after the ripening of seeds.

Neither grazing regime is favourable, as both showed a decline in population, particularly in the premature and flowering stages. Previous research indicates that sheep browse *Gladiolus* more selectively (61%) than cows (48% (Kose and Moora, 2004);). From 2014 to 2016, we observed that browsing habits differ annually, and while sheep browse almost half of the juveniles from the grass, the cows' browsing can vary yearly from 20 to 40%, although the availability of plants is similar. Two-leaved plants' leaves are more visible in grass and are browsed significantly more by sheep. Additionally, the flowering shoots are highly distinguishable from the rest of the grass and are eaten selectively by sheep. Yearly differences may indicate the heterogeneity of grazing patterns in different subsites (i.e. different paddocks), i.e. the patterns of animal behaviour may also affect the population and structure. For example, one of the cattle treatment sites, which was selected in 2002 and features the only population in a large area, has become a favourable resting place for animals. Plants almost disappeared from there, but a large number have spread to the surrounding 50 ha. Field observations indicated that after late grazing with sheep in 2003 and 2004, in the following years, a large number of *G. imbricatus* seedlings appeared near the paths of sheep and in their resting places. Similar zoochory was reported by land managers throughout the restoration period. The prescribed grazing pressure (0.8−1.2 LU/ha) was probably too high; Lyons et al. (2017) reported a long-term positive response to grazing pressure of 0.2 LU/ha in upland calcareous grasslands, although this is a habitat with much lower productivity. The low year-round horse grazing pressure (0.3 in the vegetation period and 0.2 in winter) was found to be favourable for rare species and communities in dry calcareous grasslands (Köhler et al., 2016) and are recommended for dry sandy grasslands (Henning et al., 2017). On the other hand, Tóth et al. (2018) suggest that livestock type is more crucial than grazing intensity in short-grass steppes and that sheep may be more selective grazers in cases of low grazing pressure (Tóth et al., 2018). This could be the case for *G. imbricatus*.

We suggest that management schemes that favour grassland biodiversity and rare plant species must consider the grazing habits of the available grazers, grazing pressure and timing. The diverse management patterns of grasslands have been suggested to be more effective for preserving arthropod diversity (Bucher et al., 2016), pollinators (Moroń et al., 2008; van Klink et al., 2016), amphibians and breeding birds and feeding migratory waders (Arbeiter et al., 2018; Rannap et al., 2017). This is probably important for plants. Small- and large-scale heterogeneity is characteristic of natural ecological conditions, which must be considered while planning optimal and effective restoration treatments (Valkó et al., 2018; Wehn et al., 2018a,b).

We showed that the short-term part of our experiment leaves an overly positive impression about the effectivity of restoration management support scheme (i.e. experiment within the time-frame of restoration support scheme), while the long-term continuation of the same management types shows their negative effect on population restoration of *G. imbricarus*. The latter negative results, however, are attributed to the following maintenance support by agri-environmental schemes (i.e. experiment within the time-frame of agri-environment scheme) after the maximum three year support for habitat restoration. Additionally, restoration contracts are more flexible when it comes to choice of management type than agri-environmental schemes. Specifically mowing is not a conventional measure for coastal meadows maintenance under the agri-environmental support schemes and its application needs special permits. Late-summer mowing (with mulching), however, is probably a more cost-effective on the upper parts of coastal meadows (Bonari et al., 2017; Henning et al., 2017; Liira et al., 2009; Szépligeti et al., 2018) and supports more efficiently certain rare plant species than prescribed grazing. There have been doubts about EU Common Agricultural Policy ability to support achieving the biodiversity targets (Pe'er et al., 2014). We suggest that the problem might start from inadequate restoration and management methods, but the short-term monitoring prescribed for restoration schemes is not able to detect these problems. We suggest that the most favourable management types for upper parts of coastal meadows is rotational treatment in which mowing, grazing and no management are applied in different years, which promotes seed ripening and distribution, creates various microsites and disturbances. Finally, as we observed the boosting reaction of *G.imbricatus* in the consequence of changed grazing-mowing management type to the late-summer end-milling cutting at the meadow neighbouring the experiment, litter-free ground in the spring can be an additional critical factor for *G. imbricatus*, however, these late-summer removal treatments should be tested and promoted in future.

