

**Biotic and abiotic filters in translocation
experiments with the three threatened plant
species *Gentiana cruciata* L., *Gentiana
germanica* Willd. and *Myricaria germanica* (L)
Desv.**

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Abstract

Translocations are becoming a common tool for conservation of threatened plant species despite risk, cost and labor intensity. Next to the number of transplanted individuals and genetic diversity, the choice of suitable translocation sites with the right abiotic and biotic conditions is essential for translocation success. Understanding the role and impact of abiotic and biotic filters on early translocation success could therefore improve translocation practices.

Here we present two explorative translocation experiments. In a first translocation experiment we tested the influence of positive (facilitation) and negative biotic interactions (competition) of surrounding vegetation on early translocations success. We translocated 180 individuals of the threatened *G. cruciata* and *G. germanica*, under three treatment conditions: 1) transplanting into existing vegetation, 2) transplanting into bare ground after removal of existing vegetation, 3) transplanting together with common plant species of typical calcareous grasslands after removal of existing vegetation. In a second translocation experiment we examined the relationship of abiotic conditions and environmental stochasticity for the translocation success of the threatened *M. germanica*. 108 *M. germanica* individuals were translocated to three sites along the Kander river, covering different exposures to floods (height over water level) and a range of soil conditions (sandy to rocky).

Despite overall high gentian mortality after overwintering, *G. cruciata* survived better when planted directly into existing vegetation, benefiting mostly of higher soil moisture. This indicates density dependent facilitative effects of surrounding vegetation on early translocation success. *G. germanica* performance was not affected by translocation treatments. *M. germanica* performed best close to the water level although with decreased chance of survival due to higher risk of flooding. Optimal translocation sites should factor in this trade-off and spread around intermediate height levels. Additionally, germination was best on sandy substrate.

Our results suggest that surrounding vegetation could be used to increase early transplantation success and that this should be explored further to increase understanding of spatial and temporal effects of surrounding vegetation on transplants. Further, we want to stress the importance of site selection for translocation success and the impact that environmental stochasticity can have in some habitats. Lastly, explorative translocations in collaboration with practitioners enhance the value of translocation experiments, by advancing knowledge whilst supporting conservation efforts. Scientifically assisted translocations should be encouraged and close collaboration between conservation practitioners and plant ecologists fortified.

Introduction

Global biodiversity decline and species loss is ongoing and happening at a worrying pace (Ceballos et al., 2015; Dirzo & Raven, 2003). Habitat destruction, being a main driver of biodiversity loss, is a key focus of conservation efforts (Godefroid et al., 2011). However, despite increasing attention to habitat conservation efforts in recent years, these measures are not always enough to preserve biodiversity (Heywood, 2017; Maunder, 1992; Volis, 2019). For the conservation of threatened plant species in particular, additional measures are needed to avert extinctions.

Species introductions, reintroductions and augmentations, gathered under the term translocations, have become increasingly important as a complementary conservation tool to reduce species loss (Godefroid et al., 2011; Wolf et al., 1996). Translocations aim to establish or increase the number of viable, self-sustaining populations (Menges, 2008). Especially rare and threatened plant species, with often small and fragmented populations, benefit from direct, species specific measures (Leimu et al., 2006; Maunder, 1992; Menges, 2008). Improvement of genetic diversity, population size and population interconnectivity endorse the recovery and viability of threatened species (Maunder, 1992; Menges, 2008). However, translocation is still a fairly young discipline in conservation biology. Failures are not uncommon and uncertainties in translocation planning still manifold (Godefroid et al., 2011).

The evaluation of translocation success is difficult (Godefroid et al., 2011; Menges, 2008). Successful translocations should improve persistence of focus species in the long run. Therefore, long-term monitoring is necessary to confirm translocation success (Drayton & Primack, 2012; Godefroid et al., 2011; Menges, 2008). Although long-term success should remain the main focus of translocation efforts, early translocation success should not be disregarded (Guerrant Jr & Kaye, 2007). Successful early establishment implies that more individuals reach mature reproductive state, thus increasing the chance of population growth and survival (Dalrymple et al., 2012). Early establishment can be helpful to understand and assess the effect of translocation methods and practices and can give early indications about the coherence of decision making in translocation projects. Furthermore, to maximize benefits from translocation efforts regardless of success, translocations should be designed as experiments to better understand the ecological processes and species-specific requirements involved in translocation of threatened plants (Falk et al., 1996; Guerrant Jr & Kaye, 2007).

Many different factors need to come together, for successful establishment after translocation. Beside the influence of the size of the source population, the number of plants from which seeds were collected and the number of transplanted individuals, transplants go through different filters determining the establishment outcome. They essentially go through the same processes described in modern community assembly (HilleRisLambers et al., 2012). Modern community assembly is a holistic and mechanistic approach to understanding establishment of species. It is a framework that allows to integrate ecological concepts for a better understanding of community structures. It has been suggested as an approach to synthesize the field of invasion ecology (Pearson et al., 2018) and could be used as a framework for translocations. The mechanistic approach of community assembly theory is interesting, as it aims to dissect different factors influencing establishment success. Understanding the individual effects driving translocation success could help develop better practices and improve efficacy of translocations by providing applicable guidelines for practitioners.

According to community assembly theory, translocated plants need to pass two main filters: the biotic and the abiotic environmental filter (HilleRisLambers et al., 2012). The biotic filter comprises of biotic interactions within the community whereas the abiotic filter comprises interactions with the environment. However, these interactions are not independent from each other. Feedbacks are common and make it more difficult to disentangle and quantify single effects on community assembly (Chesson, 2000; HilleRisLambers et al., 2012). Therefore, both interactions and their feedbacks should be considered in translocation experiments.

Understanding how rare and threatened species can coexist with other species in a sustainable community is crucial for translocation practice. Competition and facilitation are important biotic interactions in communities (Callaway & Walker, 1997). The sum of these interactions can strongly influence the establishment of threatened plant species (Van Der Wal et al., 2000). While competition is commonly considered in the design of translocation projects (Midoko-Iponga et al., 2005; Van Der Wal et al., 2000), facilitation is still often neglected (Brooker et al., 2008). Facilitative effect could be exploited to improve translocation efficacy and could be a valuable tool for restoration and conservation of species (Brooker et al., 2008; Gómez-Aparicio et al., 2004; Rayburn, 2011). Yet only few examples of translocations of threatened plant species focusing on facilitation of neighboring plants exist (Bizecki Robson, 2013; Lanno & Sammul, 2014; Ren et al., 2010). Investigating the net effect of surrounding vegetation on translocations of threatened species could help develop recommendations of translocation methods targeting competitive relief or endorsing facilitative effects.

Abiotic conditions are just as important as biotic conditions for translocation success of threatened plant species (Maschinski et al., 2012). There are two main components of the abiotic filter that are particularly important for rare species: Environmental conditions and stochasticity (Maschinski et al., 2012). A good match between abiotic conditions of the translocation site and abiotic niche requirements of the threatened plant species determines establishment potential (Izuddin et al. 2018) and should be carefully considered before any translocation (Godefroid et al., 2011; Noël et al., 2011). Determining translocation sites by similarity to source habitat is usually a good starting point (Brzosko et al., 2018). In addition to abiotic site conditions, stochasticity such

as extreme climatic or disturbance events further shape establishment of plant individuals after translocation (Groves et al., 2020; Mahoney & Rood, 1998; Prati et al., 2016). Stochastic events can have opposing effects on translocation success. Disturbance can, for example, increase translocation success by creating habitat heterogeneity and subsequently increase seedling recruitment (Mahoney & Rood, 1998). Conversely, disturbance can result in higher mortality or even the eradication of transplants (Prati et al., 2016). While many stochastic events are impossible to foresee, some can be anticipated and might even be an important part of a certain habitat. In any case, the possibility and importance of stochastic events should be assessed and included in the considerations of site selection and the development of appropriate transplanting strategies.

