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Variation in life-cycle between three rare and endangered floodplain violets in two regions: implications for population viability and conservation

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Abstract: We studied the demography of *Viola elatior*, *V. pumila*, and *V. stagnina*, three rare and endangered Central European floodplain species, to (i) analyse variation in life-cycles among congeners and between regions (Dyje-Morava floodplains, Czech Republic; Upper Rhine, Germany), (ii) to define sensitive stages in the life-cycles, and (iii) to identify possible threats for population viability and species conservation.
Matrix models were based on the fate of marked individuals from a total of 27 populations over two years. We analysed population growth rate (λ), stage distribution, net reproductive rate (R_0), generation time, age at first reproduction, and elasticity and calculated a life table response experiment (LTRE).
Most populations were declining and λ did not differ between species or regions during the observed interval. Despite higher probabilities for survival and flowering in the Dyje populations, R_0 was higher in the Rhine populations. Also other demographic traits showed consistent differences between regions and/or species. Complex life-cycles and large variation in λ precluded unequivocal identification of sensitive stages or vital rates for conservation. Variation between regions may be a consequence of differences in habitat quality.
Our results suggest that deterministic processes such as reduced management, succession, habitat destruction, and lack of disturbance through reduced or eliminated flooding present the strongest threat for the viability and persistence of populations of the three floodplain violets as compared with stochastic processes. However, the persistent seed bank of the species may buffer populations against environmental variation and represents a reservoir for recovery after resumption of suitable land-use management.

Key words: *Viola elatior*; *Viola pumila*; *Viola stagninaI*; conservation; demography; life table response experiment (LTRE); matrix models

Introduction

The growth and viability of populations ultimately depend on the vital rates: survival (*stasis* and *regression*), growth and reproduction (*fecundity*; cf. Caswell 2001). Environmental conditions (both abiotic conditions and biotic interactions) exert selective forces that may lead to the development of specific suites of traits in certain habitat types, along successional trajectories or along clines from the centre to the margin of the species range (Sagarin & Gaines 2002). Across species of different families, habitat-trait relationships go hand in hand with considerable differences among species, life-forms and functional groups in their life-cycles (Silvertown et al. 1993; Grime 2002) but to date there are only a few comparative studies that explicitly focused on life-cycle differences among congeneric species (Newell et al. 1981; Solbrig et al. 1980, 1988; Svensson et al. 1993; Tolvanen et al. 2001).

However, in light of biodiversity loss and species conservation, there is an urgent need for detailed knowledge on variation in life-cycle among closely related species and within both common and rare species (e.g., Oostermeijer et al. 1996), because human domination of the earth's ecosystems and of biogeochemical processes increased the rates of species extinctions (Vitousek et al. 1997). Land-use changes are expected to exert the largest effects on biodiversity (Chapin et al. 1997; Vitousek et al. 1997; Sala et al. 2000). While land-use changes at the global scale denote the total conversion of ecosystems, e.g. from tropical forest to grassland or from grassland to crop fields, there may also

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be profound changes in ecosystem structure, function and composition, as a consequence of intensification or de-intensification of land-use, especially within the cultural landscape of Europe (Korneck et al. 1998; Eriksson et al. 2002; Jacquemyn et al. 2003). Intensification of land-use will have direct negative effects through increased disturbance, fertilisation and the application of biocides and will lead to species and habitat loss and a homogenisation of landscapes (Korneck et al. 1998; Brys et al. 2005; Reger et al. 2007). The abandonment of land-use and the following unguided succession processes will displace species of semi-natural habitats adapted to regular management (Jacquemyn et al. 2003). Due to the increased fragmentation of habitats, many (also formerly widespread) species have become rare and restricted to small and/or isolated populations (e.g., Endels et al. 2002; Eriksson et al. 2002; Honnay et al. 2005). In Germany, 28.4% of the total flora of flowering plants and ferns of 3319 species is red-listed (Korneck et al. 1996, 1998).

Rarity is closely related to the risk of extinction because species with narrow niche breadth are more likely to suffer from variation or directional changes in external or internal conditions than widespread and common generalist species (Gaston & Kunin, 1997). Within a species, the proportion of occupied sites and average population densities decline from the centre to the margin of its range (e.g., Lawton 1993; but see Sagarin & Gaines 2002 for a critical review). Therefore, peripheral plant populations are often more isolated (Lawton 1993; Lesica & Allendorf 1995) and contain fewer individuals than core populations (Durka 1999; Lammi et al. 1999; but see Kluth & Bruelheide 2005).

