



OPEN Understanding the effects of weather parameters on the population dynamics of an endangered geophyte supports monitoring efficiency

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Due to their complex life cycles geophytes are often neglected in conservation programs, despite they are important elements of early spring communities. Their life cycle is strongly affected by weather parameters, i.e. temperature, precipitation, and light, but the effects of these parameters are often contradictory and show high intra-annual variability even within species. Deeper knowledge about the abiotic factors affecting the population dynamics of geophytes is needed to support the designation of effective conservation plans. We aimed to explore the link between weather parameters and population dynamics of *Colchicum bulbocodium*, an endangered and strictly protected geophyte. We monitored three life cycle stages (flowering, growing, fruiting) of 1069 individuals in permanent plots for six consecutive years. Our results showed that life cycle of *C. bulbocodium* was strongly related to the actual weather parameters; the lagged effect of the previous year was weaker. Increasing temperature and lack of cold periods had negative effect on all life stages. We highlighted that population estimation based on the number of flowering individuals in a single year can underestimate population size by 40–83%. Monitoring in years following wet and cold springs and cold winters could increase the accuracy of population estimations of the flowering individuals.

Keywords *Colchicum bulbocodium*, Temperature, Precipitation, Monitoring, Dormancy, Phenology

Climatic changes in the Anthropocene can be witnessed by the increasing temperature, shrinking lengths of cold periods, fewer frost days and nights, reduced snow cover, earlier snowmelt, and changing precipitation patterns¹. These abiotic changes lead to changes in living organisms as well, among which the phenological shifts are the most spectacular ones, and were extensively studied in the past decades². In plants, phenological shifts were detectable both in herbaceous species and in trees²; earlier and milder spring periods often result in advanced start of early life cycle events such as blooming, flowering and greening out, while a prolonged vegetative period can cause a delay in late phenophases, i.e. fruiting, leaf senescence^{2–6}. Beside the changes directly caused by the temperature, earlier start of flowering and altered duration of flowering can be caused also by changes in precipitation availability^{6,7}.

Early-spring geophyte species can especially be sensitive to climate change, as their life cycle events are strongly dependent on the weather parameters, especially on temperature⁸. Temperature in general was found to have major effect on the growth and development of the storage organs of geophytes, as higher temperature resulting in smaller storage organs⁹. As geophytes below a certain bulb size usually do not produce flowers, increasing temperature that limits the bulb growth expresses its negative effects on reproduction success as well, and in a long run, on population dynamics of geophyte species^{10,11}. Increasing temperature also changes flowering phenology^{5,12–14}, which, combined with the mismatching response of other taxa, can lead to the disruption of plant-pollinator interaction, further reducing reproduction success^{13,14}. Aside from the effect of the increased

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temperatures in limiting bulb growth and disrupting plant-pollinator interactions, low temperatures in late spring, i.e. late frosts, can also have negative effects on some species by decreasing the reproduction success of flowering individuals¹¹. Other weather parameters, like the amount of precipitation, usually have minor effects compared to that of temperature, mainly because of the ability of geophytes to cope with drier conditions by storing water in their belowground storage organs^{8,15,16}. Few exceptions exist, like *Anemone nemorosa*, where water deficiency leads to delayed spring phenology¹⁷. A third factor that may affect geophytes' population dynamics is light availability. Jacquemyn et al. (2010) found that light availability affected the flowering dynamics of *Orchis purpurea*, by enabling frequent, year to year flowering at lower costs under bright conditions compared to shaded places¹⁸. However, similar relation in other geophyte species (*Gagea lutea*) may not exist or may vary from year to year^{9,19}. These contrasting results may be related to differences in temperature conditions, which can overwrite the weaker effects of other factors⁹. Besides, parallel with the abiotic factors, biotic factors may also express their effects, i.e. by changing light conditions, and add a further layer to the factors affecting geophyte phenology. All these findings indicate that our knowledge about the response of geophytes to the effects of weather parameters and other abiotic factors is still incomplete and that more studies are needed to understand them.

Deeper knowledge on the factors affecting the population dynamics of geophytes could help to support the designation of evidence-based conservation plans. The conservation of geophytes is especially important, as they may be threatened not only by the changing abiotic conditions, but also by direct and indirect human activities. Geophytes have a long history of human use: they have long been part of human diet due to their storage organs rich in carbohydrates^{20–22}, they were and still are used for medicinal purposes due to their chemical compounds^{23,24}, and are often used for ornamental purposes because of their decorative flowers^{25,26}. All these means of utilization make them frequent targets of overexploitation and illegal trade^{22,23,25}.

Population monitoring is the base of conservation, as it aims to gather information about the state and dynamics of populations, and to indicate the need of intervention for conservation. However, geophytes can be easily overlooked during vegetation surveys due to their specific life cycles: in general they are detectable only in early spring so their numbers are often underestimated during monitoring surveys or they can be missed entirely^{27,28}. Unfavourable conditions and inadequate management can lead to unnoticed changes of their populations. As they have crucial role in maintaining spring communities, for example providing nectar for pollinators¹³, changes in the timing of flowering and in the number of flowers may result in significant changes in the early-spring communities related to them. That is why knowledge on specific life cycles, and proper timing of monitoring are of great importance when studying geophytes. For accurate population surveys, long-term monitoring is inevitable, given that individuals can enter, and remain in dormant state for multiple years; and relying on counting only aboveground parts of individuals only in certain years may be misleading^{29,30}. The work of monitoring practitioners would also be more effective if they could estimate the part of the populations hidden belowground. For this, filling the knowledge gap about the biotic (i.e. surrounding vegetation, moss cover, amount of litter) and abiotic parameters (i.e. weather parameters) that trigger dormancy and prolonged dormancy of geophytes would be of great help.

In our study we aimed to gather information about the weather parameters affecting the population dynamics of the spring meadow saffron, *Colchicum bulbocodium* Ker-Gawl., an endangered and strictly protected geophyte³¹. *C. bulbocodium* has synanthous leaves, i.e., flowers and leaves of the individuals appear in the same season. The individuals set flowers between February and March²⁶, when temperature in bulb-level (10 cm soil depth) reaches 7 °C³². Flowering individuals have short leaves, which continue to grow after flowers withering. The leaves of vegetative, non-flowering individuals appear and develop later, when most flowers withered. Vegetative period, during which leaves are out, individuals photosynthesize and accumulate resources in the bulbs, lasts until May, when leaves start withering³³. Green capsules start to develop along the withering of flowers and appear aboveground in early May^{26,33}. Capsule development (fruiting period) continues until late May/early June, when capsules mature and open up in their apex to release seeds (Fig. 1). Seeds bear elaiosomes, are dispersed by ants and germinate in autumn or spring³⁴. Bulbs are renewed annually, and the regeneration of the new bulb ends in July, when the bulbs enter into a dormant state.

