

DETERMINANTS OF SPECIES RARITY: POPULATION GROWTH RATES OF SPECIES SHARING THE SAME HABITAT¹

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Determining differences between common and rare species is commonly used to identify factors responsible for rarity. Existing studies, however, suffer from two important drawbacks. First, studies compare species that are closely related phylogenetically but occupy different habitats. Second, these studies concentrate on single life history traits, with unknown relevance for population growth rates. Complete life cycles of one rare and one common *Cirsium* species sharing the same habitat were compared. Population growth rate was slightly lower in the rare species, translating into a large difference in local extinction probability. Seed predation intensity did not differ between species. However, it can be demonstrated that in connection with the data on complete demography, seed predation is the key factor causing a lower population growth rate in the rare species. These results are the first estimation of factors responsible for commonness or rarity of plants in terms of population growth rate without confounding differences in ecology. They demonstrate that conclusions based on single traits may be misleading and that only a comparison based on a complete life cycle can provide unequivocal evidence for concluding which factors are really those responsible for species commonness or rarity.

Key words: *Cirsium*; congeneric species; dry grasslands; dynamics; matrix models; population growth rate; seed predation; seed size.

Understanding the processes determining the commonness or rarity of plant species can provide information necessary for effective conservation of rare species (Magurran and Henderson, 2003), one of the key issues in conservation biology (Bevill and Louda, 1999; Pachepsky et al., 2001; Murray et al., 2002). Given the same environmental requirements and human influence, species rarity can be influenced by species demography, colonization ability, and ability to adapt to changing environments (e.g., Cole, 2003; Kwit et al., 2004; Yates and Ladd, 2004).

Essential insights into rarity can be gained by comparing closely related species (e.g., Huber, 1996; Krahulec et al., 1999). Comparisons of species pairs that differ in rarity can be used to identify ecological and genetic traits associated with rarity. While this kind of comparison seems to be an attractive way to approach the processes underlying patterns of rarity, information gained from comparative studies of common–rare species pairs so far is surprisingly scattered, inconsistent, and defies generalization (e.g., Bevill and Louda, 1999, and references therein; Moora et al., 2003; Simon and Hay, 2003). This may be due to two main drawbacks in the existing studies.

First, many of these studies are concerned with single species attributes, e.g., differences in reproduction and vegetative growth, competitive ability, or habitat preferences (e.g., Rabinowitz and Rapp, 1981; Fiedler, 1987; Karron, 1989; Byers and Meagher, 1997; Menges et al., 1999). Traits are usually

selected based on our knowledge of the biology of the species. Still, because only one to a few aspects of the life cycle are usually studied and are thus not formally put in the framework of the whole life cycle it is not clear whether the observed differences can be interpreted as those responsible for the rare vs. common difference (see Lloyd et al., 2002, 2003).

Second, most of the existing studies on this topic compare species that are closely related phylogenetically, but that occupy different habitats (e.g., Fritzsheridan, 1988; Baskin et al., 1997; Lloyd et al., 2002; Debussche and Thompson, 2003). This may, however, limit the ability to distinguish between demographic causes of rarity and consequences of different habitat conditions, and the observed patterns cannot be safely used to explain the causes for commonness vs. rarity.

In this paper, I compare the complete demography of a pair of rare and common *Cirsium* species sharing the same habitat, viz., chalk grasslands in northern Bohemia, Czech Republic. Although the species share a common habitat, they may experience different pressures from interacting species such as insects. This may be important because many *Cirsium* species are known to suffer from strong seed predation by many different insects (see reviews in Crawley, 1989, 1997; Louda, 1989; van der Wal et al., 2000). Therefore, I also explore to what extent seed predation can be used to explain differences in rarity between the two species.

Specifically, I aim to answer the following questions: (1) What are the differences in population biology between the rare and common species? (2) Are these differences able to explain the differences in rarity of these species? (3) What is the effect of seed predation on the performance of the two species? (4) Can seed predation be used as an explanation for the difference in rarity between the two species?