5. Conclusions

Our study reveals that when coastal meadow restoration and maintenance managements target the general aims of agri-environmental schemes, such as the promotion of low-sward grassland and habitats for shoreline-breeding waders and migratory birds, while other more specific conservational aims may have been neglected. Therefore, restoration and agri-environmental management schemes need more precise multi-target planning, i.e. must consider all conservation values of the ecosystem. While grazing is the most common restoration and maintenance measure for coastal meadows, we

recommend diversification of management types by promoting late-season mowing and reducing grazing intensity. Sheep grazing must be avoided or regulated to low intensity levels. The short-term evaluation results of restoration and management methods can be misleading, and the long-term multi-indicator monitoring of management contracts must be implemented.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00761.

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Appendices for "Long-term effect of different management regimes on the survival and population structure of *Gladiolus imbricatus* in Estonian coastal meadows"

Global Ecology and Conservation

Marika Kose, Jaan Liira, Kadri Tali

This PDF file includes:

Table A. 1. The results of mixed models about the effect of treatment on the leaf height of *G.imbricatus*.

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Table A. 1. The results of mixed models about the effect of treatment on the leaf height of *G.imbricatus*.

	Juveniles			Premature			Generative		
Effect	df	F-statistic	P	df	F-statistic	P	df	F-statistic	P
Treatment	3;131	3.08	0.0296	2;108	3.72	0.027	2;107	9.6	0.0001
Covariance parameters	Estimate	Z-statistic	P	Estimate	Z-statistic	P	Estimate	Z-statistic	P
Random:									
SubSite(Treatment)	56.4	1.28	0.0996	123.5	1.18	0.12	32.5	1.05	0.1467
Residual	68.7	8.09	<0.0001	91.4	7.35	<0.0001	99.1	7.31	<0.0001

Table A. 2. The results of mixed models about the differences of vegetation parameters between years and treatments.

	Vegetation maximum height 2014-2016			Vegetation upper leaf layer height 2014-2016			Species richenss 2014-2016		
Effect	df	F-statistic	P	df	F-statistic	P	df	F-statistic	P
Treatment	3;224	11.95	<0.0001	3;224	7.59	<0.0001	3;4	154.09	0.0001
year	2;224	10.97	<0.0001	2;224	22.83	<0.0001	2;8	9.57	0.0075
Treatment*year	6;224	2.95	0.0086	6;224	2.76	0.013	6;8	4.9	0.0216
Covariance parameters	Estimate	Z-statistic	P	Estimate	Z-statistic	P	Estimate	Z-statistic	P
Random:									
SubSite(Treatment)	114.6	1.27	0.1027	105.9	1.29	0.099	-0.09	-0.26	0.797
Residual	402.0	10.58	<0.0001	308.0	10.58	<0.0001	17.73	10.58	<0.0001

