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Research Article

Effect of population reinforcement method, site, and plant characteristics on early establishment of the rare endemic plant species *Minuartia smejkalii*

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Many habitat-specialist plant species have been endangered by fragmentation or destruction of their habitats. *Minuartia smejkalii* is a serpentinophyte endemic to the Czech Republic. It is highly threatened by recent habitat destruction and fragmentation, calling for effective conservation measures.

We evaluated two conservation methods to reinforce *M. smejkalii* populations: sowing seeds collected from natural populations and transplanting pre-grown individuals in three consecutive years to sites currently or recently occupied by the species. We checked for seed emergence (recruitment) and followed the survival and performance of the transplants and recruits to identify factors responsible for the establishment success for up to three years after transplantation.

Recruitment from sown seeds was unsuccessful, but overall, 83% of transplants survived the first year and 49% until the third year. Survival depended on the year of transplantation, size of the transplanted individual and mother plant characteristics. Mother plant characteristics were important for growth and flowering in the first year, but not for survival. Across years, initial size and age were more important for size and number of flowers than mother plant identity. Population differences had a larger effect on size and number of flowers in the first year than across years.

Seedlings established from seeds of the transplants in four of the five populations. This led, despite mortality of transplants, to a four to six times larger population size after three years in two populations, compared to the number of transplanted individuals.

Overall, our findings emphasize that for long-lived perennials with poor seedling establishment, repeated transplantations across years and sites are key for population reinforcement.

Keywords: conservation, endangered, reintroduction, seed, serpentine, sowing

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Introduction

Specialist plant species with few small local populations growing in extreme conditions are especially vulnerable to habitat fragmentation (Wolf 2001, García-Barriuso et al. 2012, Pimm et al. 2014, Cheptou et al. 2017), which increases extinction risk by further reducing population sizes, genetic diversity, and dispersal potential (Shaffer 1981, Melbourne and Hastings 2008). In addition to protection of their habitats (Maschinski et al. 2004, Ren et al. 2012, Betz et al. 2013), these species often require assisted enhancement of population size and genetic diversity (McNaughton 1989, Maunder 1992, Hodder and Bullock 1997, Newmark et al. 2017, Heywood 2019). Population reinforcement, an increasingly crucial tool for rare species (Maunder 1992, Hodder and Bullock 1997, Drayton and Primack 2000, Rout et al. 2009, Godefroid et al. 2011, Betz et al. 2013), encompasses both reintroducing and establishing species at previously occupied sites (Maschinski et al. 2023), and supporting currently small plant populations by adding individuals (Akeroyd 1995, IUCN 2013).

However, empirical evidence shows species reintroduction to be intricate and often lacking long-term success (Drayton and Primack 2012, Godefroid et al. 2025). This may result from incomplete knowledge of habitat requirements, competition, weather events, or interactions with invasive species (Fahselt 2007, Godefroid et al. 2011, Drayton and Primack 2012, Godefroid et al. 2025). Nonetheless, it remains a viable in situ conservation option for species with limited seed dispersal potential, especially in fragmented habitats.

Seeding as direct introduction method conserves resources and allows seedlings to adjust to new environments (Godefroid et al. 2011, Bucharova et al. 2017). However, unsuitable conditions or predation may hinder germination and establishment on site (Albrecht and Maschinski 2012). Moreover, because large numbers of seeds would potentially be required for successful establishment (Knight 2012), limited seed availability and lower establishment rates in natural habitats compared to controlled conditions make on-site sowing risky. To the contrary, the amount of seeds required for transplantation is lower since the germination and growth of seedlings are conducted in controlled environments (e.g. incubators or greenhouses). Nevertheless, it disrupts plants during the transition to new habitats and interferes with genetic selection and phenotypic adjustments which are happening in nature (Vora 1992, Drayton and Primack 2000, Dayrell et al. 2018, Ensslin et al. 2023). This may cause preferential establishment of transplants originating from mother plants with certain genetic backgrounds, phenotypes, or origins (e.g. maternal effects; Roach and Wulff 1987, Kahmen and Poschlod 2000, Veselá et al. 2021) influencing transplantation success in the long term (Bucharova et al. 2017). Experience suggests population reinforcement is more successful when seedlings or adult plants are introduced compared to seeds, and the transplantation sites are protected and appropriately managed post-transplantation (Drayton and Primack 2000, Godefroid et al. 2011, Dalrymple et al. 2012, Sugier et al. 2013, John et al. 2016).

Understanding which reintroduction method (sowing or transplantation) works best is particularly relevant for threatened species confined to rare, extreme, and fragmented habitats and low seed production. Reintroduction efforts, demanding significant time and labour, should ideally exhibit a high success rate to preserve seed material. Unfortunately, despite their growing importance for conservation, published results generally remain limited compared to actual endeavours, and tend to highlight successful outcomes, encumbering improvement (Godefroid et al. 2011). Moreover, even seedling recruitment from reintroduced individuals or sown seeds (indicating high reinforcement success) is no guarantee for the long-term persistence of a new population (Vora 1992, Drayton and Primack 2000). However, it raises the question whether offspring from transplants (recruited individuals) exceed their parents' survival chances as they are naturally dispersed close to suitable locations and safe sites and thus may have a higher likelihood of reaching suitable microsites at the right time.

Obligate serpentinophytes exemplify highly specialised species restricted to specific soil conditions and confined to highly localised sites. These species endure a stressful, low-competition environment of high metal concentrations, low nutrient contents and limited water retention capacity in shallow soils (Kruckeberg 2002, Caillaud et al. 2009). Consequently, serpentine species are susceptible to being outcompeted when growing in less extreme habitats, likely due to a trade-off between stress tolerance and competitive abilities (Kruckeberg 1984, Rajakaruna and Harrison 2011). Many serpentine species, including the Czech endemic *Minuartia smejkalii* (Dvořáková), are critically endangered due to habitat destruction, requiring immediate and targeted conservation actions.

The 'Life for Minuartia' project aims to enhance population sizes at existing *M. smejkalii* localities and reintroducing the species to recently extinct locations. Our preliminary attempts to improve the *M. smejkalii* populations through sowing seeds yielded limited success, indicating the potential need for a different approach. Apart from low germination rates in situ, this species demonstrates a short dispersal distance and prospects of natural range expansion are doubtful (Zhu et al. 2021) even with potential improvement of habitat quality through management. Additionally, several studies have investigated the dispersal, biology, and genetics of the species in common garden experiments within the project (Lozada-Gobilard et al. 2020, 2023, Stojanova et al. 2020, 2021, Zhu et al. 2021).

