

Dispersal and microsite limitation of a rare alpine plant

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Received: 8 April 2011 / Accepted: 26 September 2011 / Published online: 21 October 2011
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Abstract Knowledge on the limitation of plant species' distributions is important for preserving alpine biodiversity, particularly when the loss of alpine habitats because of global warming or land use changes is faster than colonization of new habitats. We investigated the potential of the rare alpine plant *Campanula thyrsoides* L. to colonize grassland sites of different suitability on a small mountain plateau in the Swiss Alps. A total of 15 experimental sites were selected according to their differences in habitat suitability for adult *C. thyrsoides*, which was measured by the Beals index. At each site we applied a disturbance treatment, added seeds at different densities and monitored the survival of seedlings over two consecutive years. The number of surviving seedlings was not positively related to habitat suitability for adult *C. thyrsoides*. Furthermore, *C. thyrsoides* appears to be strongly dispersal limited at the regional scale because seed addition to unoccupied habitats resulted in successful germination and survival of seedlings. Since an increase of seed density in already occupied sites did not affect the number of seedlings, we suggest that *C. thyrsoides* is microsite limited at the local scale. Microsite limitation is supported by the result that seedling survival of the species was enhanced in vegetation gaps created by disturbance. We conclude

that *C. thyrsoides* may become endangered in the future if environmental changes cause local extinction of populations. An appropriate management, such as a disturbance regime for enhancing recruitment in existing populations, may ensure the long-term survival of this rare alpine plant species.

Keywords *Campanula thyrsoides* · Dispersal limitation · Disturbance · Habitat suitability · Microsite limitation · Seed sowing experiment

Introduction

The occurrence of suitable habitats and the dispersal ability are the two main factors that influence a plant's distribution at the regional scale (Münzbergova and Herben 2005; Bullock et al. 2006). Habitat limitation is caused by environmental factors such as climate, soil conditions, and vegetation succession. Dispersal limitation is the intrinsic limitation of the plant itself to disperse seeds, to recruit seedlings successfully and to establish a fully self-sustainable population in a newly colonized habitat. There is a well-known evolutionary trade-off between the number of seeds and the seed size: high seed numbers increase the chance of dispersal to a distant suitable habitat, while heavier seeds increase the establishment probability of seedlings (see review in Moles and Westoby 2004). At the local scale, distribution is theoretically limited by the availability of either microsites or seeds

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(Münzbergova and Herben 2005). However, in nature, local distribution seems to be influenced by a complex interaction of microsite availability, seed limitation, and inter- or intraspecific competition between seedlings (Svenning et al. 2008; García-Camacho et al. 2010; Egawa and Tsuyuzaki 2011).

In the European Alps, the heterogeneous topography of the landscape may limit the dispersal ability of plants (Körner 2003; Bacles et al. 2006). Environmental conditions in some alpine habitats are stressful for germination and seedling establishment of plants because of the short time available without snow-cover (Bonde 1968). In alpine ecosystems, seedling establishment occurs either from seeds in the seed bank or seed rain (Chambers 1995) and has been observed to be strongly dependent on the dispersal mode and the successional stage of available sites (Stöcklin and Bäumler 1996; Niederfriniger-Schlag and Erschbamer 2000). Disturbances resulting from natural and human causes may positively affect seedling recruitment and variation in the timing of germination may reflect differences in seed longevity and dormancy among alpine plant species (Chambers et al. 1990).

Recently, land use changes and global warming have led to the loss of suitable habitats for many alpine plant species and to an up-ward extension in the altitudinal range of several species (Walther et al. 2002; Rudmann-Maurer et al. 2008). In a fast-changing environment (e.g., global warming), plant species with a weak colonization potential and limited dispersal need assistance in dispersal of their seeds (Primack and Miao 1992). Therefore, from the perspective of preserving alpine biodiversity, investigating the limiting factors of a species' colonization potential may allow predictions of future range changes in alpine plant communities and the formulation of species-specific management strategies for rare plants (Franzén and Eriksson 2003).

In the present study, we investigated the dispersal ability and the potential of the rare alpine plant *Campanula thyrsooides* L. to colonize habitats of different suitability on a mountain plateau (Schynige Platte) in the Swiss Alps. *C. thyrsooides* is well suited to study distribution limitations at the regional and local scales for several reasons. First, *C. thyrsooides* has a very narrow ecological niche, that is, the differences in its habitat requirements for humidity, nutrients, temperature, and light were very small in a wide comparison of *C. thyrsooides* habitats (Wüest 2008). Therefore, the species has to disperse over long distances to reach

unoccupied suitable habitats. Second, while a single individual plant of this species produces numerous seeds, the dispersal propagules have no morphological structures to support dispersal. Furthermore, pre-dispersal seed predation can cause complete seed loss (Kuss et al. 2007). These two facts suggest that the distribution of this species is dispersal as well as occasionally seed limited. Third, after colonization of a new site, at least two individuals must reproduce at the same time to successfully establish a new population, because of the strong self-incompatibility and monocarpic life cycle of *C. thyrsooides* (Ægisdóttir et al. 2007; Kuss et al. 2007).