In this study we performed two different translocation experiments of explorative character. We focused on the effects of biotic and abiotic filters on early translocation success and wanted to exemplify their importance and implications for the translocation of three threatened plant species. In a first translocation experiment, we investigated the importance of the surrounding vegetation, i.e., their competitive or facilitating effects, for early translocation success of two threatened calcareous grassland species, *Gentiana cruciata* L. and *Gentiana germanica* Willd. We translocated the plants under three treatment conditions: once we removed the existing vegetation (bare ground), once we transplanted the individuals into the present vegetation (present vegetation) and once we removed the existing vegetation and transplanted them together with individuals of common plant species typical for calcareous grasslands (community vegetation). In a second translocation experiment, we focused more strongly on the importance of abiotic site conditions and stochasticity for the early translocation success of a riparian pioneer shrub, *Myricaria germanica* (L) Desv. Both translocation experiments were performed in collaboration with practitioners of local authorities to scientifically support conservation efforts. With these two translocation experiments we wanted to answer the following questions:

- Which biotic filter influences early translocation success more strongly: competition or facilitation?
- What is the trade-off between ideal abiotic conditions and stochastic events for the early establishment of *M. germanica*?

Material & Methods

Gentiana

Study species and study sites

G. cruciata and *G. germanica* are two threatened species from dry calcareous grasslands (Lauber et al., 2018; Zollner & Wagner, 1986). The two members of the Gentianaceae are classified as vulnerable in Switzerland and are listed on the Swiss priority list for conservation of species (moderate priority) (BAFU, 2019; Bornand et al., 2016). *G. germanica* is a monocarp biennial, whereas *G. cruciata* is a polycarp perennial species, but both develop rosettes that die back over winter and regrow the following season (Hegi et al., 1931; Verkaar & Schenkeveld, 1984). *G. germanica* generally reproduces in the second year whereas *G. cruciata* rarely sets fruits at all in the first years but reproduces over multiple seasons thereafter (Hegi et al., 1931; Verkaar & Schenkeveld, 1984). Both species are self-compatible but while *G. germanica* has a high naturally occurring selfing-rate (Markus Fischer & Matthies, 1997), *G. cruciata* depends more on cross pollination (Petanidou et al., 1995). Both produce fruits with up to 100 small seeds with low dispersal ability (Markus Fischer & Matthies, 1997; Kéry et al., 2001; Verkaar et al., 1983).

Dry, nutrient-poor and calcareous grasslands (Mesobromion) are part of the Swiss priority list for conservation of habitats and are classified as vulnerable after IUCN criteria (Delarze et al., 2015; Keith et al., 2013). Nutrient poor grasslands typically host high species richness and are

therefore interesting study systems to investigate biotic interactions and understanding species coexistence. The experiment was carried out on an extensively managed municipal site of the city Bern, near the Hintere Engehalde (Figure 1a). The south-east facing, steep and dry grassland corresponds to a Mesobromion community with *Bromus erectus* Huds. as dominant and eponymous grass species. The site is within reasonable limit of historic distribution of *G. cruciata* and *G. germanica*.

Study design

Seeds from 17 *G. cruciata* and 18 *G. germanica* individuals were collected in Summer 2018 from populations near Moutier in the Bernese Jura. To account for genetic diversity of translocated plants, the seeds were collected as seed families (grouped by source individuals) from the source population. The seeds of 12 common community species, chosen to represent a typical nutrient-poor calcareous grassland community, were purchased from Artha Samen (Münsingen, Switzerland), a local wild plant nursery.

To ensure germination, *G. germanica* seeds were treated with gibberellic acid (2 mg GA₃ per ml of water) for five days before planting (Fischer and Matthies 1997). In March 2019, *G. cruciata* and treated *G. germanica* seeds were sown in round pots (12 cm round Göttinger, Germany) filled with seedling-substrate (Klasmann, Germany) and stratified by being left outside in the Botanical Garden of the University of Bern for four weeks (average 6.2 °C, min -3.6 °C, max 18.4 °C, MeteoSchweiz, 2019). Likewise, the community species were planted and stratified following the same procedure. In April 2019 the pots were taken into a greenhouse to avoid frost damage. In May 2019, 300 seedlings of both gentian species were transplanted to growing plates with cultivation soil (Substrate 167, Ricoter AG, Switzerland). Analogously, for each community species, 60 seedlings were transferred to growing plates (120 for *Bromus erectus* Huds.). All growing plates were kept in the botanical garden until translocation in September 2019. During the hottest summer days, the plants were shaded, as growing plates would have dried out during the course of a day.



Figure 1. Overview of the translocation experiment at the Hintere Engehalde with two threatened gentian species. a) Location of the translocation site, 3 km north of the city center of Bern (Swisstopo). b) View of the south-east facing slope with three fenced experimental blocks. c) Rosette of *G. cruciata* in a vegetation sub-block. d) Design of one fenced block with three treatment sub-blocks and the random allocation of both gentian species within each sub-block (+ = *G. cruciata*, o = *G. germanica*).

To investigate the importance of surrounding vegetation for the translocation of threatened plant species, we defined three treatment levels: bare ground, present vegetation and community (Figure 1c).

For the bare ground treatment, we removed the topsoil and turf about 5 cm deep and with this also the present vegetation. Therefore, it represents a translocation with no direct biotic interaction with other plants in the early stage of establishment. Thus, bare ground mostly reflects how the transplants cope with only the abiotic conditions.

For the present vegetation treatment, vegetation was left untouched, and gentians were planted directly into the existing community. In this treatment we would expect strong biotic interactions of a predominantly competitive nature with the surrounding vegetation.

For the community treatment we removed the topsoil and turf about 5 cm deep. We had previously chosen 12 common plant species representing a typical nutrient-poor, calcareous grassland community (Delarze et al., 2015). The species were selected to cover the most common plant families and functional groups (Table A1). In each plot with the community vegetation treatment, we planted ten additional community plants together with the study species. The species composition of the community around each individual was randomly assigned but balanced, as such that all 12 community species were equally represented (except *Bromus erectus* as dominant grass 2:1). By transplanting the threatened gentians together with their characteristic plant community, representing an intermediate vegetation density we aimed to decrease possible competitive effects, whilst maintaining positive interactions of neighboring plants (Chu et al., 2008; Xi et al., 2016).

The three treatments were established in three 7 x 7 m blocks on the site at the Hintere Engehalde (Figure 1b). Each block consisted of three, 1 x 5 m treatment sub-blocks. The three treatments within a block were randomly allocated. The elongated sub-blocks were 1 m apart and ran perpendicular to the slope. Each treatment sub-block consisted of 20, 0.5 x 0.5 m plots, for a total of 180 plots (60 per treatment) (Figure 1d).

The translocation was carried out mid-September 2019. The 90 individuals of each gentian species were equally distributed across the three treatments. Individuals from different seed families of both gentian species were equally allocated to the treatments and then randomly assigned to plots (Figure 1d). The 600 community species were planted in the community treatment sub-blocks at the same time as the gentian species. The blocks were fenced to limit possible trespassing and disturbance by animals, as the site was near a residential area. Additionally, the field was watered in the first two weeks after transplantation due to particularly dry weather conditions. Thereafter, the site was left untouched and was not mowed during the duration of the experiment.

Measurements

We monitored the transplants over one year. Initial measurements of height, number of leaves and biggest leaf were taken from each gentian transplant. Additionally, to control for differences in treatments and plots, and to quantify the density of vegetation of the three treatments, we estimated vegetation cover (moss and herbs) for all plots. We also recorded the soil moisture (% water content) of each plot at 3 different timepoints (HH2 Moisture Meter with ML3 ThetaProbe, Delta-T Devices Ltd, England). After initial measurements, survival, height, number of leaves and biggest leaf was recorded every three weeks before and after winter.

