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Effect of land use and climate change on the future fate of populations of an endemic species in central Europe

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ABSTRACT

The identification of optimal management strategies for a given species is a major challenge of species conservation. It becomes especially challenging when the environmental conditions are expected to change in the future, and the optimal management applied today may differ from the management that is optimal under the changed conditions (e.g. due to climate change).

This study evaluates prospect of a rare plant species endemic to semi-natural grasslands in central Europe, *Gentianella praecox* subsp. *bohemica*. The number of populations of this species has declined rapidly in the last 60 years; currently, a conservation action plan has been established in the Czech Republic, where most populations of this species occur. This study uses periodic matrix models to compare different management regimes under different scenarios of climate change and to identify the optimal management in each case.

Without management, populations of the species are not able to survive. Flowering individuals can occur for a long time after the cessation of management, but the extinction of the population is inevitable within several decades. Without management, even very large populations (1000 flowering individuals) will go extinct in less than 50 years. Total extinction (including seed bank) will follow several years after observation of the last flowering plant. The most suitable management is mowing and disturbance (by harrowing), which is also the best method for restoration of threatened populations. Mowing is less suitable, but it is fully sufficient for large prospering populations. When managed, even small populations (10–15 flowering individuals) are able to survive. When management is applied, future climate change may have a relatively small impact on the probability of survival of the species. Climate change will, however, increase the extinction probability of very small populations.

1. Introduction

One of the main negative factors affecting species survival in the current landscape is land use change (Luoto et al., 2003), which causes habitat fragmentation and loss, two major drivers of species loss worldwide (Foley et al., 2005). In Europe, the most dramatic changes came with the industrialisation of agriculture in the second half of the 20th century. Some formerly common habitats formed by traditional management decreased significantly and were highly fragmented (e.g. extensive pastures and wet meadows). Thus, plants adapted to such types of habitats became highly endangered (Eriksson et al., 2002; Procházka and Holub, 2000). Because these species are dependent on specific human activities, current nature conservation actions are, in large proportion, aimed at the management of habitats that often host many species threatened by land-use changes. However, the best management approach to take is not clear when the original management method (e.g. extensive grazing) is not feasible on such small habitat fragments.

Another threat for species decimated by land-use change is climate change (Travis, 2003). Towards the end of the 21st century, the climate in central Europe should be drier and warmer, and extreme rainfall events should be more frequent (Rowell, 2005). This change means an increased probability of severe weather disturbances due to droughts or floods. Some species are adapted to periodic catastrophic events, which are regular parts of the species' life cycles (Blom and Voesenek, 1996; Roy and Sonie, 1992). Other species, however, including meadow species, are not adapted to such extremes. The question becomes how much such a weather disturbance, such as extreme drought, that results in the death of most individuals, except seeds in the seed bank, affects the probability of survival of the population.

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For assessing future prospects of such species and detecting the most suitable approaches for their management, it is necessary to model population viability under expected disturbance regimes and different management treatments. Because all natural populations experience stochastic variation in vital rates, stochastic demographic models (Caswell, 2001; Schleuning and Matthies, 2009; Torang et al., 2010) provide an appropriate framework for analysing the effects of various environmental changes on the population dynamics of species.

Population viability is usually described using population growth rate, λ, or more reliably, stochastic population growth rate (Caswell, 2001). However, when the environment changes dramatically, the population growth rate reflecting long-term population growth is difficult to use, as it changes from year to year following the change in the environment (but see Horvitz et al., 2005). In such a case, we suggest using extinction probabilities of small populations instead of the population growth rate (Lennartsson, 2000; Lennartsson and Oostermeijer, 2001).

There have been several studies that argue that it is not meaningful to calculate extinction probabilities (Fieberg and Ellner, 2000; Ludwig, 1999). Criticisms are mostly based on studies of animal populations and emphasise that it is impossible to collect sufficient data sets to generate reliable predictions. Plants have the advantage of sessile lives; thus, it is easier to precisely follow a larger number of individuals. It is even possible to perform experiments that can collect information on the probability of all transitions in the life cycle and on the effect of different management methods on these transitions (Ramula, 2008). Moreover, Beissinger and Westphal (1998) discuss that problems with extinction probabilities lay in their interpretation. Absolute interpretations should be avoided, but relative interpretations are reliable and useful, such as comparing habitat conditions under which a plant population has a higher probability of survival. Such relative information is often demanded the most by practical conservationists, as it can, for example, indicate which management strategy to apply to preserve a given species.

Extinction probabilities are often calculated over many-year period, such as 50 years (Bucharová et al., 2010; Lennartsson and Oostermeijer, 2001) or 100 years (Menges, 1990). It may be argued that predictions over such a long period of time are not realistic, as many factors will change during that time. We fully agree with this objection. However, extinction probabilities must not be interpreted as predictions but rather as illustrations of current processes in the populations (Beissinger and Westphal, 1998). Calculations over such a long time period show the trends under the current conditions. If such projections were generated over a shorter period (e.g. 10 years), the threat of extinction may not be seen for some species, such as those forming long-lived remnant populations (Eriksson, 1996).