To directly compare methods, we reintroduced *M. smejkalii* to several localities within its natural range via direct sowing and transplantation of pre-grown individuals. For three years post-transplantation/sowing, we monitored the continuous survival of the transplants, alongside the survival and numbers of their offspring, to evaluate population development.

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We expected that:

1. Transplanting pre-grown individuals increases establishment success for *M. smejkalii* compared to on-site sowing.
2. Establishment success varies with contextual factors such as population, the year of transplantation, and specific characteristics of individuals and mother plants (e.g. size, number of flowering stems) before transplanting.
3. Transplanted and recruited individuals differ in their performance, with offspring recruited in situ performing better (survival, flowers, relative growth rate).

Material and methods

Species description

The Czech endemic *M. smejkalii* (Dvořáková) is an insect-pollinated chamaephyte and an obligate serpentinophyte that grows on small serpentine outcrops, in shallow serpentine soils, rock crevices, and in unconnected grasslands in light pine forests (alliances *Asplenion serpentinii* and *Asplenion cuneifolii–Armerion serpentinii*) (Dvořáková 1988). The species rapidly disappears from locations that are overgrown by strong competitors.

In rare cases, it is capable of vegetative propagation by splitting of tufts. During summer, tufts may get dry but regrow in the cooler autumn month. Tufts can remain dormant for one to several years but then regrow if environmental conditions improve (e.g. more suitable temperatures, water availability). However, the likelihood to regrow decreases with time and is close to zero after four years (Pánková and Sučíková unpubl.).

Individuals consist of numerous, 2–5 cm long, densely leafed sterile stems, and may produce hundreds of straight 5–15 cm long flowering stems (ramet) with on average three to twelve small flowers (up to 4 mm large) per ramet. Thus, one individual can produce on average around 1280 to – in extreme cases – close to 20 000 seeds, (Pánková and Sučíková unpubl.). The peak flowering of the species is in the second half of June, but it may flower continuously throughout the whole vegetation season. Seeds usually disperse only few centimetres and the population spread rate is extremely low (1–23 mm per year; Zhu et al. 2021). *Minuartia smejkalii* can establish a seed bank under natural conditions for a at least 10 years (currently being studied), and seeds remain viable for at least two to three years (unpubl.) when stored in a cold, dark place (e.g. a refrigerator).

The current distribution is limited to the central part of the Czech Republic and the species is classified as critically endangered (Dvořáková 1988, Grulich 2012). It is protected under European Habitats Directive 92/43/EEC as a species of priority interest and included in the Convention on the Conservation of European Wildlife and Natural Habitats. However, the taxonomic position of the species is still unclear. While Lomolino et al. (2017) included *M. smejkalii* as subspecies *Minuartia verna* ssp. *verna* ((L.) Hiern), the study of Lipánová et al. (2023) considers this species as a separate subspecies *Sabulina verna* subsp. *smejkalii.* Clear morphological and genetic differentiation between *M. smejkalii* and other species from the *M. verna* group was also confirmed by the study of Stojanova et al. (2020). Since the taxonomic status is not the subject of this study and to stress its conservation value, we will further use the endemic's name *Minuartia smejkalii*.

The natural distribution of *M. smejkalii* has been constrained to three places within an area of 500 km^2: Borecká skalka Natural Monument, Hadce u Želivky National Natural Monument and Hadce u Hrnčíř Natural Monument. Populations in the first region went extinct due to mining activities and the self-propagation of trees in the 1960s. More than half of the available serpentine rocks suitable for the species in the Želivka region were destroyed by the construction of a motorway and a dam between 1965 and 1975 (Pešout 2001). Combined with afforestation of the remaining rocks, this led to fragmentation and shading of the habitat and a drastic population decline.

Study sites

The study area, Hadce u Želivky National Natural Monument, is one of the most important serpentine localities in the Czech Republic, hosting several serpentine (sub) endemic taxa. It is made up of several separate parts according to the documented occurrence of *M. smejkalii* (Fig. 1; for more specific information on the sites, see the Supporting information).

The species occurs or formerly occurred in mosaics of forest vegetation (biotope spring heath Scots' pine forests) with steppe vegetation and protruding serpentine rocks within this area (populations Z1 to Z7; Fig. 1). Populations Z1, Z2, Z4, Z5 and Z7 grow on the steep banks of the Želivka water reservoir and represent natural occurrences of *M. smejkalii*, population Z7 however, went extinct, in 2012. Z3 is a small population growing in open parts along an old highway embankment, which was built in the 1930's and Z6 occurs on a small municipal abandoned quarry, which was destroyed by illegal dumping (for instance of gardening waste). A few individuals persist there on exposed rocks. Seeds from all extant populations within this protected area were used as seed sources as specified below.

As it has been shown that site preparation, like the removal of competitive or invasive species, is often crucial for increased establishment success (Hölzel and Otte 2003, Bissels et al. 2006, Godefroid et al. 2011, Maschinski et al. 2023), we applied this approach for our study. All sites were managed by tree cutting and removal of the humus layer with vegetation and mosses prior to reinforcement to create open low-competition sites with accessible serpentine bedrock and the dump on Z6 was removed. Before the beginning of the reinforcement in this study in 2017, the population sizes were very different and ranged between five individuals in Z1 to 181 in Z2 (Supporting information). A genetic study (Stojanova et al. 2020) suggested that it is possible to use a mixture of seeds for species reintroduction and that it is a preferable approach in small populations. Nevertheless, we decided to respect the origin of source material in populations

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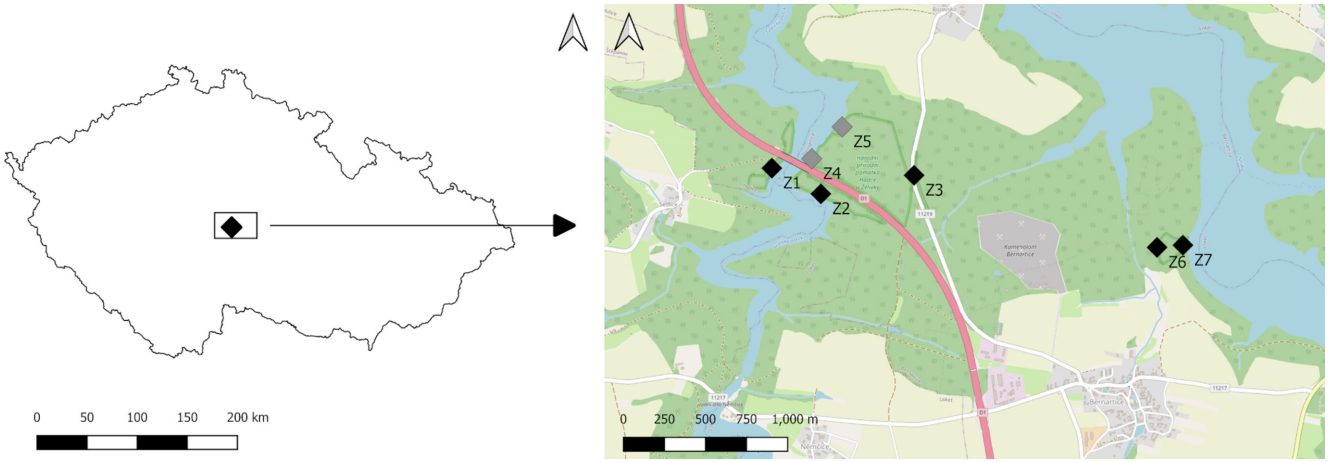