Statistical analysis

To test the effect of the surrounding vegetation for early translocation success, we used generalized linear mixed effect models (glmer) and linear mixed effect models (lmer) from the lme4 package (Bates et al., 2015). We used generalized linear mixed effect models (glmer) with a binomial error distribution for survival data and with a Poisson distribution for number of leaves performance data. For biggest leaf performance, we used linear mixed effect models (lmer). Height was not included, because it did not represent growth accurately, due to the general low height of young rosettes. We focused our analysis on the effects shortly after translocation (before winter) and after winter. We included block as random factor according to our experimental design. The full model included treatment and soil moisture as fixed effects in addition to initial leaf size (initial measurement of biggest leaf) and seed family as covariates. We could not include interactions, as the models would not converge with the added complexity. We simplified the models comparing nested models using likelihood ratio tests and removing non-significant terms. We analyzed significant categorical terms using pairwise comparison with Tukey p-value adjustment (emmeans

package; Lenth, 2020). To avoid pseudo-effects, initial leaf size was not included in the analysis of biggest leaf size. All statistical analysis was performed using R version 4.0.2 (R Core Team, 2020).

Myricaria

Study species and site

M. germanica is a riparian pioneer shrub listed as vulnerable in Switzerland with moderate national priority (BAFU, 2019; Bornand et al., 2016). It typically occurs on sand and gravel banks of dynamic rivers (Egger et al., 2017). This resistant shrub can tolerate periods of drought and flooding. However, it depends on occasional disturbance events such as floods to mitigate competition from more competitive shrub species (Kudrnovsky, 2013; Lener et al., 2014). On average, they grow seven years old before being either outcompeted by other fast growing riparian shrubs and trees or being eradicated by bigger disturbance events (Schweingruber et al., 2007). However, some individuals grow 21 (Schweingruber et al., 2007) to 70 years old (Frisendahl, 1921), indicating the impact of dynamic processes on the habitat of *M. germanica*. Main competitors and co-occurring shrubs of *M. germanica* are willow shrubs (Kammerer, 2003; Rieben, 2009). Together they characterize the riparian willow communities (Salicion eleagni; Delarze et al., 2015), a habitat classified as endangered and of high national priority in Switzerland (BAFU, 2019). The persistent tamaricaceae reproduces through small wind dispersed seeds, that quickly germinate after dispersal (within 24h; Egger et al., 2017). Genetic exchange of the insect-pollinated shrub is known to be bidirectional along rivers but is still often limited by increasingly fragmented populations (Werth & Scheidegger, 2014).

The Kander river (Figure 2a), having its source at the Kanderfirn, is a typical example of a tamed mountain torrent (Grosjean, 1962). Channelization and containment efforts along the Kandertal up to lake Thun have led to strong riverbed erosion and the disappearance of riparian habitats (Flussbau AG SAH, 2008; Meyer et al., 2013). However, the problem has been recognized and renaturation efforts have been strong in the last decade (“Kander.2050”; Flussbau AG SAH, 2008). In 2005 the region of Augand has been widened and the riverbed consolidated, facilitating controlled overflow and the connectivity of water and river wetland. Today, the main population of *M. germanica* at the Kander river is limited to the Gasterntal, with few isolated individuals downstream (Infoflora.ch/de/daten; Magnin, 2020, personal observation). Historically however, *M. germanica* spread along the whole Kandertal (Infoflora.ch/de/daten). The partially restored dynamic in the Augand region make this site ideal for translocation of *M. germanica*.

Study design

Seeds were collected from 50 individuals of the source population in the Gasterntal in July 2018. On the same day, they were randomized and sown into deep (30 cm) growing pots filled with fine sand. The growing pots were placed into 5 cm deep water to guarantee continuous water availability in the first months. The plants were overwintered in a greenhouse the first year and grown outside otherwise.

Riparian habitats are often disturbed and heterogenous (Naiman and & Décamps, 1997). Abiotic environmental conditions vary within short distances and stochastic events, such as floods, additionally shape the habitat (Naiman and & Décamps, 1997). We focused on two major components of the abiotic environment of *M. germanica*: Flooding disturbance and soil composition. To investigate the impact of flooding mediated disturbance and soil composition on early translocation success of *M. germanica*, we selected three different sites in the Augand region (Figure 2b). The sites differ in their abiotic conditions, ranging from stony to sandy and higher to lower height over water level (exposure to flood) (Figure A2). Additionally, site selection was helped by evaluations of age and dynamics of sand and gravel banks, by river consulting engineers (Flussbau AG SAH, 2019, unpublished report). Using their expertise and hydrological data from the Kander-Hondrich measuring station, we chose different heights over water level as indicators of flooding frequency and intensity. 0.5 m over water level corresponds to a biennial flooding event, 1

m over water level is in the range of a thirty-years high water event. We included a range from approximately 0.5 to 2 m over water level (measured at average yearly discharge rate of ca. 20 m³/s) (Figure 2d). For soil composition we included gradients from sandy to stony in our site selection. Three experimental blocks were designated at each site. Each block consisted of four plots of three individuals spaced 1 m apart. The plots ran parallel to the river and covered diverse microsite conditions on a height over water level gradient. To optimize the range and the gradients of conditions covered in each block, the distance between plots varied between 1.5 and 3 m (Figure 2c). The conditions chosen for our experimental blocks, resulted being around the demarcation from mostly bare sand and stone to abundant riparian vegetation. In October 2019, 108 *M. germanica* plants were translocated to the three sites in the Augand region. The transplants were randomly assigned to the plots.

In an additional common garden experiment, we assessed the importance of soil composition for the germination of *M. germanica*, as germination ability in a translocation site is a crucial part of population rejuvenation and therefore of translocation success. Seeds from 25 individuals were collected in the Gasterntal in July 2020. On the same day, 50 seeds were sown 2 m downriver of each plot for a total of 36 sowings. The seeds were generously watered once after sowing. Additionally, another common garden experiment was prepared in the Botanical Garden of the University of Bern. 27 pots (square 11 cm Göttinger, Germany) were prepared with different soil compositions collected from the three sites, covering the whole range of soil composition found in the field. Seeds were sown and counted. The pots were then placed in water filled trays and watered regularly, to represent germination with abundant water availability.