Since the future fate of organisms varies with age, stage or size, the demographic approach to conservation, i.e. population biological analyses of various aspects of the life-cycle as the fundamental unit for the description of organisms (Caswell 2001), promises to supply the necessary information for the conservation of rare and endangered species (e.g., Schemske et al. 1994; Menges 2000; Caswell 2001; Morris & Doak 2002; Nicolč et al. 2005).

The study species, *Viola elatior* Fr., *V. pumila* Chaix and *V. stagnina* Kit. ex Schult. (syn. *V. persicifolia* auct., non Schreber) are among the most endangered species across Europe deserving special conservation efforts (Schnittler & Günther 1999) and red-listed in many European countries (e.g., Korneck et al. 1996). Under the assumption of ecological niche stability, the species, which are today restricted mainly to the valleys of large lowland rivers with regional continental climate (Burkart 2001), were most probably more widely distributed and more frequent at the end of the last glaciation when climatic conditions in Central Europe were more continental. An analysis of grid maps suggests that the species have undergone a severe decline of about 50% during the last decades (Eckstein et al. 2006a), which caused strong fragmentation and isolation of populations (Eckstein et al. 2004; Eckstein et al. 2006a, b). As such, they belong to the 'new rares', which are probably more vulnerable to isolation and range contractions than 'naturally' rare plants (Huenneke 1991).

The aims of the present study were to (i) analyse and quantify differences in life-cycles among the endangered congeneric species and between regions with different position to the species ranges, (ii) try to identify sensitive stages in the life-cycles based on the demographic approach, and (iii) summarise published evidence for stochastic and deterministic effects on population viability to evaluate possible threats to species conservation.

Material and methods

Study species and regions

The study species and their habitats have been described in detail in Hölzel (2003), Eckstein et al. (2004), Eckstein & Otte (2005), and Eckstein et al. (2006 a). All three species are perennial iteroparous hemicryptophytes with a long-term persistent seed bank (Hölzel & Otte 2004). In Central Europe, they occur mainly in the corridors of large lowland rivers. All three species show a Western Eurasian distribution (Hultén & Fries 1986), with *Viola stagnina* being relatively frequent also in the hemiboreal vegetation zone in Scandinavia.

The study was carried out in the Upper Rhine valley (Germany; in the following referred to as 'Rhine') and in the floodplains of the rivers Dyje and Morava in southern Moravia (Czech Republic; in the following 'Dyje'). The German populations are at the western margin of species ranges, while the Czech populations are close to the core distribution ranges (Hultén & Fries 1986).

Study design

The study was based on observations on the fate of all individual plants that occurred in marked permanent plots of 0.25 m^2 (50 × 50 cm). Within each region, we selected three (*V. stagnina*), five (*V. pumila*) and five (*V. elatior*, Dyje) to six (*V. elatior*, Rhine) populations, which represented the characteristic vegetation types: the populations of *V. pumila* and *V. stagnina* were situated on extensively used sub-continental meadows mown once a year; the populations of *V. elatior* were situated in ecotonal habitats, such as grassland fringes and openings or clearings of alluvial forests adjacent to floodplain meadows. Depending on population size and extension, three to eight permanent plots were established in 2001 along a line transect across each population. Plots were selected to represent the variation in shoot density present across populations. In total, we investigated 1898 individuals in 122 plots from 27 populations. This study design, which seeks to attain a large (i.e. representative) spatial sample of populations, together with logistic constraints and stochastic events (activities of wild boar), precluded excessive temporal replication. Therefore, the data only represent a single life-cycle transition. Since the sampling period was not extreme with respect to climate, we assume that it more or less represents an average year. However, as the temporal variation is unknown, the data should be interpreted with caution. Using largely the same data set, an analysis of the effects of management and environmental variation on density and frequency of life-cycle stages, i.e. the population stage structure, was presented by Eckstein et al. (2004). In contrast, the present paper develops a life-cycle of the three species and presents a detailed comparative analysis of the fates of individually marked plants based on the intrinsic population parameters obtained by matrix population models (cf. Caswell 2001).

Life-cycle stages

Seeds germinate in spring, and seedlings develop a few leaves by the end of summer. During May to early June, generative plants may bear one to several open-pollinated (chasmogamous) flowers, which are potentially cross-pollinated and mature into capsules from early June to early July. Later in the season, cleistogamous flowers, which remain closed and are obligatorily self-pollinated, may be formed by the same individual (Eckstein & Otte 2005). The life-cycle stages used in the present paper were based on the presence of flowers and the number of shoots (cf. Eckstein *et al.* 2004):
(i) seedlings (s), defined by the presence of cotyledons,
(ii) small vegetative (v1), non-flowering plants, with one shoot,
(iii) large vegetative (v2), non-flowering plants with two or more shoots,
(iv) small generative (g1), flowering plants with one or two shoots,
(v) large generative (g2), flowering plants with three or more shoots.

