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Research

The decline of *Gentianella campestris*: three decades of population development of an endangered grassland plant in Sweden

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Species-rich semi-natural grasslands are declining all over northern Europe, and many plant species confined to such grasslands are currently under threat. We studied the development of populations of one such species, the field gentian *Gentianella campestris*, during three decades in the County of Södermanland, south of Stockholm, Sweden. *Gentianella campestris* is Red Listed as Endangered in Sweden. It is a strict biennial, and as far as known with only a transient seed bank. Large population fluctuations are a characteristic of this species, and its life history makes the species inherently sensitive to factors causing population reductions. We found that the number of sites with *G. campestris* has declined with over 60% in the last three decades. The total number of flowering individuals also show a strong decreasing trend, although there was an increase the last year (2020) at a few remaining sites. Cessation of grazing management is a major cause of the decline, but populations also disappeared from managed sites. It is possible that the management has been inappropriate, and circumstantial evidence suggests that summer drought might be an additional cause of population decline. Data from 2018, a year with an exceptional summer drought, supports this explanation. A sowing experiment indicated that recruitment of new populations is unlikely in the present-day landscape where most vegetation is unsuitable for *G. campestris*. Due to the poor prospects for long-term maintenance of grazing management in still remaining semi-natural grasslands, and the decline even at sites with current management, *G. campestris* faces a risk of becoming regionally extinct within the coming decades.

Key words: drought effects, grazing management, population extinction rates, seed sowing experiment, semi-natural grasslands

Introduction

Many anthropogenic landscapes in Europe still maintain traces of the long history of management preceding the modernization of agriculture and forestry during the last 100–150 years (Emanuelsson 2009, Eriksson and Cousins 2014, Plieninger et al. 2015). One of the features of this modernization was the abandonment of mowing and grazing at 'semi-natural grasslands', i.e. pastures and meadows with a long history

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of continuous management, and without significant impact of additional sowing, artificial fertilizers or plowing. Semi-natural grasslands have declined drastically during the last century. Estimates of this decline suggest that the semi-natural grassland area has decreased by more than 95%, for example in England (Fuller 1987, Ridding et al. 2015), Finland (Luoto et al. 2003) and Sweden (Eriksson and Cousins 2014, Cousins et al. 2015). This decline is particularly serious for semi-natural meadows, where in Sweden only about 1.7% of the area remains as compared with 1927 (Swedish Board of Agriculture 2019). In Sweden, around 270 000 hectares of species-rich semi-natural grasslands remain, mostly (ca 98%) maintained by livestock grazing (Swedish Board of Agriculture 2005). These grasslands harbor an exceptional plant species richness at small spatial scales (Eriksson et al. 2006, Öster and Eriksson 2012, Wilson et al. 2012), and remaining species-rich grasslands are of special interest for conservation (Veen et al. 2009, Berglund et al. 2014, Plieninger et al. 2015).

As result of this decline of semi-natural grasslands, many of their typical species are also declining. Currently, about a third of all species on the Swedish Red List is associated with agricultural landscapes, mostly with semi-natural grasslands (Eide et al. 2020). One of these species is the biennial *Gentianella campestris* (L.) Börner (Fig. 1), the field gentian, which is currently classified as Endangered in Sweden (SLU Artdatabanken 2020). Although the mechanisms behind the decline of *G. campestris* have not been examined closely, it is believed that cessation of management of semi-natural grasslands is the main cause of its decline, as populations typically disappear after 5–15 years if management ceases (Lennartsson 2015). There may also be additional factors causing a decline of this species, for example isolation of remaining semi-natural grasslands, and inappropriate grazing management. Furthermore, *G. campestris* is generally sensitive to competition, and is negatively affected by fertilizers (Lennartsson 2015). Another factor that might be responsible for the decline of *G. campestris* is summer drought, which can be deleterious to the survival of the rosettes (Lennartsson 2000). Drought also has negative effects on seed production (Lennartsson and Svensson 1996).

In this paper, we describe and examine the decline of *G. campestris* using data from the late 1980s onwards, until today. Most of the data was gathered from the County of Södermanland (Fig. 2), located in southeastern Sweden, south of Stockholm. However, we expect that our results and conclusions are valid also for other parts of this species' distribution. Our main objectives were to synthesize the survey data, to use indirect evidence to identify mechanisms behind the decline of *G. campestris*, and to discuss the prospects for preventing further decline and ultimately regional extinction of *G. campestris*.



Figure 1. The field gentian, *Gentianella campestris*. Photo: the authors.

Natural history of *Gentianella campestris*

Gentianella campestris (Fig. 1) exhibits variation in life cycle, morphology and flowering phenology (Lennartsson 1997, Winfield et al. 2003), which has led to the recognition of two, sometimes three, subspecies. *Gentianella campestris* ssp. *baltica* has an annual life cycle, and *G. campestris* ssp. *campestris* and *G. campestris* ssp. *islandica* have a strict biennial life cycle, but are distinguished by whether a main stem is present (ssp. *campestris*) or absent (ssp. *islandica*) (Lennartsson 2015, Lennartsson et al. 2018). *Gentianella campestris* ssp. *campestris* is considered to have two phenological varieties, the early flowering *G. campestris* var. *suecica* and the late flowering var. *campestris* (Zopfi 1991, Lennartsson 1997, Plenk et al. 2016). This study concerns *G. campestris* ssp. *campestris* (henceforth referred to as *G. campestris*). The survey data mainly refer to the late flowering variety, which is most common.