To answer the questions, I collected data on complete demography of each species in three populations over three transition periods as well as data on several other traits possibly responsible for the common vs. rare difference (seed predation,

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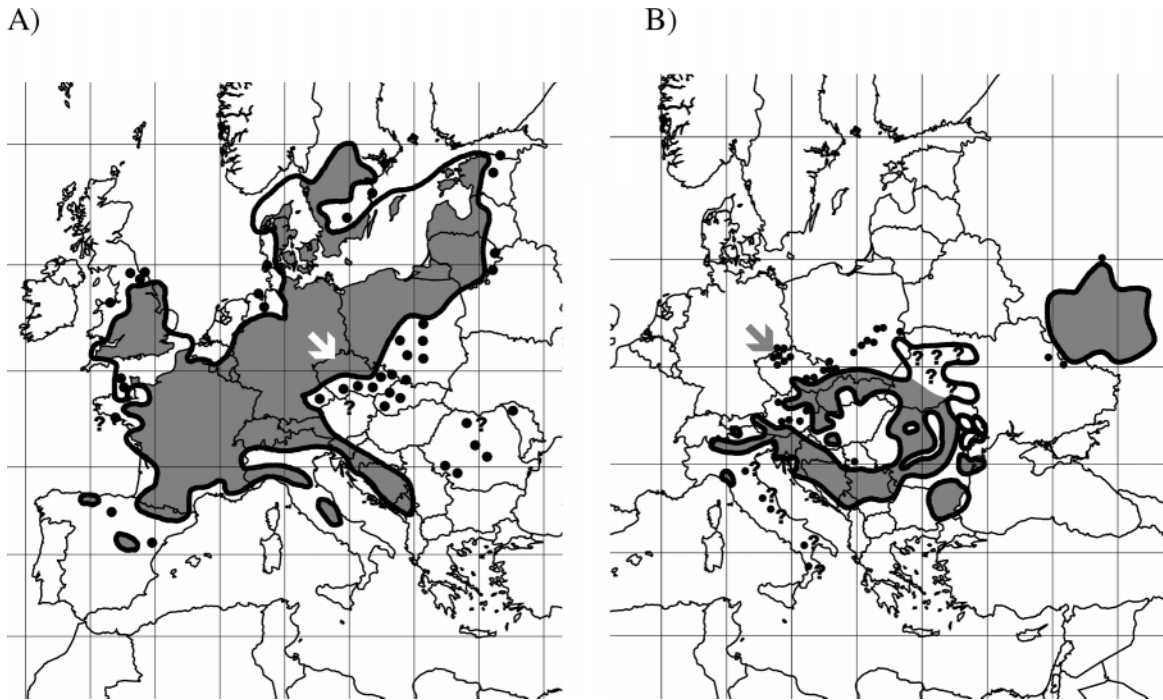


Fig. 1. Distribution range of the species and the location of the study area (marked by arrow). (A) *Cirsium acaule*. (B) *Cirsium pannonicum*. Figures are modified after Meusel and Jäger (1982). Question mark indicates doubtful occurrence of the species.

ability to survive in the seed bank, seed germination rate, and ability to self-fertilize). I used population matrix models to explore differences in population growth rates between the two species and tested the effect of seed predation on growth rates. To demonstrate that the two species really share the same habitat, I also compare species composition at localities with the two species.

MATERIALS AND METHODS

Study species and region—*Cirsium pannonicum* (L.f.) Link is a perennial herb up to 80 cm high with leaves entire or denticulate with rigid spinules 1–5 mm long. The species rarely produces vegetative ramets. Its range covers eastern, central, and northeastern Europe, extending south to northern Italy and northward to 55° N in Russia (Tutin et al., 1964–1983; Fig. 1). In the Czech Republic the main distribution is in the eastern and central part of the country with the western border of the distribution in the western part of the country (Dostál, 1989).

Cirsium acaule Scop. subsp. *acaule* is a perennial acaulescent herb with leaves having 2–5 spinose-dentate lobes. The species is able to form vegetative ramets; the furthest are not, however, more than about 15 cm away (personal observation). The distribution ranges from northern England and Estonia south to southern Spain and the central part of former Yugoslavia (Tutin et al., 1964–1983; Fig. 1). In the Czech Republic the main distribution is in the western and central part of the country with a few isolated localities in the east, and extending to central Slovakia (Dostál, 1989).

Both species are restricted to chalk grasslands in the study region, i.e., in the České středohoří Mountains in northern Bohemia, Czech Republic. For both species, this region is the area with one of the highest concentrations of localities within the Czech Republic. Both species are attacked by a suite of inflorescence-feeding insects, mainly *Rhinocyllus conicus* Frölich and *Larinus planus* (F.). All of the inflorescence-feeding insects consume flower heads and developing flowers and seeds prior to or after full seed development. The two *Cirsium* species are not direct sister species (Tutin et al., 1964–1983), and my definition of relatedness is based on the two species being of the same genus.