The life-cycle stages as defined above differed markedly in their fates, i.e. their probabilities for survival, growth and reproduction (see below).

Matrix analyses

In each permanent plot all individual plants were recorded with their coordinates. With the density of shoots encountered in the field, we were able to assign each shoot to a particular single- or multiple-shoot plant. This approach was verified by careful excavations of a few multiple-shoot plants outside our plots. Plots were re-visited in 2002, and the fate of all individuals (birth, death, survival in the same stage, regression into a lower stage, growth) was recorded. Using these data we prepared a 5 × 5 Lefkovitch matrix based on life-cycle stages (Caswell 2001; Appendix 1) for each population. Matrix elements (a_{ij}) represent probabilities for the transition between stage j in 2001 to stage i in 2002, except for the transitions a_{14} and a_{15} in the first row (Appendix 1), which express the average number of seedlings in 2002 produced per small or large flowering plant in 2001, respectively ('anonymous reproduction'; Caswell 2001). Anonymous reproduction also contains the dynamics of seeds in the seed bank. Since data on the number of cleistogamous capsules, which appear later in the year, are lacking, we assumed the same fertility in small and large generative plants. Consequently, $a_{14} = a_{15}$ for the mean matrices, except if one of the stages was missing in one of the populations. To improve the generality of our results, all further analyses were based on a mean matrix per species × region combination that contained the mean values for each matrix entry of 3–6 single populations (Appendix 1).

To describe and compare the species' population dynamics we calculated the observed population growth rate (λ_{O}) and the bootstrapped estimate for λ (λ_{B}) together with accelerated 95% confidence intervals (Dixon 1993; McPeek & Kalisz 1993; Manly 2001). For the bootstrapping procedure we assumed a binomial distribution based on the observed numbers and probabilities of each stage class for matrix entries that represented transition probabilities. For fertilities we resampled (with replacement) new means for a_{14} and a_{15}based on our empirical estimates from the single populations (n = 3–6) for each species-region combination. We restricted our bootstrap sample to matrices where no column sum of transition probabilities was larger than 1, since, by definition, transition probabilities for each stage class including death can only amount to 1. We did not apply a restriction with respect to the minimal column sums allowed, since any threshold would be arbitrary. However, column sums below 0.3 (i.e. a mortality of more than 70%) hardly occurred during resampling.

From the matrix analysis we obtained the stable stage distribution (SSD). Differences between observed stage distribution (OSD) and SSD were calculated as

$$\mathrm{Keyfitz's}\Delta = 0.5 * \sum |x_i - w_i|,$$

where x_i and w_i are the observed and the expected proportions of stage i, respectively, to see whether the mean populations were in tune with their environment (Caswell 2001).

After decomposing the population matrix into one matrix containing only transition probabilities and another containing only fecundity, we estimated age-specific traits from our stage-specific model as described in Caswell (2001: 116ff). We calculated net reproductive rates (R_0), which give the mean number of offspring by which a newborn individual will be replaced by the end of its life, generation time (T), and the age at first reproduction (A_{FR}) for seedlings conditional on survival. For each mean matrix we calculated elasticity (de Kroon et al. 1986), which represents the response of population growth rate to proportional changes in life-cycle transitions, i.e. the slope of log λ to log a_{ij}. We chose elasticity instead of sensitivity (response of λ to absolute changes in transitions), since elasticity sums to unity across each matrix, which makes comparisons of elasticity among species easier. Additionally, life-cycle elasticities, summarised for vital rates representing growth, stasis plus regression and fecundity can be compared with the elasticities spectrum of other species from the literature (Silvertown et al. 1996).

To analyse possible life-cycle differences between the two true meadow species *V. pumila* and *V. stagnina* and the ecotonal *V. elatior*, and between regions (Rhine, Dyje), we calculated a two-way life table response experiment (LTRE; Caswell 1996, 2001). LTRE is a retrospective approach, which decomposes the effects of species, region and their interaction on the observed difference in λ into contributions from different life-cycle transitions or vital rates (Caswell 1996). To this end, the differences in each matrix element (Δa_{ij}) between *V. elatior*, *V. pumila* and *V. stagnina* (mean matrices across regions), respectively, and an overall mean matrix (the mean matrix across species and regions served as 'reference matrix') are calculated. Then the sensitivity of λ to changes in each matrix element (sa_{ij}) was determined at a matrix 'half-way' between the two matrices compared (Caswell 1996, 2001). Finally, the contribution of each matrix element (ca_{ij}) was calculated as

$$ca_{ij} = \Delta a_{ij} * sa_{ij}.$$

Similarly, the effects of region were calculated by comparison of regional mean matrices (across species) and the overall mean matrix. The models for main effects and their interaction were parameterised as given in Caswell (2001: eq.10.5–10.11). All contributions representing *survival* (P, stasis plus regression), *growth* (G) or *fecundity* (F) were summarised for each life-cycle stage. Positive (negative) contributions of certain life-cycle transitions indicate that these