Germination of *G. campestris* occurs during spring, and a small rosette develops the following summer (Lennartsson and Oostermeijer 2001). A taproot and bud overwinter and flowering occurs in the summer–autumn of the following year (Lennartsson and Oostermeijer 2001). The early flowering variety flowers in late June and early July, and the late flowering variety flowers from mid-August to early September. Some individuals have an intermediate flowering phenology (Lennartsson et al. 1997), implying that the distinction between the phenological varieties is not fully clear. Individuals produce 5–15 purple flowers (Lennartsson et al. 1997)

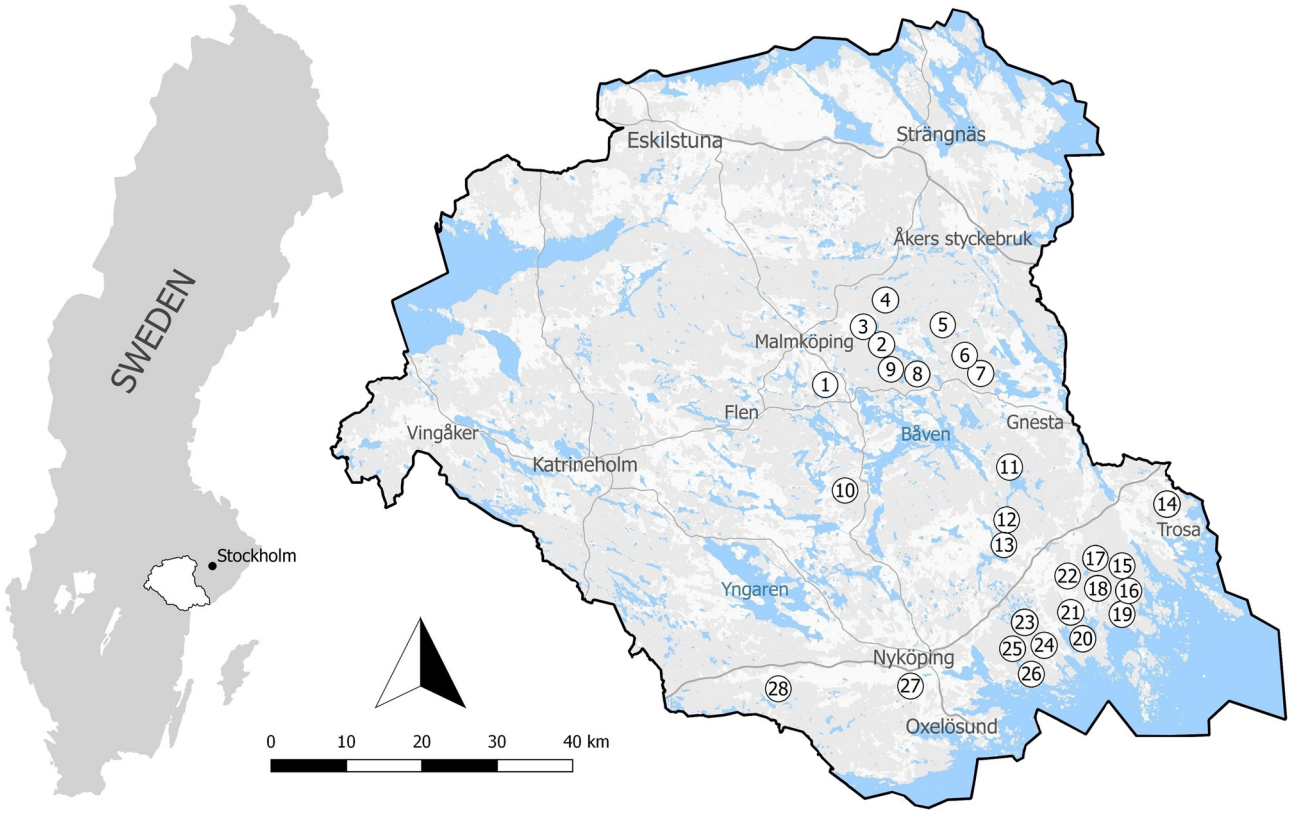


Figure 2. Map showing the County of Södermanland, and its location in Sweden. The 28 sites in the CS-1 dataset are marked, following the numbering used in Table 1.

and occasionally up to 60 flowers (Glav Lundin and Eriksson unpubl.). The flowers are pollinated by bumblebees, but *G. campestris* is capable of self-pollination and may produce a full seed set without pollination by insects (Lennartsson 2015, Lennartsson et al. 2000). Each fruit produces 50–110 seeds (ca 0.19 mg). After reproduction, the individual dies.

Gentianella campestris is considered to have a short-lived seed bank (Milberg 1994). Lennartsson and Oostermeijer (2001) found that most seeds germinated in the year after they had been produced, around 6% germinated the year thereafter, and possibly a few seeds remained dormant longer. According to the same study, seedling mortality is high; only few seedlings ultimately develop into a rosette. Accumulation of litter has a negative effect on germination and establishment of seedlings (Lennartsson and Svensson 1996).