C. bulbocodium is a suitable model species for studying the effects of weather parameters on the population dynamics of early spring geophytes. Due to its complex phenology and population dynamics, population monitoring of this species is often inaccurate which largely complicates the design of species conservation plans. We aimed to understand the effect of weather parameters on the population dynamics of *C. bulbocodium* by studying a large population in East-Hungary for six consecutive years in 20 permanent plots. We selected this population as this is one of the biggest populations in the region that enabled us to follow the demography in a representative number of plots. In our study we considered both actual and lagged weather parameters to study their effects on population dynamics of *C. bulbocodium* (Fig. 1). This is because studies involving geophytes mostly focus on their growth, reproduction and phenological changes in response to the weather parameters and light conditions of the actual year^{8,9,11,35,36}. However, it is also important to study the effect of lagged weather effects on the population dynamics of species^{37,38}. As Jahn et al. (2023) suggested, weather parameters that affect growth of the storage organs in geophytes, i.e. the weather parameters of the year preceding observations, should be studied more deeply, as it has fundamental effect on the life cycle next year³⁵. Besides, as *C. bulbocodium* is a weak competitor³⁹, the effects of the surrounding vegetation should also be considered, when population dynamic is studied. For this purpose, in our study we also aimed to gather information about the effects of the biotic factors characteristic of the study site.

We addressed the following questions: (i) Do the number of individuals in different life stages show fluctuations across years? (ii) Which weather parameters have the largest influence on the number of individuals in certain life stages? (iii) How can monitoring programs be designed to account for the complex phenology and population dynamics of the species and also incorporate weather effects?

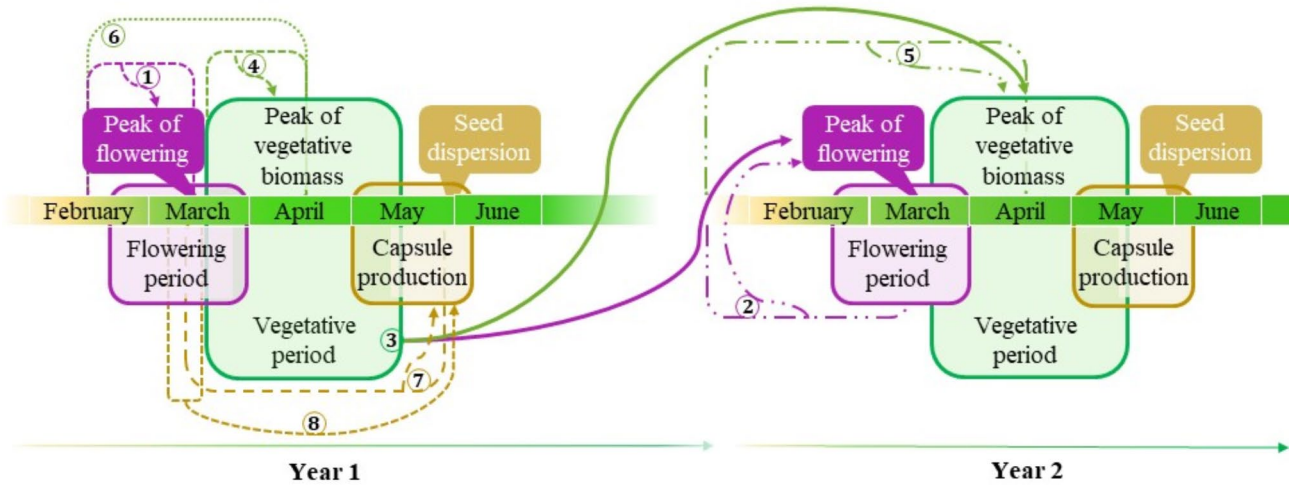


Fig. 1. Main life cycle stages of *C. bulbocodium* in two consecutive years (marked with polygons with solid line contour) and the study periods, whose weather parameters affect the life stages (marked with numbers and polygons with non-solid line contours (except no. 3)). Numbers: (1) from early spring to peak flowering period, (2) from fall of the previous year to flowering period of the actual year, (3) vegetative period of the previous year, (4) leaf development period, (5) from fall of the previous year to the peak of the vegetative period of the actual year (6) from early spring to peak vegetative period, (7) period between flowering and fruiting and (8) flowering period. The arrows start in the period whose effects were studied in the case of life stage, where they end. Colour of the polygons and of the arrows indicate to which life stage is related the studied period (except in case of no. 3, which may have a lagged effect on multiple life stages, so the colour of the polygon is different than that of related life stages). The line type of the polygons with the same colour represents different periods affecting the same life stages. For detailed description see Supplementary Table S1.

Results

General patterns in population dynamics

During the six study years, we identified in total 1069 individuals in the twenty permanent plots (Supplementary Table S2). We found significant differences in almost all studied variables between the study years (Fig. 2, Supplementary Table S3, Supplementary Table S4). We observed that the timing of the peak of the flowering was similar, but the timing of the peak of capsule maturation differed between the study years (Supplementary Table S2).

The number of flowering individuals identified was highest in 2018 and the difference was significant for all years except 2023. We detected the lowest number of flowering individuals in years 2019 and 2021 (Fig. 2A, Supplementary Table S4).

The total number of detectable individuals (i.e. those with leaves) was similar across the years. The number of individuals within leaf-number categories differed in all cases across years except the 4L (four-leaved individuals) category (Supplementary Table S4). Both 1L and 2L individuals (one- and two-leaved individuals) were fewest in 2018 and more abundant in all other years, while 3L (three-leaved individuals) individuals showed the opposite trend (Fig. 2C, Supplementary Table S4).

The proportion of flowering individuals compared to the total number of detectable individuals differed significantly between the years. It was the highest in 2018 (56.74%) and lowest in 2021 (16.61%) followed by 2019 (17.95%) (Fig. 2D, Supplementary Table S3–S4).

The number of individuals entering dormancy (DE) and having stable leaf number (LS) was similar across the years, while significant changes were observed in other behaviour categories (Supplementary Table S4). There was a decreasing tendency in the number of individuals with decreasing leaf number (LD), being lowest in 2022, while an increasing tendency was observed in the case of individuals with increasing leaf number (LI), despite being lowest in 2021. The number of individuals which breaks dormancy (DB) was highest in 2018 and lowest in 2023, but no tendency was detectable across the years.

The number of capsules produced was highest in 2023, but not significantly different from 2018 to 2020 (Fig. 2A, Supplementary Table S4). The lowest number of capsules was counted in 2019. Capsule production