Table 1. Observed population growth rate (λ_O), bootstrap estimate of λ (λ_b) with lower and upper 95% bootstrap confidence intervals CI(l) and CI(u), respectively, net reproductive rate (R_0), generation time (T), and age at first reproduction (A_{FR}) of *Viola elatior*, *V. pumila* and *V. stagnina* in their important Central European regions of occurrence (Dyje, Czech Republic; Rhine, Germany).

Region	Species	λ_O	λ_B	CI(l)	CI(u)	R_0	T	A_{FR}
Dyje	*Viola elatior*	0.844	0.788	0.493	0.946	0.340	6.38	4.02
	Viola pumila	0.761	0.704	0.400	0.870	0.140	7.19	4.17
	Viola stagnina	0.888	0.827	0.663	0.912	0.061	23.47	4.85
Rhine	*Viola elatior*	0.810	0.803	0.625	0.898	0.273	6.17	4.17
	Viola pumila	0.881	0.863	0.652	0.989	0.366	7.94	4.60
	Viola stagnina	1.121	1.076	0.750	1.276	1.870	5.50	3.28

transitions have a higher (lower) absolute value and/or a higher (lower) importance in certain species or regions than in the overall mean matrix. Matrix analyses were done using the program 'Poptools', version 2.6.7 (Hood 2005).

Log-linear analysis

For each species separately, we tested for the effects of *region* and *life-cycle stage* on the fate of individuals by using log-linear analysis (Caswell 2001; Quinn & Keough 2002). To meet assumptions of log-linear models of no more than 20% of categories having expected frequencies less than about five (Quinn & Keough 2002), we had to pool small and large generative plants into one stage class. Fates were defined as follows: (i) death, (ii) survival (i.e. stasis plus regression) and (iii) growth into a higher stage class. Log-linear analyses were done using Statistica (version 6.0, StatSoft Inc., Tulsa, USA).

Results

Matrix analysis

Observed population growth rates (λ_O) for the 2001–2002 transition were <1 for all species-region combinations, except for the Rhine populations of *V. stagnina* (Table 1). Bootstrap estimates of λ (λ_B) were slightly lower than λ_O, and their 95% confidence intervals were very close to but did not include a value of $\lambda_B = 1$, again with the exception of *V. stagnina* from the Rhine. Values for λ_B did not differ significantly among species within the same region or between regions (Table 1). Across species, the proportion of flowering plants was slightly higher in populations of the Dyje floodplains than at the Rhine (data not shown). Flowering was not synchronised among species since the proportion of flowering plants decreased between years in *V. elatior* and *V. pumila* but increased in *V. stagnina*. Despite similar or higher proportions of flowering plants in the Dyje populations, net reproductive rates (R_0) of *V. pumila* and *V. stagnina* were lower here than in the Rhine populations (Table 1). This was mainly due to large differences in the numbers of expected offspring of *V. stagnina* between regions.

First reproduction of seedlings of the species was observed at an age of about four years (Table 1), i.e. an average seedling produced seeds three years after the year of its germination. Seedlings of *V. stagnina* from the Dyje populations reproduced at an age of five years, while they reached maturity at three years, i.e. slightly earlier than *V. elatior* and *V. pumila*, in the Rhine floodplains.