The seeds are released during late autumn and winter. They lack specific adaptations to dispersal and while seed dispersal is facilitated by wind (Verkaar et al. 1983), the seeds typically land only a few decimeters away from the mother plant (Lennartsson 2015). In the traditional agricultural landscape, hay transports may have contributed to long-distance dispersal of seeds, and it seems likely that seeds may be dispersed by hoofs of livestock. However, due to the fragmented state of today's agricultural landscape, long-distance dispersals is unlikely.

Methods

Field sites and surveys

The starting point for this study is a survey of remaining semi-natural grasslands in Sweden, initiated during the 1980s and conducted independently in each of Sweden's counties. Although we use some data from other counties in Sweden, the main data is from the County of Södermanland (Fig. 2). Semi-natural grasslands in this county are generally species-rich at small scales, sometimes with more than 40 species of flowering plants per 0.25 m^2 (Eriksson et al. 2006, Öster and Eriksson 2012). Species richness is strongly related to historical continuity of management, mowing and grazing (Cousins and Eriksson 2002, Eriksson and Cousins 2014). The most species-rich semi-natural grasslands are found at sites with a top soil of silt, and the pH in dry to moist semi-natural grasslands ranges between 4.8 and 5.7 (Cousins and Eriksson 2002). The vegetation matrix is typically dominated by grasses such as *Agrostis capillaris* L. and *Festuca ovina* L., and common forbs such as *Achillea millefolium* L. and *Trifolium repens* L., and often with a significant presence of stands of *Calluna vulgaris* (L.) Hull (Anonymous 1992, Öster and Eriksson 2012). Examples of other common forbs are *Leucanthemum vulgare* Lam., *Polygala vulgaris* L. and *Antennaria dioica* (L.) Gaertn. (Anonymous 1992, Eriksson et al. 1995).

A survey dataset (henceforth termed CS-1) was gathered as part of a project initiated in the early 1990s with the aim to study semi-natural grasslands in the County of Södermanland from a perspective of plant species richness, plant population dynamics and semi-natural grassland conservation. Eriksson and Cousins (2014) give an overview and summary of the main conclusions from this project.

Gentianella campestris was chosen as one of the target species, and with help from the Nature Conservation Unit at the County Administrative Board of Södermanland, 28 sites were chosen (Fig. 2, Table 1). The criteria for inclusion were that the site had been identified as a valuable semi-natural grassland, and that surveys made during the late 1980s had documented that *G. campestris* was present at the site (Anonymous 1992). All sites were more or less isolated fragments of semi-natural grassland, surrounded by vegetation (arable fields, forests) that are unsuitable for many of the plant species inhabiting the site (among them *G. campestris*). The area of the sites ranged from 1.1 to 26.8 hectares (median area: 4.0 ha), based on the records of 'open pasture' in Anonymous (1992). Although some of the sites may have contained several patches of *G. campestris*, each site was henceforth considered to have hosted one population.

All sites were surveyed yearly 1993–1996. Initially (1993), all sites except two were managed by grazing, but over time management was abandoned at several sites. After 1996, a decision was made to reduce the field effort. Surveys were conducted some years, but in 2005–2006 all sites were again surveyed, and this was repeated in 2014 with the exception of two sites, that had been transformed so strongly that a visit was considered meaningless. In 2015–2016, and 2018–2020, all sites considered potentially still hosting *G. campestris* were surveyed. In 2020, five sites where *G. campestris* previously had been assessed as extinct were re-visited in order to check this assessment. Table 1 summarizes the survey data.

The field surveys were made between mid-August and early September, i.e. at a time when *G. campestris* is flowering. At each visit, the surveyor walked slowly across the site, counting the number of flowering individuals. In addition to the authors, two experienced field assistants participated in the surveys 1993–2006. Thus, although some bias due to the person conducting the survey is expected, this is regarded as rather limited.

In addition to the dataset CS-1, we had access to survey data from the Nature Conservation Unit at the County Administrative Board of Södermanland. In 2017, using consultants hired for this task, re-surveys were made at known sites for *G. campestris* from the 1980s, and also at sites a priori considered as potentially hosting *G. campestris*. In addition to record the presence of *G. campestris*, this survey also evaluated the management status of each site. Weak (assessed by an average height of the grass sward > 10 cm) and absent management were considered as 'unsatisfactory' management for *G. campestris*, whereas ongoing grazing management was considered as 'satisfactory' management. This dataset is henceforth termed CS-2, and is summarized in Anonymous (2017).

Population data and analysis

The County Administrative Board conducted the initial surveys 1988–1990. In overviews and analyses of the development of number of populations, we decided to set the starting year to 1988. For CS-1, we used data on the number of remaining populations and actual population sizes (number of flowering individuals). For CS-2, we used number of populations, i.e. whether *G. campestris* was recorded or not.

We used the data to calculate an extinction rate for populations. Such calculations may be complicated due to the difficulties to determine when a population is really extinct (Boakes et al. 2016). *Gentianella campestris* populations may fluctuate considerably between years, and, because of the short-lived seed bank, even occasionally have no flowering individuals at all despite not being extinct. Thus, for the CS-1 dataset we decided to use a conservative criterion of extinction. We considered a population to be extinct if during at least two (in most cases three) consecutive surveys no flowering individuals were found. For both datasets CS-1 and CS-2 we examined the relationship between management and population extinction, and for CS-1 we examined the relationship between site area (based on Anonymous 1992) and population extinction.