In our study, we evaluated *Gentianella praecox* subsp. *bohemica*, a typical representative species endangered by land use and climate change. It used to commonly grow on wet pastures and meadows. With changes in land use, the number of populations has drastically decreased; currently, there are only 111 populations, ranging in size from several individuals to several thousands of individuals. However, sizes of individual populations vary highly from year to year. Thus, this plant is currently of great interest to nature conservation (ec.europa.eu/environment/nature/natura2000, last accessed 19.9.2011). Recently, an action plan for the restoration of this plant has been developed in the Czech Republic. Creating an effective action plan requires reliable scientific information (IUCN/SSC, 2002, 2008).

We estimated the susceptibility of small populations of *G. praecox* subsp. *bohemica* to extinction under three different management regimes: no management, mowing and mowing followed by disturbance by harrowing, which was part of the traditional management practice. Financial resources are always limited; thus, we identified the minimal suitable management (the costs for the three management types differ) that will ensure the existence of the population under given conditions (e.g. population size and frequency of extreme events). Because in some areas, the populations are in threatened states due to the lack of appropriate management, we also estimated the probability of successful restoration from the seed bank of almost extinct populations and identified the best management for their restoration. Moreover, we simulated the possible influence of future climate change (an increased frequency of extreme drought) on population prospects.

2. Methods

2.1. Study species

G. praecox (A. et J. Kerner) E. Mayer subsp. *bohemica* (Skalický) Holub is a small (usually 10–25 cm tall), strictly biennial plant. It flowers in autumn (mostly September), which is followed by seed production. Seeds either germinate in the next spring, or they are stored in the seed bank. Germinated seeds slowly develop during the first season into rosettes. The 1-year-old plant forms a rosette the next year, carrying flowering stems in the autumn. Thus, the individuals (except the seeds in the seed bank, which can survive in the same stage) have to grow or they die (Fig. 1). The species is pollinated by insects. The number of individuals in a given population fluctuates highly from year to year.

G. praecox subsp. *bohemica* is an endemic taxon of the Czech Massif. Its historical distribution included the Czech Republic, the Bavarian part of the Šumava Mountains (Böhmerwald, Germany), the northern part of Austria and the southern part of Poland. It typically inhabits secondary grasslands, with traditional management of grazing and mowing (Kirschner and Kirschnerová, 2000). With agricultural intensification, the traditional management of the semi-natural grasslands decreased their size considerably, resulting in a steep decrease in the number of populations of the taxon (Brabec, 2005). Recently, it was identified at only 111 localities over the entire distribution range (Brabec, unpublished). Thus, it is rare and of interest to nature conservation (Procházka and Holub, 2000; ec.europa.eu/environment/nature/natura2000, last accessed 19.9.2011).

2.2. Study sites

The experiment was established at four localities (Table 1) in the centre of the current distribution area of the species: southern and south-western Bohemia, the Czech Republic. All of the studied

Table 1
Experimental populations in south and south-western Bohemia, the Czech Republic.

Locality	Onšovice	Dobročkov	Chvalšiny	Hroby
Position	N 49°06′46″,E 13°46′53″	N 48°54′38″, E 14°09′17″	N 48°50′57″, E 14°12′10″	N 49°23′36″, E 14°51′22″
# of flowering individuals per year (2000–2010)	May-00	0–3445	219–2825	63–7050
Vegetation type	Dry grassland	Dry grassland	Mesic grassland	Mesic grassland
Altitude (m)	630	660	610	500