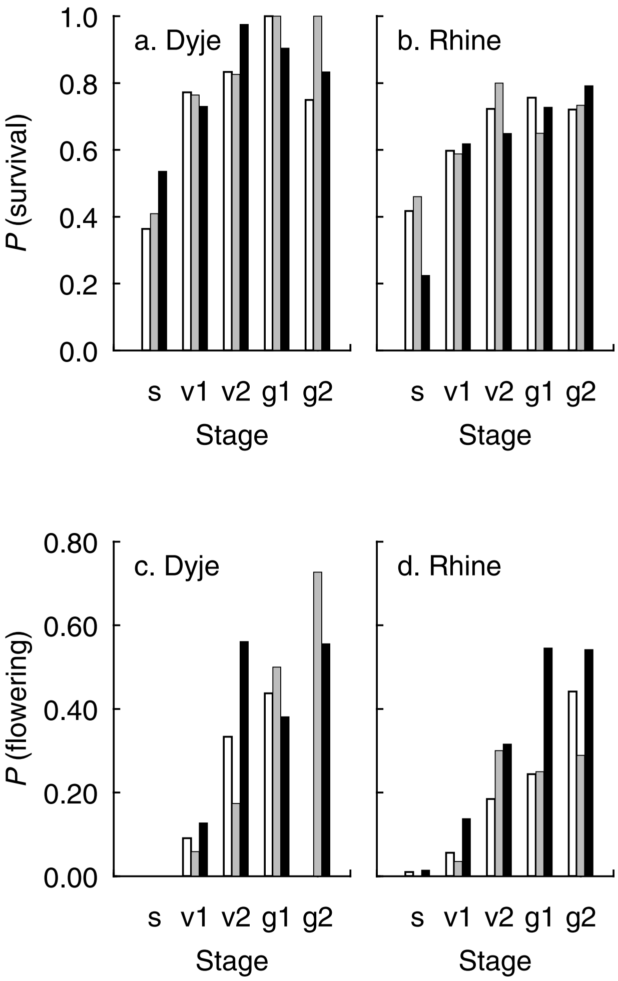

Fig. 1. Probability of survival (a., b.) and flowering (c., d.) of different life-cycle stages (s, seedling; v1, small vegetative; v2, large vegetative; g1, small generative; g2, large generative) of *Viola elatior* (white bars), *V. pumila* (grey bars) and *V. stagnina* (black bars) from the Rhine (b., d.) and Dyje (a., c.) floodplains.

When the observed stage distributions were compared between species pairs, *V. elatior* and *V. pumila* showed the highest degree of similarity, while OSD of *V. stagnina* differed strongly from the other two species. Observed stage structures of species pairs were more similar in populations of the Dyje river than at the Rhine (data not shown). *Viola pumila* showed

Table 2. Observed (OSD) and expected stable stage distribution (SSD) of *Viola elatior*, *V. pumila* and *V. stagnina* from populations at the Dyje and the Rhine. Keyfitz's Δ measures the distance between SSD and OSD for each species-region combination. Stages: s, seedling; v1, small vegetative; v2, large vegetative; g1, small generative; g2, large generative.

	OSD	SSD	Difference	Keyfitz's Δ
Viola elatior, Dyje				
s	0.308	0.224	0.084	0.134
v1	0.277	0.323	−0.046	
v2	0.246	0.196	0.051	
g1	0.108	0.194	−0.086	
g2	0.062	0.064	−0.002	
Viola elatior, Rhine				
s	0.354	0.262	0.092	0.126
v1	0.382	0.412	−0.030	
v2	0.135	0.220	−0.085	
g1	0.055	0.066	−0.011	
g2	0.075	0.040	0.034	
Viola pumila, Dyje				
s	0.256	0.239	0.017	0.036
v1	0.376	0.369	0.007	
v2	0.214	0.228	−0.015	
g1	0.068	0.057	0.012	
g2	0.085	0.107	−0.022	
Viola pumila, Rhine				
s	0.217	0.287	−0.070	0.077
v1	0.346	0.298	0.047	
v2	0.275	0.250	0.025	
g1	0.075	0.070	0.005	
g2	0.088	0.095	−0.007	
Viola stagnina, Dyje				
s	0.007	0.022	−0.014	0.183
v1	0.360	0.197	0.163	
v2	0.272	0.321	−0.049	
g1	0.162	0.142	0.020	
g2	0.199	0.319	0.120	
Viola stagnina, Rhine				
s	0.611	0.559	0.051	0.143
v1	0.095	0.231	−0.137	
v2	0.053	0.054	−0.001	
g1	0.084	0.090	−0.005	
g2	0.158	0.066	0.092	

the smallest differences between expected and observed stage distributions (Table 2), which was indicated by a low Keyfitz's Δ. In *V. elatior*, the largest positive deviations from the expected stage proportions (i.e. more observed than expected from SSD) were observed for seedlings, the largest negative deviations for large vegetative (Rhine) and small flowering plants (Dyje). In *V. stagnina*, deviations from the SSD were almost exactly opposite in the two regions, and the largest contribution to the observed dissimilarity was through small vegetative and large flowering plants.