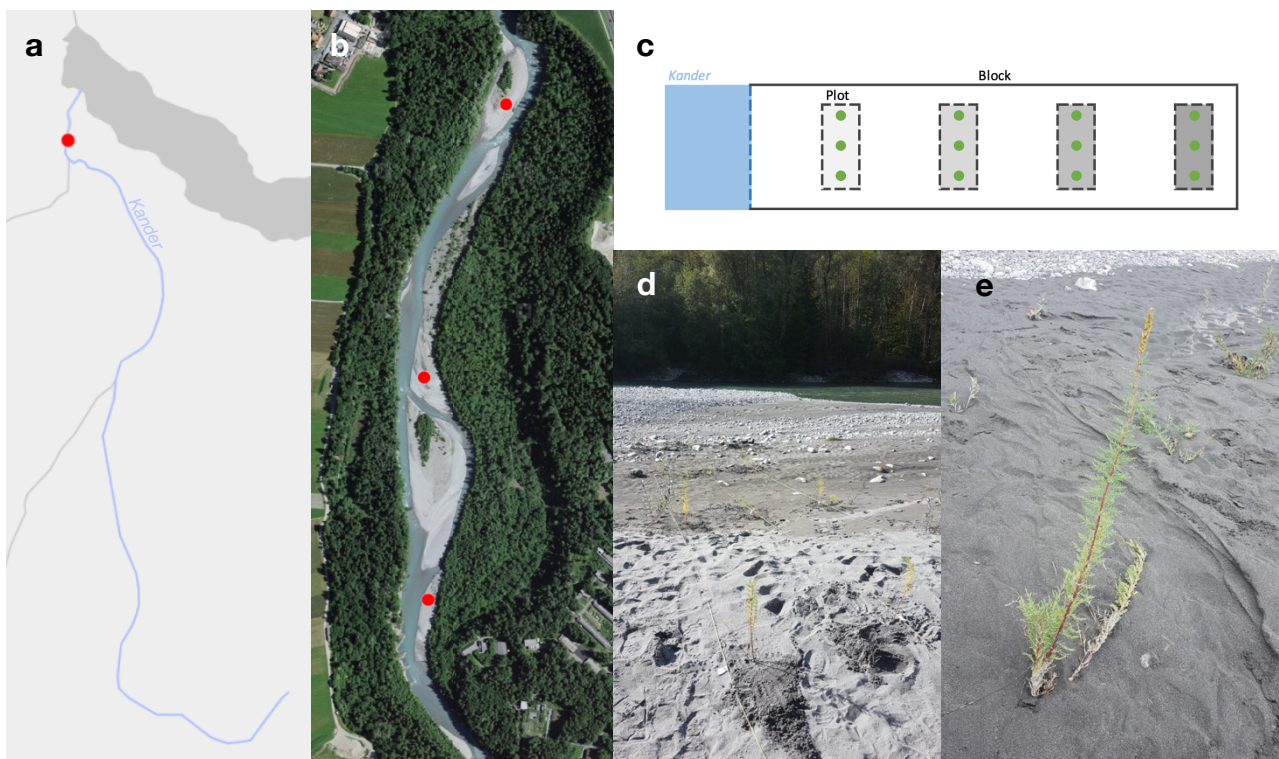


Figure 2. Overview of the translocation experiment in the Augand with the riparian shrub *M. germanica*. a) River course of the Kander from the Gasterntal to lake Thun with the location of the natural reserve Augand. b) Location of the three translocation sites within the natural reserve. Three blocks of 12 *M. germanica* individuals were planted at each site. c) Plants were planted in four plots on different heights over the water level. d) Block after translocation with plots along elevation over the water level. e) Flowering *M. germanica* which has recently been submerged.

Measurements

The abiotic conditions for each plot were recorded after the translocation in October 2019. We measured height over water level and distance to the river using a laser distance meter with tilt

sensor (Disto X4, Leica Geosystems AG). Vegetation cover and soil composition was recorded around each individual *M. germanica* transplant. Pictures taken from 1 m above the transplants were used to estimate percentage of vegetation cover and percentage of sand (< 1 cm) respectively stone (> 1 cm) cover, as indicator of soil composition. Initial transplant performance was measured as plant height and number of branches (>10 cm) shortly after the translocation. After winter, survival, flowering, plant height and number of branches was continuously measured every 5 weeks until autumn 2020 (Figure 2e.).

For the germination field experiment, the soil composition was estimated by percentage of sand respectively stone coverage on a 50 x 50 cm square around the seeds. Analogously, the soil composition was estimated for each pot in the common garden experiment at the Botanica Garden of Bern. The number of germinated seeds was recorded 1, 3, 7 and 14 days after sowing in both experiments.

Statistical analysis

To test the effect of flooding disturbance and soil composition on early translocation success of *M. germanica*, we used mixed effect models from the lme4 package (Bates et al., 2015). For binary survival and flowering status data we used generalized linear mixed effect models (glmer) with binomial error distribution. Growth as differences of height and number of branches after one year was analyzed with linear mixed effect models (lmer). Only living individuals were included in growth analysis. We included block identity nested in site identity as random effect to account for our experimental design. The fixed effects of the full models consisted of height over river, percentage of sand (soil composition) and percentage of vegetation cover, including all interactions. Only survival was not analyzed with interactions, as the model would not converge with the added complexity. We did not use distance to the river in the models, as it strongly correlated with height over river and did not represent the risk assessment from river consulting engineers as well. We simplified the models comparing nested models using likelihood ratio tests and removing non-significant terms. We analyzed significant categorical variables using pairwise comparison (emmeans package; Lenth, 2020). The branch difference response variable was log transformed to satisfy model assumptions.

The effect of soil composition on germination ability was tested with a linear model with sand coverage as explanatory variable. Germination suitability of the experimental gradients was analyzed with generalized linear mixed effect model (glmer) with binomial error distribution to account for proportional data. We included soil composition and height over river as fixed terms. To account for our block design, we included block identity nested in site identity as random effect. All statistical analysis was performed using R version 4.0.2 (R Core Team, 2020).

Results

Gentiana

Of the 90 respective individuals planted per gentian species, 80 *G. cruciata* and 84 *G. germanica* survived translocation before winter. After winter 14 *G. cruciata* and 29 *G. germanica* reemerged (Figure 3a). The growth of the two species was generally low, both before and after winter, with overall even smaller individuals after winter (Figure 3a and b).

Before winter, both, surrounding vegetation treatments (bare ground, present vegetation, community vegetation) and soil moisture, did not influence the survival or the growth of the gentian species (Table 1). After winter, the findings were different. While the surrounding vegetation still did not influence the survival of *G. germanica*, *G. cruciata* individuals planted in the existing vegetation (present vegetation) survived significantly better than individuals planted in bare ground or together with individuals from the same community (community vegetation) (Tables 1 and 2). Similarly, soil moisture only influenced *G. cruciata*. Higher soil moisture slightly increased survival of *G. cruciata*

but had no influence on *G. germanica*. Growth of both gentian species was still not influenced by surrounding vegetation treatments and soil moisture after winter (Table 1).

The two covariates, initial biggest leaf size and seed family did not influence survival nor growth of the gentian species before winter (Table 1). After winter however, initial leaf size significantly influenced survival of both gentian species, with bigger initial size increasing the chance of successful overwintering (Table 1).

Table 1.

Outcome of generalized linear mixed effect models testing for survival and growth of *G. cruciata* and *G. germanica* before and after winter. Treatment (bare ground, present vegetation, community vegetation), soil moisture, seed family and initial biggest leaf size effects on translocation survival of *G. cruciata* and *G. germanica* after overwintering. Block effects were included as random term. Significances were determined with likelihood-ratio tests of nested models. Estimates are only given for significant and marginally significant terms. Significant factors were subsequently analyzed by pairwise comparison (Table 2).

Before winter												
<i>G. cruciata</i>												
	Survival				Number of leaves				Biggest leaf			
	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value
Treatment	-	2.15	2	0.34	-	2.79	2	0.25	-	3.79	2	0.15
Soil moisture	-	1.58	1	0.21	-	1.75	1	0.19	-	0.43	1	0.51
Seed family	-	10.21	8	0.25	-	3.66	8	0.89	-	10.24	8	0.25
Initial biggest leaf size	-	0.27	1	0.60	-	2.21	1	0.14	-	-	-	-
<i>G. germanica</i>												
	Survival				Number of leaves				Biggest leaf			
	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value
Treatment	-	1.75	2	0.42	-	0.49	2	0.78	-	3.62	2	0.16
Soil moisture	-	0.41	1	0.52	-	0.02	1	0.88	-	0.02	1	0.88
Seed family	-	9.14	9	0.42	-	7.22	9	0.61	-	13.41	9	0.14
Initial biggest leaf size	-	2.51	1	0.11	-	0.01	1	0.97	-	-	-	-
After winter												
<i>G. cruciata</i>												
	Survival				Number of leaves				Biggest leaf			
	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value
Treatment	-	6.95	2	0.03	-	0.25	2	0.88	-	1.45	2	0.48
Soil moisture	0.75	3.37	1	0.07	-	0.01	1	0.97	-	1.13	1	0.29
Seed family	-	10.50	8	0.23	-	1.59	5	0.90	-	8.01	5	0.16
Initial biggest leaf size	0.55	3.18	1	0.07	-	0.78	1	0.38	-	-	-	-
<i>G. germanica</i>												
	Survival				Number of leaves				Biggest leaf			
	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value	Estimate	χ^2	df	p-value
Treatment	-	3.29	2	0.19	-	0.19	2	0.91	-	0.209	2	0.90
Soil moisture	-	1.28	1	0.26	-	0.11	1	0.75	-	0.03	1	0.86
Seed family	-	15.99	9	0.07	-	3.52	9	0.94	-	12.04	9	0.21
Initial biggest leaf size	0.86	7.74	1	0.01	-	0.01	1	0.95	-	-	-	-

Even though we did not have enough replications per seed family to test the effect of specific seed families on the survival or growth of the gentian species, we could test whether there were general differences between the survival or growth of seed families. And indeed, we found that the covariate seed family had a marginally significant influence on the survival of *G. germanica*, while it did not

influence the survival of *G. cruciata* (Table 1). Growth after winter was also not influenced by initial biggest leaf size and seed family (Table 1). Additionally, we found that soil moisture and vegetation cover are correlated. This indicates that our treatment levels with different vegetation densities influence soil moisture (Figure A1).