We also used CS-2 and two other datasets to calculate population extinction rates. Lennartsson and Svensson (1996) presented results of surveys made 1992–1994 based on known localities of *G. campestris* from the 1940s in the Province of Uppland (north of Stockholm). The time interval was set to 1945–1994 (the last year 1994 was used as it gives the most conservative estimate of extinctions). This dataset is termed UPP-1. Lennartsson (2015) also presented results from a follow-up of the survey made by Lennartsson and Svensson (1996), where the remaining populations of *G. campestris* 1992–1994 were re-surveyed 2004. The time interval was set to 1992–2004 (the first year was set to 1992 since it gives the most conservative estimate of population extinctions). This dataset was termed UPP-2. For the datasets CS-2, UPP-1 and UPP-2, the criterion of extinction used for CS-1 was not applicable since the surveys were made just once at the beginning and end of the survey period. We considered a population to be extinct if no flowering individuals were found at the end of the survey period. Thus, it may be that the CS-2, UPP-1 and UPP-2 to some extent overestimate population extinctions in comparison with the data set CS-1.

The mean survival rate (s) of a population could be calculated using $N_2 = N_1 \times s^T$, where N_1 and N_2 are the number of populations at the beginning and the end of the survey period, and T is the number of years between the two surveys. Extinction rate is then $1 - s$.

As mentioned above, the CS-2 dataset included both sites at which *G. campestris* had been recorded 1988 (Anonymous 1992) and additional sites were this species was a priori expected. In order to use the dataset CS-2 for calculation of extinction rate, we restricted the analysis to those sites in the CS-2 survey that were identified as sites hosting *G. campestris*

Table 1. Number of flowering *Gentianella campestris* at the 28 sites included in the CS-1 dataset. nd = no data. Site and ID are according to Anonymous (1992). The text for details of the surveys during different years.

Site	ID	1993	1994	1995	1996	1997	1998	1999
1. Stora Råstock	82–35	73	24	7	126	nd	nd	nd
2. Hässelby-Henäng	82–22	0	0	0	0	nd	nd	nd
3. Alm-Norräng	82–23	18	4	3	26	2	12	37
4. Mora Gård	82–11	46	25	97	28	0	250	4
5. Stora Åsa	61–2	266	19	13	440	367	268	332
6. Kärvsätter	61–34	4	0	0	0	nd	nd	nd
7. Viby (Kesätter)	61–35	114	0	0	14	10	127	1
8. Herröknanäs	61–11	0	0	nd	nd	nd	nd	nd
9. Vreta	61–10	1	0	12	16	17	12	1
10. Herrgölet	82–80	573	533	915	3431	216	681	169
11. Fräkenvassen	61–69	0	0	nd	nd	nd	nd	nd
12. Onsberga-Vreten	80–37	10	30	74	55	93	81	65
13. Västra Malma Vreten	80–12	174	34	29	482	72	32	34
14. Hunga Norrgården	88–11	1	0	11	0	0	0	0
15. Långmaren	88–25	109	251	12	995	2395	112	816
16. Nynäs-Mellanstugan	80–68	77	8	4	17	nd	nd	nd
17. Nyckelby-Norrgård	88–17	0	4	0	35	1	4	14
18. Litselby	88–24	1119	58	47	717	96	9	45
19. Nynäs-Sandvik	80–73	4	2	5	37	nd	nd	nd
20. Hånö-Horsvik	80–88	100	31	0	3	2	22	16
21. Hånö Säteri	80–86	2	0	nd	nd	nd	nd	nd
22. Grinda-Skyle	80–66	103	15	4	151	nd	nd	nd
23. Björksund-Blindkällan	80–83	60	156	77	256	nd	nd	nd
24. Björksund-Grytmar	80–85	6	0	0	3	nd	nd	nd
25. Björksund-Baggebol	80–84	178	1	4	260	nd	nd	nd
26. Ånga	80–114	600	17	99	166	nd	nd	nd
27. Lindbacke	80–106	41	2	0	109	nd	nd	nd
28. Bergtorpgården	80–98	102	24	16	19	nd	nd	nd

Site	2001	2005	2006	2014	2015	2016	2018	2019	2020
1.	33	168	78	0	1	25	79	106	124
2.	nd	0	0	0	0	0	nd	nd	nd
3.	86	245	77	0	44	3	0	0	12
4.	30	1195	137	0	17	45	0	0	35
5.	568	303	185	424	749	691	135	70	3150
6.	0	0	0	nd	nd	nd	nd	nd	nd
7.	0	2	0	0	nd	nd	nd	nd	nd
8.	nd	5	1	0	nd	0	nd	nd	nd
9.	7	0	0	0	nd	nd	nd	nd	nd
10.	168	302	111	5	0	135	5	1	147
11.	nd	0	0	nd	nd	nd	nd	nd	nd
12.	11	176	365	0	0	nd	nd	nd	0
13.	0	0	0	0	nd	nd	nd	nd	nd
14.	2	0	0	0	0	nd	nd	nd	0
15.	212	180	388	10	113	25	1	0	9
16.	0	1	0	0	nd	0	nd	nd	0
17.	2	75	7	0	0	0	0	0	0
18.	23	33	38	0	15	0	0	0	0
19.	4	58	8	0	0	0	0	0	0
20.	84	33	18	3	56	0	0	2	0
21.	nd	0	0	0	nd	nd	nd	nd	nd
22.	43	4	101	0	0	nd	0	0	0
23.	213	86	175	0	0	nd	nd	nd	0
24.	0	8	111	0	0	nd	nd	nd	0
25.	414	264	227	0	nd	nd	0	0	0
26.	37	24	114	0	21	4	0	0	0
27.	nd	308	436	0	0	0	0	0	0
28.	nd	0	2	0	0	nd	nd	nd	nd

in Anonymous (1992). In the Result section, data from CS-2 was also used for examining presence of *G. campestris* in relation to management, and then the number of sites used differ from the calculation of extinction rate.