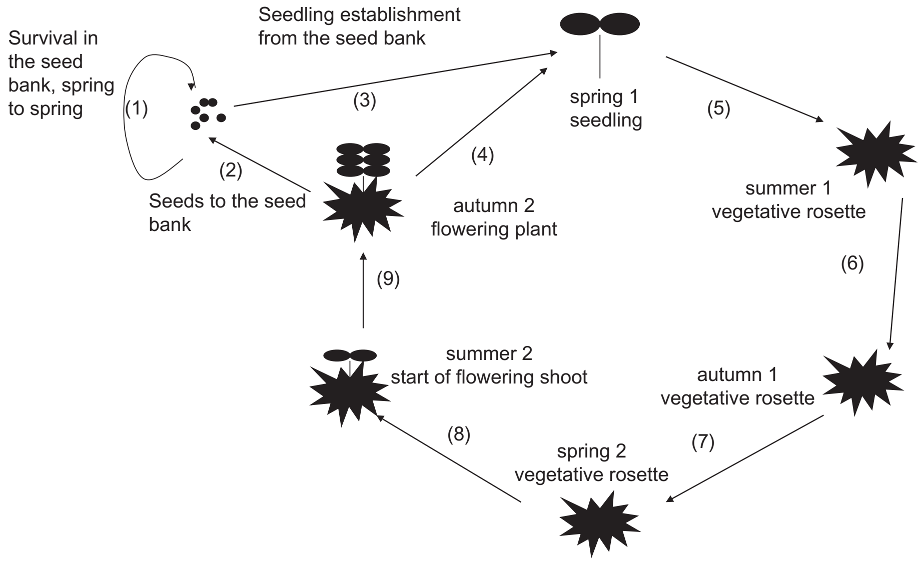

Fig. 1. Life cycle of *Gentianella praecox* subsp. *bohemica*. The plant is strictly biennial. Seedlings germinate in the first spring, the plant grows, overwinters and produces seeds in the next autumn. Seeds either give rise to seedlings the next spring, or they form the seed bank. Each transition (marked by an arrow in the picture) was assessed in the experiment and is present in the transition matrices (Table 2).

Table 2
Structure of annual set of matrices describing the life cycle of *Gentianella praecox* subsp. *bohemica*.

	Autumn *t*			Spring *t*			Summer *t*		
	Seed	One year old plant	Two year old plant	Seed	One year old plant	Two year old plant	Seed	One year old plant	Two year old plant
	Spring t + 1			*Summer t + 1*			*Autumn t + 1*		
Seed	(1) Survival in the seed bank		(2) Seeds to seed bank	1			1		
One year old plant	(3) Seedling establishment from the seed bank		(4) Seedling establishment from the autumn seed production		(5) Growth			(6) Growth	
Two year old plant		(7) Survival over winter				(8) Growth			(9) Growth

First transition is autumn-spring, when seedling establishment and survival of plants over winter occurs. Survival in the seed bank was also assigned to this transition, since we knew only between-years survival in the seed bank, not between-seasons. *t* is annual life cycle (autumn to autumn). The transitions spring-summer and summer-autumn contain growth only. Numbers (#) refer to the corresponding transitions in the life cycle (Fig. 1). Data or one annual matrix set describes behavior of plants in population in 1 year, thus originate from three subsequent experiments established within three subsequent years, i.e., three experimental life cycles (establishment for autumn seed production from first, survival of 1 year old plants from second, survival of 2 years old plants from third experimental life cycle).

localities were large (>500 flowering individuals), as we needed a sufficient number of individuals to perform the experiments. Moisture conditions varied from mesic, dominated by *Arrhenatherum elatius,* to drier, dominated by *Brachypodium pinnatum*, representing the variability of the natural habitats of *G. praecox* subsp. *bohemica*. The grasslands are species-rich and host many rare species, such as *Gymnadenia conopsea*, *Platanthera bifolia*, *Botrychium lunaria* and *Lilium martagon*. The grasslands were irregularly mown or grazed before the beginning of the experiment.

2.3. Data collection

2.3.1. Survival of individuals – seed sowing experiment

At the four experimental localities, a sowing experiment was performed for 2–5 years (2000–2005). At each locality, six plots (60 × 40 cm) divided into six subplots (15 × 15 cm with a 2.5-cm buffer zone) were established every year during the sowing experiment (Supplementary Appendix A). Three types of management were performed in a random design in the subplots, and each management type was applied to two subplots: unmanaged, clipping (simulation of mowing) and clipping and vegetation cover disturbance (simulation of mowing and disturbance by harrowing, part of traditional management). Clipped biomass was removed from the plots. Management was performed in October after the fruiting of the species because management at the time of flowering and fruiting is highly unsuitable for *Gentianella* species (Lennartsson and Oostermeijer, 2001).

At one of the subplots of a given management type, 600 seeds of *G. praecox* subsp. *bohemica* collected from the locality were sown in the autumn, shortly after seed maturation, to mimic the natural release of the seeds as closely as possible. Seeds were collected, air-dried and evenly sown on the soil surface the next day. No further treatment (e.g. watering) was applied on sown plots to maintain natural conditions. The high sowing density corresponds approximately to the situation when a plant with ripened seeds falls down, and all of the seeds remain in a very limited area, which occurs very often in the field (one plant produces on average 613 seeds, unpublished results). The other subplot with the given management type served as a control for natural germination. During sowing each year, seeds were sown to newly established plots.

All of the plants present in the subplots thus originated from one sowing event. In each year, there were six replicates for each treatment.

Germination, seedling establishment and the survival of plants in the experimental plots were recorded three times per year for two subsequent years until completion of the entire life cycle (the plant is strictly biennial). At each census, the number of plants present in each subplot was recorded. Thus, we obtained the proportions of established/surviving individuals between censuses. Whole plants with ripened seeds were collected, and the numbers of seeds were counted in all plant capsules to assess seed production. In addition, germination and seedling establishment from the seed bank (i.e., delayed germination of the sown seeds) were also followed the second year after sowing, which was possible because 1- and 2-year-old plants can be easily morphologically distinguished from each other.