We used a relatively new method, which is based on species co-occurrence data from vegetation relevés and a suitability index (Beals index value; Münzbergova and Herben 2004), to select a total of 15 experimental sites of different suitability for a seed sowing experiment with *C. thyrsooides*. Seed sowing experiments are a straightforward method for investigating the factors influencing a plant's distribution (Turnbull et al. 2000) and allowed us to test if germination and survival of seedlings are dependent on the habitat suitability of sites for adult *C. thyrsooides*. By adding seeds to unoccupied sites, we additionally tested for dispersal limitation at the regional scale. By sowing seeds in different densities to already occupied sites and by using control plots without seed addition, we tested for seed limitation at the local scale. Finally, by modifying the conditions for germination with a disturbance treatment, we tested whether microsite availability is enhanced by disturbance and whether disturbance would be an appropriate regime for conservation management of the rare *C. thyrsooides*. The following hypotheses were addressed in our study: (1) The higher the habitat suitability (Beals index) for adult *C. thyrsooides*, the higher the germination and survival rate of seedlings is. (2) Addition of seeds to unoccupied habitats results in successful germination and survival of seedlings. (3) Augmentation of seeds in already occupied habitats increases the number of seedlings. (4) The number of seedlings is positively related to a disturbance treatment.

Materials and methods

Study species and region

Campanula thyrsooides occurs in the European Alps, the Jura Mountains, and the Dinaric Alps (Aeschmann

et al. 2004). Typical habitats of the species are subalpine and alpine grasslands to screes on limestone or carbonate-bearing schists. The species requires a moderately disturbed regime, which may be created naturally (open soil in steep topography) or by human land use. It is assumed that disturbances positively affect seedling establishment by creating suitable microsites and reducing competition from other plants (Kuss et al. 2007). Thus, the species may be locally abundant in disturbed areas such as road shoulders, where populations may expand locally (Kuss et al. 2008), while it is rare at the regional scale and protected in the majority of the Alpine countries (Moser et al. 2002). *C. thyrsoides* is one of the few monocarpic perennials in the Alps. Plants produce a dense spike composed of 50–200 yellow and bell-shaped protandrous flowers (Scheepens et al. 2011). They die after the production of 15,000–50,000 tiny seeds with no morphological adaptations for dispersal. Seeds are trapped by the withered bracts and are only dispersed when wind, rain or animals shake the seeds out of the capsules. Modeling seed dispersal by wind resulted in 99.9% of the seeds being dispersed within 10 m distance to the mother plant.

As study region, we used a topographically highly structured mountain plateau (Schynige Platte, centered at 46° 39' 12" N; 7° 54' 42" E) in the Swiss Alps. The mountain plateau covers an area of about 10 km² and includes an altitudinal range of 1,800–2,100 m a.s.l. On the Schynige Platte, *C. thyrsoides* occurs in 24 populations mostly in grasslands or steep screes, which are spatially separated by small forest patches. The geographic distances between population pairs range from 0.5 to 3.0 km.

Estimation of habitat suitability using relevé data

The Beals index of sociological favorability (Beals 1984) estimates the occurrence probability of a species at a distinct habitat using species co-occurrence data from vegetation relevés. This index can also be used as a suitability index (Beals index value), which describes the suitability of habitats for a given plant species (Münzbergova and Herben 2004). The threshold value of suitability for unoccupied habitats corresponds to the lowest Beals index value of all relevés where the target species was found. Therefore, all habitats with a higher Beals index than this threshold are considered as suitable and the higher the Beals

index (range 0–1), the more suitable a habitat for the species is.

In 2008, 87 vegetation relevés were recorded on randomly chosen grid points and within natural populations of *C. thyrsoides* on the Schynige Platte, with each of them including an area of 49 m² (Wüest 2008). Suitable unoccupied habitats were identified based on species co-occurrence data using the relevés with and without *C. thyrsoides* of Wüest (2008) and 138 relevés of Fischer and Wachter (1991). For each of the 225 relevés, the Beals index was calculated according to the formula described in Münzbergova and Herben (2004).

Seed addition and augmentation experiment

In order to investigate the potential of *C. thyrsoides* to colonize grassland habitats of different suitability on the Schynige Platte, we selected 15 sites for a seed sowing experiment in such a way that they covered the entire spectrum of the Beals index as inferred from vegetation relevés described above (Table 1). We then classified the sites into three groups of habitat quality according to their occupancy and suitability for adult *C. thyrsoides*. Six sites were established in habitats where *C. thyrsoides* naturally occurred, that is, sites of high habitat quality. Nine sites were established in habitats unoccupied by *C. thyrsoides*. From these unoccupied habitats, three sites were considered as habitats of medium quality because they would be suitable for the species, that is, Beals index was larger than the threshold of suitability. The remaining six sites are referred as habitats of low quality (Beals index lower than this threshold).