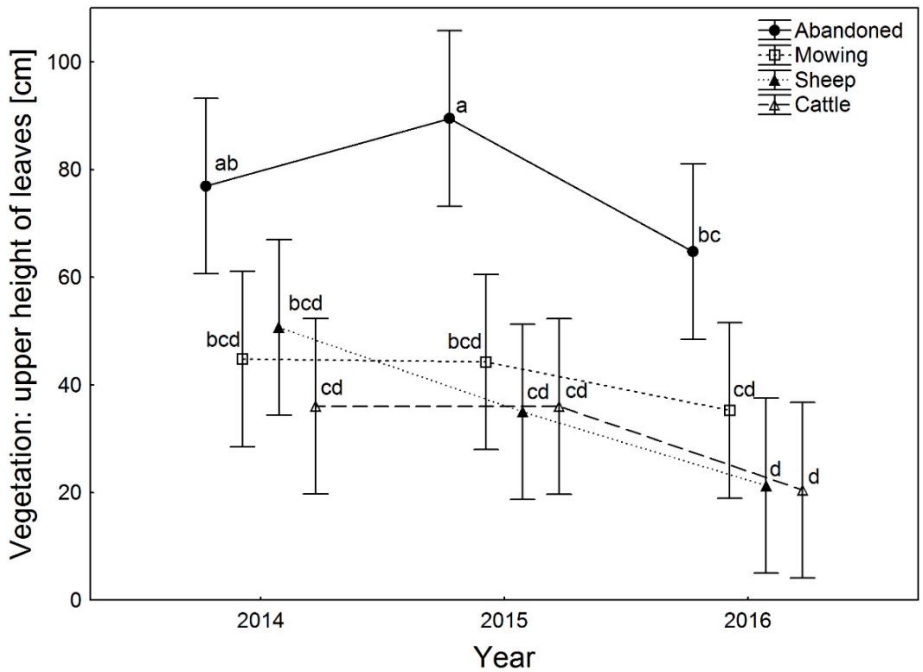

Figure A. 1. The average height of the upper height of leaves the vegetation of survey plots. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.2).

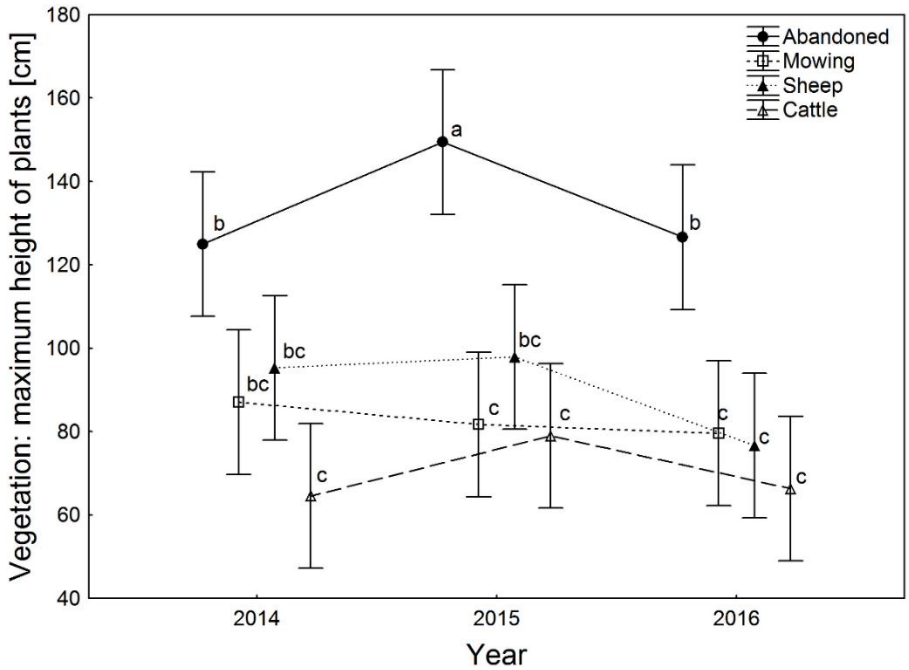

Figure A. 2. The maximum height of vegetation in plots by year. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.2).