Figure 1. Populations of *Minuartia smejkalii* in the Czech Republic in the area of Hadce u Želivky National Natural Monument (Z1–Z7). Populations in grey were only used as source material for reintroduction at Z7, but not as location for transplantations. Map data copyrighted OpenStreetMap contributors and available from www.openstreetmap.org, country shape file https://ec.europa.eu.

with naturally occurring individuals because of the precautionary principle. Moreover, a better performance of plants in their original locations was demonstrated in a range of other study systems (Kindell et al. 1996, Montalvo and Ellstrand 2000a, Hufford et al. 2008).

Population reinforcement was implemented on sites, where the populations were small or extinct: two primary sites (Z1 and Z7) and two secondary sites (Z3 and Z6). Additionally, we applied the same approach to Z2 (the largest population) as a control. The population here was the biggest and the habitat seemed most suitable. Success of the reinforcement at this site and not at the others would show that the failure is due to unsuitable habitat conditions or seed quality. In contrast, failure even at this site would indicate problems with the methodology. We performed plant transplantations at all sites. The sowing was done at all sites except Z7 because of low seed availability. The reinforcement was conducted in a distinct part of each site at sufficient distance to the natural population to be able to monitor performance of transplants and their offspring (recruits).

Seed sowing experiment

Seeds of *M. smejkalii* were collected from mother plants in the natural parts of the populations corresponding to each target site (Z1, Z2, Z3 and Z6) between 2014 and 2017. We tried to collect seeds from as many mother plants as possible without endangering the survival of the population, which was insured by only using fully ripe and opened capsules at the collection time, leaving immature capsules for natural propagation at a later point. Therefore, we were strictly limited by seed sources. Selecting individuals for the collection of seeds was random among individuals with at least three flowering stems at the time of collection. The seeds from each mother plant were stored separately in paper bags at room temperature. Specifically, we were able to obtain seeds from 9 mother plants from Z1, 39 from Z2, 23 from Z3 and 12 from Z6.

In 2017, 3 plots for seed sowing were established in Z1, 8 plots in Z2, 1 plot in Z3, and 3 plots in Z6. The plots of the seed experiment were situated approximately 10 m away from the individuals of the natural population to exclude the possibility of wind dispersal into the sowing site while still ensuring a suitable microhabitat.

The plots of 0.5 × 0.5 m were divided into 25 small subplots of 0.1 × 0.1 m and, depending on seed availability, unsown subplots per plot were used as a control (Supporting information). Half of the plots were sown with seeds at the beginning of the growing season (March 2017), the remaining plots were sown with seeds at the end of the growing season (September 2017). We used older seeds (collected 2014–2016) for the spring sowing and a seed mixture of old and fresh seeds (from 2017) for the autumn sowing. Seeds were exclusively distributed at their population of origin at a density of approximately 2750 (Z3) to 3030 (Z2) seeds per square meter (Supporting information). The plots were checked on a bi-weekly basis for emerging seedlings.

Transplantation experiment

We planted *M. smejkalii* at five sites (populations Z1, Z2, Z3, Z6 and Z7). Following the same technique as for the seed experiment, seeds were collected from mother plants in populations Z1 to Z6 in 2016, 2017 and 2018 to be used in the transplant experiment. The extant populations Z1, Z2, Z3 and Z6 received transplants from local seeds. The extinct Z7 received transplants from Z2, Z3, Z4 and Z5 to maximize genetic variability.

Part of the seeds for the seedling transplantations were germinated in an incubator (12 h light and 17°C and 12 h dark and 7°C) at the Institute of Botany of the Czech Academy of Sciences at Průhonice, Czech Republic, in Petri dishes lined with filter paper in the beginning of September 2016 and the two following years. The seeds were watered with distilled water once a week. The rest of the seeds were geminated directly in serpentine soil in the greenhouse. After

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germination, all seedlings were consecutively planted in multi-pots of 2.5 × 2.5 cm each filled with serpentine soil and overwintered in the greenhouse. Approximately six-months-old seedlings were replanted into separate pots of 7 × 7 cm with serpentine soil in 2017 (and the following years for the consecutive plantings). The pots were placed in open parts of the common garden for acclimatization (49°59′42′N, 14°33′57′E, 350 m a.s.l., average annual temperature 8.8°C, mean annual precipitation 560 mm) and watered only if the weather was extremely dry. Approximately one-year-old plants were transplanted to target sites in the autumns of 2017–2019. The number of planted individuals varied between transplantation years and sites between 1 and 1436 (Supporting information). Planting locations were chosen in a way that they were clearly separated from natural parts of the populations (by approximately 20 m) and the plots of the sowing experiment. Individuals were removed from their pots and planted including all soil to suitable places between serpentine rocks or in their proximity. The distance between individuals was at least 50 cm. Transplants were planted randomly, permanently labelled, recorded into a drawn map and photographed to facilitate re-discovery in the following years.

Data collection

The length, width, and the number of flowering and non-flowering stems of each mother plant (which served as seed source) were measured in June in natural sites and mother plant size was calculated as the area of an ellipse (because *M. smejkalii* grows predominantly vertically in separate stems, area is a better fitness estimate than plant height). We also counted the number of flowers on ten randomly chosen stems with terminated growth (dichotomous stem division) and multiplied this by the number of flowering stems to calculate the number of total flowers for each flowering plant. The number of flowers per individual stem was averaged per population and year. Prior to transplantation, we measured maximum length and width of each plant to calculate plant size as above and determined if the plant was flowering or not. Plant characteristics in the years after transplantation were evaluated likewise at the time of flowering during June and July. The data collection was done at two levels: whole site and transects (permanent plots).