In September 2008, mature seeds from 18 different natural populations of *C. thyrsoides* on the Schynige Platte were collected and mixed. On 20 September 2008, seeds of this mixture were sown in the 15 experimental sites (Fig. 1). Within each of the sites, eight experimental plots of 50 × 50 cm² were established, and disturbance and seed density treatments were randomly assigned to them in the following way: four plots were disturbed by clipping the grasses and herbs to ground level and by scarifying the upper soil layer with a three-pronged fork to simulate the activity of small mammals (e.g., Edwards and Crawley 1999), while four plots remained undisturbed. Seeds were added in three different densities (300, 3,000, and 30,000 seeds) to six of the plots, while in two plots no

Table 1 Location and characteristics of the 15 experimental sites in a seed sowing experiment with *Campanula thyrsooides* on the Schynige Platte in the Swiss Alps

Site	Beals index	Habitat quality	Lat (N)	Long (E)	Altitude (m a.s.l.)	Exp	Slope (%)	Soil pH	Ri	Rco (%)	Gco (%)	Fco (%)	Dco (%)
1	0.099	Low	167358	636149	1947	E	30	5.0	48	2	47	5	0
2	0.116	Low	167153	636155	1950	NNE	20	4.5	62	10	42	10	3
3	0.132	Low	167254	636254	1941	WNW	30	5.0	64	10	20	5	5
4	0.169	Low	167744	636942	1945	S	35	4.5	75	1	47	5	7
5	0.171	Low	166958	636147	1984	E	25	5.0	75	10	30	10	5
6	0.186	Low	167146	636751	1876	SE	60	5.0	82	3	35	8	7
7	0.200	Medium	166946	636067	2029	ESE	50	5.0	66	2	45	2	3
8	0.223	Medium	167556	636155	1972	SE	30	7.0	51	15	40	10	2
9	0.251	Medium	167322	635953	2040	SE	75	6.0	66	30	30	5	5
10	0.276	High	167184	635687	1901	SW	65	7.0	64	20	25	5	1
11	0.293	High	167176	636503	1928	SSE	80	5.0	64	7	25	8	13
12	0.305	High	167125	635690	1886	WSW	60	7.5	61	25	20	5	10
13	0.305	High	167143	635881	2005	SW	60	7.0	44	20	9	3	13
14	0.306	High	167090	635923	1996	WSW	75	7.0	48	15	28	10	14
15	0.318	High	167125	636547	1908	SE	100	5.5	70	15	30	5	8

Suitability of sites was measured by the Beals index from vegetation relevées, each including an area of 49 m². Sites are ordered from lowest to highest Beals index. Sites were grouped to habitat quality: low = unoccupied and unsuitable sites, medium = unoccupied but suitable sites, high = occupied and suitable sites for *C. thyrsooides*. *Lat* Latitude (Swiss Grid), *Long* longitude (Swiss Grid), *Exp* exposition (*E* East, *N* north, *S* south, *W* west), *Ri* species richness (number of species), *Rco* rock cover (%), *Gco* grass cover (%), *Fco* cover of Fabaceae (%), *Dco* cover of dwarf shrubs (%)

seeds were added. Seedlings were counted during three censuses: one each at the beginning and end of the growing season in 2009 and a third at the end of the growing season in 2010. We also measured the diameter of three surviving seedlings in each plot.

Mixed-effects model analyses

We analysed our data using mixed-effects modeling because of the hierarchical experimental design, with plots nested in sites. Mixed-effects modeling allowed us to handle binomial and Poisson data in the same framework as normal data, therefore transformation of the response variables was not necessary (Bolker et al. 2009). The germination rate (binomial error distribution) was fitted with a generalized linear mixed model (GLMM) and a logit link function (Crawley 2009). To assess the survival rate of seedlings, the proportion of surviving seedlings at the end of the first year to the number of germinated seedlings, and the proportion of surviving seedlings at the end of the second year to the number of germinated seedlings were calculated. Since the number of seedlings at the end of 2009 and

2010 showed a Poisson error distribution, these variables were also analysed with GLMMs, but with a log link function (Crawley 2009). In all GLMMs, we accounted for overdispersion by using a quasi-likelihood approach (Bolker et al. 2009). For the diameter of seedlings with a normal error distribution, we fitted linear mixed models (LMMs).

The simplest model included the Habitat suitability (Beals index), the two treatments Disturbance (2 levels) and Seed density (3 levels) as well as their interaction as fixed factors, while Site and Plot nested in Site were included as random effects. The sample size was $n = 90$ plots. In the more complex model ($n = 270$), a repeated measure analysis was used with Time (three censuses of measurements) included as an additional fixed factor to account for the time-dependency of seedling survival.