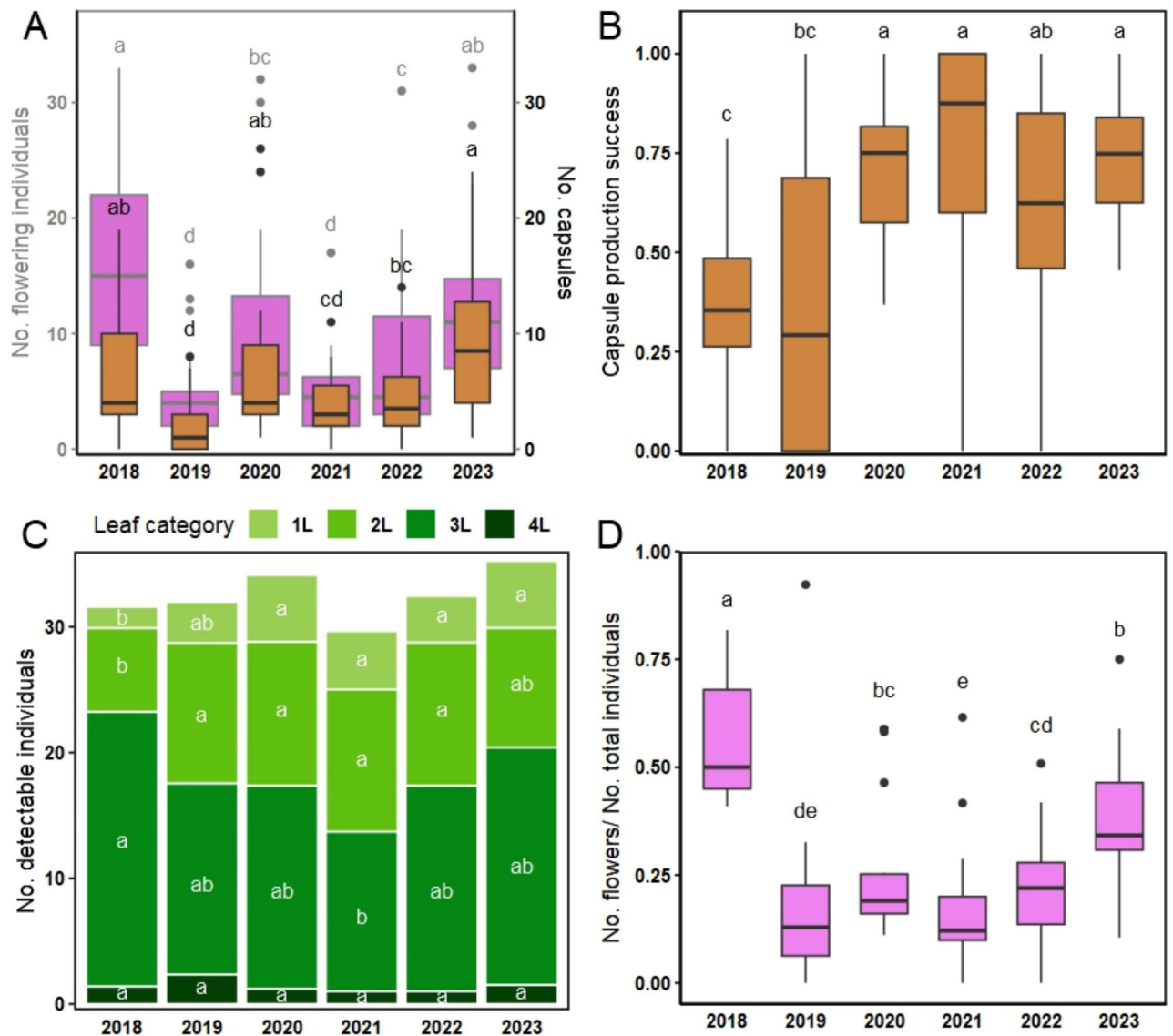


Fig. 2. Results of the generalized linear mixed models (GLMMs) analysing the effect of Year on the dependent variables: (A) Number of flowering individuals (box: magenta, letter: grey) and number of the capsules (box: brown, letter: black), (B) capsule production success of flowering individuals, (C) total number of detectable individuals and individuals belonging to the four leaf-number categories, (D) proportion of flowering individuals compared to the total number of individuals. Lower-case letters indicate significant differences between the years ($p < 0.05$, Supplementary Table S4).

success was highest in 2021 and lowest in 2018 (Fig. 2B, Supplementary Table S4). Capsule length followed similar trends as their number across the years.

Out of the four plot characteristics studied (percentage cover of herbaceous vegetation, mosses and litter, percentage of bare ground in the study plots), understorey plant cover affected negatively the number of detectable individuals and capsule production success, while litter cover affected positively the number of detectable individuals (Supplementary Table S5).

Effect of weather parameters on population dynamics

Out of the ten studied weather parameters (see Materials and methods, [Weather parameters](#)) of the early spring-peak flowering period, only two had significant effect on the number of flowering individuals: both T_{\max} and DTR affected negatively the number of flowering individuals (Fig. 3A). None of the weather parameters of the fall-flowering period (Fig. 3B) as well as the vegetative period of the previous year (Fig. 3C) had any effect on the number of flowering individuals (Supplementary Table S6).

In general, the studied weather parameters had a negligible effect on the number of detectable individuals (Supplementary Table S7). The effect of the weather parameters of the leaf development period on the number of detectable individuals was negative in the case of T_{mean} and T_{min} (Fig. 4A), and similarly, in the case of T_{mean} ,