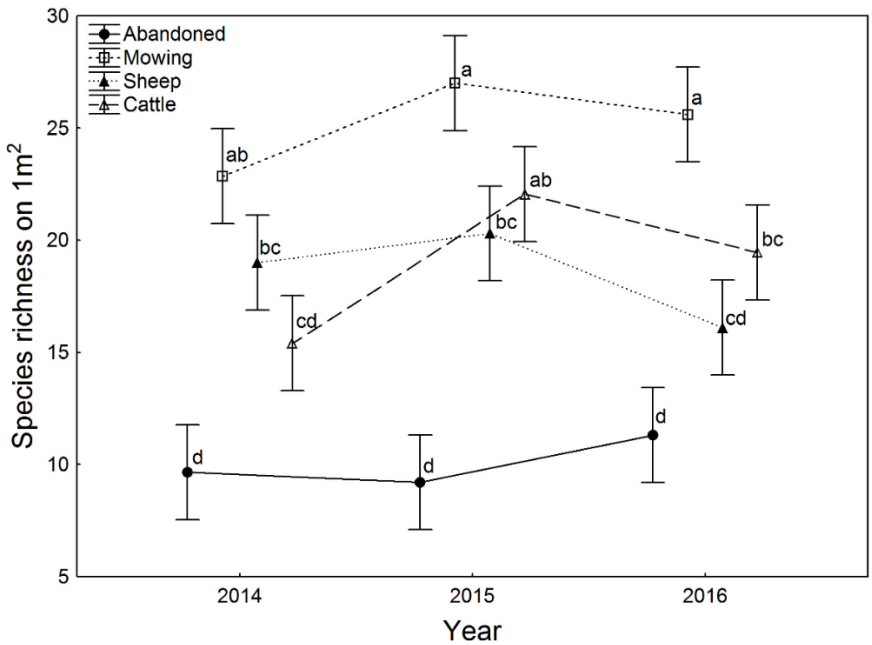

Figure A. 3. The species richness in plots by year. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.2).

Table A. 3. The results of the mixed model about proportional distribution of one-leaved (juveniles) and two-leaved (premature) plants by bulb morphology.

	Bulb-leaf distribution		
Effect	df	F-statistic	P
Treatment	3;4	0.77	0.5698
Stage	3;12	10.12	0.0013
Treatment*Stage	9;12	4.63	0.0081
Covariance parameters	Estimate	Z-statistic	P
Random:			
SubSite(Treatment)	-0.012	-1.87	0.0608
Residual	0.061	2.45	0.0072

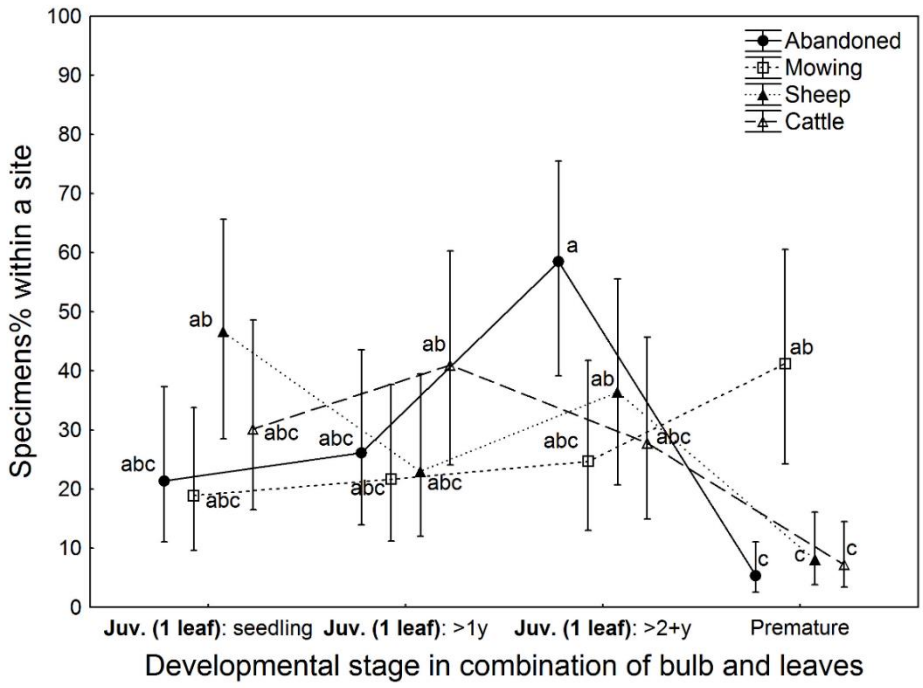

Figure A.4. The proportion of one-leaved (juveniles) and two-leaved (premature) plants by bulb size and morphology. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.3)

Table A. 4. The test results of mixed model about differences in the proportion of browsed plants of *G. imbricatus* among stages by year and treatment.