Both models were fitted and tested using the statistical package R (R Development Core Team 2009). The model parameters were estimated with the glmmPQL function in the R-package MASS (Ripley 2005). Significance of the fixed effects was tested with *F*-tests (Faraway 2005), as recommended for GLMMs

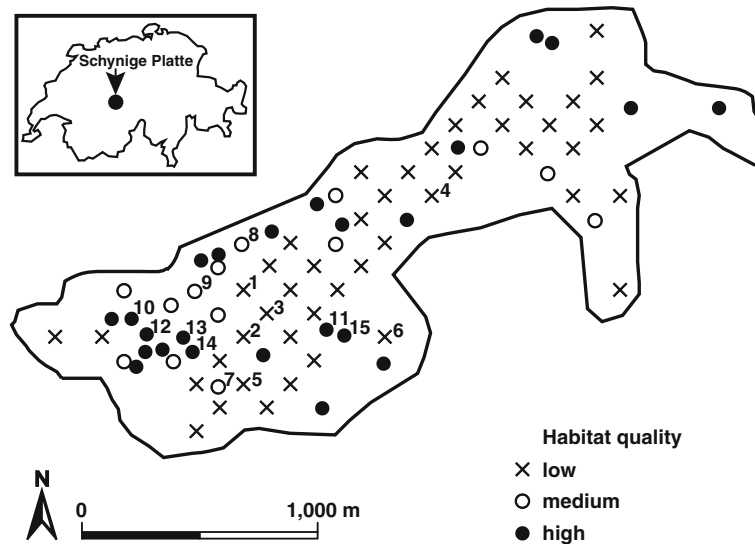


Fig. 1 Map of the study region on a mountain plateau (Schynige Platte) in the Swiss Alps with habitats of different quality for *Campanula thyrsoidea*. Habitat quality: low = unoccupied and unsuitable sites, medium = unoccupied but suitable sites, high = occupied and suitable sites for *C. thyrsoidea*. Suitability

of sites was measured by the Beals index (for details see “Materials and methods”). The 15 experimental sites used in the study are marked with numbers top right of their locations. Other sites are vegetation relevées from 2008

with overdispersion (Bolker et al. 2009). A priori contrasts were used to test for differences caused by different seed densities. As contrasts, low vs. medium seed density and medium vs. high seed density were tested. Likelihood ratio tests (Pinheiro and Bates 2000) were performed for testing random effects. Model assumptions (Pinheiro and Bates 2000) were checked using diagnostic plots constructed with the R-packages *GGPLOT2* (Wickham 2010) and *LATTICE* (Sarkar 2009).

Additional analyses

To determine whether habitat suitability was related to environmental variables at the sites, such as slope or pH value of the soil, we performed a Pearson’s correlation analysis between the Beals index and site characteristics (Table 1) using the statistical package R (R Development Core Team 2009). Soil pH was measured with a Hellige-Pehameter (AVM Analyseverfahren, Freiburg, Germany). To test for seed limitation in occupied sites, we compared the mean number of seedlings in control plots (without seed addition) to the one in plots in which seeds were added, by using one-sided *t*-tests.

Results

Effects of habitat suitability and time

The habitat suitability measured by the Beals index had a significant negative effect on germination rate, the number of surviving seedlings, but not on survival rates after 1 and 2 years (Tables 2, 3). Germination rate was lowest (mean 0.18%; Table 4) in occupied and suitable sites, and increased with decreasing habitat suitability (Fig. 2a). There was no such trend between survival rate and habitat suitability (Fig. 2b). Time had a much stronger negative effect on the number of seedlings than habitat suitability (Table 3). Seedling diameter did not differ among sites of different occupancy and habitat suitability (Tables 2, 4). Finally, the habitat suitability correlated positively with slope, soil pH, rock cover and cover of dwarf shrubs, and negatively with grass cover (Table 5).

Effects of disturbance

Disturbance had the strongest positive effect on all measured variables, with the exception of the number of seedlings (Tables 2, 3). In disturbed plots, germination

Table 2 Summary of mixed-effects model analysis testing the effects of habitat suitability, disturbance treatment and seed addition density on germination, seedling diameter and survival of *Campanula thyrsooides* in a seed sowing experiment

Source of variation	Model effects		Source of variation	Model effects	
	df	Test statistics		df	Test statistics
Germination rate			Seedling diameter		
Habitat suitability	1	10.83**	Habitat suitability	1	0.90
Disturbance	1	12.53***	Disturbance	1	13.0**
Seed density	2	2.99(*)	Seed density	2	4.19*
Contrasts low vs. medium		−0.33	Contrasts low vs. medium		0.62
Contrasts medium vs. high		−2.43*	Contrasts medium vs. high		2.75**
Disturbance:Seed density	2	1.83	Disturbance:Seed density	2	0.46
Site	1	17.35****	Site	1	6.35**
Survival 2009			Survival 2010		
Habitat suitability	1	0.13	Habitat suitability	1	0.47
Disturbance	1	4.23*	Disturbance	1	6.49*
Seed density	2	1.1	Seed density	2	0.34
Contrasts low vs. medium		1.07	Contrasts low vs. medium		0.57
Contrasts medium vs. high		1.57	Contrasts medium vs. high		1.09
Disturbance:Seed density	2	1.87	Disturbance:Seed density	2	0.87
Site	1	0.82	Site	1	3.97*