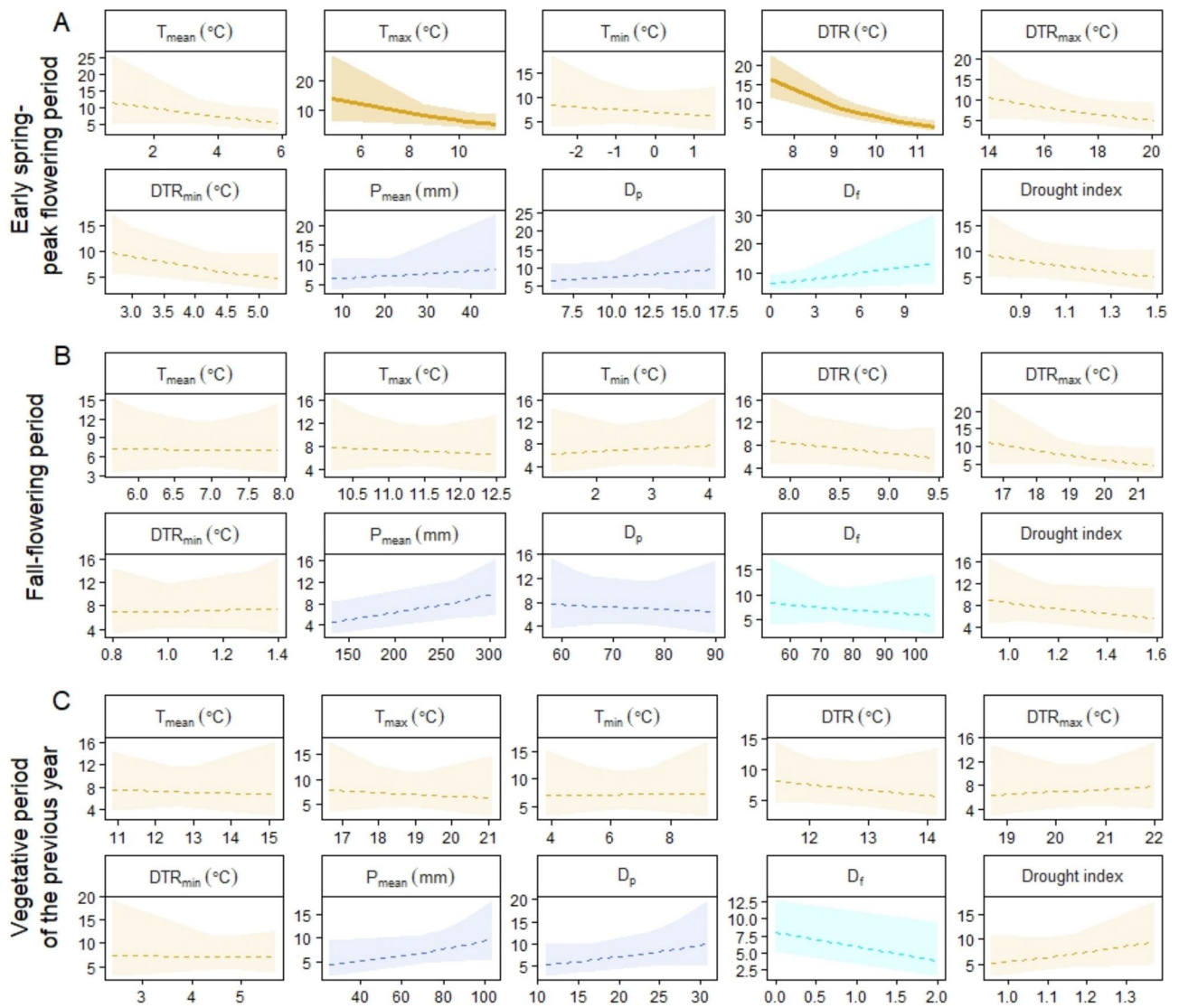


Fig. 3. Results of the generalized linear mixed models (GLMMs) analysing the effect of weather parameters of (A) the early spring–peak flowering period, (B) fall–flowering period and (C) the vegetative period of the previous year on number of flowering individuals. Solid lines indicate significant effects ($p < 0.05$, Supplementary Table S6). Notations: T_{mean} = Mean temperature, T_{max} = Mean of daily maximums, T_{min} = Mean of daily minimums, DTR = Diurnal temperature range, DTR_{max} = Maximum of DTR, DTR_{min} = Minimum of DTR, D_f = Number of frost days ($T_{\text{mean}} < 0$ °C), P_{sum} = Amount of precipitation, D_p = Number of days with precipitation ($P_{\text{day}} > 0$ mm).

T_{min} and DTR of the vegetative period of the previous year (Fig. 4C). The weather parameters of the fall – spring period (Fig. 4B) had no effect on the number of detectable individuals.

Weather parameters affected the individuals belonging to three leaf-number categories, while individuals of the 4L category were not affected by any parameter (Supplementary Table S7, Supplementary Table S8). T_{mean} and T_{min} of the leaf development period affected negatively the individuals belonging to 1L category. T_{min} also negatively affected the 2L category, while DTR_{max} and drought index had positive effect on this category. DTR_{min} and drought index affected positively individuals in 3L category (Fig. 5A). Weather parameters of the fall – spring period had no effect on 1L category, T_{max} and DTR had positive effect on 2L category while DTR had a negative effect on 3L category (Fig. 5B). Out of the weather parameters of the vegetative period of the previous year, only P_{mean} had a positive effect on the 3L category (Fig. 5C).

Weather parameters had also a significant effect on the behaviour categories. Weather parameters of the early spring–peak vegetative period had negative effects on the number of individuals belonging to dormancy breaking (DB) (T_{min} , P_{mean}) and decreasing leaf number (LD) (P_{mean}) categories, while positive effects on the individuals belonging to the same categories, i.e. dormancy breaking (DTR, DTR_{max} , D_f) and decreasing leaf number (DTR_{min}), were also found. The weather parameters of the fall–peak vegetative period affected mostly

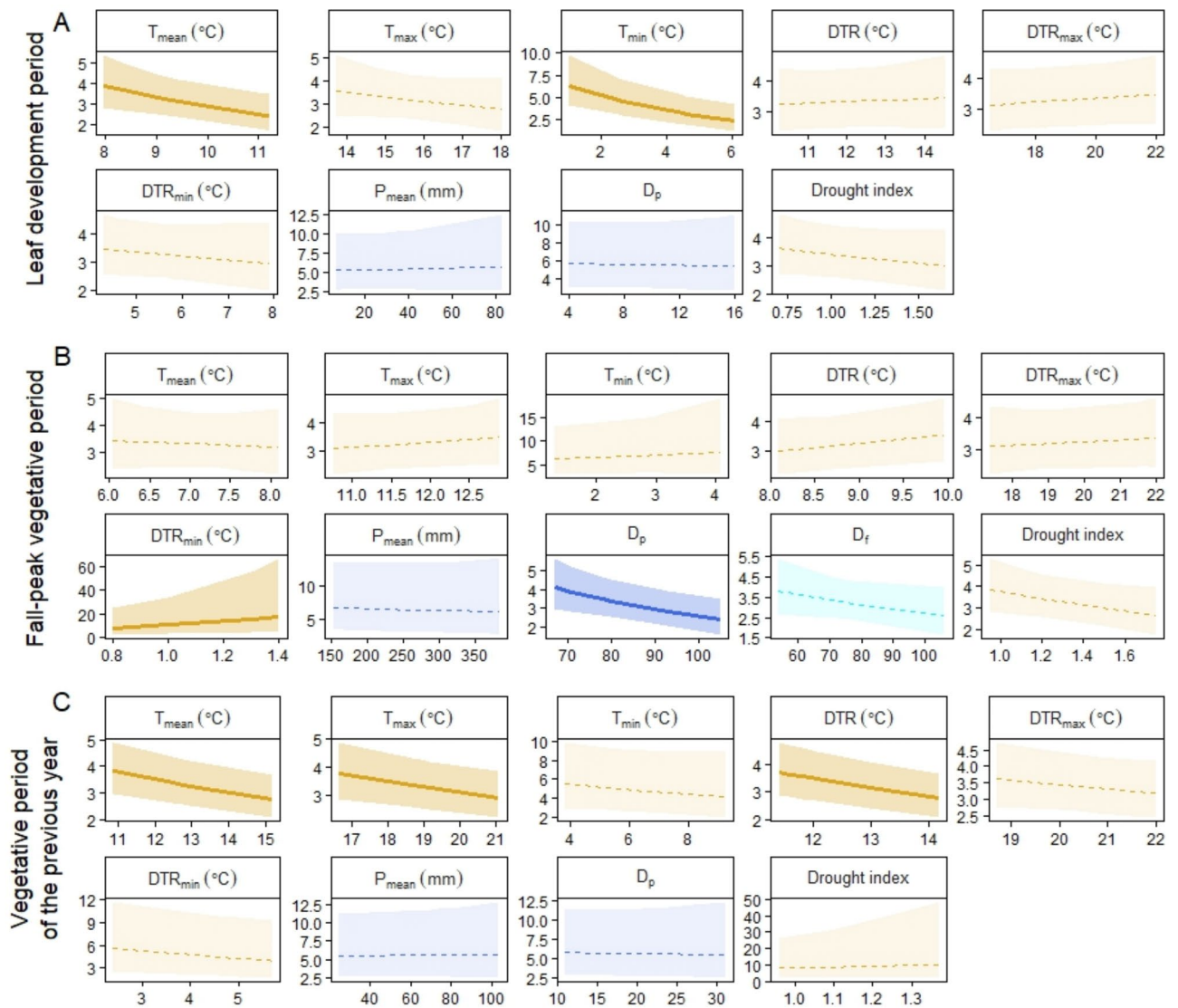


Fig. 4. Results of the generalized linear mixed models (GLMMs) analysing the effect of weather parameters of (A) the leaf development period, (B) fall-peak vegetative period and (C) vegetative period of the previous years on the number of detectable individuals. Solid lines indicate significant effects ($p < 0.05$, Supplementary Table S7). Notations: T_{mean} = Mean temperature, T_{max} = Mean of daily maximums, T_{min} = Mean of daily minimums, DTR = Diurnal temperature range, DTR_{max} = Maximum of DTR, DTR_{min} = Minimum of DTR, D_f = Number of frost days ($T_{\text{mean}} < 0$ °C), P_{sum} = Amount of precipitation, D_p = Number of days with precipitation ($P_{\text{day}} > 0$ mm).

the dormancy breaking category, T_{mean} , T_{max} , T_{min} , DTR_{min} , P_{mean} had a negative effect, while DTR_{max} , D_f and drought index had positive effects. A negative effect of T_{max} and DTR_{min} was also found on the number of individuals entering dormancy (DE), while the effect of drought index was positive. T_{max} and DTR_{min} also affected individuals with stable leaf number (LS) in a positive way. Number of individuals with decreasing leaf number was negatively affected only by DTR_{min} , while the number of individuals with increasing leaf number (LI) was affected positively by DTR and negatively by D_p . Weather parameters of the vegetative period of the previous year had mostly negative effects on the number of individuals entering dormancy (T_{min} , P_{mean}), breaking dormancy (drought index), decreasing leaf number (DTR, P_{mean} , D_p) and increasing leaf number (DTR), while positive effects were found in case of the number of individuals with increasing leaf number (P_{mean} , D_p) (Supplementary Table S9, Supplementary Fig. S1).