Detailed surveys of 426 dry grasslands in the study region showed that there are only 13 *C. pannonicum* populations, but at least 90 *C. acaule* populations (personal observation). Literature records suggest that *C. pannonicum* used to be more common in the region but declined in the last several decades (Kubát, 1970). The difference in number of populations in the region reflects differences in number of populations in the whole country (Dostál, 1989). Single populations of both species, however, may consist of up to a few thousand individuals. Definition of rarity of *C. pannonicum* when compared to *C. acaule* is thus based mainly on the number of existing populations. When classifying the two species using the Rabinowitz et al. (1986) classification of rarity, I suggest that both species would fall into the category “predictable,” with wide ranges, large populations, and relatively narrow habitats. The distribution range as well as range of habitat types are, however, somewhat narrower in the rare species (Figs. 1, 2).

Survival and transitions across life stages—To describe the whole life cycle of the species, I marked 150 individuals with at least 30 individuals in each stage (seedling, vegetative, reproductive) at each of the three populations (Appendix S1, see Supplemental Data accompanying online version of this article for coordinates and characteristics of the localities) of each species in 2001. The minimum number of individuals per stage was set to assure that a more or less equal number of individuals in each stage was marked, which is the most accurate method of demography data collection (Münzbergová and Ehrlén, in press). The individuals were marked in three permanent plots per locality (each plot was approximately 2 m²). I started by marking all individuals in the one corner of the plot and moved to the corner across diagonal. When there were already 20 marked individuals of one stage in that plot, further individuals of this stage were skipped to make sure that each stage was represented by at least 10 individuals per plot. The use of three plots was a compromise between an attempt to cover different parts of the locality and to keep track of the individual marked plants. Each individual was marked with plastic and metal labels that were placed just behind the plant. A census was completed every June from 2001–2004. Survival of each individual and its size were recorded. If there were fewer than 30 living, marked individuals per stage at the time of the census, new individuals were marked to maintain the minimum number of individuals per stage for the next

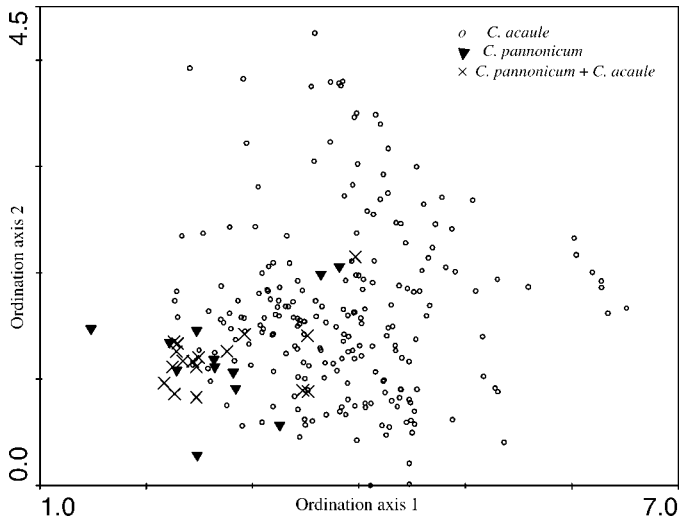


Fig. 2. Comparison of species composition of sites with occurrence of the species of interest. Graph shows position of samples with *Cirsium* on the first and second ordination axes based on detrended correspondence analysis of 2984 relevés from dry grasslands. Samples without any *Cirsium* species are not shown.

transition period. At each census, the leaves and inflorescences were counted, and the length of the longest leaf was measured. The studied period covered a very wet summer in 2002, a very dry summer in 2003, and intermediate conditions in 2001 and 2004 (weather data is available at website <http://www.chmi.cz/meteo/ok/infklim.html>). Therefore, the weather variation captured in the data is rather high, and the relative consistency of the patterns between years can be taken as an indication that the results are robust.