Elasticities

Across species elasticities for survival were between 0.25 and 0.75, those for growth between 0.25 and 0.50, and those for fecundity between 0 and 0.25 (Fig. 2). Elasticities for the Rhine and Dyje populations were very similar in *Viola elatior*, whereas variation between regions was larger in *V. pumila* and, especially, in *V. stagnina*. The elasticity of λ for fecundity was close to zero in the Dyje populations of *V. stagnina*, whereas the Rhine populations of this species had the highest elasticity for fecundity of all species-region combinations.

Stage-specific elasticities were relatively similar in both regions in *V. elatior* and *V. pumila* (Fig. 2). However, while the fate of small vegetative plants had the largest effect on λ in the former, small and large adults had a roughly equal effect in the latter. In contrast, there were large differences in the contribution of different stages to λ between regions in *V. stagnina*. In the Dyje populations, the fate of large plants was most important with almost no effect of variation in seedling fates, whereas along the Rhine flowering plants and seedlings had the largest effects.

LTRE

The predicted population growth rates (λ) based on our LTRE were within 2.5% of the observed values for λ, which showed that our linear models were very accurate (Caswell 1996, 2001). Absolute differences in life-cycle transitions between species-region combinations and the overall mean matrix were about ± 0.3, whereas differences in fecundity were even >0.3 (not shown). In

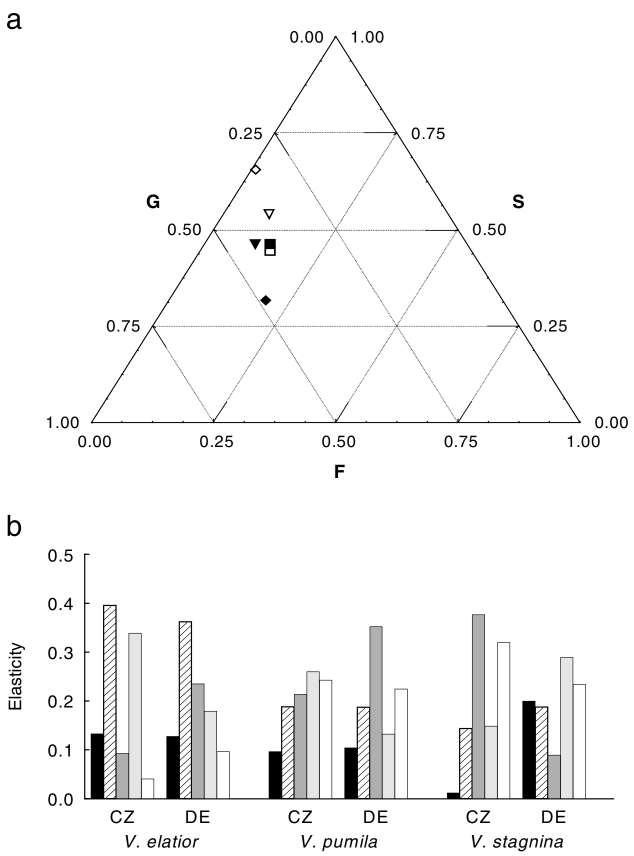

Fig. 2. Elasticity of population growth rates to survival (S), growth (G), and fecundity (F) for *Viola elatior* (squares), *V. pumila* (triangles) and *V. stagnina* (diamonds) from the Rhine (filled symbols) and Dyje (open symbols) floodplains (a) and stage-specific elasticities in the Dyje (CZ) and Rhine (DE) populations (b). Stages: seedling (black); small vegetative (hatched); large vegetative (dark grey); small generative (light grey); large generative (white).