During the experimental period, an extremely dry year occurred (2003). The summer was so dry that almost all of plants died, and only the populations in the seed bank survived. Such a dry year occurs with probability of 1:20–1:50 in the study area (period 1950–2007, internal climatic data from our institute). Thus, we were able to record the fate of the population in the instance of a catastrophic event – extreme drought. We subsequently distinguished "dry year" data (from 2003) from "normal year" data (from all other years).

2.3.2. Survival in the seed bank

Eighteen fine-mesh sacks, each containing 300 seeds (collected at a given locality), were buried at each of the four localities in the autumn of 2000 or 2001. In autumn for the subsequent 7–8 years, 2 (in exceptional cases, only 1) sacks were excavated, and undamaged seeds were counted. Undamaged seeds were considered to be alive, following the approach of Fischer and Matthies (1998b). Additionally, we cut open several undamaged seeds to be sure that seeds with this representative appearance were actually intact.

2.4. Matrix construction

A periodic matrix model (Caswell and Trevisan, 1994) was used for analysing the extinction probability of *G. praecox* subsp. *bohemica*. Periodic matrix models are used to describe the effects of cyclic environmental variation, both seasonal and interannual, on population dynamics. If an environmental cycle (e.g. annual) is of length m, with matrices $B^{(1)}, B^{(2)}, \ldots, B^{(m)}$ describing the population growth during the m phases of the annual cycle, then population growth over the entire cycle is given by the product matrix

$$A = B^{(m)} \times B^{(m-1)} \times \cdots \times B^{(1)}$$

In the case of this study, we have an annual cycle of length 3 (transitions autumn-spring, spring-summer and summer-autumn), which is thus represented by three separate transition matrices. The following stages were distinguished: seeds in the seed bank, seedlings, first-year rosettes in the summer and autumn and 2-year-old plants in the spring, summer and autumn. The first matrix represented the autumn-spring transition, which was the transition connected with reproduction (e.g. seedling establishment from current seed production and from the seed bank), survival in the seed bank and over-wintering of 1-year-old plants. The second matrix represented the transition from spring to summer, and the third represented the transition from summer to autumn. These two matrices contained only information on growth of 1- and 2-year-old plants. Survival of seeds in the seed bank was assigned 1 here because we only knew between-year survival, not survival between seasons within a year. The annual setting of these three transitions following each other described 1 year of dynamics for the population (Table 2).

The probability of seedling establishment was estimated as the number of seedlings in the sowing plots in the spring divided by the number of sown seeds in the previous autumn. The probability of transition between all of the other size categories was obtained from the sowing experiment as the proportion of individuals in the plot in the current census divided by the number of individuals in the plot in the preceding census, summed across all subplots with the same type of management in the given year at the given locality (note that all individuals in a single plot are of the same stage). The probability of survival in the seed bank was estimated from the burial experiment as the number of viable seeds in the bags in 1 year divided by the number of viable seeds in the bags the year before, summed over all localities and years. We estimated this proportion by combining the data over all of the years and locales, rather than separate values for each locality and time interval, as data variability was huge and without any strong trends between years/localities.

We started the sowing experiment for estimating individual survival in several subsequent years. For most of the years, we knew the behaviors of both the 1- and 2-year-old plants. However, for some years, we did not know all of the transitions. This situation occurred in the 1st and last year, and it was also the case in 2003, due to the extreme mortality in that very dry year (Supplementary Appendix A).

Univariate analysis of the influence of environmental characteristics on vital rates in our data indicated that the largest differences were between management types and types of year (normal/dry year) in most cases (data not shown). Missing data were thus replaced by weighted means (by numbers of individuals entering the transition) for years with similar weather (normal/dry year) and management type at a given locality. The type of year had no effect on seed production per plant (data not shown), and missing values for seed production were thus replaced by the weighted means of the data over all years from a given locality and management type. This procedure resulted in as many annual sets of matrices (each annual set consisting of three matrices of transitions between seasons) and as many life cycles as we established in the experimental design (by sowing) minus 1 (due to the dry year in 2003). In total, we obtained 14 annual sets of matrices for each management type: three annual sets of matrices from two localities, and four annual sets of matrices from two localities.

Despite high sowing density (3 × 600 seeds per locality, management and year), there were quite a few individuals for the construction of the transition matrices in some annual cycles, due to the high mortality of seedlings in some years and management types (in extreme cases, only several individuals were available, especially under the no management regime). Thus, we also decided to construct pooled sets of matrices over all localities for each type of year (dry and normal) and for each management type, which were more robust than the separate sets of matrices described above. We pooled all individuals from all localities in a given type per year, thus obtaining two types of matrix sets for each management type: a set of matrices for a dry year and a set of matrices for a normal year.