Three life stages, with comparable definitions between species, were recognized in the data: seedlings, vegetative plants, and reproductive plants. This allowed direct comparison of stage performance between the species. Seedlings of these species lose cotyledons in very early stages of development, and cotyledons can thus not be used to define seedlings. The maximum size that an individual could reach within one year was thus used as a limit of the smallest category. These individuals also never flowered in the subsequent year. On rare occasions, a formerly larger plant shrank into this category, and the category thus contains not only real seedlings, but also some plants that became small again. This category was defined as plants with leaves shorter than 3 cm or with fewer than three leaves in *C. pannonicum* and plants with leaves shorter than 5 cm or with fewer than three leaves in *C. acaule*. All larger vegetative individuals of *C. pannonicum* were placed in the second stage. Further splitting of this stage was not possible due to very high variation in length of largest leaf among both sites and years without obvious effects on plant performance in the subsequent year. On the other hand, there was very low variation in the number of leaves in the rosettes of these larger vegetative individuals. In *C. acaule* there was very little variation in leaf number and in leaf length among the larger rosettes, so likewise only one stage of large vegetative plants was defined. Reproductive plants were considered the third category in both species.

Seed production and germination—At the time of fruiting (i.e., at the end of June 2001–2003), 20 flowering ramets were randomly selected at each locality, and the number of inflorescences per ramet and the number of seeds per inflorescence were counted. Later, fifteen 20×20 cm plots were marked on a transect at each locality and 100 seeds were sown in each plot. Seed germination was recorded in each plot, as well as in a control plot directly adjacent to each sowing plot, the following June.

Cirsium requires disturbance for germination (e.g., van Leeuwen, 1981). Study sites were influenced by continuous small-scale erosion, which created small disturbances throughout the study. Larger scale disturbances were not common at the sites. Therefore, seeds were sown in untreated vegetation,

conditions representative of those under which the species naturally germinate.

Survival in the seed bank—To estimate species' ability to survive in the seed bank, 20 nylon bags each containing 100 seeds were buried at one of the three demographic localities in late September 2001 for each species. Four bags were buried at each of five different sites at the locality. Ten bags (two from each site) were excavated in late September 2002 and 2003, and the seeds were tested for viability.

Seed viability was estimated by placing all seeds from one bag into a petri dish. The seeds were regularly watered with distilled water and kept under a fluctuating regime (12 h light at 20°C, 12 h dark at 10°C) in a growth chamber. Germinating seeds were regularly removed. The dishes were maintained until all seeds germinated or decayed (approximately 6 mo). The same procedure was used to estimate the viability of fresh seeds in the first year. This value was then used as a baseline value to estimate the decline in seed germination rate. This procedure provided information on potential survival in the seed bank given that the seeds did not germinate in the previous year.

For delayed germination, I monitored seedling emergence in the seedling recruitment plots in subsequent years. This provided information on delayed germination for seeds sown in 2001 in 2003 and 2004: 1- and 2-yr delays and for seeds sown in 2002 in 2004 a 1-yr delay.

Seed predation—To estimate the importance of seed predation in the species, 100 flower heads per population were sampled in each population of *C. pannonicum* and *C. acaule* in 2002, 2003, and 2004 at the time of fruiting of the species. Altogether 35 population/year samples were collected for *C. pannonicum* and 15 population/year samples for *C. acaule* over the study period (see Supplemental Data accompanying online version of this article for coordinates and characteristics of the localities). All these populations occur within an area of 40 km² without any major gradients of habitat conditions. The lower number of *C. acaule* populations sampled is due to the fact that in some years no flowering plants could be found in some populations. Such absence of flowering may be associated with avoidance of seed predation (e.g., Buonaccorsi et al., 2003), but data from more years would be required to assess this.

Each flower head was opened, and the number of fully developed seeds without any evident damage was counted. Further, evidence for seed predation (presence of damaged seeds, insect larvae, adult beetle, or insect frass) was recorded for each flower head. Flower heads with any sign of seed predation were marked as affected by seed predation; flower heads without any such evidence were marked as unaffected.

Seed mass—Seed mass was estimated by weighing 10 groups of 10 randomly chosen seeds from each of three demographic populations with the pappus removed before weighing. This trait was used only to show differences between the two species.

Habitat requirements—To compare habitat requirements of the two species I used relevés from dry grasslands from the Czech national phytosociological database (Chytrý and Rafajová, 2003). I used all relevés of dry grasslands from the area delimited by 13°15'–15°30' E and 50°00'–50°40' N. There were 2984 relevés in total. Data on species composition of these relevés were summarized by detrended correspondence analysis (DCA) using Canoco (ter Braak and Šmilauer, 1998). DCA is a multivariate technique assuming a bell-shaped species distribution along an underlying environmental gradient. This enables the extraction of a few ordination axes that summarize maximum variation in species composition. The two *Cirsium* species were excluded from the data set before the analysis. Positions of the relevés on the 1st and 2nd ordination axis from this analysis were then used to compare species composition at localities of the two *Cirsium* species.