Table 2.

Pairwise comparison of the three treatments bare ground, present vegetation and community vegetation for *G. cruciata* after winter. Pairwise comparison from estimated marginal means of the minimal adequate generalized linear mixed model with treatment, soil moisture and initial leaf size as fixed terms and block as random effect. P-values were determined with Tukey adjustment method for multiple comparison.

	Estimate	SE	z ratio	p-value
vegetation - bare	2.45	0.98	2.51	0.03
vegetation - community	2.91	1.05	2.77	0.02
bare - community	0.46	0.99	0.47	0.89

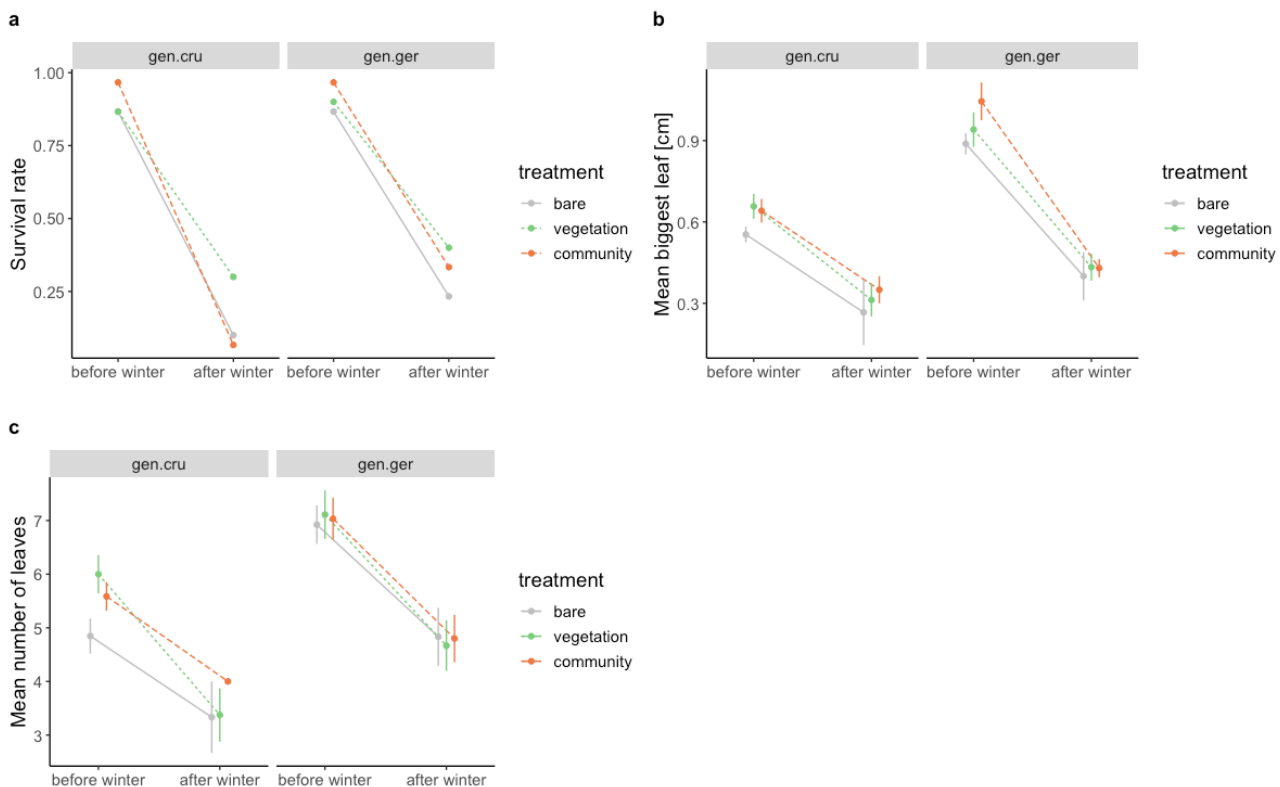


Figure 3. Overview of growth and survival of *G. cruciata* and *G. germanica* after overwintering. a) Survival rate, b) mean biggest leaf and c) mean number of leaves of gentians under three planting conditions. Bars indicate standard errors.

Myricaria

103 of 108 (95% survival) translocated *M. germanica* individuals survived the first year in the field. Individuals closer to the water level seemed more vital, with more foliage and young leaves. However, most plants did not grow in height over the course of the first year but instead some developed more branches (Figure 3). Over the first summer after translocation, 22 individuals set flower.

The few individuals that did not survive the first year were all situated close to the water level (Figure 4a). In general, height over water level influenced survival of *M. germanica*, with lower

chance of survival at lower height over water level (Table 3, Figure 4a). However, surviving individuals close to water level developed more branches and had an increased probability to set flower (Table 3, Figure 4b and c). Plant size was not affected by height over water level. Conversely, soil composition only influenced plant height but not survival or flowering of *M. germanica*. *M. germanica* individuals on stony substrate remained taller than on sandy substrate (Table 3, Figure 4d).

Table 3.

Results of the mixed effect models for performance of *M. germanica* after translocation. Effects of height over water level, soil composition and vegetation cover on survival, flowering, number of branches and plant height of *M. germanica*. The models include random effects for blocks nested within sites. Significances were determined with likelihood-ratio test of nested models. Estimates are only given for significant terms.

	Survival			Flowering			Number of branches			Plant height		
	Estimate	χ^2	p-value	Estimate	χ^2	p-value	Estimate	χ^2	p-value	Estimate	χ^2	p-value
Height over water level	5.26	7.96	0.005	-3.27	5.69	0.02	-0.43	11.68	0.001	-	0.06	0.80
Soil composition	-	2.70	0.10	-	0.09	0.77	-	0.87	0.35	-8.23	5.53	0.02
Vegetation cover	-	2.40	0.12	-	2.09	0.15	-	0.46	0.50	-	0.98	0.32

Otherwise, soil composition had no effect on development of branches and flowers (Table 3).