2.5. Performance of the populations

Population performance under different conditions was expressed as the extinction probability of a given population. The stochastic simulation approach, which included demographic stochasticity (Caswell, 2001), was used to combine the annual sets of three matrices describing within-year dynamics (i.e., the three within-year matrices were always kept together). Populations of certain population vectors were projected by randomly drawing one annual set of matrices of the given type for each year. Matrices could be drawn with a certain probability, and the sum of the probability for all matrices equals 1. At each time step, the population vector was multiplied with a given matrix. There were three time steps within a year. The resulting population vector after each step was replaced by a value drawn from a Poisson distribution with the given mean to simulate demographic stochasticity. This projection was run over 100 years (i.e., 300 steps). The entire simulation was repeated 1000 times, and the extinction/survival of the population at the end of each simulation was recorded.

The extinction probabilities over 100 years were used to extrapolate the current processes in the populations and, thus, to illustrate the long-term effects of the given population dynamics. Running the model over 100 years enabled us to see the long-term effects, especially in unmanaged populations. When run over a shorter period (e.g. 20, 30 or 50 years), the effect of management absence did not seem to be as lethal because there were still some seeds present in the seed bank and the population did not go extinct, despite the fact that extinction was only matter of a few additional years.

First, we ran the model with pooled matrices. Each estimate of transition probability and, thus, each estimate of extinction probability was confined with an error because of the limited number of individuals that could be sampled. To estimate this error, we bootstrapped the original data used to derive the original matrices 1000 times (Alvarez-Buylla and Slatkin, 1994), created new matrices from the bootstrapped data and used these bootstrap matrices to estimate the extinction probabilities of populations as described above. Based on the results, 95% confidence intervals of the extinction probabilities were constructed (Efron and Tibshirani, 1994). For this, a MATLAB script developed by Münzbergová (2006, 2007) was used.

Second, we ran all of the models using separate matrices. Separate matrices were sometimes based on several individuals only. The bootstrap of the data resulted in extremely wide confidence intervals, suggesting that these matrices are based on too few individuals to precisely describe reality. Moreover, results based on separate matrices were largely within confidence intervals obtained from pooled matrices. Thus, only results based on pooled matrices are presented.

The initial population vectors in all of our simulations were arbitrary. Using different initial vectors, however, did not qualitatively change the results. Thus, only one initial vector was used for all simulations (see below).

2.5.1. Effect of management and population size on population survival (Model 1)

Populations of *G. praecox* subsp. *bohemica* are often small (reaching a maximum of approximately 15 individuals. Thus, we determined how small a population can and still have a reasonable chance for survival under different management conditions. Population vectors of 1–100 flowering individuals were projected by randomly drawing one set of matrices of a given management type (one set for a dry year, one set for a normal year), with a frequency of dry years of 1:20. For the management type with the highest extinction probability (i.e., the absence of management), we also calculated the time to extinction. The time to extinction was calculated both as the time to total extinction, including the seed bank, and as the time to putative extinction, when no flowering plants appear but when some individuals are still present in the form of inconspicuous 1-year-old rosettes and/or in a seed bank.

2.5.2. Population restoration (Model 2)

When a population is unmanaged, it inevitably goes to extinction. The most obvious sign of an upcoming extinction is the absence of flowering plants. In this case, it is still possible to restore the population from the seed bank by the introduction of management. The success of such a restoration depends on time, such as for how long no flowering plants were observed. In the model, we projected a population consisting of 50 rosettes and 50 flowering plants with no-management matrices. This projection inevitably led to a population decrease, and after a certain amount of time, there were no flowering plants. The model was still projected for a predefined time (1–15 years) with matrices describing no management, simulating the time until the responsible management office recognises that something is wrong with the population and implements management. After this predefined time without any flowering plants, we switched the transition matrices to matrices describing a selected management strategy (mowing or mowing and disturbance). We then ran the model over 100 years. We recorded in which time step the management was induced and the percentage of successfully restored populations. Dry years were again incorporated, with a probability of 1:20.

2.5.3. Climate change and population survival (Model 3)

A simulation of climate change, expressed as an increased frequency of dry years, on population prospects was performed using the same approach as in Model 1, but we varied the frequency of dry years from 1:1 to 1:50. The initial population vector contained 10 flowering individuals.

3. Results

3.1. Effect of management on population survival (Model 1)

The extinction probability of a population decreases with increasing population size (Fig. 2). There were strong differences between management types. Even very small populations (fewer than 10 flowering individuals) have a very high probability for survival under the management of mowing and disturbance. When mown only, small populations have a much smaller probability for survival. For populations larger than 10–20 flowering individuals, both mown and disturbed and only mown populations have an extinction probability of almost zero. However, even very large populations (100 flowering plants) when unmanaged have zero or a very small probability for survival (Fig. 2). However, the lower limit of the confidence interval decreases with increasing population size, suggesting that even large unmanaged populations may, under current conditions, survive for 100 years.