Recruitment experiment

To examine whether the regional number of populations of *G. campestris* was seed limited (Eriksson and Ehrlén 1992), recruitment experiments were carried out in which seeds were added to sites where *G. campestris* was not present. If seed addition leads to recruitment, there are unoccupied but suitable sites available, which the target species has not yet been able to colonize. The experiment was done at sites which were subjectively considered as potentially suitable for *G. campestris*. Twelve semi-natural grassland sites were chosen (selected from Anonymous 1992), but including only sites where the surveys during the 1980s did not record *G. campestris*. At each site 4000 seed were sown (2000 seeds in each of two 1-m^2 plots). Sowing was done in 1993, and the sites were visited from 1995 (when flowering individuals would be expected) onward, until it was evident that no flowering individuals remained.

Results

Population development and extinctions

The number of populations used in the CS-1 survey declined from 28 in 1988 to four in 2018 and 2019, followed by an increase to six in 2020 (Fig. 3). Note that the years 1997–1999 and 2001 were not included in Fig. 3 since not all populations in the CS-1 dataset were surveyed these years. Using our conservative criterion of extinction (two consecutive surveys without a flowering plant found), seven populations remained in 2020 (Table 1), a decline by 75%. The revisits at five sites where populations had been assessed as extinct earlier during the survey period (sites 12, 14, 16, 23 and 24; Table 1) confirmed the assessment. No flowering *Gentianella campestris* was found at these sites. There was no relationship between population extinction and site area (logistic regression; $p = 0.88$).

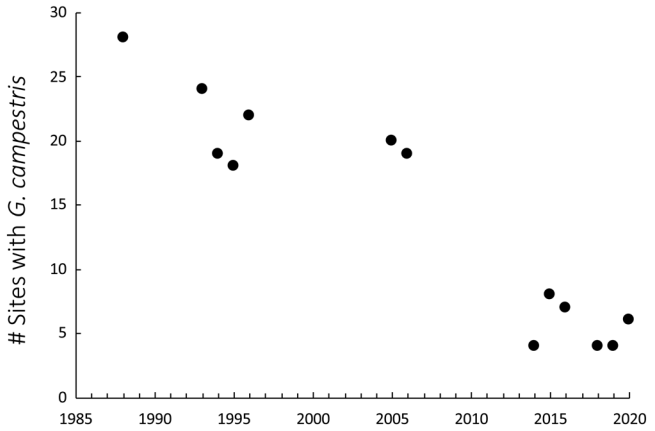


Figure 3. The number of sites with records of flowering *Gentianella campestris* in the CS-1 survey. The starting data (1988) was set from the survey made by the County Administrative Board in Södermanland based on records of flowering *G. campestris*. The follow-up surveys were made from 1993. Note that the years 1997–1999 and 2001 are not included in this figure, since not all sites were surveyed these years. The decline over the study period is strongly significant ($R^2 = 0.87$, $p < 0.001$).

In the CS-2 survey conducted 2017, flowering *G. campestris* was found at 38 out of 75 sites (Anonymous 2017). Restricting the sample to only those sites in the CS-2 dataset where *G. campestris* had been recorded 1988 (Anonymous 1992), the decline was from 65 to 25 sites, i.e. a decline with 62%.

Local populations of *G. campestris* exhibited pronounced fluctuations in size with, at some sites, several thousand flowering individuals in some years and only a few in other years (Table 1). Fig. 4 gives two examples of local dynamics, illustrating how the fluctuations were manifested at single sites. At one site, Långmaren (Fig. 4A), 109 flowering individuals were recorded when the CS-1 survey started 1993, but in 1997, the number peaked at 2395 flowering individuals. Thereafter, the population declined; in 2018 only one flowering individual was found, in the survey 2019 there was no flowering individuals, and in 2020 we found nine. The population at Stora Åsa (Fig. 4B) is unusual in the sense that it showed an overall positive trend, even though at this site the population was also small during 2018–2019. In the last year of the survey (2020) this population was among the highest recorded in the CS-1 dataset, with 3150 flowering individuals.

Overall, the total number of flowering *G. campestris* (based on the CS-1 dataset) during the first four years varied from ca 1200 (1994) to over 7300 (1996). During the last series of surveys from 2014 onward, the total number of flowering individuals has generally been lower. The lowest number were recorded 2018 (220) and 2019 (179). In 2020, a recovery was recorded, with 3477 flowering individuals.