Proportion of flowering individuals compared to the total number of individuals, including dormant individuals, was affected by the weather parameters of early spring-peak vegetative period: positively by the P_{mean} and D_f and negatively by DTR. P_{mean} of the fall-spring period had also a positive effect, while the vegetative period of the previous year did not affect the proportions of flowering individuals (Supplementary Table S10, Supplementary Fig. S2).

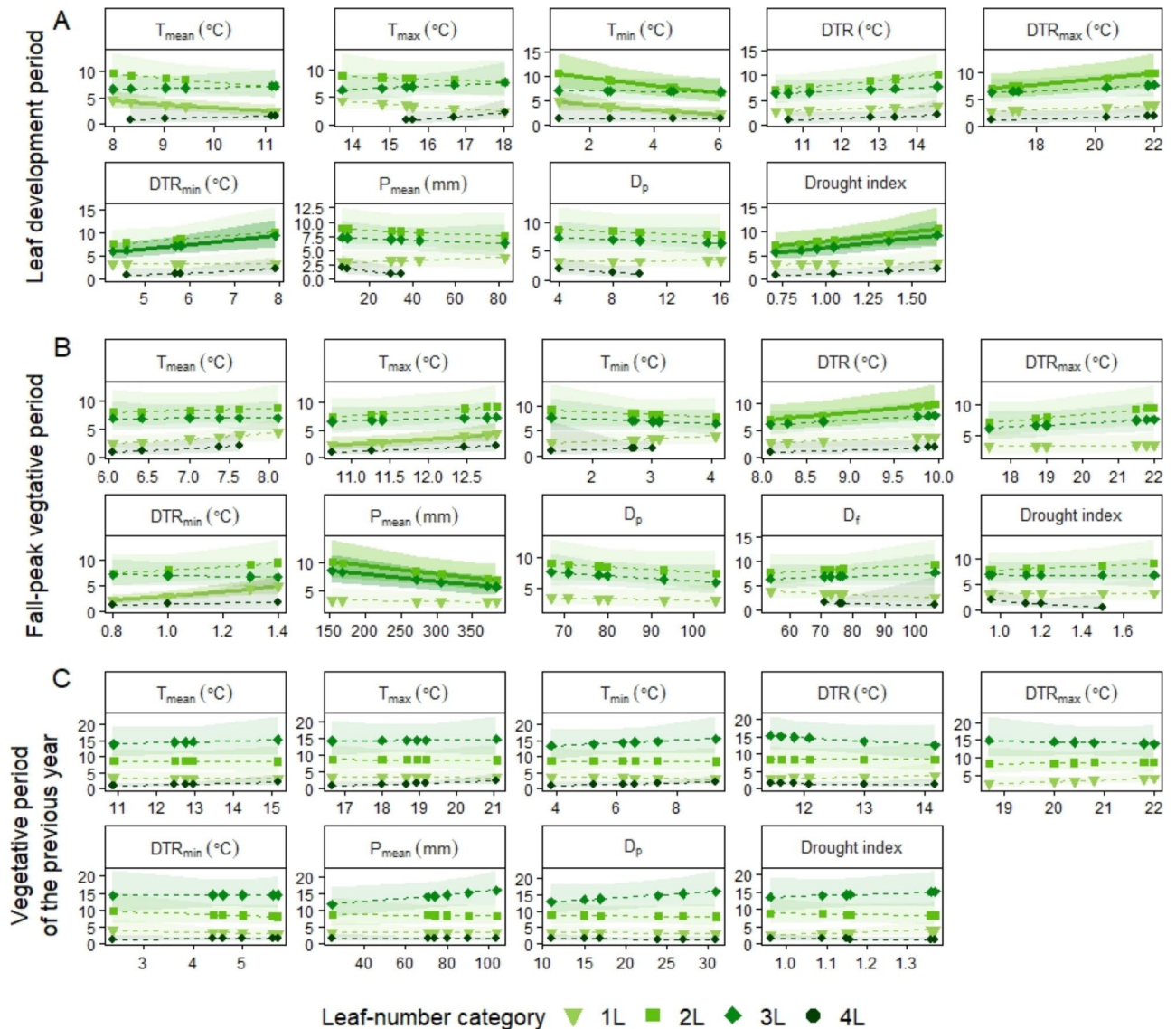


Fig. 5. Results of the generalized linear mixed models (GLMMs) analysing the effect of weather parameters of (A) the leaf development period, (B) fall-peak vegetative period and (C) vegetative period of the previous years on the number of detectable individuals by leaf-number categories. Solid lines indicate significant effects ($p < 0.05$, Supplementary Table S8). Notations: 1–4L: individuals with 1–4 leaves; T_{mean} = Mean temperature, T_{max} = Mean of daily maximums, T_{min} = Mean of daily minimums, DTR = Diurnal temperature range, DTR_{max} = Maximum of DTR, DTR_{min} = Minimum of DTR, D_f = Number of frost days ($T_{\text{mean}} < 0$ °C), P_{sum} = Amount of precipitation, D_p = Number of days with precipitation ($P_{\text{day}} > 0$ mm).

None of the nine studied variables related to weather during flowering period affected capsule production success (Fig. 6A). Out of the nine studied weather parameters of the period between flowering and capsule maturation three (T_{mean} , T_{min} and T_{max}) had significant negative effect on the capsule length (Supplementary Table S11, Supplementary Fig. S3) and capsule production success (Fig. 6B, Supplementary Table S12).