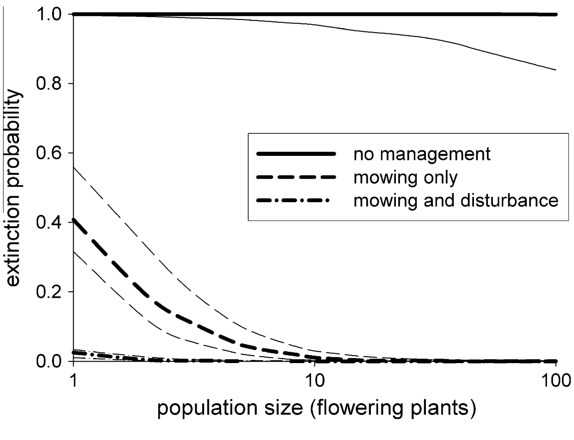

Fig. 2. Extinction probability in 100 years as a function of population size (Model 1). The 95% confidence intervals are indicated by thin lines. In unmanaged populations, a wide confidence interval is given by the low germination and high mortality of plants and, thus, the low number of individuals available for assessing transitions in the experiment.

The slow disappearance of flowering plants is interesting. After the end of management, even small populations of approximately 10 individuals will still produce some flowering plants for an average of 12 years (Fig. 3). Large populations (e.g. 100 and 1000 flowering plants) will produce flowering individuals without being managed for much longer after the cessation of management – 25 and 39 years on average, respectively. Because no flowering plants appear in the population, the population will go completely extinct (including vegetative individuals and the seed bank) within approximately 8 years.

3.2. Population restoration (Model 2)

The probability of successful restoration of a population from the seed bank decreases with the time since the observation of the last flowering plant (Fig. 4). When using the most effective restoration management (i.e., mowing and disturbance), there is a more than 80% probability of the successful restoration of the population from the seed bank after no flowering plants have been observed for 3 years. With an increasing time of observing no flowering plants, the probability decreases considerably, with only a 30% restoration success 6 years after the observation of the last flowering plant and with less than a 3% restoration success 10 years after the observation of the last flowering plant.

When only mowing is used, the probability of successful restoration is significantly lower from 2 years after the observation of flowering plants (confidence intervals do not overlap); after 6 years, the probability of successful restoration is lower than 10%, and after 10 years, it is lower than 1%.

Flowering plants were present for some time even without management. For example, the run of a model of a successful restoration of a population presented in Fig. 5 shows a relatively long time in which a reasonable number of flowering plants are present before they finally disappear, and then there is a steep increase in flowering plants after the introduction of management.

3.3. Climate change and population survival (Model 3)

The probability of extinction of populations increases with the increasing probability of dry years (Fig. 6). Again, there is an important difference between management types. Unmanaged populations do not survive under any frequency of dry years. In mown populations, the extinction probability is approximately the same up to a 1:10 frequency of dry years; it then steeply increases. In mown and disturbed populations, the extinction probability is almost 0 until a 1:5 frequency of dry years; it then increases steeply.

4. Discussion

In this study, we used extinction probabilities of small populations to assess the effect of different management types on the population survival prospects of a rare and endangered species, *G. praecox* subsp. *bohemica*. Management type (mowing or mowing plus disturbance by harrowing) has an impact, especially on populations in certain critical situations (e.g. a very small number of individuals, population restoration or a high frequency of dry years), but in large, prospering populations, the management type has a rather small impact on the probability of population survival.

In contrast to the very little difference in the effect of mowing and mowing and harrowing in most cases, the absence of management had a dramatic effect on the population persistence; populations of all sizes were not able to survive without management over a long time period. Even a very large population (1000 flowering individuals) would go extinct within less than 50 years. This estimation is still rather optimistic because unmanaged semi-natural grasslands will undergo succession, including shrub establishment, and conditions will become even less suitable for the establishment and growth of *G. praecox* subsp. *bohemica*.

The process of the slow disappearance of plants from the locality after the cessation of management is interesting. Flowering plants still appear for several years; if the population was large, it is possible to observe flowering plants for more than 20 years after the cessation of management. The number of flowering plants may sometimes rapidly increase between years, even without management; this is due to stochastic environmental and demographic changes and the extensive seed bank. Thus, responsible management officers can easily revert to the belief that nothing is wrong because the population prospers even without management.

If managed, even very small populations (fewer than 10 flowering individuals) have a high chance for survival. Lennartsson (2000) reports a similarly high survival probability of *Gentianella campestris* under the best management strategy. In populations larger than 10 individuals, there is almost no difference between management types (mowing or mowing and disturbance). This result has practical implications – in large stable populations, the simpler and thus cheaper management (mowing only) should be enough to preserve the species.

An unmanaged population may seem to be extinct when no flowering individuals appear. However, there is still some chance for the recovery of the population from the seed bank. Our results show that restoration of a population from the seed bank is possible up to 8 years from the time that the last flowering plant was observed, but a reasonable chance for survival (approximately 80%) elapses after a maximum of 3–4 years. For restoration of a population from the seed bank, the best management is mowing and disturbance; mowing only is less successful. Here again, the absolute interpretation in the form of a number of years has to be treated with caution for the sake of policy decisions.