Habitat suitability was measured by the Beals index (for details see “Materials and methods”). Plots ($n = 90$) are nested in sites. Test statistics are F -values for fixed effects (Habitat suitability, Disturbance, Seed density, Disturbance:Seed density), t -values for a priori contrasts, and χ^2 values for random effects (Plot, Site). df Degrees of freedom

Asterisks represent significance levels: (*) $P < 0.08$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

Table 3 Summary of mixed-effects model analysis testing the effects of time, habitat suitability, disturbance treatment and seed addition density on the number of seedlings of *Campanula thyrsooides* in a seed sowing experiment

Source of variation	Model effects	
	df	Test statistics
Number of seedlings		
Time	2	580.03****
Habitat suitability	1	8.20*
Disturbance	1	3.31(*)
Seed density	2	46.09****
Contrasts low vs. medium		−4.87****
Contrasts medium vs. high		11.42****
Disturbance:Seed density	2	0.71
Site	1	27.52****

Habitat suitability was measured by the Beals index (for details see “Materials and methods”). Plots ($n = 270$) are nested in sites. Test statistics are F -values for fixed effects (Time, Habitat suitability, Disturbance, Seed density, Disturbance:Seed density), t -values for a priori contrasts, and χ^2 values for random effects (Plot, Site). Time represents a factor of three different censuses of measurements. df Degrees of freedom

Asterisks represent significance levels: (*) $P < 0.08$, * $P < 0.05$, **** $P < 0.0001$

rate, survival rates, diameter of seedlings, and the number of seedlings were always higher compared to undisturbed plots (Table 4; Figs. 3, 4). The disturbance treatment also had a positive effect on the number of seedlings in control plots, with on average 2.2 seedlings in undisturbed plots and 8.0 seedlings in disturbed plots.

Effects of seed density

The number of added seeds significantly affected germination rate, seedling diameter, and the number of seedlings, but not survival rates (Tables 2, 3). The number of seedlings increased with increasing seed density (Fig. 4). Contrast tests indicated that the number of seedlings was different ($P < 0.0001$) between plots of low and medium seed density, and of medium and high seed density (Table 3).

The number of seedlings in control plots (mean = 5.1) was not significantly different from that observed in plots in which seeds were added in high density (mean = 9.0; $t = -1.14$, $df = 11$, $P = 0.28$).

Table 4 Means (SE) for germination rate, seedling diameter and survival rates in a seed sowing experiment with *Campanula thyrsooides*. Means were calculated for the habitat quality, seed addition density and disturbance treatment separately

	Habitat quality		
	Low	Medium	High
Germination (%)	1.22 (0.3)	1.36 (0.5)	0.18 (0.1)
Diameter (mm)	5.9 (0.4)	4.0 (0.3)	5.4 (0.4)
Survival 2009 (%)	32.85 (5.4)	31.53 (6.5)	39.92 (7.5)
Survival 2010 (%)	12.94 (3.0)	13.21 (4.5)	17.40 (6.0)
	Seed density		
	300	3,000	30,000
Germination (%)	1.18 (0.4)	0.77 (0.3)	0.54 (0.1)
Diameter (mm)	5.1 (0.6)	4.6 (0.3)	5.6 (0.3)
Survival 2009 (%)	27.81 (9.4)	31.76 (6.1)	39.96 (4.6)
Survival 2010 (%)	10.42 (5.7)	13.54 (4.1)	16.84 (3.4)
	Disturbance		
	Undisturbed	Disturbed	
Germination (%)	0.73 (0.2)	0.93 (0.3)	
Diameter (mm)	4.5 (0.3)	5.8 (0.3)	
Survival 2009 (%)	26.59 (4.6)	41.07 (5.3)	
Survival 2010 (%)	8.00 (2.4)	19.52 (3.8)	

$n = 90$. Suitability of sites was measured by the Beals index (for details see “Materials and methods”). Habitat quality: low = unoccupied and unsuitable sites, medium = unoccupied but suitable sites, high = occupied and suitable sites for *C. thyrsooides*. Seed density number of added seeds

Table 5 Correlation analysis of habitat suitability with characteristics of 15 experimental sites in a seed sowing experiment with *Campanula thyrsooides*

	<i>r</i>
Slope (%)	0.84****
Soil pH	0.70**
Species richness	-0.20
Rock cover (%)	0.61*
Grass cover (%)	-0.62*
Cover of Fabaceae (%)	-0.13
Cover of dwarf shrubs (%)	0.66**

$n = 15$. For details to the habitat suitability measured by the Beals index see “Materials and methods”. *r* Pearson’s correlation coefficient, *Species richness* number of species assessed in vegetation relevées

Asterisks represent significance levels: * $P < 0.05$, ** $P < 0.01$, **** $P < 0.0001$

Moreover, the number of seedlings in control plots did not differ significantly from that in plots in which seeds were added in medium (mean = 1.2; $t = 1.13$, $df = 11$, $P = 0.28$) or low density (mean = 0.1; $t = 1.45$, $df = 11$, $P = 0.18$).