Discussion

The six-year-long survey of *C. bulbocodium* in the study site revealed that the population size is stable, but year-to-year differences in the number of individuals representing the studied life stages, especially flowering and fruiting stages, are present. These differences can be associated to the studied weather parameters, especially to the ones of the actual years, while lagged effect of the weather of the previous year was of less importance. We confirmed that temperature-related weather parameters were more important than precipitation-related ones: cold weather was required for flowering and successful capsule production, while increased temperature and drought induced dormancy or maintained dormancy of already dormant individuals. We also highlight that monitoring schemes based on flower-counting are inaccurate to estimate population size and reproduction success but can be improved by taking into account factors affecting the different life stages. More accurate

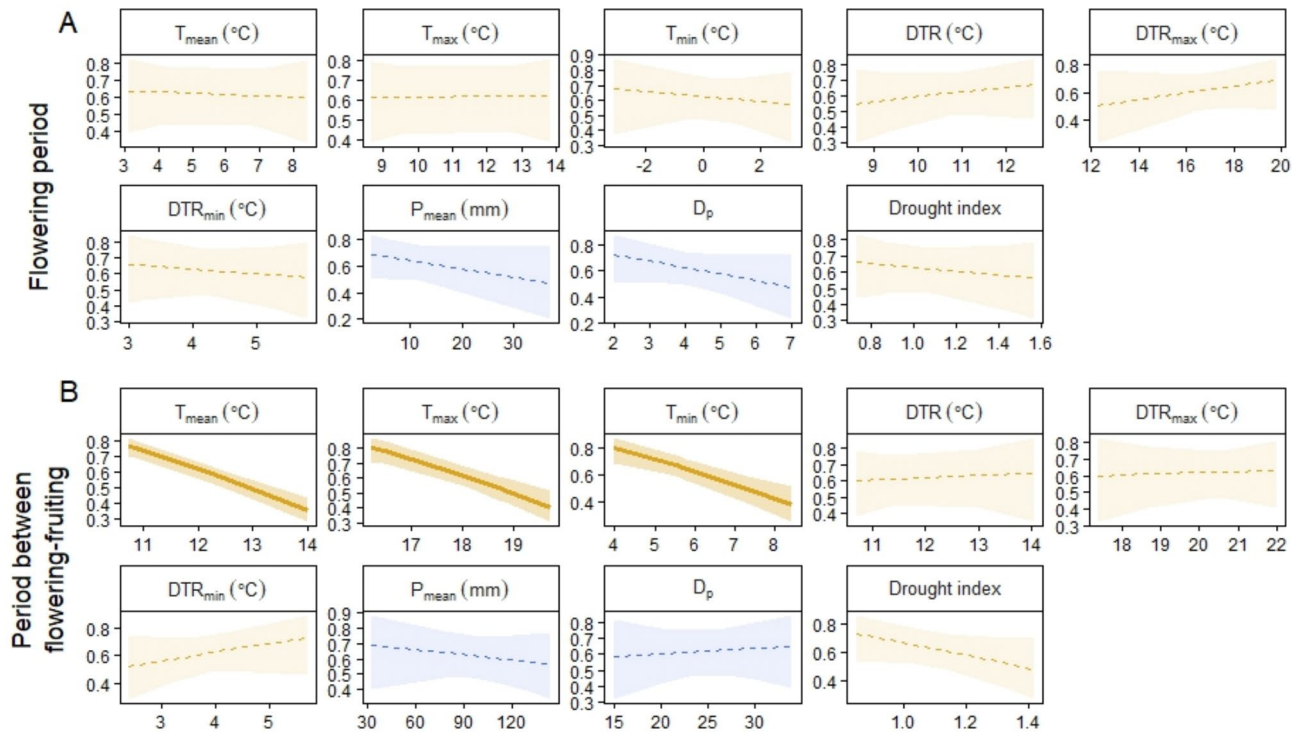


Fig. 6. Results of the generalized linear mixed models (GLMMs) analysing the effect of weather parameters of (A) the flowering period and (B) the period between flowering–fruiting on capsule production success. Solid lines indicate significant effects ($p < 0.05$, Supplementary Table S12). Notations: T_{mean} = Mean temperature, T_{max} = Mean of daily maximums, T_{min} = Mean of daily minimums, DTR = Diurnal temperature range, DTR_{max} = Maximum of DTR, DTR_{min} = Minimum of DTR, D_f = Number of frost days ($T_{\text{mean}} < 0$ °C), P_{sum} = Amount of precipitation, D_p = Number of days with precipitation ($P_{\text{day}} > 0$ mm).

estimations can be achieved by monitoring following cold winters and wet and cold springs or by applying long-term monitoring if possible.

In our study we confirmed an overall stability in the studied population, since the number of detectable individuals was similar across the study years. This is in line with previous findings, which confirm, that perennial plant populations tend to be more stable⁴⁰ than short-lived species populations^{40,41}. The difference in the inter-annual fluctuations of populations size documented in short-lived and perennial species^{30,40,42,43} can be explained by the strategies of the species: short-lived species maintain their populations by continuous extinction-reestablishment cycles, having efficient seed production and seed dispersal for colonizing suitable habitat patches. In contrast, perennials tend to maintain their populations in the same location allocating more resources to survival than to reproduction⁴⁰. In line with this strategy, the presence of the underground vegetative organs of geophytes is the most effective strategy that helps them to maintain their population stability on the long term^{30,40}. However, in *C. bulbocodium* we also found, that the number of individuals belonging to the different leaf number categories, that compose the total number of detectable individuals, was different between the years. The largest part of the studied population consisted of individuals with actual or possible regenerative potential, i.e. mature individuals with 2–4 leaves, but young individuals were represented with an increasing number over the years. An increasing tendency of young individuals over the years is expected also from the success of capsule production: year-to-year differences were also present, but the trend was different from that of the number of flowering individuals and increased over the study years. The stable population size despite the increasing capsule production success and increasing presence of young individuals may indicate a (i) high seedling recruitment associated with low survival rate or a (ii) high seedling recruitment and high survival

rate that counterbalances the mortality of older plants. As our six-year-old data however is still not enough to precisely determine the fate of plants (i.e. mortality), we can only account for prolonged dormancy. To determine which is the key mechanism that drives the population dynamics of *C. bulbocodium*, further monitoring of seedlings and dormant individuals is needed.

We found that weather parameters of the actual year, i.e., that may be responsible for dormancy breaking of bulbs, were more important, than weather parameters of the previous year, i.e. that affect bulb growth. Bulb size plays a crucial role in the phenology of geophytes, especially in flowering^{11,18,35,44,45}. A smaller bulb size due to unfavourable conditions during the vegetative period may be expressed in lower number of flowering individuals in the forthcoming year. However, we did not find such effect, which can be explained by the fact that (i) conditions during the vegetative period were favourable in all years to support bulb growth and flowering in the next year, or (ii) under promising conditions in early spring reproduction was initiated, expressed by flower production, despite the possible costs in the future. It seems more likely that flowering initiation in our case is not size limited, but this happens in the expense of capsule- and seed production. The resources spent for fruiting in the case of geophytes can be provided both by assimilation and by resources stored in the bulbs¹². The former strategy was found in the case of *Trillium apetalon*, a species which uses the foliar photosynthetic products for fruit production⁴⁶, while the fruit production of *Corydalis ambigua* depends only on resources stored in old tubers¹², corresponding to the latter strategy. Our results indicate that *C. bulbocodium* uses a similar strategy to that of *Trillium apetalon*, as capsule and seed production seems to be mostly relying on assimilation products. As seed production may consume a large part of the assimilation products, which could hamper the bulb growth, a trade-off may exist between reproduction and survival. In warm springs, individuals may focus on survival rather than reproduction, allocating less of the assimilation products in capsules and seed production, resulting in higher fruit-abortion, and increased accumulation into the storage organs¹⁰. Our findings on capsule length further supports this assumption: in warmer years not only the number of produced capsules was lower, but capsules were also shorter, than in the following colder springs.

Lagged weather effect was found only in the case of number of detectable individuals, as in a year following a warm vegetative period a lower number of individuals was detectable. This is in accordance with the findings of Jahn et al. (2023), who found lower cover of spring ephemerals following warm springs. They also found a positive effect of precipitation on the cover of ephemerals, which were only partially supported by our results: a larger amount of precipitation promoted the increase of leaf number and hampered its decrease, and also hampered the individuals to enter prolonged dormancy. When individuals were already in prolonged dormancy state, despite precipitation per se had no effect on dormancy, drought seemed to prolong this state. As production of leaves is costly, higher number of leaves may occur only after favourable, wet years while water-deficiency during growing season leads to decreased growing capacity of bulbs¹¹.