Data analysis—The difference in proportion of flower heads affected by seed predation was tested using ANOVA with number of insect-damaged flower heads per population as the dependent variable (this was possible as an equal number of flower heads were sampled in each population; always

TABLE 1. Effect of seed predation on number of developed seeds in different years in the two *Cirsium* species. Locality (Species) indicates that locality is nested within species.

Independent variable	df	df error	Residual deviation	P
Species	1	95	625	<0.001
Year	2	96	725	0.12
Predation	1	1683	34 418	<0.001
Locality (Species)	24	1657	26 058	<0.001
Species × Year	2	92	621	0.70
Species × Predation	1	1656	26 040	<0.001
Year × Predation	2	1652	25 679	<0.001
Locality (Species) × Year	13	1615	23 109	<0.001
Locality (Species) × Predation	24	1628	25 114	<0.001
Species × Year × Predation	2	1613	23 089	<0.001
Locality (Species) × Year × Predation	11	1602	22 964	<0.001

only one flower head per plant was sampled) and with year, species, and their interaction as independent variables. Differences in the number of developed seeds per flower head between species, populations, years, and flower heads with and without seed predation were tested using GLM with Poisson distribution. When testing the effects not including seed predation, mean number of seeds per flower head per population per year was used in the test to take into account that flower heads within localities were not independent.

To analyze local population dynamics for each species, data on transition probabilities from each population and each transition interval (2001–2002, 2002–2003, 2003–2004) were combined with mean seed production per flower head in each population and each year (see Kaye and Pyke, 2003, for a similar approach). This was done because seed predation data came from more populations than the data on transitions between stages, and also because the intensity of seed predation was expected to be the most variable component of the life cycle of the species. This procedure yielded 9 (3 populations × 3 transition intervals used to study full species demography) × 15 for *C. acule* and 35 for *C. pannonicum* (number of populations in single years used to estimate seed predation) demography matrices in total. All matrices were combined using stochastic simulations as described in Caswell (2001), with equal probabilities of drawing each matrix. The model yielded the dominant eigenvalue of the matrices for each species (λ) and the elasticity of single life cycle transitions of each species.

Further, I estimated the fate of a local population that was randomly assigned one of the matrices each year. The population started with 100 indi-

viduals distributed according to the stable stage distribution of both *Cirsium* species, and population growth was projected over 100 years. The number of runs (out of 1000) when the population went extinct was counted and used to estimate the probability of local population extinction for each species.

To estimate confidence intervals of population growth rates and elasticities, I bootstrapped the original field data on transitions of single individuals between stages. This yielded 100 new transition probability matrices for each species and population. All the matrix modeling procedures described were applied to each resulting matrix to yield 100 new estimates of each value. These were used to construct confidence intervals for each of the values as described in Efron and Tibshirani (1994). All the matrix calculations were made using Matlab, version 5.3.1 (The MathWorks, Inc., Natick, Massachusetts, USA).

RESULTS

There was a large overlap in species composition of sites with the two *Cirsium* species (Fig. 2). It was also clear that *C. pannonicum* has stricter habitat requirements than *C. acule*. Still the species share many localities; all study populations were at localities within the overlapping region.

Cirsium pannonicum had a marginally, significantly greater ($F_{1,46} = 3.96$, $P = 0.05$) proportion (51%) of insect-damaged flower heads than *C. acule* (37%). There was no overall difference in seed predation between years ($F_{1,46} = 3.4$, $P = 0.08$), and also the interaction between year and species was not significant ($F_{1,46} = 1.8$, $P = 0.19$).

There were significantly more developed seeds in flower heads without than with seed predation, and the rare *C. pannonicum* had significantly more developed seeds per flower head than the common *C. acule* (Table 1, Fig. 3). Also, the decrease in number of developed seeds per flower head due to seed predation was stronger in the common *C. acule* (Fig. 3, Table 1). The effect of year and the interaction of year and predation on number of developed seeds were insignificant (Table 1). All the other interactions were significant (Table 1).