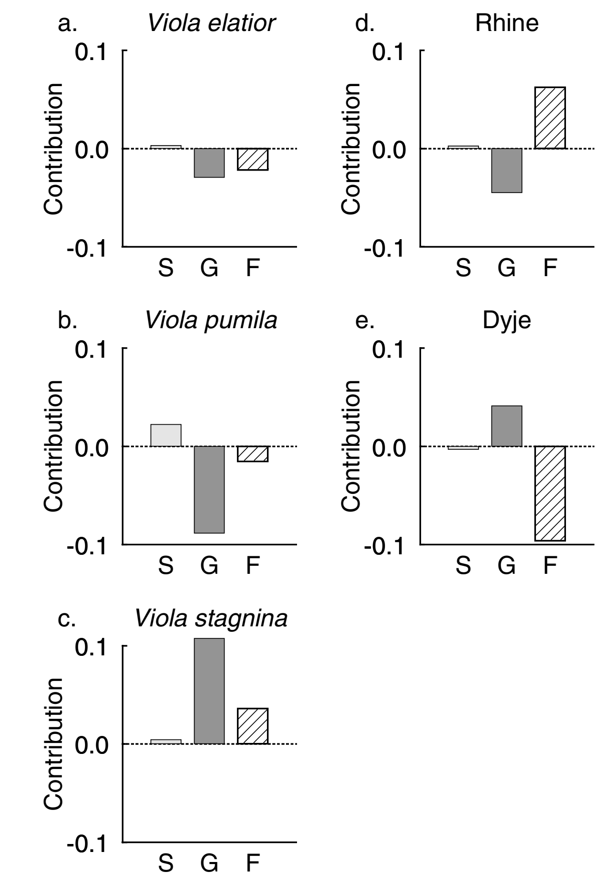

Fig. 3. Life table response experiment (LTRE) on the effects of species (a. – *Viola elatior*, b – *V. pumila*, c – *V. stagnina*) and regions (d – Rhine, e – Dyje) to the differences in population growth rate (λ). Given are the contributions of survival (S, stasis plus regression, light grey bars), growth (G, dark grey bars) and fecundity (F, hatched bars) to the differences in λ as compared to an overall mean matrix across species and regions.

comparison with the overall mean matrix ($\lambda = 0.9085$), populations across regions of *Viola elatior* ($\lambda = 0.8602$) and *V. pumila* ($\lambda = 0.8261$) had lower growth rates. These differences were accounted for by negative contributions of growth and fecundity (Fig. 3). Higher λ of *V. stagnina* across regions ($\lambda = 1.0565$) was owing to positive contributions of growth and fecundity (Fig. 3).

Across species, the Dyje and the Rhine populations had population growth rates of 0.8464 and 0.9294, respectively. Survival did not contribute to the difference in population growth between the overall mean matrix and the regional matrices across species. Negative contributions of growth transitions were outweighed by positive contributions of fecundity in the Rhine populations, whereas the pattern was exactly opposite in the Dyje populations (Fig. 3). There was a species-region interaction, which was indicated by a much closer match between observed and predicted λ when the interactions term was considered than when only accounting for the additive effects of species and region (not shown). Especially the performance of the Dyje populations of *V. stagnina* and of the Rhine populations of *V. elatior* was overestimated when considering only additive effects. In summary, the high performance of the Rhine populations of *V. stagnina* had a strong influence on both the mean λ of this species across regions and on the mean λ of Rhine populations across species. Especially fecundity contributed to the difference in λ between the Dyje and Rhine populations of *V. stagnina*.

Log-linear analysis

Results from the log-linear analyses showed that there were significant differences in fate among stages, even when the effect of regions already was accounted for in the model (significant L and L(|R) effects, Table 3). The probability of survival from 2001 to 2002 varied between 0.2 and 1.0 among stages and regions (Fig. 1). It generally increased with stage class and showed little variation among species. Seedlings experienced a much higher mortality (45–80%) than adult stages (<40%). Low mortalities of adult stages and low numbers of observed individuals in some small Dyje populations lead to survival probabilities of 1.0 for flowering plants of *V. elatior* and *V. pumila*, which obviously are an over-estimation in the long run. Similarly, probability of flowering during the next year increased with stage class (Fig. 1). It increased from 0–1% in seedlings and 4–13% in small vegetative plants to 20–70% in the other

Table 3. Log-linear analysis on the effects of *region* (R; Dyje, Rhine) and *life cycle stage* (L; seedling, small vegetative, large vegetative, reproductive) on the fate (death, regression/stasis, growth) of the individuals of *Viola elatior*, *V. pumila* and *V. stagnina*. The columns 'delta Chi^2' and 'delta DF' give the differences in Chi^2 and degrees of freedom between a null-model and one that includes the effect of a certain factor on fate. Abbreviations: L(|R) and R(|L) denote the effect of factor L (R) when the effects of factor R (L) on fate is already included in the null-model, and R * L denotes the interaction between *region* and *life-cycle stage*.

	Factor	delta Chi^2	delta DF	p
Viola elatior	R	5.87	2	0.0531
	L	161.26	6	<0.0001
	R(|L)	4.59	2	0.1008
	L(|R)	159.98	6	<0.0001
	R * L	6.27	6	0.3936
Viola pumila	R	0.45	2	0.7985
	L	261.41	6	<0.0001
	R(|L)	6.85	2	0.0325
	L(|R)	267.81	6	<0.0001
	R * L	8.31	6	0.2163
Viola stagnina	R	117.85	2	<0.0001
	L	398.94	6	<0.0001
	R(|L)	25.89	2	<0.0001
	L(|R)	304.70	6	<0.0001
	R * L	10.58	6	0.1023

stages. In Rhine populations, *V. stagnina* showed the highest flowering probabilities. The probability of repeated flowering was as high as or higher than the probability for vegetative plants to flower during the next year in most cases (Fig. 1). Zero probability of repeated flowering of large plants of *V. elatior* was most probably a sampling effect due to a small sample size ($n = 4$). Differences between regions in the fate of individual plants were not or marginally significant in *V. pumila* and *V. elatior* (Table 3), while the population turn-over in *V. stagnina* was significantly higher in the Rhine populations than in the Dyje populations, even when the effect of stage was accounted for.