It is necessary to interpret the estimated survival probability of small populations discussed above with extreme caution (Beissinger and Westphal, 1998). While the relative interpretation – the difference among the management types – is valid, the estimated minimum size of a viable population has some limitations. A population consisting only of, for example, 10 flowering individuals (especially if it is growing in a very small area), is vulnerable to local catastrophic events, such as small-scale habitat destruction, and may consequently be lost before it can recover.

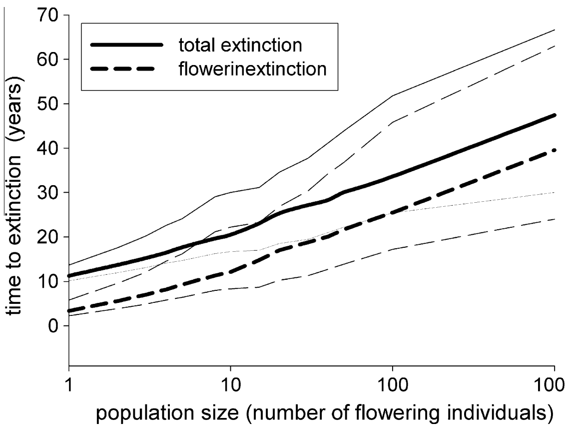

Fig. 3. Time to extinction of a population as a function of population size (Model 1), under the no management condition. The times to total extinction and to extinction of flowering plants are shown. The 95% confidence intervals are indicated by thin lines.

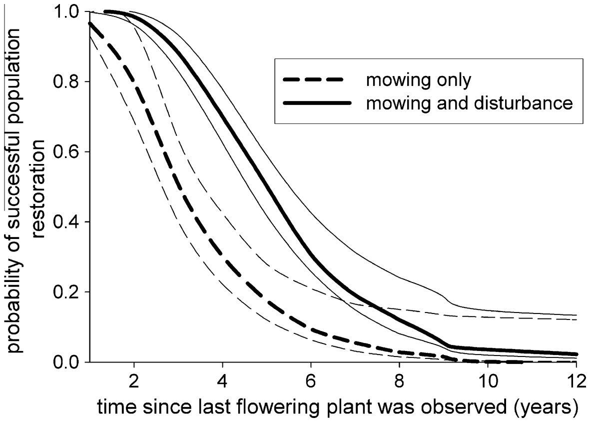

Fig. 4. The probability of the successful restoration of a population related to the time based on how long no flowering individuals have been present in the population (Model 3). The 95% confidence intervals are indicated by thin lines.

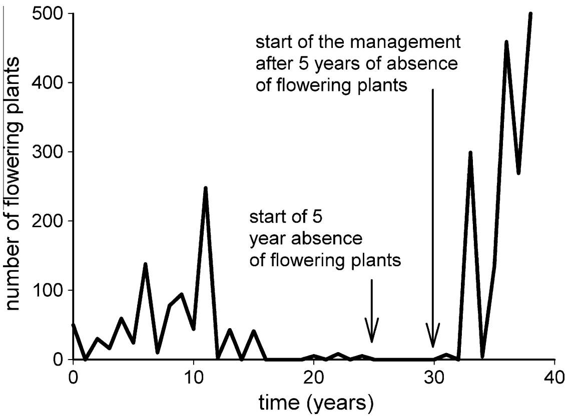

Fig. 5. Example of one run of the model for population restoration. For an estimation of the probability of restoration of a population from the seed bank (see Fig. 4), 1000 such runs were performed for each "time since last the flowering plant was observed". In this example, the "time since the last flowering plant was observed" was set to 5 years.

In addition, predictions concerning small populations also do not include other possible negative consequences of small population size, which may be linked to genetic changes in these populations, such as inbreeding (Ellstrand and Elam, 1993; Ouborg and Vantreuren, 1995), or other factors such as the Allee effect (Stephens et al., 1999). Negative effects of small population size on plant fitness have been documented in the *Gentianella* genus (Fischer and Matthies, 1997, 1998a). The data in our study were obtained from large populations, which suffer from none of the negative effects described above. In such a population, induction of management should be followed by a rapid increase in population size within 3 years. If there is no such rapid increase in reality, there is something wrong, likely due to a small population size or environmental changes (e.g. human-induced extreme desiccation of the locality). Such a scenario was actually observed recently in the field after inducing experimental management for several isolated (and, for several decades, very small) populations.