There was no significant difference between population growth rates of the two species when assuming no seed predation. However, when the observed field level of seed predation was taken into account, population growth rate of the rare *C. pannonicum* strongly decreased and was thus significantly lower than that of the common *C. acule* (Fig. 4). Significance was estimated using the overlap of the confidence intervals of the values. The difference in growth rate also translated into large differences in extinction probability of local populations of the species (Table 2). This was estimated using hypothetical populations of 100 individuals (10 flowering and 90 vegetative). The ratio of flowering and vegetative

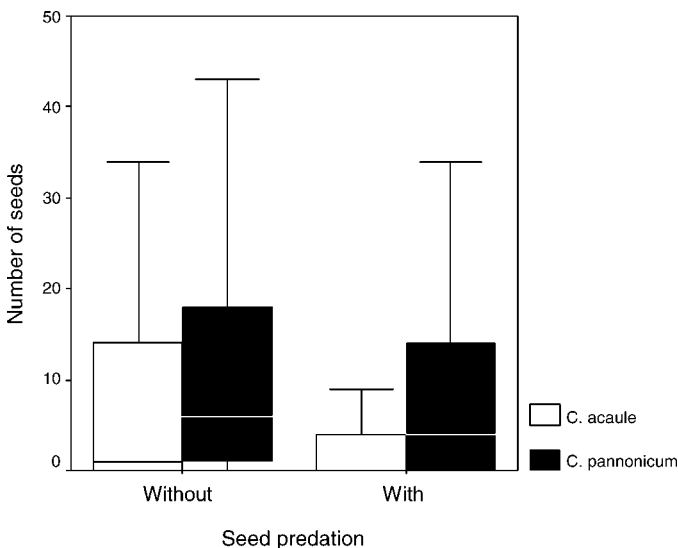


Fig. 3. Number of developed seeds in flower heads with and without seed predation in the two *Cirsium* species. Median, upper and lower quartiles, and non-outlier minimum and maximum are shown.

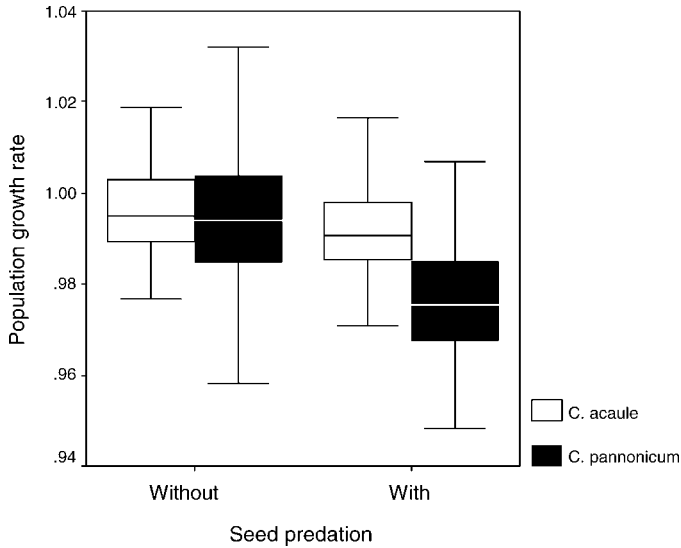


Fig. 4. Local population growth rate of *Cirsium acaule* and *C. pannonicum* with and without seed predation, estimated using data on the full demography of the species. Median, upper and lower quartiles, and non-outlier minimum and maximum values are shown for population growth rate gained using bootstrap analysis.

individuals used in these simulations approximately corresponds to the mean stable stage distribution of the two species.

Growth transitions and the survival of individuals in the flowering stage were higher in *C. acaule*, whereas transition from flowering individuals to the vegetative stage and the other way round were higher in *C. pannonicum*. Elasticities of the single life-cycle transitions showed the opposite pattern, with higher importance of survival transitions in *C. acaule* and higher importance of reproduction and seedling survival in *C. pannonicum* (Table 2).

Both species are able to self-fertilize without any decrease in seed production. Also, the ability to survive in the seed bank is similar in the two species. All results comparing the two species are presented in Table 2.

DISCUSSION

Habitat requirements of the two species—One prerequisite of this study was the assumption that the species share the same habitat. The comparison of species composition of localities of the two species confirmed that they are very similar. This is further supported by the existence of several localities where these two species co-occur. However, it is still possible that there are some differences in habitat requirements between the two species at the microsite level because no detailed study on microsite requirements of these two species was carried out.

TABLE 2. Comparison of traits that could be interpreted as the key parameters responsible for the common–rare difference in the two *Cirsium* species. Mean of each value plus standard error of the mean is given (if applicable).