Discussion

Habitat suitability and seedling establishment

Germination rate and the number of seedlings of *C. thyrsooides* were significantly lower in experimental

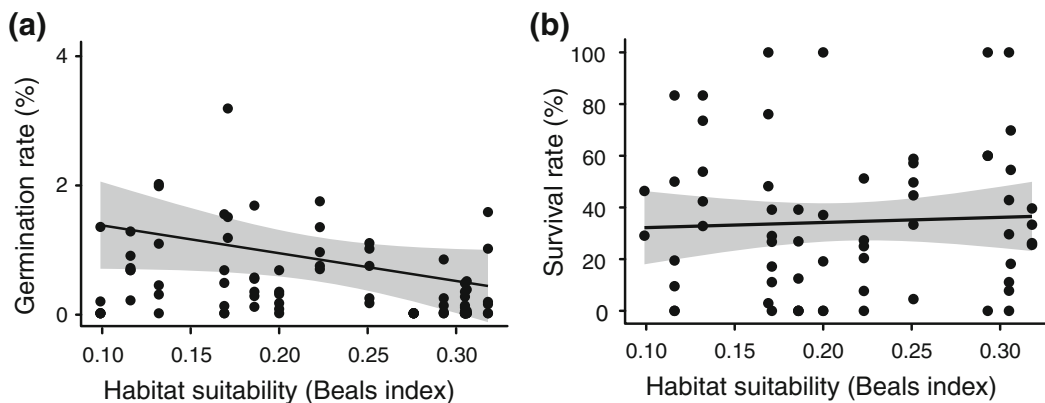


Fig. 2 Seedling establishment of *Campanula thyrsooides* in a seed sowing experiment with **a** germination rate at the beginning and **b** survival rate at the end of 2009 as a function of habitat suitability (measured by the Beals index; for details see

“Materials and methods”). The lines represent the fit obtained by the model analyses and the gray shaded areas are the 95% confidence intervals

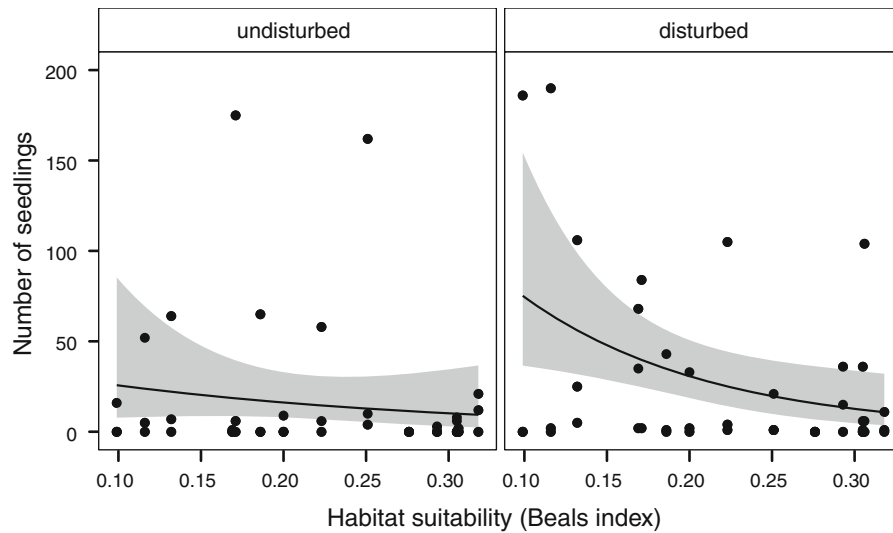


Fig. 3 The number of seedlings in 2009 in a seed sowing experiment with *Campanula thyrsooides* as a function of disturbance treatment and habitat suitability (measured by the

Beals index; for details see “Materials and methods”). The lines represent the fit obtained by the model analyses and the gray shaded areas are the 95% confidence intervals

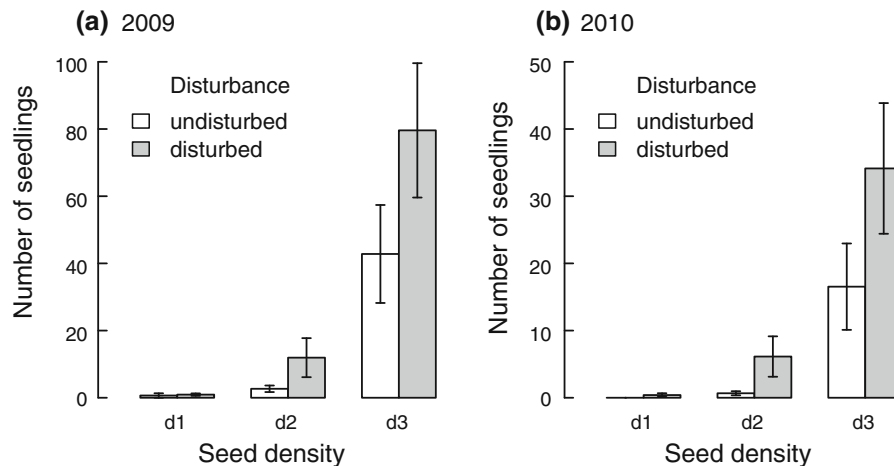


Fig. 4 The effects of seed addition density and disturbance treatment on the number of seedlings in **a** 2009 and **b** 2010 in a seed sowing experiment with *Campanula thyrsooides*. Seed density: *d1* 300 seeds, *d2* 3,000 seeds, *d3* 30,000 seeds