At the level of the whole site, we evaluated the status of each transplanted individual in the following years as flowering, non-flowering, dry, absent (but potentially still able to regenerate in following years) and lost (when both plant and label could not be found). Survival was encoded as 0 or 1. Individuals were counted as alive (= 1) if they could be found, even though they were dry at time of observation. Individuals that were absent in one or two years but re-emerged in the next year were also counted as alive in the years they had been missing previously (0.26% of total individuals). Individuals which were absent (no aboveground parts visible or disappeared for unknown reasons including the tag) and did not re-grow later were considered dead (= 0). Additionally, we counted the total number of newly recruited plants at the whole part of the site, where the transplantation had been done.

Transects with a width of two meters passed through the area of newly transplanted individuals and covered the heterogeneity of the environment and at least 50% of the transplanted individuals to reduce sampling effort in the years following transplantations. The transect length and number of transects per population were dependent on population size and plant distribution in the terrain. In these transects, we measured and calculated the same parameters as above (size, flowering and non-flowering stems and flowers).

Recruits within the transects in the years after transplantation were numbered and tagged and similarly recorded and measured in consecutive years as the transplanted individuals.

The relative growth rate (RGR) of individual plants was computed for each measurement time (tx, with x being 1, 2 or 3 years since transplantation) compared to the initial measurement before transplantation (t0)

$$\mathrm{RGR} = \frac{\ln\left(\mathrm{Size}_{tx}\right) - \ln\left(\mathrm{Size}_{t0}\right)}{tx - t0} \quad (1)$$

Statistical analyses

The analysed plant parameters comprised survival, size (transformed to its natural logarithm), relative growth rate and number of flowers of each individual.

Package 'lme4' (Bates et al. 2015) was used to analyse the effects of population identity, year of transplantation, year after transplantation and initial size (natural logarithm) and the interaction of initial size and population on plant performance (survival, size, growth rate and number of flowers) in R (www.r-project.org). The data were analysed using generalized mixed-effects models (glms) as repeated measures with individual plant ID as random term. We assumed binomial distribution for survival, Poisson distribution for flower number and Gaussian distribution for the other variables. These analyses were conducted for all populations and transplantation years.

Significant fixed effects were identified using stepwise model reduction (*drop1* in 'lme4'). Goodness of fit of the full models as R^2 was assessed using package 'MuMIn' (Burnham and Anderson 2002). The explained variance (as sum of squares) was then calculated as percentage contribution by applying the function *anova* from package 'stats' to the models (including only significant factors) based on R^2. This method was applied in order to use a unified calculation on the different model kinds, which did not allow a more straightforward analysis due to the inherent model characteristics. This approach was also used on the models mentioned below.

Since we expect the variation in the characteristics in the first year after transplantation, as the most sensitive phase (Primack and Drayton 1997), to differ from the following years, we analysed the data from the first year separately with glms with the same predictors, dependent variables and assumed distributions as above.

To compare recruits and transplants, we only used measurements from 2020 of seedlings recruited in 2019, because

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too few seedlings had emerged in 2018, and compared them to individuals in the first year after transplantation (data collected in 2018 for plants planted in 2017) for populations Z1, Z2 and Z6 – the only populations with recruits. We used the same models as for the performance of plants in the first year after transplantation and additionally included a binomial term of seedling origin (transplanted or not) and its interaction with population identity and initial size.

The effect of mother plant identity, mother size and number of flowering stems was tested on a subset of the data for the first year after transplantation and across following years for individuals planted in 2017 (excluding population Z3 due to insufficient data) substituting the effect of population (because mother plants are nested in population) and adding either mother plant identity, the size of the mother plant or its number of flowering stems. The other years of transplantation were not used in the analyses due to insufficient replicates of mother plants and the fact that population Z7 comprised mother plants from different populations.

The function *glht* from package 'multcomp' (Hothorn et al. 2008) in R was used to determine significant differences for pairwise comparisons of factor levels.

Results

Population development from seeds and transplants

Germination of *M. smejkalii* seeds in the field was not successful, despite using a larger number of seeds and of different collection times. Only in one sowing plot at population Z6 thirteen seedlings could be found, however, there were more seedlings in a control plot.

In the first year after transplanting, 76% of transplanted plants across all populations and years were flowering and produced seeds. The percentage of flowering individuals increased with time (Fig. 2b). In three of the five populations (Z1, Z2, Z6) a few seedlings emerged from seeds of the transplanted individuals one year after transplantation, i.e. in 2018 (Table A1). More seedlings recruited in these populations in the following year (2019; Fig. 2a), 20 in Z1 (6 within the transects), 354 in Z2 (213 in transects) and 2828 in Z6 (1385 in transects), with most of the recruits flowering a year after emergence (i.e. Year 1; Fig. 2b).

Before the beginning of the study, *M. smejkalii* was extinct at site Z7 and had almost gone extinct at site Z3 (only two plants remaining in 2015). Two years after reintroduction in