Traits	<i>C. acaule</i>	<i>C. pannonicum</i>	Difference
Reproductive attributes			
Decrease of seed production after self-fertilization	0	0	0
Germination rate	0.12	0.19	0
Seed weight (mg)	2.8 ± 0.16	1.6 ± 0.42	+
Survival in seed bank	0.139	0.105	0
Seed production per plant	8.76 ± 0.738	11.12 ± 0.656	–
Seed predation			
Probability of flower head predation	0.37 ± 0.07	0.51 ± 0.04	0
Percentage decrease of seeds per flower head due to seed predation	33 ± 0.07	50 ± 0.05	0
Demography			
Extinction probability after 100 years	0.158	0.488	+
Elasticity of life cycle-transitions			
Seedling→seedling	0.0158 ± 0.0023	0.0263 ± 0.0017	–
Vegetative→seedling	0.0086 ± 0.0004	0.0063 ± 0.0004	+
Reproductive→seedling	0.0124 ± 0.0007	0.0240 ± 0.0012	–
Seedling→vegetative	0.0174 ± 0.0006	0.0270 ± 0.0011	–
Vegetative→vegetative, including clonal growth	0.8641 ± 0.0058	0.7663 ± 0.0072	+
Reproductive→vegetative	0.0238 ± 0.0010	0.0457 ± 0.0014	–
Seedling→reproductive	0.0036 ± 0.0005	0.0033 ± 0.0006	0
Vegetative→reproductive	0.0326 ± 0.0013	0.0664 ± 0.0021	–
Reproductive→reproductive, including clonal growth	0.0228 ± 0.0020	0.0346 ± 0.0036	–
Life-cycle transitions			
Seedling→seedling	0.322 ± 0.008	0.372 ± 0.009	–
Vegetative→seedling	0.025 ± 0.001	0.020 ± 0.001	+
Reproductive→seedling (only germination)	0.061 ± 0.001	0.065 ± 0.001	–
Seedling→vegetative	0.381 ± 0.010	0.274 ± 0.009	+
Vegetative→vegetative, including clonal growth	0.938 ± 0.003	0.862 ± 0.002	+
Reproductive→vegetative	0.764 ± 0.010	0.773 ± 0.010	0
Seedling→reproductive	0.013 ± 0.002	0.030 ± 0.004	–
Vegetative→reproductive	0.031 ± 0.002	0.072 ± 0.003	–
Reproductive→reproductive, including clonal growth	0.155 ± 0.007	0.128 ± 0.007	+

Note: In transition probabilities and elasticities + indicates values that simply are higher. + = the trait is significantly better for the common *C. acaule*; – = the trait is significantly worse for *C. acaule*; 0 = no difference between the species (details are explained in the Materials and Methods).

The range of localities of *C. acaule* is wider than that of *C. pannonicum* (Fig. 2). In spite of this, the habitat requirements of these species are probably as similar as possible in two different species, and thus life history traits of these species can be compared without confounding the comparison by different ecologies, the common drawback of many of such comparisons.

It is of course very common that closely related species have different habitat requirements (e.g., Stebbins, 1957; Neuffer and Eschner, 1995; Lloyd et al., 2002). Different habitat requirements are, however, known to result in different population dynamics even within a single species (e.g., Oostermeijer et al., 1994; Brys et al., 2004). Thus, any demographic differences are in this case more likely a symptom of rarity than a cause. Therefore, while I fully recognize that this is not always possible, I suggest that when attempting to identify demographic causes of species rarity, authors should try to search for congeneric species of the same or similar habitats rather than for direct sister pairs in very different habitats.

Data from a large-scale sowing to introduce *C. pannonicum* into a range of different types of dry grasslands in the region showed a high number of suitable, unoccupied localities for the species (Münzbergová, 2004). The suitability of the unoccupied localities was estimated by whether seedlings in the experimental plots survived after 3 years. In this species the number of seedlings surviving in the plots at the unoccupied localities was similar to the number at occupied localities. Therefore, it is unlikely that the very low number of existing populations of *C. pannonicum* would be due to very few suitable localities.