Within years, a few populations dominated, but the identity of these varied among years (Table 1). For example, 61% of all recorded plants in 1993 occurred in the three largest populations. The corresponding figure for the following years 1994–1996 were 76, 78 and 70%, respectively. Only one population (Herrgölet, site 10; Table 1) was among the top-three all four years. A decade later, in 2005, the three largest populations (52% of the flowering individuals that year) were different from all those that were top-three during 1993–1996. Thus, the rank order in size among populations varied between years. The dominance of single populations increased during the last years. In 2020, 91% of all recorded flowering individuals were found at one site (site 5, Stora Åsa; Table 1). Based on the population developments between 2014 and 2020, we would regard this site as harboring the only really viable population left.

The calculated population extinction rates, based on the CS-1 dataset (using the criterion of extinction described above) and the datasets CS-2, UPP-1 and UPP-2, ranged between

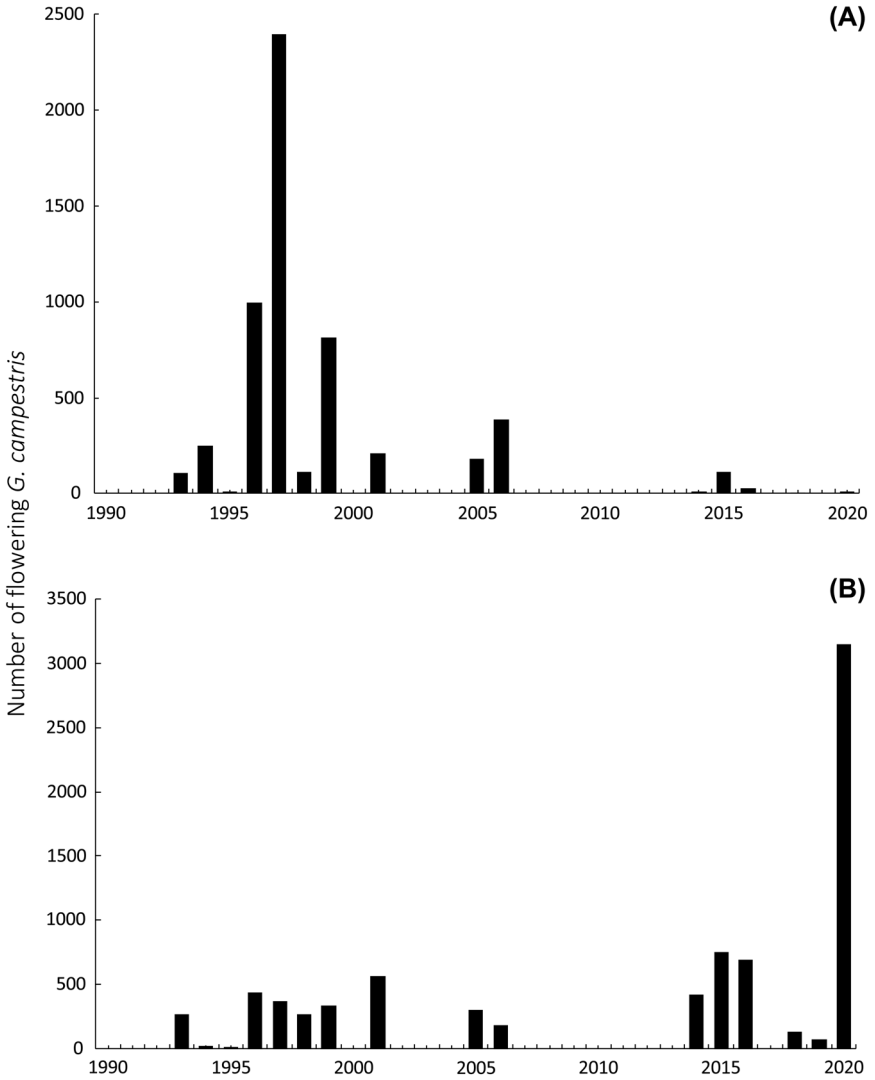


Figure 4. Two examples of local population dynamics of *Gentianella campestris*, based on the CS-1 survey. (A) Långmaren; (B) Stora Åsa. Note that this figure includes also the years 1997–1999 and 2001 which were not included in Fig. 3 (since not all sites were surveyed these years).

3.2% and 4.2% per year (Table 2). A weighted average (based on the number of populations at the start of each observation series) yielded a population extinction rate of 4.0% per year.

Recruitment experiment

In the recruitment experiment (Table 3) flowering individuals were observed at three of the twelve sites. Based on the number of seeds sown and the recorded number of flowering individuals, the maximum recruitment rate (at site III; Table 3) was 0.9%. At that site, flowering individuals were observed until 2003, but after that year no flowering *G. campestris* were recorded. Assuming a strict two-year cycle (year 1: flowering and seed production, year 2: germination, and development of a rosette, year 3: flowering and seed production), we expected that flowering individuals

Table 2. Population extinction rate of *Gentianella campestris* calculated for four datasets. The text for description of the data and the method of calculation. The table summarizes the number of populations recorded the year the survey started (N_1) and ended (N_2), and the calculated yearly population extinction rate. The model used is described in the text.

Dataset	N_1 (year)	N_2 (year)	Extinction rate (fraction of extinct populations/year)
CS-1	28 (1988)	7 (2020)	4.2%
CS-2	65 (1988)	25 (2017)	3.2%
UPP-1	418 (1945)	50 (1994)	4.2%
UPP-2	48 (1992)	31 (2004)	3.6%

Table 3. Results of a seed sowing experiment in *Gentianella campestris*. Seeds were sown at twelve sites (unoccupied by *G. campestris*) in 1993, and flowering individuals were recorded until it was evident that no further flowering individuals remained.