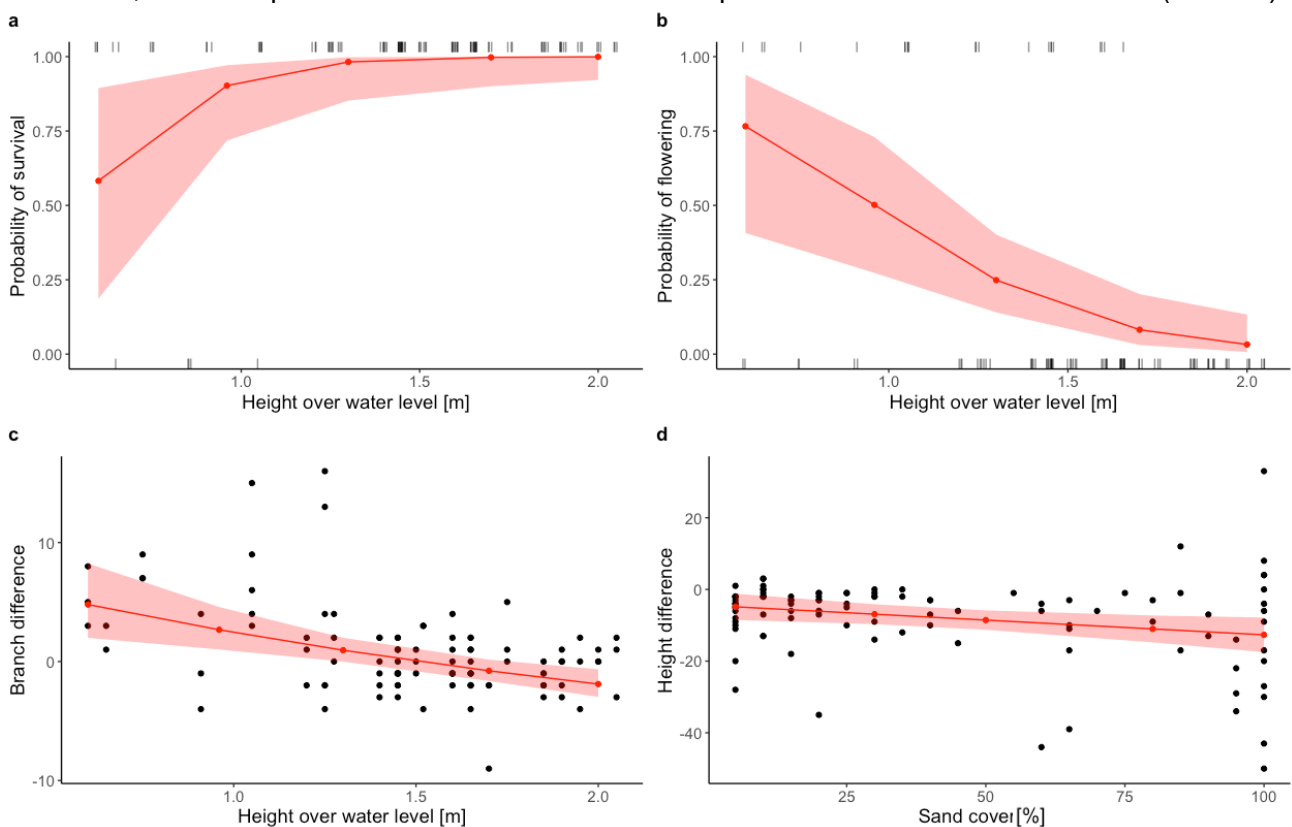


Figure 4. Overview of raw data and model predictions of significant terms for translocation performance of *M. germanica*. a) Effect of height over water level on survival. b) Effect of height over water level on flowering. c) Effect of height over water level on number of branches. d) Effect of soil composition on plant height. Red points indicate model estimates and red bands show 95% confidence intervals.

Vegetation cover also did not affect *M. germanica* in the first season for any of the considered measurements (Table 3).

M. germanica germinates very quickly. In our experiment, most seeds germinated within the first days. In the field, we found germinating seeds only on 5 of 36 plots, whereas germinating seeds

were found in all pots of the common garden experiment. Germination rate in pots was 30% after 14 days. In the field, germination was better at low height over water level ($\text{Chi}^2 = 105.24$, $p < 0.001$, Figure 5a) and not influenced by the soil composition ($\text{Chi}^2 = 2.72$, $p = 0.10$). In the common garden experiment under constant water availability, sandier substrate improved germination dramatically ($F(1,25) = 55.67$, $p < 0.001$, $R^2 = 0.68$, Figure 4b).

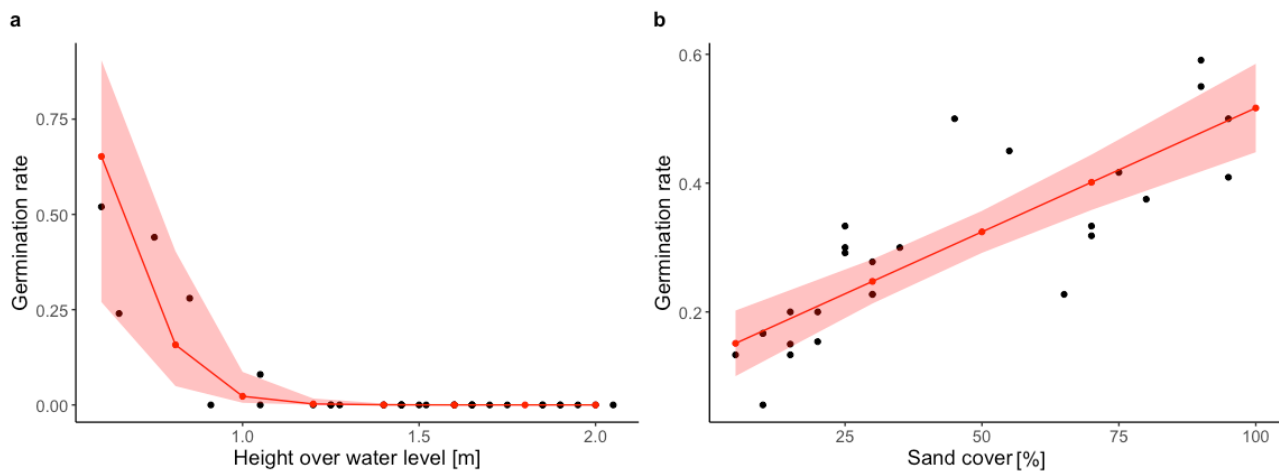


Figure 5. Overview of raw data and model predictions for germination of *M. germanica*. a) Effect of height over water level on germination in the field. b) Effect of soil composition on germination rate in pots. Red points indicate model estimates and red bands show 95% confidence intervals.

Discussion

Gentiana

Survival for both gentian species after one season was low and growth of the survivors only limited. Literature suggests that the size of the translocated plant can have a significant impact on survival and establishment with bigger individuals generally surviving better (Grossnickle, 2012). As the translocated gentian individuals were quite small in our study, this might have led to an overall high mortality. This is also reflected by the positive effect of initial biggest leaf size on survival of both gentian species, suggesting size dependent survival. This should encourage the development of good nursery protocols before translocation experiments.

Despite overall low survival, we found that *G. cruciata* survived better when planted directly in present vegetation compared to bare ground or together with common plants of the same community (community vegetation). This suggests a positive effect of surrounding vegetation on survival of *G. cruciata*. Facilitation of threatened species from surrounding vegetation has been observed in other studies and is considered an important promoter of coexistence in communities (Soliveres et al., 2015). However, facilitation and competition both have density-dependent components (Dickie et al., 2005). It has been shown that facilitation can shift to higher densities under environmental stress, outweighing competitive interactions even at high densities (Goldberg et al., 1999; Zhang & Tielbörger, 2020). In our study we found that plots with the treatment present vegetation retained more water than bare ground or community vegetation plots, whereas bare ground and community vegetation plots did not differ in soil moisture. Soil moisture regulation by surrounding plants has also been shown in other translocation experiments (Yang et al., 2010). *G. cruciata* seemed to benefit from the higher water retention especially in the higher density plots under the present vegetation treatment. Our results therefore suggest that in our study, facilitation is more important than competition in early translocation survival of *G. cruciata*. A result that might

have been promoted by rather dry conditions (65% of norm precipitation in Bern) when rosettes reemerged after overwintering (MeteoSchweiz, 2020).