The weather parameters of the actual spring expressed stronger effects, than the vegetative periods of the previous years. Especially the effects of temperature-related parameters were important, similarly to the findings of other studies, which found that temperature has a superior role compared to precipitation^{8,35}.

Temperature plays a crucial role in both the dormancy breaking of bulbs and in the growth and development of individuals. Increasing mean, minimum, and maximum temperatures, as well as drought in general decreased the chance of individuals to break dormancy. In contrast, the presence of frost days increased the proportion of dormancy breaking *C. bulbocodium* individuals. These results are in accordance with the findings of other studies, which found that geophytes can germinate, grow, and develop better under colder conditions^{47–50}. These studies agree that geophytes require a warm – cold – warm period to properly complete their life cycle. Without this temperature sequence *Fritillaria meleagris* individuals grown in vitro were not able to break dormancy and to develop properly⁵⁰, while in *Corydalis bracteata* individuals the sugar content of buds was insufficient, possibly leading to bud-abortion⁴⁸. In the background of these negative effects, changes in molecular pathways can be found. Without the warm–cold–warm temperature sequence, especially without the cold period, certain sugar transport routes are not activated and the development of geophytes cannot be completed^{48,51}. Increased temperature during the vegetative period was found to lead to shorter leaf activity, earlier leaf senescence, and lower bulb yield^{48,52–54}. These changes are also related to altered molecular pathways: increased temperature leads to increased photosynthetic rate in many early flowering species, however, cellular growth in storage organs cannot keep up with increasing demand of storage capacity. Fast sugar allocation leads to negative feedback and results early leaf senescence and low bulb size compared to plants grown under colder temperatures. Under lower temperatures, these negative feedbacks occur later, supporting a longer leaf activity as well as prolonged bulb growth^{52,53}.

The effect of temperature can manifest also indirectly by affecting the development of surrounding vegetation, and in this way the light availability⁵⁵. However, the studies focusing on light-limitation of geophytes rarely consider the understorey vegetation and focus mainly on canopy closure, despite the presence of herbaceous vegetation in some habitats may be similarly important as the canopy, by changing light-conditions. Based on our observations, we considered that the shading effect of herbaceous vegetation should be considered too, as it occurs earlier than canopy closure. As *C. bulbocodium* is a weak competitor for light^{39,56}, the development of the surrounding herbaceous vegetation can limit its growth, assimilation capacity as well as its fitness. In accordance with these studies we also found that the number of detectable individuals was negatively affected by the surrounding dense vegetation and also, that capsule production success was negatively affected by increased understorey plant cover. A negative effect of shading on fitness was also found in *Erythronium japonicum*⁵⁷ and in six other species as well⁵¹, while other species, like *Gagea lutea*, can be insensitive to light conditions⁹. The results published so far are controversial and highlight that mechanisms underlying the observable changes are affected both by light- and temperature, so their effects cannot be separated³⁵. The effect of litter cover was opposite to that of understorey plant cover, as the presence of litter layer affected positively the number of detectable individuals. *C. bulbocodium* individuals could easily overgrow the present litter layer; furthermore,

the litter could express a positive effect on them by moisture retention and providing thermal protection against increased temperature^{58–60}. Baltzinger et al. (2012) found, that *Anemone nemorosa* also benefits from the presence of litter layer, although in that case the positive effects manifested in leaf protection during late frosts⁶¹. While the presence of litter can buffer the negative effects of abiotic conditions, litter accumulation above a certain level can shift its effects from positive to negative^{62,63}, so management measures should be taken to prevent it.

The efforts invested in our study, i.e. three monitoring dates annually for six years, can be considered as a high sampling intensity⁶⁴. With this intensity we were able to detect not only the easily detectable flowering individuals, but also “hiding” individuals. Furthermore, we were able to reveal a major setback of the widely applied monitoring practices (i.e., counting the flowers one occasion per year): the inability to accurately measure population size and population dynamics based only on the number of detectable individuals. Similar results were obtained by Aronne et al. (2023) who highlighted that most autecological studies of threatened species focus only on the flowering, which is a major bottleneck for effective species conservation⁶⁵. In our case, the proportion of flowering *C. bulbocodium* individuals compared to the total number of individuals showed great inter-annual variability (17–60%), mainly due the great variability detected in the number of flowering individuals. Similarly, year-to-year differences were also found when capsules production success was considered, with a trend different from that of the number of flowering individuals. The inaccuracy to estimate population size and reproduction success based on flowering individuals could be reduced by taking into account factors affecting the individual life stages of species, for example actual and lagged weather parameters that induce or maintain dormancy (drought, warm weather), induce flowering (cold weather) or capsule production (cold weather).

Conclusions

C. bulbocodium is a species with complex population dynamics, with dormancy-prone bulbs and great inter-annual variability in the number of flowering individuals, which represents in general only one third of the total individuals. Therefore, flower-counting-based monitoring schemes inaccurately represent the population size, and provide misleading estimations about the reproduction success of the species. The inaccuracies can be related to factors affecting the life stages of the plant, like the temperature-related weather parameters, which should be taken into account to correct estimations. Furthermore, we highlight that for an accurate estimation of population size and detection of population dynamics, monitoring at a single date is not sufficient, as it can underestimate population size by 40–83%. Long-term monitoring is required, or if that is not possible, monitoring in the years following wet and cold springs and cold winters could increase the accuracy of population estimations of the flowering individuals, while surveys in cold springs can estimate reproduction success the most accurately. Long-term monitoring could also account for individuals with prolonged dormancy and so may further increase estimation accuracy. In the era of climate change gaining information about the changes of the population dynamics of endangered plant species and about the underlying factors is crucial to assess vulnerability and to develop accurate management plans for conservation.

Materials and methods

The studied population and field survey

C. bulbocodium is an early spring geophyte with a disjunct distribution from the Pyrenees to the Caucasus and the Lower Volga region. In western Europe (i.e. the Pyrenees and the Alps) it occurs in alpine meadows, between 1000 and 2500 m asl., while from Central- and East-Europe to the Volga region it inhabits steppe and forest-steppe vegetation in lower altitudes. In Hungary, due to the destruction of its natural habitats and its illegal collection in the past, its populations have undergone a severe decline and present day it has only a few, isolated populations²⁶.

The population studied is located in the Northern Great Plain at 150 m asl in Újléta, close to the city of Debrecen (East-Hungary). Only a few individuals were collected for herbarium from the study region in the early 20th century, but the studied population was discovered only in the end of the century^{26,33}, resulting in a lack of long-term phenological records in the region. Since *C. bulbocodium* is strictly protected, we did not collect any parts of the plant during our study and used a non-destructive sampling protocol, in close cooperation with the ranger service of the Hortobágy National Park. The site is characterised by forest steppe vegetation formed on sand. The vegetation structure is characterised by loose woody vegetation dominated by *Quercus robur* and *Crataegus* spp., but the study site is largely overgrown by the invasive alien tree *Robinia pseudoacacia*. The soil of the site is sandy soil with low humus content. We started the monitoring of the *C. bulbocodium* population in Újléta in March 2018. We established twenty permanent plots of 2 m × 2 m in the peak of flowering in March. The plots were permanently marked with coloured steel nails in their four corners and also GPS coordinates were recorded in the centres of the plots. The permanent plots were monitored yearly between 2018 and 2023, three times each year (Supplementary Table S2), to cover all detectable life stages (Table 1; Fig. 1). As we observed some minor shifts in the timing of life stages across the years, we scheduled the surveys to match with the peak of the life stages (see Supplementary Table S2) and executed them in one day, as to reduce observation bias caused by different observation dates. The same persons performed the surveys in all years to reduce observer bias.