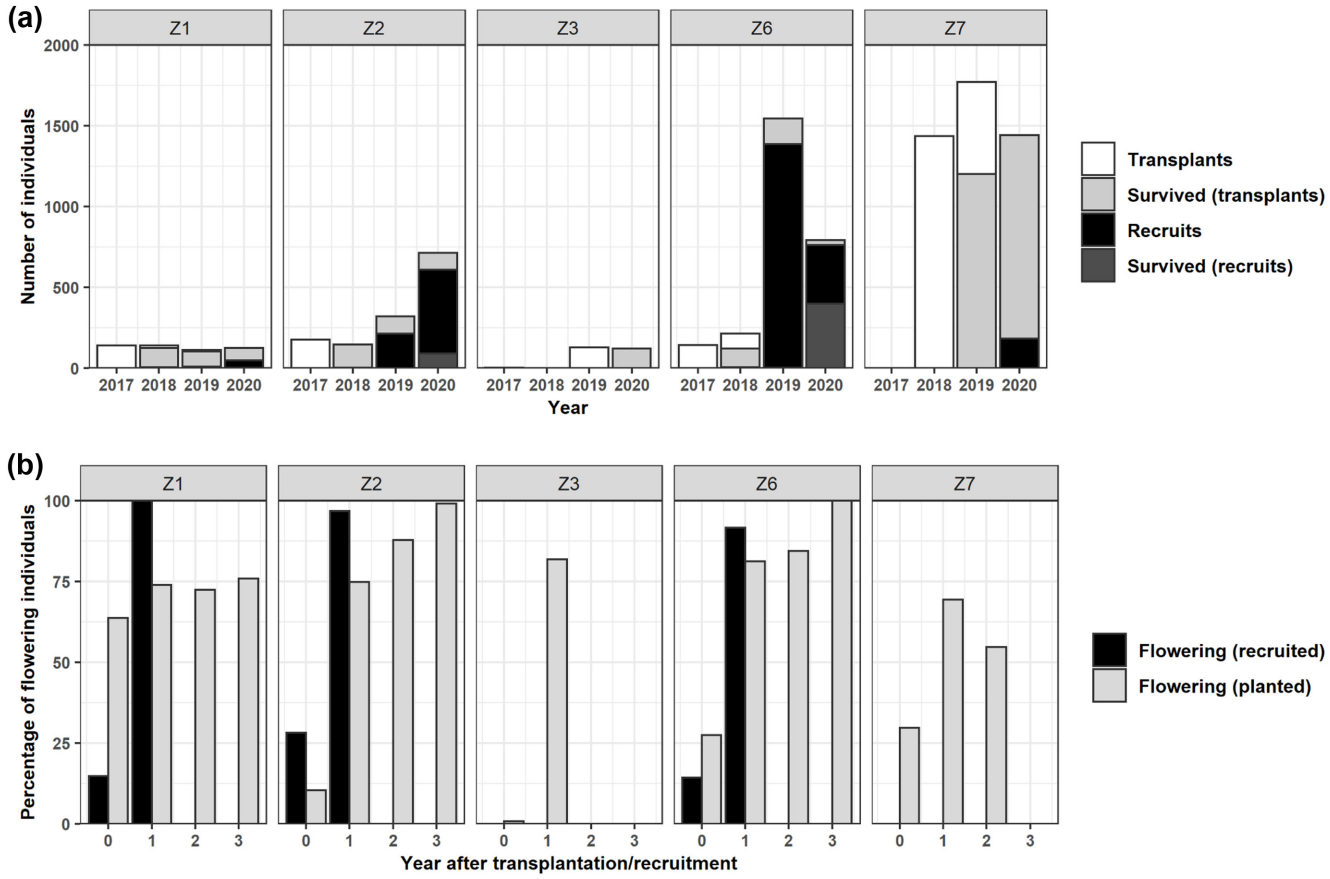

Figure 2. Population development within transects. (a) Population development across years with regards to survival of planted individuals, recruited seedlings and their survival (the exact composition of surviving plants according to in which year they emerged/were planted is not shown here, for more see the Supporting information). (b) Percentage of flowering and non-flowering individuals in the different populations for each year (year zero equals the year of transplantation or first emergence) across 2017–2020.

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Table 1. Percentage of seedlings that survived the years after transplantation, (a) by population and (b) per transplantation year. For the number of planted seedlings in each year and population, see the Supporting information. Means are weighted by number of surviving individuals per population or transplantation year, respectively. *for population Z3, only the survival of seedlings planted in 2019 was included because only one seedling was planted in 2017.

(a) Population	First year (%)	Second year (%)	Third year (%)
Z1	88.18	69.71	42.03
Z2	81.71	60.57	58.86
Z3	94.53*	–	–
Z6	82.63	36.50	11.35
Z7	82.36	55.64	
Weighted mean	83.35	55.65	49.05
(b) Year planted	First Year (%)	Second year (%)	Third year (%)
2017	82.93	59.62	37.41
2018	86.91	49.92	
2019	87.09		
Weighted mean	82.84	52.32	37.41

2018, Z7 comprised 1441 individuals, of which 13% were recruits, however, the number of individuals was still in total lower than the number of originally planted individuals (Fig. 2a, Supporting information). At site Z3, the population comprised 121 plants at the end of the study, eight less than originally planted (129; Supporting information), but there was no recruitment one year after transplantation. However, at the other sites (Z1, Z2 and Z6), the reinforced parts of the populations increased throughout the years due to seedling recruitment (Fig. 2a, Supporting information).

Determinants of transplant performance

Population identity explained moderate variation in most characteristics across years, particularly for RGR and transplant size (Fig. 3a, Supporting information), whereas it contributed little to survival and number of flowers. Population Z6 had the lowest survival (Table 1a) and the smallest size of transplants across years (Fig. 4a).