A model of population restoration critically depends on precise data, especially data on the survival of the seed bank. In *Gentianella* species, both persistent and transient seed banks were reported (Fischer and Matthies, 1998b; Kelly, 1989; Lennartsson and Oostermeijer, 2001; Milberg, 1994; Pons, 1991). Our study shows that *G. praecox* subsp. *bohemica* has a persistent seed bank, with a 53% probability of survival of a seed in the seed bank for over a year. In the burial experiment, we assumed that healthy-looking seeds were viable, following the method of (Fischer and Matthies, 1998b). We did not perform staining using 2,3,5-triphenyltetrazolium chloride (further reported as tetrazolium staining), as used by (Milberg, 1994), because this method has been shown to not be fully reliable for *Gentianella* species (Kelly, 1989). We simply cut open several undamaged seeds to verify that seeds of the representative appearance were actually intact. However, our results may be biased towards overestimating the number of surviving seeds, especially for seeds buried for a longer period of time. Such an overestimation would mean that undamaged seeds excavated later after burial should show lower levels of germination compared to seeds excavated earlier. However, the germination of these seeds sown in the field was proportional to the number of viable seeds counted; in some cases, it was even higher in older seeds (Brabec, unpublished, compare with Fischer and Matthies (1998b)).

According to our results, the impact of an increased frequency of dry years on population dynamics of managed populations of *G. praecox* subsp. *bohemica* would be rather small. An increased frequency of dry years simulates climate change (Lennartsson and Oostermeijer, 2001; Torang et al., 2010) because one of the main effects of climate change is increased extremes in weather, including extremely dry summers (Rowell, 2005). The small impact of dry years, when all the individuals except seeds in the seed bank die, is assured by the high number of seeds stored in the seed bank. Several studies have reported increased seedling establishment in the spring following a dry year because the drought created gaps in the dense vegetation, providing additional space for seedling establishment (Gross et al., 1998; Horvitz et al., 1998; Smith et al., 2005;; Torang et al., 2010). In our study, we could not assess this effect, as we had almost no seeds (except at one locality) for sowing experiments the year following the dry year. Establishment from the seed bank the year after the dry year was not significantly different from other years. In unmanaged plots, almost no plants germinated, regardless of year, which is probably because the thick layer of litter prevented any seedlings from establishing, independent of the amount of living biomass. On managed plots, management treatment itself releases competition and enables seed germination and seedling establishment.

We are also aware that future climate change will bring much larger changes than only an increased frequency of dry years. Climate change will influence the entire set of environmental conditions, resulting in shifts in phenology and species distribution as well as changes in the community composition and the entire dynamic context of the biota (Walther et al., 2002). To a large degree, the impact of all of these changes on the population dynamics

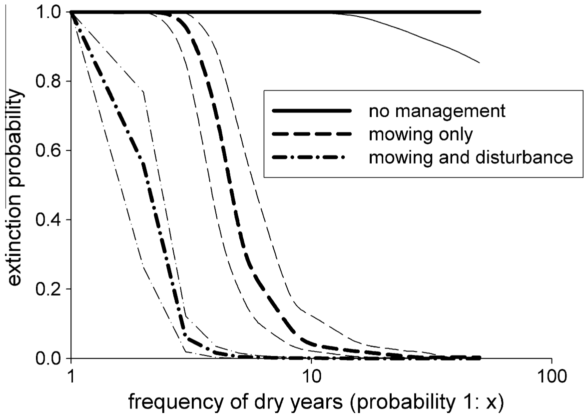

Fig. 6. Extinction probability of a small population (10 flowering individuals) as a function of the frequency of extremely dry years (Model 2). The 95% confidence intervals are indicated by thin lines.

of a single species is not known and is hardly predictable. However, increasing extremes in weather are definitely one of the major drivers of biota changes because a few extreme events, such as drought, can drastically change species prospects, distribution and even evolution (Easterling et al., 2000).

Grasslands, with occurrences of *G. praecox* subsp. *bohemica*, also host other rare species. Because all species of semi-natural grasslands need regular management (Dullinger et al., 2003; Ockinger et al., 2006), the effect of the induction of management is expected to be positive for most of the species present.c

5. Conclusions for nature conservation

Even very small populations (10–15 flowering individuals) of *G. praecox* subsp. *bohemica* are able to survive if the locality is managed. However, a population of any size is not able to survive if it is not managed. Management should be performed in the autumn after the fruiting of the species because poorly timed management has the same or an even worse effect as does no management at all (Lennartsson and Oostermeijer, 2001).

The best management for populations is mowing and disturbance by harrowing. However, in stable and large populations, mowing only is sufficient for preserving the existence of a species at the given locality. Mowing and disturbance by harrowing should be employed in cases in which the population situation is somehow critical – it is small, it has suboptimal habitat conditions (e.g. too dry) or the population is being restored from the seed bank. Restoration of a population from the seed bank by inducing optimal management has a reasonable chance for success (80%) from an approximate maximum of 3 years after the last flowering plant was observed.

Unmanaged small populations, or populations restored from a seed bank, should respond to the induction of management within 2–3 years by a rapid increase in the number of flowering individuals. If this is not the case, either the environment is flawed (e.g. there are human-induced changes in vegetation or moisture), or the population suffers from some negative effects of small population size (e.g. inbreeding, allelic loss due to genetic drift or the Allee effect). In the case of restoration from the seed bank, it may also be simply too late.

The conclusions of this paper were implemented into a prepared conservation action plan for *G. praecox* subs. *bohemica* in the Czech Republic.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.09.016.

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