Survey I: In mid-March (peak of flowering period) we counted the number of flowering individuals and marked each with a red plastic bead (for aiding the search for fruiting individuals in the fruiting period, see Survey III).

Survey II: In mid-April we thoroughly searched the permanent plots for the leaves of *C. bulbocodium* individuals and recorded the total number of individuals present in each plot. As leaf number is an indicator of development stage of individuals, we marked every individual with a temporary mark of one of four different colours indicating their leaf number: (i) one-leaved, young individuals (1L); (ii) two-leaved individuals (2L);





				
Life stage	Bulb*	Flowers	Leaves	Capsules
Season of detectability	-	March	April	May/June
Difficulty of detection	-	Low	Very high	High
What the life stage indicates	Total number of individuals (non-dormant + dormant)	Number of individuals with reproductive potential	Number of non-dormant individuals	Number of successfully reproduced individuals

Table 1. Detectability of life stages of *C. Bulbocodium*. *As *C. Bulbocodium* is a strictly protected species, bulbs are not suitable for monitoring. The photo of the bulb is just an illustration (photo of a bulbous garden plant, not *C. Bulbocodium*, © B. Deák). © Flower and leaves: R. Kiss, capsules: T. Migécz.

(iii) three-leaved individuals (3L) and (iv) four-leaved individuals (4L). In the centre of the markings a dot indicated if the individual was flowering in March. We took photos of the plots with the markings (see the [photo management](#) section for more information).

Survey III: In late May or early June, when most capsules were matured but not opened yet, we surveyed the capsule-production (fruiting) success by searching for previously flowering individuals (using bead-marks, photo-records) and recorded their capsule production success. We measured the length of five randomly selected capsules in each plot. At the end of this survey, we removed the bead-markings from the study site.

During Survey II and III we also recorded plot characteristics: the percentage cover of herbaceous vegetation, mosses and litter as well as the percentage of bare ground in the plots.

Photo management

Unique IDs were assigned to each individual starting from 2018 based on their positions on the photos. Individuals in the same position across the years were marked with the same ID, while new IDs were given to the newly appeared individuals. Based on coloured markings on the photos, presence-absence data of each individual was recorded and individuals were assigned to one of the four leaf-number categories (1L, 2L, 3L, 4L) in each year. Based on yearly presence-absence data and leaf-number categories of individuals we also distinguished dormant individuals, that were not detectable in certain years.

We assigned a behaviour category to each individual in each year based on their leaf-number and dormancy state in the previous year. The six established behaviour categories accounted for leaf-number change, i.e., decreasing (LD), increasing (LI) and stable (LS) leaf number, and change in bulb-dormancy, i.e., entering (DE), breaking (DB) or stable (DS) dormant state. For this, we took into account individuals observed at least four times during the six study years. Unfortunately, two photos in years 2019 and 2023 were blurry or missing; therefore, we needed to exclude the individuals represented in these photos from the categorization to behaviour types. Further individuals were excluded when they could not be tracked accurately due to their aggregated positions. In total we included in this analysis 474 out of 1069 individuals, and DS category was ultimately excluded due to low number of individuals in this category.

Weather parameters

Weather parameters originating from the closest meteorological station (Debrecen Airport) were derived from the Meteorological Database of the Hungarian Meteorological Service (OMSZ)⁶⁶ and Operational Drought and Water Scarcity Management System of the General Directorate of Water Management (OVF)⁶⁷. The following weather parameters were calculated for eight time periods (Fig. 1, Supplementary Table S1, Supplementary Table S13): temperature (daily mean (T_{mean}), mean of daily maximums (T_{max}), mean of daily minimums (T_{min}), diurnal temperature range (DTR), maximum of DTR (DTR_{max}), minimum of DTR (DTR_{min}), precipitation (sum of daily precipitations (P_{sum}), number of days with precipitation (D_p), number of frost days (D_f) and drought index. The periods considered were: (1) early spring–peak flowering period, (2) fall – flowering period, (3) vegetative period of the previous year, (4) leaf development period, (5) fall–peak vegetative period, (6) early spring–peak vegetative period, (7) period between flowering and fruiting and (8) flowering period. These periods were chosen as they are expected to have a main influence on dormancy breaking (1, 2, 5), on bulb growth (3, 4, 6) and on reproduction (7, 8)^{14,33,47}.

Statistical analyses

All statistical analyses were performed in the R statistical environment (version 4.3.2)⁶⁸ using *glmmTMB* (GLMMs)⁶⁹, *ggeffects* (estimated marginal means)⁷⁰, *MuMin* (marginal and conditional R^2)⁷¹, and *ggplot2* (plots)⁷² packages. Dependent variables were number of flowering and detectable individuals, number of individuals in the behaviour categories, ratio between flowering and total number of individuals, number and length of capsules and capsule production success. Akaike's Information Corrected Criterion (AICc) was used to decide whether Plot ID, Year, leaf-number category (in case of detectable individuals) or autoregressive correlation structure (AR1), accounting for repeated measurements, improved the models (in this case were used as random

factors) or could be excluded from the full models. Except of drought index, all weather parameter data were scaled, not centred. For more information see Supplementary Table S1.

General analyses

GLMMs were used to study the effect of Year (fix factor) and plot characteristics on the dependent variables: number of flowering individuals, capsule number and length, capsule production success and number of individuals in the five behaviour categories. To study differences in the case of detectable individuals and number of detectable individuals by leaf number, interaction between Year (factor) and leaf-number category (factor) was included in the models (Supplementary Table S1). When indicated by AICc, Plot ID or ARI structure, accounting for repeated measurements, was also included in the models (Supplementary Table S1).

Weather parameters

Generalized linear mixed models (GLMMs) were used to test the effects of weather parameters on the dependent variables (number of flowering individuals, number of detectable individuals, number of detectable individuals by leaf number category, changes between behaviour categories, the number of flowering individuals compared to the total number of individuals, capsules length and production success) (Supplementary Table S1).

Data availability

The datasets analysed during the current study are available from the corresponding author on reasonable request.

Received: 8 July 2024; Accepted: 17 October 2024

Published online: 29 October 2024

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Acknowledgements

The study was supported by the Hungarian National Research, Development and Innovation Office (Grant Number: NKFI PD 137632 – RK). The work of the authors was also supported by the NKFI KKP 144096 (OV) and the NKFI FK 135329 (BD) grants. We are grateful to Szilvia Radócz and Ferenc Báthori for their help during some of the surveys.

Author contributions

RK, OV, BD, LD, LS conceived and designed the experiment; RK, KL, LG, ÁT, TM, LS and LD took part in the field surveys; RK and BD made the statistical analysis; RK designed the figures; RK and OV wrote the manuscript. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-024-76942-5>.

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