Site	1995	1996	1997	1998	1999	2000	2001	2002	2003
Number of flowering *Gentianella campestris* individuals									
I	1	4	0	0	0	0	0	0	0
II	0	17	3	0	0	0	0	0	0
III	13	23	0	39	0	0	4	0	3

IV–XII: No flowering individuals were observed.

would appear 1995 since the sowing was done in 1993. If the individuals flowering in 1995 were successful in producing seeds, a new set of flowering individuals would appear 1997, and so on. However, flowering individuals appeared 1996 at all three sites, so some of the seeds sown in 1993 must have remained dormant and germinated in 1995 instead of 1994.

Management and population extinctions

The general understanding that ceased management of semi-natural grasslands is the major cause behind the decline of *G. campestris* was confirmed at many sites during the field studies. Among the 21 sites in the CS-1 dataset where *G. campestris* has disappeared, ten sites have suffered from abandonment of grazing management. The seven sites with remaining populations of *G. campestris* were managed throughout the study period. The relationship between ceased management and population extinction was significant ($\chi^2 = 5.2$; $p = 0.023$). Following abandonment, *G. campestris* disappears within a few years. However, sometimes the local extinction process may take considerably longer time. One example is the site Onsberga-Vreten (site 12; Table 1), where management had ceased already when the CS-1 observation series started in 1993. This site maintained a quite large population until the survey 2006, i.e. 13 years. Ultimately, this population went extinct the following years. Management has recently been resumed at this site, but no flowering *G. campestris* was recorded in 2020. However, abandonment of management is not the only cause of population extinction. Among the 21 sites where *G. campestris* has disappeared, 11 sites were still managed by grazing.

In the CS-2 survey 2017, management status was noted by the consultants. Among the 38 sites where *G. campestris* was found, 82% was classified as 'satisfactory' management. Among the 37 sites where *G. campestris* was not found, 65% was classified as 'unsatisfactory' management. The relationship between management status and occurrence of *G. campestris* was significant ($\chi^2 = 16.7$; $p < 0.001$).

Discussion

This study reveals two major features of the population dynamics of *Gentianella campestris*. Firstly, the populations exhibit strong population fluctuations. Even though the data were gathered by different persons, and this may imply that some of the variation is a result of person-related bias, the extent of the variation is such that this conclusion must be regarded as robust. Large variations of population size is expected given that *G. campestris* is a strict biennial, with the potential to produce vast numbers of seeds, but also that the recruitment rate is sensitive to local environmental conditions that in themselves vary between years, for example precipitation. Thus, it seems reasonable to suggest that similar fluctuations in population size was a feature of this species even during times when it was much more common. Large fluctuations in local populations have probably always been associated with a relatively high rate of local population extinctions. Before the decline of semi-natural grasslands, commencing over 100 years ago, large and connected areas of grassland (Cousins et al. 2015) and transport of hay and livestock (Bruun and Fritzbøger 2002) would have promoted establishment of new populations, balancing local extinctions.

The second major feature is that *G. campestris* is currently declining drastically. This decline can be described by different figures. For example, in the province of Uppland, only 31 populations remained in 2004, out of 418 recorded in 1945 (Table 2), a decline by 92.6% over this period. For the County of Södermanland, the results of this study suggest that between 62% and 75% of the populations have disappeared during the last three decades. Calculated as population extinction rates, the four examined data sets suggest that approximately 4.0% of the populations disappear yearly. This exact figure may be a slight overestimate, since three of the datasets necessitated using a criterion of extinction based on just one single year with no records of flowering *G. campestris*. As evident from site 3, 4 and 20 (Table 1), even using two consecutive years with no flowering individuals may overestimate extinction rates. However, when recovering, those sites had only few flowering individuals, and at most sites with several years of no records, *G. campestris* is obviously extinct (Table 1). Thus, even if the calculated rate of extinction may be somewhat higher than the true figure, we consider it robust to conclude that *G. campestris* experiences a rate of decline of a magnitude close to the one calculated.

This decline of *G. campestris* is probably a continuation of a process of shrinking semi-natural grassland area that has been going on during the last century. The area of semi-natural grasslands in the County of Södermanland has declined with more than 95% over the last 100 years (Cousins et al. 2015). Abandonment of management was identified as the major cause of the decline in *G. campestris* in the Province

of Uppland between 1945 and 1994 (Lennartsson and Svensson 1996), and this conclusion is supported by the present study. Although the CS-1 dataset includes one site where *G. campestris* had maintained a population more than 13 years after abandonment of management, the general picture is that populations disappear within a few years if grazing ceases.

However, the decline also occurred at sites with ongoing management. Local population extinctions at sites with ongoing management may reflect that the grazing management has been inappropriate. In our study, the distinction between 'satisfactory' and 'unsatisfactory' management was made subjectively, and perhaps this does not reflect what is truly a satisfactory management for *G. campestris*. We have no data on this issue, but Lennartsson (2015) gives several examples of ongoing management which has been very negative for *G. campestris*, for example a too high grazing pressure throughout the entire season.