sites of high habitat suitability for adults measured by the Beals index. This negative relationship contradicts our hypothesis and results of another study with *Succisa pratensis*, where the Beals index correlated positively with the number of seedlings (Milden et al. 2006). In a long-term study that investigated the effects of habitat suitability on the establishment of seedlings in several grassland species, positive correlations between the Beals index and the abundance of seedlings were generally weak and there was a trend of an increasing positive

correlation over time (Ehrlén et al. 2006). It is likely that environmental conditions for successfully reproducing adults of *C. thyrsooides* are better in occupied compared to unoccupied sites, and that with time and increasing plant growth the number of plants would decrease in unoccupied and unsuitable sites (Gustafsson et al. 2002). However, within the two consecutive years of our experiment, the number of seedlings decreased in all sites similarly, and survival rates did not differ between sites of different habitat quality (Table 4).

Our results suggest that the Beals index is only valid for the habitat requirements of adult *C. thyrsoides*, based on which habitat suitability was assessed (Wüest 2008). The habitat suitability measured by the Beals index may not represent the suitability of a habitat for colonization by seedlings, but rather the probability of a habitat to be occupied by an already established population. We know from integral projection models that populations of *C. thyrsoides* can moderately grow and persist even at an extremely low establishment rate of seedlings (Schynige Platte: seedling establishment rate < 0.1%; Kuss et al. 2008). Therefore, habitat conditions for successful recruitment in natural populations have most probably changed since colonization because of the ongoing vegetation succession. We assume that *C. thyrsoides* needs open and newly created habitats to establish populations and that after a population has been established, it can persist for a long time, even when the habitat is changing. The correlation analysis supports that recruitment of natural populations may be negatively influenced by vegetation succession. Occupied sites had an increased cover of dwarf shrubs, while in unoccupied sites with lower suitability for *C. thyrsoides*, the vegetation was dominated by grasses (Tables 1, 5).

The long persistence of *C. thyrsoides* at already occupied sites might be explained by a seed bank, which is known from other *Campanula* species (e.g., Greve Alsos et al. 2003), although we have no indication from literature or field for a persistent seed bank in *C. thyrsoides* (Hegi 1975; Kuss et al. 2007). A soil seed bank might increase persistence of populations in already occupied sites, but apparent colonization of new unoccupied sites can hardly be related to a seed bank because the area of the Schynige Platte has been monitored for *C. thyrsoides* since 2005. However, a seed bank would not change our interpretation that *C. thyrsoides* has a weak colonization potential.

Limitation at the regional scale

Habitat limitation is not an important factor for the actual distribution of *C. thyrsoides* on the Schynige Platte because only a small fraction (26%) of all suitable habitats was occupied by the species in recent vegetation relevées (Wüest 2008). Therefore, and because seeds lack morphological structures for wind or animal dispersal (Kuss et al. 2007), we hypothesized that dispersal limitation could be much more

important than habitat limitation for the regional distribution of this species. Indeed, our seed addition experiment indicates that *C. thyrsoides* is strongly dispersal limited, since adding seeds to unoccupied habitats resulted in successful germination and survival of seedlings. In a seed sowing experiment with several plant species on a glacier foreland in the Eastern Alps, it was suggested that dispersal limitation might be a common feature of alpine plant species (Erschbamer et al. 2008).

Nevertheless, recording seedling survival over more than 2 years, as was done in our study, would provide better estimates of dispersal limitation, since only long-term data could show whether seedling recruitment in unoccupied sites would lead to a viable population (Gustafsson et al. 2002). Although the survival rate of seedlings decreased drastically from the first to the second year (Table 4), we do not expect a significant decrease in the number of juveniles in the following years. This low mortality of plants in the near future is expected because the early establishment is the most critical phase in the life cycle of many plant species (Cook 1979), including that of *C. thyrsoides*, because its survival probability increased with plant size in a demographic study (Kuss et al. 2008). Most of the young plants that survived the first winter in 2009 will probably grow into adults and will reproduce with an average flowering age of about 10 years (Kuss et al. 2008).