	Proportion of browsed plants 2014-2016		
Effect	df	F-statistic	P
Treatment	1;16	2.59	0.1273
Stage	2;16	26.47	<0.0001
Treatment*Stage	2;16	7.50	0.0050
Year	2;16	0.24	0.7884
Treatment*Year	2;16	13.77	0.0003
Stage*Year	4;16	0.10	0.9801
Treatme*Stage*Year	4;16	3.03	0.0487
Covariance parameters	Estimate	Z-statistic	P
Random: SubSite(Treatment)	0.041	0.64	0.2596
Repeated: Stage(Subsite) by Year	-0.073	-1.04	0.3001
Residual	0.405	2.45	0.0072

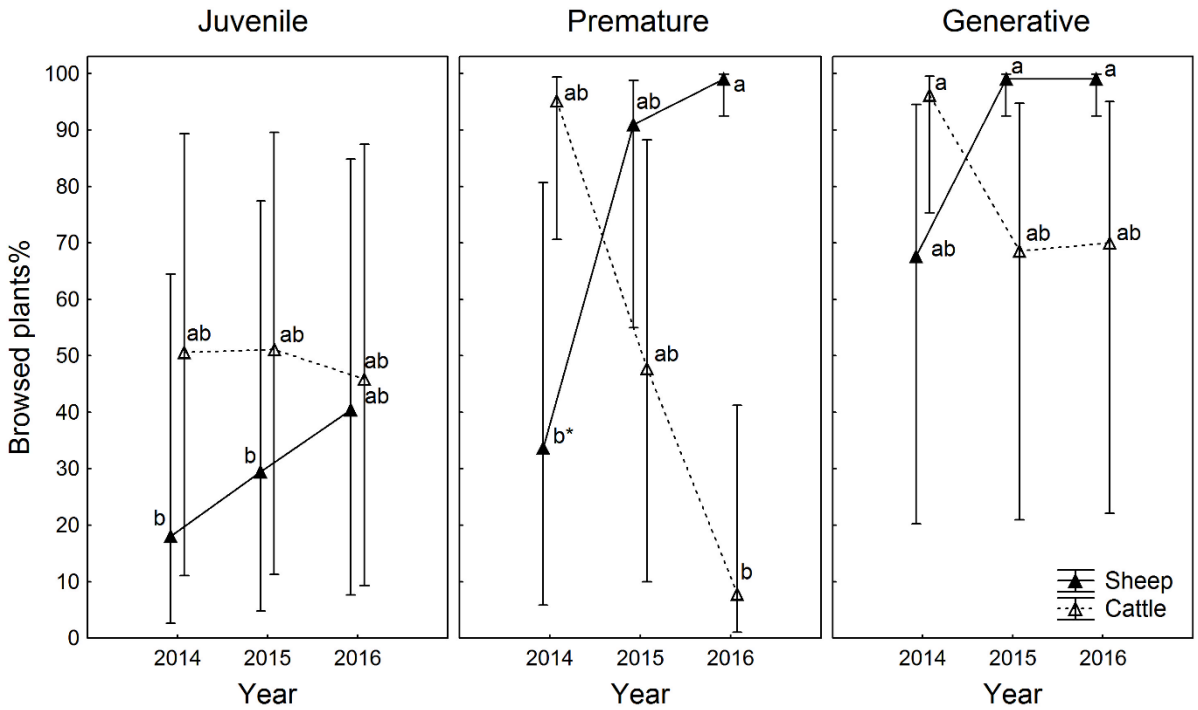

Figure A. 5. The leaf-browsing proportions of *G. imbricatus* specimens across stages in three years. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.4).