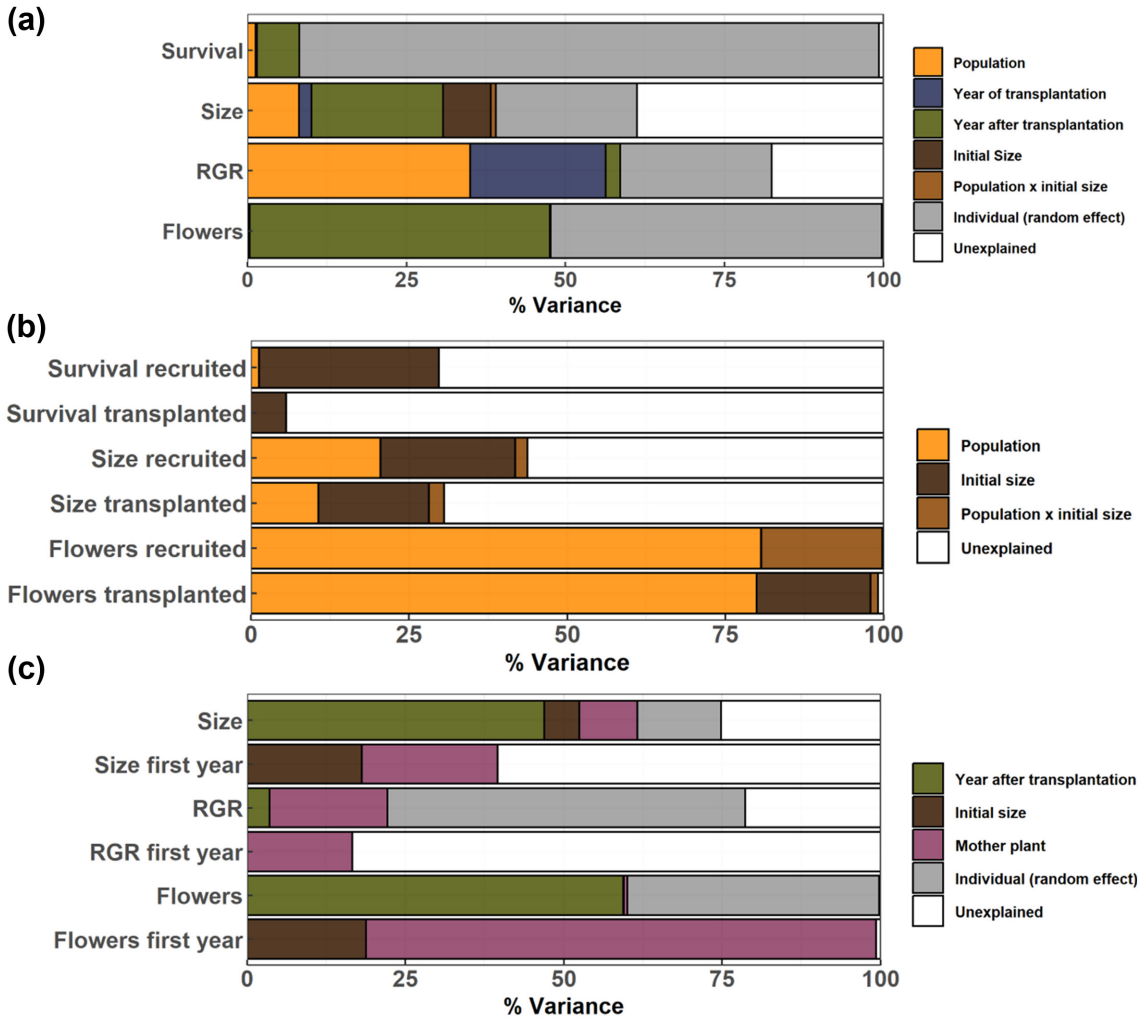

Figure 3. Variance partitioning. Variance partitioning of models only including significant factors (a) across years for the planted individuals, (b) for planted and recruited individuals one year after transplantation or first recording, (c) for the effect of mother plants of the individuals planted in 2017 from populations Z1, Z2 and Z7 one year after transplantation and across three years.

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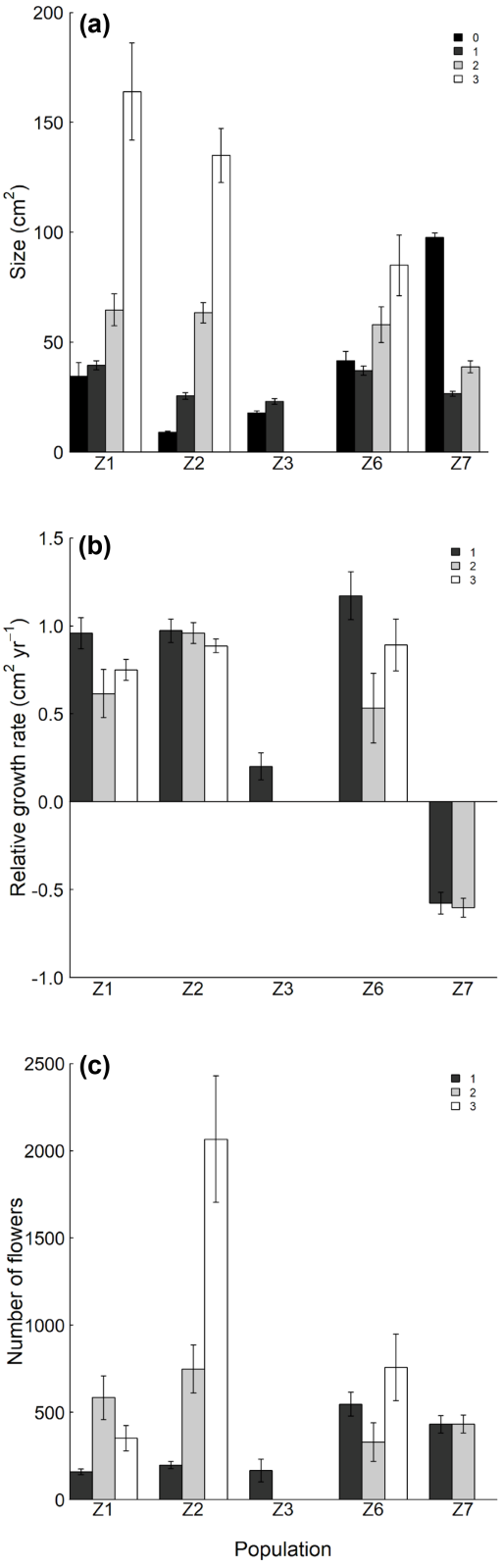

Figure 4. Measured characteristics of transplants before and after transplantation. (a) Size, (b) relative growth rate, and (c) number of flowers of individuals in the year of transplantation (0) and following years in each population (1, 2, 3; colours correspond to these different years). Shown are means ± SE.

In the first year after transplantation, population identity was the strongest predictor for flower number and RGR, but not for size or survival (Supporting information). The year of transplantation explained less variation than population for all the dependent variables both one year after transplantation and across years but contributed still almost a quarter of variation for RGR (Fig. 3a, Supporting information).

Initially larger transplants were also significantly larger in the first and in the following years after transplantation and had higher survival in the first year (Supporting information) with effects of initial size being comparable to effects of population identity for size across all years. However, initial size explained most of the variation in size in the first year after transplantation. Larger transplants had more flowers in the first year after transplantation (Supporting information), but across years, the importance of initial size declined relative to plant age, indicating that early advantages persisted but were gradually offset by other factors.

Overall, mother plant identity affected all characteristics of the individuals except for survival (Fig. 3c, Supporting information). However, only a part of this variation was associated with the size and number of flowering stems of mother plants (Fig. 3c). Offspring of mothers with more flowering stems were smaller, had fewer flowers and grew slower in the first year.

Comparison of recruited and transplanted individuals

Almost 43% of the recruits from 2019 in population Z2 had survived to the following year and about 29% in Z6 (Supporting information). In population Z1 one third of the seedlings was still present, however, it was only two individuals. Recruited individuals differed in their size, flower number and relative growth rate, but not in their survival among populations. The variation explained by population was, however, very low except for flower number (Fig. 3b). The survival after one year depended largely on the initial size of recruited individuals (Fig. 3b, Supporting information).

Variation in individual size one year after emergence was equally determined by initial size of recruited individuals and population identity (Fig. 3b). New individuals were the smallest in Z6 and the largest in population Z1 (Supporting information). The initial size was indicative for a larger size in the following year except for in population Z1 and a significant predictor for number of flowers, but explained less than 0.1% of the variation (because the effect of initial size differed between populations; Fig. 3b).