Limitation at the local scale

Our hypothesis that distribution of *C. thyrsoides* at the local scale is fully seed limited must be rejected, since augmentation of seeds in already occupied sites did not result in a higher number of seedlings compared to control plots. Consequently, an already established population of *C. thyrsoides* produces enough seeds to ensure its local spread and we must accept the alternative hypothesis that the species is partially microsite limited. Microsite limitation is supported by the result of the artificial disturbance. Disturbance increased the number of seedlings considerably (Figs. 3, 4), probably because ideal microsites facilitated germination of seedlings. Such microsites created by disturbance may include increased light availability and higher soil temperatures, which were measured in plots free from vegetation in another sowing experiment (Chambers et al. 1990). Interspecific competition

was also reduced by our disturbance regime, but intraspecific competition could still be present in disturbed plots, which is assumed to be higher than competition between seedlings of different plant species (Svenning et al. 2008). Intraspecific competition for nutrients might at least partially explain the low survival rate in the second year, which was nearly half of that observed in the first year (Table 4), when seedlings were smaller and their roots were less intermingled.

Furthermore, the average germination rate in permanent plots of a natural population of *C. thyrsooides* on the Schynige Platte was estimated to be 0.078% (Kuss et al. 2008), while in a greenhouse study germination on wet filter paper was ca. 1,000 times higher at 75% (Ægisdóttir et al. 2007). Thus, the low seedling recruitment in natural populations of *C. thyrsooides* is rather caused by a lack of microsites than a limited availability of seeds. In addition, when simulating population growth in *C. thyrsooides*, increasing the seedling establishment rates resulted in a dramatic increase of the population size (Kuss et al. 2008). Although we have no indication for seed limitation, seed predation could occasionally play a role for the local distribution of *C. thyrsooides* (Kuss et al. 2007) because pre-dispersal seed predation is a crucial factor affecting seed availability (Juenger and Bergelson 2000; Szentesi and Jermy 2003; Orrock et al. 2006).

Conservation implications

Summarizing our results, the species *C. thyrsooides* may become endangered on the Schynige Platte in the future because of its weak colonization potential in combination with its narrow ecological niche, monocarpy, and strong self-incompatible breeding system known from previous studies (Ægisdóttir et al. 2007; Kuss et al. 2007; Wüest 2008). Although genetic diversity was generally high in all populations in this region (Frei et al. submitted), we would consider the currently established natural populations of *C. thyrsooides* as threatened, if the present availability of suitable habitats diminished because of global warming. Shifts in the distribution of alpine plant species in response to increased summer temperatures have been repeatedly reported (Grabherr et al. 1994; Walther et al. 2002; Parmesan and Yohe 2003). The expected range extension of plants because of global warming is

likely to be related to their different dispersal abilities (le Roux and McGeoch 2008), and we suggest that particularly dispersal limited species such as *C. thyrsooides* will be negatively affected by climate change.

A long, traditional management history is obviously important for the persistence of many plant species (Eriksson 1998). Thus, another putative risk for the population maintenance of *C. thyrsooides* might be changes in the current land use practises (Körner 2003). For several centuries and to this day, the area of the Schynige Platte has been used as summer pasture for cattle (Lüdi 1948). Pastures, which are more heterogeneous and characterized by light gaps in the vegetation from disturbances by grazing animals, favor the establishment of seedlings much more than homogeneous mown grassland does (Bullock et al. 1995; Coulson et al. 2001). Nonetheless, such disturbances by cattle are obviously not enough for the establishment of new populations at suitable unoccupied sites, especially since *C. thyrsooides* often grows on steep slopes where cattle is absent and where, as a result, dwarf shrubs dominate. An appropriate management strategy for conservation of the rare and strongly dispersal limited *C. thyrsooides* at the regional scale might therefore be to assist the dispersal of this species by sowing seeds from local plant populations in suitable habitats and to prevent vegetation succession by a sustainable land use management.

At the local scale, a disturbance regime would be worthwhile during the first years after sowing, which has been shown to increase seedling establishment in *C. thyrsooides* (Table 2), as well as in other grassland species (Klinkhamer and De Jong 1988). Such artificially disturbed sites are best suited for germination and early survival in *C. thyrsooides*; over 180 seedlings m^{-2} were growing on a site previously disturbed by road construction work (Furka Pass, author's personal observation).

Conclusions

Our results suggest that habitat suitability based on the Beals index for established populations of *C. thyrsooides* is not well suited to determine whether a habitat is also suitable for germination and successful establishment of seedlings in this rare alpine plant. Disturbance affected the number of seedlings positively, indicating

the importance of vegetation gaps for the abundance of *C. thyrsoides*. The strong dispersal and microsite limitation of *C. thyrsoides* as well as the succession in sites where populations established long ago may endanger this species on the Schynige Platte and in other regions in the Alps. Rare plant species, including *C. thyrsoides*, with a weak colonization potential will be disadvantaged if habitats continue to shrink and no species-specific management strategies are implemented, as we propose in the present study.

Acknowledgments The authors would like to thank Bärbel Horat for vegetation relevé data and the calculation of the Beals index values, Jens Schützek for collecting seed material, Reinhard Frei for support in the field, Stefanie von Felten and Yann Hautier for statistical advice, Kathrin U. Frei and Martin Heggli for their help with the language, and three anonymous referees for constructive comments on the manuscript. The study has been supported financially by the Swiss National Science Foundation (project no. 3100AO-116785) to Jürg Stöcklin and the Freiwillige Akademische Gesellschaft to Eva S. Frei.

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