Reproductive traits—Reproductive traits both supporting and opposing the rarity of *C. pannonicum* could be identified. Similar to patterns in other rare–common species pairs (e.g., Rabinowitz and Rapp, 1981, 1985; Fiedler, 1987; Aizen and Patterson, 1990; Baskin et al., 1997), the common *C. acaule* has larger seeds, which is expected to result in faster seedling development of this species (Khera et al., 2004; van Molken et al., 2005). On the other hand, seed production was higher in *C. pannonicum*, showing that, contrary to conclusions of many others (e.g., Fiedler, 1987; Baskin et al., 1997; Young and Brown, 1998), this trait alone cannot explain the rarity of the species. However, in connection with full demography, it could be demonstrated that seed production is the key factor favoring the common species (Fig. 4). This shows that the context of a trait, not its absolute value, is important when searching for traits responsible for species rarity.

Another commonly considered trait responsible for the common–rare difference between species is ability to self-fertilize (e.g., Purdy et al., 1994; Baskin et al., 1997; Young and Brown, 1998). In this study, this trait, however, did not differ between the species and can be rejected as a factor contributing to the observed differences in commonness and rarity between the two study species.

Population growth rate—Mean stochastic population growth rates of both species was slightly below one, indicating that populations of both species are declining. Population growth rate of *C. pannonicum* was significantly lower than that of *C. acaule*, but the difference was very small. However, this difference translated into a much larger difference in the probability of population extinction over 100 years. Given the low connectivity of the landscape, and thus low probability of re-

colonization in the current landscape, the higher extinction probability can serve as an explanation of the much lower number of existing populations of *C. pannonicum*. The 100-year transition interval used here is partly arbitrary and was used to demonstrate possible effects of differences in population growth rates. The use of several different time intervals, however, produced qualitatively similar results (not shown).

The results of any projection of population development over time critically depend on how well the data capture all the potential variation in abiotic conditions of the sites over the projection period (e.g., Lindborg and Ehrlén, 2002). It is clear that my 4-year data can hardly fully achieve this. Therefore, I suggest that the long-term predictions in this study should be interpreted as a relative comparison between the species, rather than in absolute terms, and that data over much longer period would be needed to decide whether populations of both species are really strongly declining as it seems from the estimates of the growth rates.

The life cycles of both species were divided into comparable categories. This enables direct comparison of the importance of these categories. Stasis in vegetative and flowering stage and clonal growth were higher in *C. acaule*, whereas transitions from flowering individuals to vegetative stage and the other way round were higher in *C. pannonicum*.

An analysis of elasticities of the single life-cycle transitions showed that survival transitions were more important in *C. acaule*, while reproduction and seedling survival was more important in *C. pannonicum*. This is congruent with the observed stronger effect of seed predation on population growth rate in *C. pannonicum*.

Effect of seed predation—Seed predation is considered a factor strongly affecting the population viability of many plant species. The genus *Cirsium* is well known to be strongly affected by seed predation and is a common model in studies of the effect of seed predation in plant populations (e.g., Louda and Potvin, 1995; Guretzky and Louda, 1997; Stanforth et al., 1997; Edwards et al., 2000; Rowland and Maun, 2001). In agreement with these studies, seed predation had a strong impact on the population growth rates of both species.

Without seed predation the population growth rates of both species were almost the same, as were the population extinction probabilities. Also, the probability of seed predation was only marginally significant in the two species, and seed production per both flower heads affected and unaffected by seed predation was higher in the rare *C. pannonicum*. However, when incorporating the seed predation effects into the demography matrix, seed predation appears to have a much stronger effect on *C. pannonicum* than on *C. acaule*, causing large differences in population growth rates of the species in the field. This shows that equal rates of seed predation due to the same predators in two closely related species sharing the same habitat can have dramatically different effects on population growth rate. Thus the higher importance of seedling recruitment in the life cycle of *C. pannonicum* in combination with seed predation seems to explain its rarity. This conclusion is well supported by the data showing that *C. pannonicum* has traits (greater frequency of transitions from vegetative to reproductive, regular flowering, tall inflorescences, many smaller seeds) that promote seed dispersal as a mechanism for population persistence, while *C. acaule* has a population growth strategy biased toward vegetative persistence and clonal growth.

Conclusions—The combination of full demography with data on the intensity of seed predation in two related species differing in rarity and sharing the same habitat demonstrated significantly lower population growth rates in the rare species. This difference resulted in higher probability of local population extinction. The main reason for the lower population growth rate in the rare species was the higher sensitivity of the rare species to sexual reproduction. This result is the first quantification of differences between rare and common species at the population level that provides quantitative conclusions about the effects of single traits, which would not be possible if the traits were not connected in a common framework. It is also the first demonstration of differential effects of seed predation on the life cycles of two congeneric species.

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