Extinctions at sites with ongoing management may also reflect an inherent feature of *G. campestris*, i.e. its strongly fluctuating dynamics. This would not be a problem if these population extinctions were balanced by a similar rate of population colonizations. However, very few newly established populations have been recorded. A few cases are mentioned in Lennartsson (2015), but during almost 30 years of field studies in the County of Södermanland, we have not yet encountered any 'new' (i.e. not known before) population of *G. campestris*. Thus, a likely contributing cause behind the decline is the strong fragmentation of semi-natural grasslands that makes colonization of new sites difficult.

The results from the sowing experiment gives an additional hint on the obstacles of establishing new populations. Despite a propagule pressure of 4000 seeds per site, none of the sites were successfully colonized more than temporally (for three of the twelve sites, and only one population remained until ten years after sowing). Given the highly fragmented remaining semi-natural grasslands, the likelihood of successful dispersal of a sufficient number of seeds across long distances of modern production forest or arable fields must be extremely small. One should note, however, that it is possible that the sites chosen for this experiment were not truly suitable for *G. campestris*, for example due to lack of disturbance, which is important for recruitment in other species of gentians (Fischer and Matthies 1998). If this is the case, the number of seeds per se may not be the problem, but rather the management regime at the sites. It may also be that the conditions suitable for recruitment occurs only certain years, something that is not captured in a single experiment conducted once. For example, the great increase in number of *G. campestris* in 2020, particularly at sites 5 and 10 (Table 1) may reflect that the drought during 2018 created bare ground suitable for seedling recruitment the following year, ultimately resulting in abundant flowering individuals 2020.

There are also other possible causes behind the decline of *G. campestris*, for example summer drought. Although the rank order in size among populations varies between years, suggesting that the fluctuations are not generally synchronous among sites (a result obtained also by Eriksson and Ehrlén 2001), the populations of *G. campestris* in 2018 were overall very small. The summer 2018 was extremely hot and dry. The deviation from the average temperature in July 2018 compared to the average temperature in July between 1961 and 1990 was around +4.5°C all over Sweden (SMHI 2018a), and the average monthly rainfall in Södermanland in July 2018 was less than 25% of the average rainfall between 1961 and 1990 (SMHI 2018b). If drought is a factor affecting *G. campestris* negatively, this would affect all populations within the same region in the same way. One way to alleviate such drought effects is to maintain local scale heterogeneity, for example in grazing pressure (Lennartsson 2015). Such heterogeneity has been found positive for local species richness in general (Öster et al. 2007, Bonari et al. 2017). Temporal heterogeneity (Allen et al. 2014), for example starting grazing generally late during the season and also vary the starting date of grazing between years, may be beneficial to *G. campestris* as this management resembles the historic management of meadows (Eriksson et al. 2015). Indeed, Lennartsson (2015) concludes that management with late or irregular grazing should be the best option for maintaining populations of *G. campestris*.

A general conclusion is that the decline of *G. campestris* is mainly driven by abandonment of management (grazing, mowing), and that inappropriate management, fragmentation of grasslands and increasing incidence of summer drought exacerbate the situation for this species.

So is there any hope that *G. campestris* may be rescued from further decline and ultimately total regional extinction? As continued management of semi-natural grassland is the major condition needed for population survival, the most important question is whether farmers in the future will maintain this management. To give an extensive answer to that question would require another study, but it is possible to make a few remarks. The current system of subsidies for maintaining grazing in semi-natural grasslands (a part of the Common Agricultural Policy, CAP, of the European Union, and further supported by Sweden as a part of Swedish Environmental Goals), is essential to counteract any further decline. However, many farmers across Sweden, who maintain grazing management in semi-natural grasslands, are not optimistic about the future (Waldén and Lindborg 2018).

Considering that fragmentation of semi-natural grasslands is an obstacle for dispersal among suitable or potentially suitable sites for *G. campestris*, one would not only need to maintain currently existing semi-natural grasslands, but also expand the area, and the dispersal routes connecting semi-natural grasslands. To achieve something similar to the dispersal routes in the pre-modern agricultural landscape (Poschlod and Bonn 1998, Bruun and Fritzbøger 2002) is unrealistic, but functional connectivity (Auffret et al. 2015) may be increased if semi-natural grasslands are connected with grasslands that are not (yet) as species-rich as traditionally managed semi-natural grasslands (Cousins and Aggemyr 2008, Öster et al. 2009). Such larger pastures may also be

more profitable for the farmers (Holmström et al. 2018). Potentially, also newly created habitats such as road verges (Huhta and Rautio 2007, Auestad et al. 2011) and power-line corridors (Berg et al. 2016, Svensson et al. 2017) may contribute to provide at least temporary suitable habitat for *G. campestris*.

Several species of gentians are declining all over Europe (Pritchard 1972, Oostermeijer et al. 1992, Fischer and Matthies 1997, Oostermeijer et al. 2002, Königer et al. 2012), and the field gentian *G. campestris* is no exception. Extrapolating the trends of decline in *G. campestris* reported in this paper implies that this species is probably gone within the next century. Counteracting these trends would necessitate that not only specific sites (regarded as 'valuable') are maintained and appropriately managed, but also that management has a landscape perspective (Lindborg et al. 2008, Eriksson 2016) accounting also for seed dispersal processes, thus promoting colonization founding new populations. Overall, however, it is difficult to remain optimistic about the future of the field gentian.

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Author contributions

Linnea Glav Lundin: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Ove Eriksson**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

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