Transplanted and recruited individuals differed in their survival, size, and number of flowers (Supporting information). More than twice as many individuals survived the first year when they were transplanted (Fig. 2, Supporting information), but survival of recruits did not differ between populations. Transplanted individuals were larger than recruits one year after their first recording (Fig. 5a). Relative growth rates did not differ (Fig. 5b). However, recruited individuals had more than double the number of flowers (Fig. 5c). These patterns differed between populations. While in Z1 and Z2

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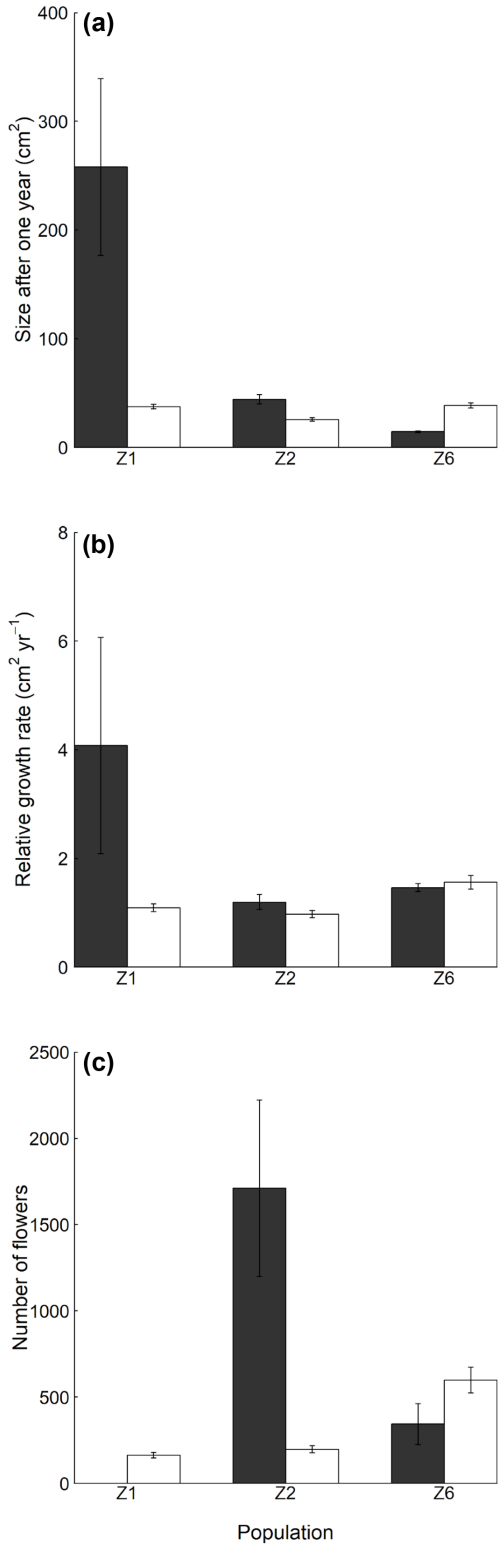

Figure 5. Measured characteristics of transplanted and recruited individuals one year after transplantation. Size (a), relative growth rates (b), and total number of flowers (c) per individual of transplanted (white) and recruited (dark grey) individuals after one year. Recruited individuals in population Z1 only comprised two flowering individuals (but flowers were not counted). Shown are means ± SE.

recruits had a higher growth rate, were larger and had more flowers than transplanted individuals, Z6 showed the opposite trend for all parameters. The increase in number of flowers with initial size was steeper for transplants than for recruits.

For both transplanted and recruited individuals, the majority of variation in survival and size depended on initial size. However, for the number of flowers, the interactive effect of population and initial size explained more variation (~19%) for recruits than initial size per se (~1%; Fig. 3b), but most variation was due to population identity itself.

Discussion

Population reinforcement methods for *Minuartia smejkalii*

In our study, sowing *M. smejkalii* directly at the sites yielded almost no seedlings (0.14% of total sown seeds germinated), no matter at which time they were sown. We made the same observation in a preliminary study in 2006 but using a lower number of seeds.

This may seem controversial, as transfer of local plant material (hay) or seed mixtures for site restauration is a common practice (Hölzel and Otte 2003, Bucharova et al. 2019), especially for annuals, but previous studies have also demonstrated the superior success of transplantation over seed sowing for rare and endangered perennial species (Guerrant and Kaye 2007, Reckinger et al. 2010, Godefroid et al. 2011, 2025). Some studies have tried to establish species at new potentially suitable locations within the range of a species by seeding (Pavlik et al. 1993, Drayton and Primack 2000, Albrecht and Maschinski 2012), which may be associated with a higher risk of failing due to unfavourable microhabitats or other conditions limiting introduction success (Münzbergová 2004). Nevertheless, in our study the plots for the sowing experiment were close to the naturally occurring plants at suitable microsites at the same location and habitat. It has been shown that low genetic diversity in small populations may negatively affect establishment and colonizing ability (Polans and Allard 1989, Crawford and Whitney 2010). However, previous studies on our populations provided information that *M. smejkalii* currently does not exhibit a low genetic diversity despite being a highly threatened endemic specialist (Stojanova et al. 2020).

Thus, it cannot be clearly determined why seed germination on site was unsuccessful in our study, which is unfortunately not uncommon for reintroduction experiments (Godefroid et al. 2011, Dalrymple et al. 2012, Drayton and Primack 2012). Seeds might have needed safer sites (Harper 1977, Kettenring and Galatowitsch 2011) directly between other *Minuartia* plants to germinate and establish as was the case with the successful seedling recruitment from transplanted individuals. The plots of the sowing experiment are still being checked, but as of the end of this study, no seedlings could be found.

The total number of seeds we used varied between sites and was lower in two populations than the average of

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previous studies (average seed number of 1551 in the meta-analysis of Godefroid et al. 2011), but in the two other populations, seeds exceeded this number by up to five times. Other reviews reported around 5640 propagules as the average applied in reintroduction efforts (Dalrymple et al. 2012), which is lower than the maximum number of seeds sown in our study. Considering the total number of seeds per plant and the probability of a seed to become a seedling is around 0.00007 to 0.002% (or: one seedling is on average produced out of 850–11 000 seeds – depending on population – as found in natural populations of the species by Sučíková et al. unpubl.), the number of distributed seeds was likely still too low. Unfortunately, we were restricted by seed availability and the endeavour not to harm genetic diversity and dispersal in the existing populations. The success of recruitment on site compared to our sowing may thus be also due to the stochastic effect of a high number of seeds produced by a flowering transplant (the mean seed number per individual we calculated across all natural populations was almost 1280).

Other studies found lower germination rates in natural sites compared to greenhouses for other rare species (Vora 1992, Lofflin and Kephart 2005). Germination and cultivation in the common garden were likewise successful in our study using seeds collected at the same time and shortly stored under the same conditions as the seeds sown in situ in 2017.