For *G. germanica* the different treatments and therefore the surrounding vegetation did not affect survival. Instead, we found that seed family influenced survival of *G. germanica*, implying the importance of diverse source material for translocation. Collecting seeds from many different source plants from a large population is important to increase the adaptive potential of the translocated species and therefore increase the chance of survival in different biotic and abiotic conditions (Forsman, 2014; Leimu et al., 2006; Vergeer et al., 2004). The importance of genetic diversity for translocation success of threatened plants has been shown in several studies (Bischoff et al., 2008; Prati et al., 2016; Schäfer et al., 2020). However, survival of *G. cruciata* was not influenced by seed family. This could indicate low genetic diversity in the source population of *G. cruciata*, demonstrating a widespread problem of small populations of threatened species (M. Fischer & Matthies, 1998; Willi et al., 2006). Inbreeding depression has been found in small populations of *G. cruciata* as well as *G. germanica* in other studies (Markus Fischer & Matthies, 1997; Petanidou et al., 1995). In our study, the source population of *G. cruciata* in Moutier (BE) seems to be genetically impoverished whereas the *G. germanica* populations still shows more genetical diversity and adaptive potential (Markus Fischer et al., 1997).

We found no significant variation in growth in neither of the two gentian species. Neither number of leaves nor biggest leaf size was influenced by our treatments. However, treatment effects were probably obscured by the low survival and growth.

Species specific knowledge about rare species can help focus efforts on rewarding methods and aspects of translocation. Understanding effects of facilitation on translocation of rare species is valuable for researchers and practitioners alike and should be more commonly considered in translocation efforts. Especially the density-dependence of facilitation could be interesting for translocation practice of threatened plant species, as high vegetation density is often solely associated with competition. Our result suggest that facilitation can be stronger than competition for early establishment, especially at high density.

Myricaria

The early survival of *M. germanica* after translocation was high with 95% survival after one year. We should note that no exceptional flooding event was recorded in 2020. The highest discharge rate measured was 112 m³/s, just around the 120 m³/s threshold of biennial flooding events. Therefore, effects related to flooding might not be particularly strong in our study period.

Nevertheless, individuals closer to the water level had a lower chance of survival due to uprooting and erosion through flooding. However, the survivors found closer to the water looked more vital with more branches and foliage in addition of having a higher chance to set flowers. They showed an overall change in growth pattern from straight growing to bushy individuals, as they developed more branches due to flood related breakage of branches (Hupp, 1983). Changed growth patterns due to altered investment in different organs is typical after translocation (Grossnickle, 2012). Nevertheless, the individuals close to the water level were lush and performed better, especially with regard to flowering. Additionally, germination was higher at lower height over the water level, mostly because of better water availability. While closeness to the water level is a good indicator for the risk of flooding in the vicinity of a stream, abiotic conditions such as nutrient availability are often more favorable towards the water level in riparian systems, thus increasing the chance for *M. germanica* to perform well (Naiman and & Décamps, 1997). This interaction creates a trade-off between favorable abiotic conditions and the stochastic flooding events driving mortality and suggests better performance but higher mortality towards the water level. Such relationships are commonly found in riparian communities and should be considered for site selection (Johnson et al., 1995; Mahoney & Rood, 1998; Polzin & Rood, 2006).

Beside the importance of height above water level, we also found effects of soil composition on performance of *M. germanica* after translocation, with taller individuals on rocky substrate and smaller individuals on sand. However, over the whole growing period we found an overall decrease in plant size, due to the loss of branches. As sandy sites tended to be closer to water level (regions

of sediment deposition), they were most likely more disturbed by flooding than stony sites, potentially leading to an increased number of branches broken at these sites. This is also reinforced by the correlation of sand and height over water level (Figure A3). Furthermore, soil composition also affected germination of *M. germanica* with higher rates on sandy substrate. The fine-grained sand is better at retaining water and therefore generates more suitable conditions for germination (Mahoney & Rood, 1991). Riparian species often have substrate requirements for successful germination and establishment that should be taken into account for ex-situ cultivation and translocations (Mahoney & Rood, 1998).

Surrounding vegetation did not affect survival or performance of *M. germanica* in the first stage of establishment. However, biotic interactions might become important filters for long-term establishment (Karadimou et al., 2015). Competition with other pioneer shrubs, especially willows, could become a restrictive force on a longer time scale.

Mainly abiotic and stochastic effects were important for early translocation success of *M. germanica*. The pioneer shrub performs best close to the water level but with increased risk of flooding. Therefore, we suggest that *M. germanica* should be translocated along a height over water level gradient, to mitigate risks imposed by flooding. As *M. germanica* naturally lives for around seven years on average, the height of a 10-year flooding event can be a reasonable approximation for the mean height over water level to use. Although assessing river dynamics and hydrological processes with height over water level might be a strong simplification (Bendix & Hupp, 2000), it is a usable criterion and guideline for practitioners. Soil composition is also worth considering, as fine wet substrate is required for successful germination of *M. germanica*.

Translocation with *M. germanica* exemplified the role and amplitude that abiotic conditions and stochasticity can have on early translocation success. Abiotic site conditions and stochastic processes are decisive for successful establishment and reproduction. Site selection is therefore particularly crucial in the dynamic habitats of riparian communities. While we found strong evidence of abiotic filters on early translocation success of *M. germanica*, biotic interactions seem less important for early establishment.

Conclusion

We found some support for density-dependent facilitation effects of surrounding vegetation on early translocation of the threatened gentian species *G. cruciata*. Positive interaction effects outweighed competitive effects at higher neighbor density. The density dependence of facilitative effects has rarely been examined in translocation experiments but should be considered more for future translocations. Positive biotic interactions could potentially be utilized to improve success of translocation practices. Although facilitation may be beneficial for early translocation success in some cases, longer term effects should also be explored in future studies to investigate the development of net interaction effects over time. Beside temporal effects, facilitation is also influenced by the present abiotic conditions (stress-gradient hypothesis; Maestre et al., 2005). Hence, understanding the species-specific abiotic environment requirements and the conditions at the translocation site therefore remain essential to better understand biotic interactions.

For the translocation of *M. germanica*, site selection and habitat requirements were the main focus. Abiotic environmental conditions most strongly influenced early translocation success, especially height over water level. Although we show the essential abiotic factors for early translocation success, monitoring should be prolonged to increase understanding of important factors for long-term translocation success. Additionally, following recruitment of new individuals could further advance knowledge about habitat requirements, especially with regard to successful reproduction.

Both biotic and abiotic factors impact early translocation success, but the importance and magnitude of these factors strongly depends on habitat type. The importance of both factors should be determined to find ideal habitats for translocation and to increase transplantation success. Well-founded understanding of species-specific habitat requirements and critical habitat-specific factors are indispensable for conclusive translocation planning. Additionally, we highlight the importance to design translocations as scientific experiments as they help to explore species-specific

requirements and help advance translocation practices, ultimately guiding future conservation efforts (Falk et al., 1996; Guerrant Jr & Kaye, 2007; Wendelberger & Maschinski, 2016). The translocation of *M. germanica* was designed as research-oriented translocation, to increase understanding of habitat requirements, whilst advancing restoration of *M. germanica* along the Kander river. In this case the insights of this study directly helped planning further translocations along the Kander river. Scientifically assisted translocations are valuable for both scientists and practitioners, advancing the understanding of underlying factors driving translocation outcome whilst implementing conservation measures. Collaborations maximize the value of translocation experiments and help further develop translocation practice as a promising tool for conservation and restoration.

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Appendix

Table A1.

Community vegetation species. Typical calcareous grassland species planted together with *G. cruciata* and *G. germanica* in the community vegetation treatment.

<i>Bromus erectus</i> Huds.	Poaceae
<i>Briza media</i> L.	Poaceae
<i>Onobrychis viciifolia</i> Scop.	Fabaceae
<i>Sanguisorba minor</i> Scop.	Rosaceae
<i>Galium verum</i> L.	Rubiaceae
<i>Salvia pratensis</i> L.	Lamiaceae
<i>Primula veris</i> L.	Primulaceae
<i>Scabiosa columbaria</i> L.	Caprifoliaceae
<i>Dianthus carthusianorum</i> L.	Caryophyllaceae
<i>Plantago media</i> L.	Plantaginaceae
<i>Centaurea Scabiosa</i> L.	Asteraceae
<i>Ranunculus bulbosus</i> L.	Ranunculaceae

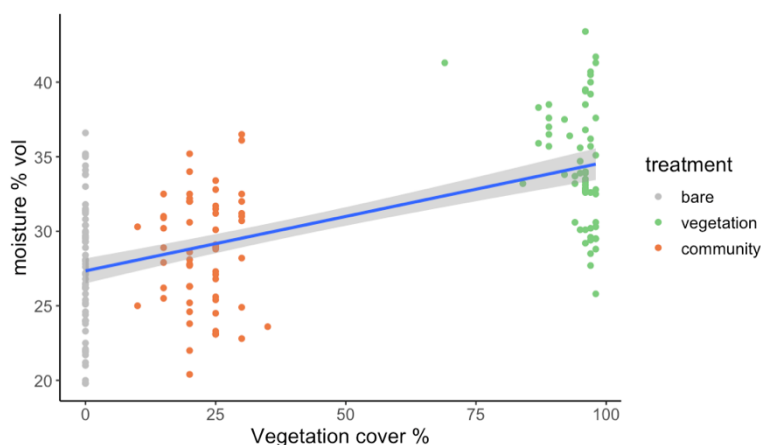


Figure A1. Relationship between soil moisture and vegetation cover across treatment plots of *G. cruciata* and *G. germanica*.

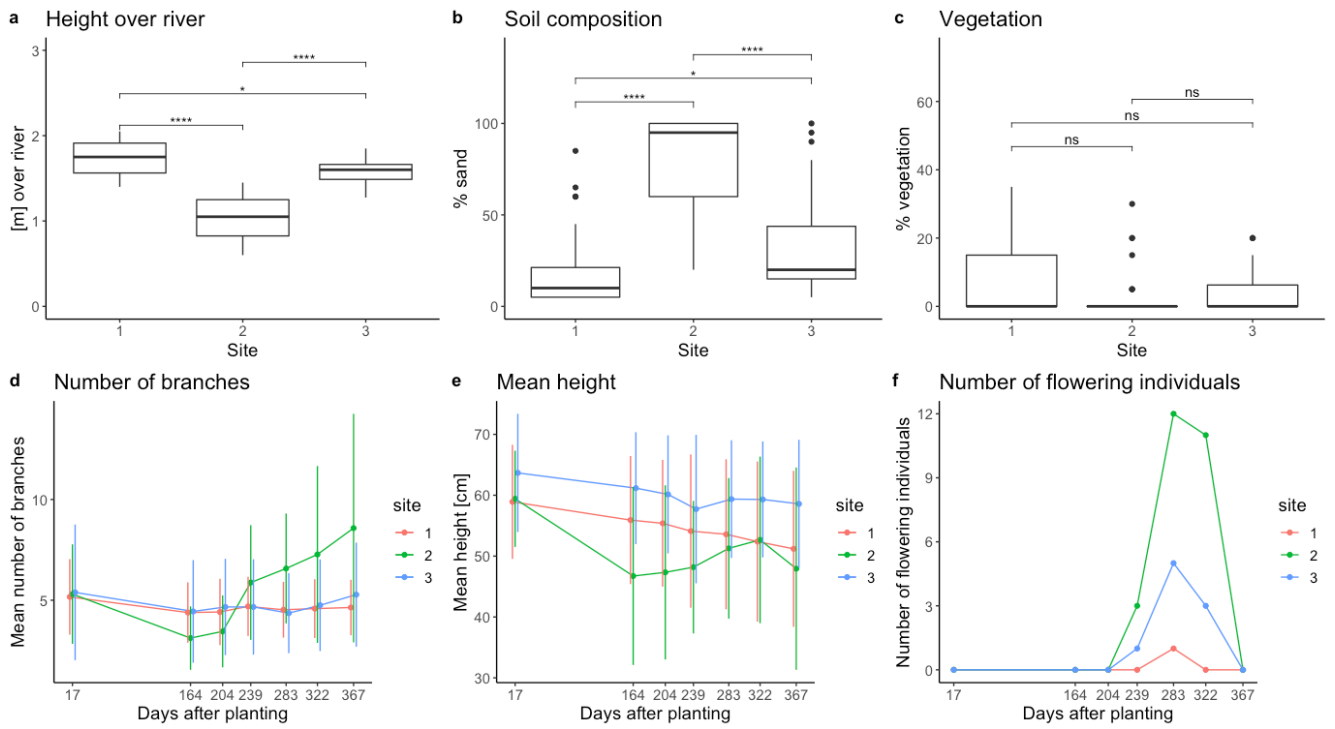


Figure A2. Abiotic site conditions and average plant development at the three sites in the Augand.

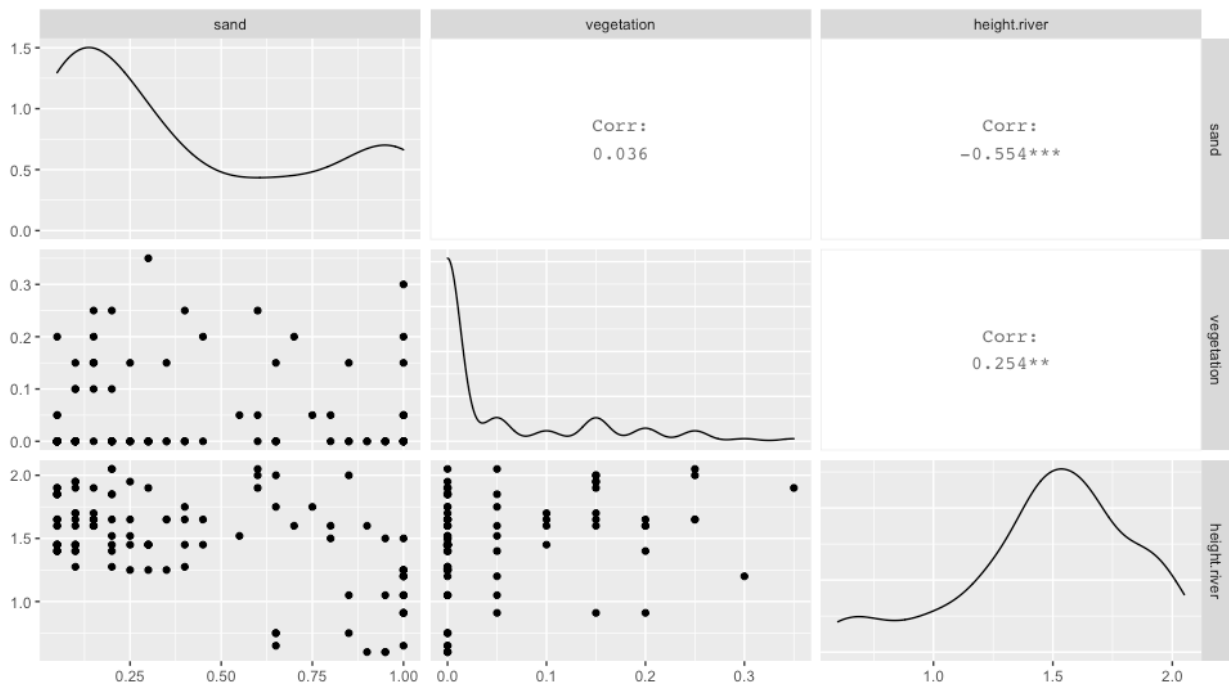


Figure A3. Correlation matrix of explanatory variables for *M. germanica*.

Declaration of Consent

on the basis of Article 30 of the RSL Phil.-nat. 18

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 literar of the University Act of 5 September, 1996 is authorized to revoke the title awarded on the basis of this thesis.

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