While not all planted individuals survived until the last analysed census, overall survival rates lay within the range found in other studies and a decrease over time is an often-reported outcome of transplantations, even after initial success (Pavlik et al. 1993, Godefroid et al. 2011, Dalrymple et al. 2012, Gao et al. 2020, Jonas et al. 2023). Overall, around 50% of transplanted individuals survived until the last census, they produced seeds and successfully increased population size with recruited offspring. This can be considered a great success in population reinforcement as it indicates that the population could further stabilize and maintain itself and potentially increase in size (Pavlik et al. 1993, Primack and Drayton 1997, Drayton and Primack 2000, Monks et al. 2012). Transplanting the species into private gardens has been likewise successful (Bucher et al. 2025). Moreover, other perennial species have shown longer time periods before recruitment (Albrecht et al. 2019, Jonas et al. 2023). Overall, our results are promising with regards to an improvement for the populations of *M. smejkalii*, but as studies have shown, longer term observations (five to ten years) may yield different results (Falk et al. 1996, Guerrant and Kaye 2007, Drayton and Primack 2012).

Except for Z3, where the number of natural individuals was slightly larger (Supporting information), all reinforced parts contained finally higher numbers of individuals than was observed in the natural population parts. The reinforced parts thus can potentially serve as an additional seed source for consequent plant dispersal. This is especially important since modelling population growth and colonization potential through natural seed dispersal showed that not all populations would be able to persist unaided (Zhu et al. 2021).

Together, these findings confirm our expectations that transplanting greenhouse-grown individuals is currently the most reliable way to reinforce *M. smejkalii* populations, consistent with outcomes for other rare perennials (Guerrant and Kaye 2007, Reckinger et al. 2010, Godefroid et al. 2011).

Determinants of establishment success

Survival and growth of transplanted *M. smejkalii* varied among sites and years, reflecting environmental heterogeneity and interannual weather differences. Mortality after transplantation can in our study be attributed to a multitude of reasons depending on the specific location, which we could not fully capture in our study. Droughts in 2018 and 2019 (Supporting information) may have hindered establishment. While individuals of this species can tolerate dry periods through dormancy, they may require several years to recover, especially if small or newly established. Resource limitation and restricted root space could also reduce survival in later years, particularly in rocky habitats. Extreme precipitation might have further increased mortality at steep sites, where run-off can dislodge plants.

However, the high variation in survival between transplantation years shows that the applied approach and effort of planting repeatedly in different years is a good method to counteract seedling mortality due to unfavourable climate and habitat conditions in specific years (Falk et al. 1996, Drayton and Primack 2000, Stewart and Byrne 2025).

The abiotic and biotic factors that predominantly influence seedling recruitment, establishment, growth, and reproduction vary throughout these phases (Grubb 1977, Knappová et al. 2013). Thus, it could be expected that the influence of population, mother plant characteristics and initial seedling characteristics on survival and plant characteristics differs between the first and following years after transplantation. A positive correlation between seedling size and survival has been shown previously (Kindell et al. 1996) and is not that unexpected, because larger individuals have a higher chance to photosynthesize more and reach soil resources with a larger root system. However, the beneficial effect of the initial size of transplants on survival disappeared after one year but persisted for other characteristics. Other studies showed that initial size advantages only lasted until other constraints (e.g. resource competition) slowed growth of initially larger individuals while smaller individuals caught up developmentally (Münzbergová and Plačková 2010, Liu et al. 2021).

Another important predictor of seedling establishment and transplant performance could be properties of the maternal plants, collectively called maternal effects (Roach and Wulff 1987, Herman and Sultan 2011) here represented by size and number of flowering stems of the mother plants. We expected that larger mother plants, because of a genetic advantage, e.g. in being larger and more dominant, would also result in larger offspring with these abilities (Roach and Wulff 1987). However, we observed the opposite. Mothers with more flowering stems led to smaller, slower growing individuals in the first year, which also had fewer flowers. This may be the result of a trade-off in which those mother

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plants produced more, but smaller seeds, leading to smaller individuals due to lower resources in the seeds as observed for other species (Strykstra et al. 1998). Seed size was however not measured in this study. It has been shown that the quality of seed material affects transplantation success (Godefroid et al. 2011), but these studies focus on a high versus low genetic variability, which was not a limiting factor in our system (Stojanova et al. 2020). While seed size and quality have been found to be less plastic characteristics than seed number (Weiner et al. 1997), other studies have shown strong effects of maternal conditions on the seeds (Veselá et al. 2021). In conclusion, maternal characteristics affected early transplant performance (growth and flowering) but had little influence on long-term survival.

Thus, we found evidence for our expectations that several contextual factors influence establishment success. However, despite variation among sites and years, post-establishment success was largely determined by individual characteristics in established plants, especially several years after transplantation.

Differences between recruited and transplanted individuals

Some of the differences between recruited and transplanted individuals may result from observing recruited individuals in an earlier developmental stage than transplants, thus it may be expected that they were still smaller even after one year, but this was only the case in one population. As initial size was an important factor for survival for both groups, this difference may partly account for the greater establishment success of transplants within the study period.

Interestingly, a larger proportion of recruited individuals flowered in their second vegetation season and produced more flowers than transplanted plants. This may indicate that seedlings establishing naturally on site can better adjust to local microsites – possibly through more efficient root placement or resource uptake – which could provide a modest 'home-site advantage' (Montalvo and Ellstrand 2000b).

Population-specific differences were evident, with recruits outperforming transplants in flowering and growth at the natural sites (Z1 and Z2) but not at the secondary site (Z6). While some of this variation may reflect sample size differences, it also suggests that local habitat conditions modulate but do not fundamentally alter the general pattern of higher transplant survival and greater recruit flowering potential. Overall, these results confirm our expectation that transplanted and recruited individuals differ in performance, however, with transplants ensuring short-term persistence and recruits contributing to long-term population renewal.

Conclusion

Transplanting pre-grown individuals markedly increased establishment success compared to direct sowing, confirming that *M. smejkalii* is poorly capable of recruiting from introduced seeds under natural conditions. Several factors such as site, year, and transplant characteristics influenced survival and reproduction, but they mainly modulated rather than changed the overall success pattern. Finally, transplanted individuals and their recruited offspring differed in performance, with transplants showing higher short-term survival while offspring displayed greater flowering potential, suggesting a complementary contribution of both groups to long-term population persistence.

Overall, our findings emphasize that for long-lived perennials with poor seedling establishment, repeated transplantations across years and sites are key for population reinforcement.

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Author contributions

Alrun Siebenkäs: Data curation (equal); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Karolína Sučíková**: Data curation (supporting); Investigation (supporting); Writing – review and editing (equal). **Zuzana Münzbergová**: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (supporting); Resources (lead); Supervision (lead); Writing – review and editing (equal). **Hana Pánková**: Conceptualization (lead); Data curation (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6wwpzgnct (Siebenkäs et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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