Discussion

In the present study, the fate of individuals in permanent plots was followed over one transition. This temporal non-replication of matrices will preclude the possibility for stochastic modelling (i.e. modelling population growth through randomly selecting different matrices of different years), because temporal variation should not be substituted by spatial variation in stochastic models (Jongejans & de Kroon 2005). On the other hand, the present study is based on a large data set, comparing the life-cycle of three congeneric species. It relies on observations from a total of 27 populations (6–11 populations per species) from two different regions with respect to the species range.

Population growth rates of all but one species-region combination were <1 during the study interval. Confidence intervals around λ based on matrix entries averaged across populations showed that species and regions did not differ significantly in growth rates. Since λ is influenced by climatic conditions, this indicates that conditions did not differ substantially (at least with respect to their effect on λ) between regions. A long-term λ of around 1 can be expected in perennials as long as the populations do not go extinct (e.g., Solbrig et al. 1980; Newell et al. 1981; Silvertown et al. 1993; Svensson et al. 1993; Oostermeijer et al. 1996; Nicolè et al. 2005).

Life-cycle analysis revealed considerable differences among species and between regions in a number of characteristics. Based on the pooled number of transitions per species-region combination, probabilities for survival were higher for the Dyje populations than for the Rhine populations (Fig. 1). Similarly, the probability of flowering was as high or higher for vegetative plants, and the probability of repeated flowering was higher in *V. pumila* in the Dyje populations than in the Rhine populations. The Dyje populations of *V. elatior* and *V. stagnina* contained a higher proportion of flowering plants than did the Rhine populations. Despite this, the net reproductive rate (R_0) was higher in the Rhine populations of *V. pumila* and *V. stagnina* and only slightly lower than in the Dyje populations in *V. elatior*. This, together with higher seedling densities of *V. elatior* and *V. stagnina* in populations at the Rhine (Eckstein et al. 2004), indicated that habitat quality may be worse in the Dyje floodplains than along the Rhine. We suggest that two aspects may be important: (1) In the Dyje populations, capsules of the study species were infested by larvae of *Orbitis cyaneus* (L.), a beetle (Coleoptera) of the *Curculionidae* family, while this phenomenon has not been observed in the Rhine populations. Larvae live inside the capsules, feeding on developing seeds. Consequently, infested capsules develop only a few or no mature seeds. In marked individual plants outside the permanent plots, infestation rates of capsules varied between 9.7 and 66.7% across capsule types (chasmogamous, cleistogamous), species and years (2002, 2003; Lučeničová, unpubl.). These data suggest that insects can substantially reduce seed production. (2) Another important difference between study regions is the frequency of management, mostly mowing or mulching (Eckstein et al. 2004). The Rhine populations are situated exclusively in nature conservation areas or are managed under conservation contracts, whereas the Dyje populations are found mainly in irregularly managed meadows. Many species from semi-natural habitats respond negatively to habitat deterioration, abandonment and fragmentation (e.g., Jacquemyn et al. 2003; Brys et al. 2005; Lindborg et al. 2005), whereas regular management reduces the asymmetry in competition for light and slows down the accumulation of litter and encroachment by bryophytes, thereby improving population viability and individual performance (Lepš 1999; Lennartsson & Oostermeijer 2001; Endels et al. 2002; Brys et al. 2005). Seedling density was negatively correlated with bryophyte cover, and regular management had positive effects on seedling density and population stage structure in *V. elatior* and *V. stagnina* (Eckstein et al. 2004). These findings are corroborated by significant or marginally significant effects of region on the fates of individuals in *V. stagnina* and *V. elatior* in the present study.

Though germination of *V. elatior* and *V. pumila* increased with increasing litter cover especially under dry conditions (Eckstein & Donath 2005; no data for *V. stagnina*), the release of seeds onto a dense carpet of litter, which impedes seed-soil contact, generally has negative effects on seed survival and germination (Facelli & Pickett 1991 and references therein). The above aspects of habitat quality are not exclusive but may act in concert to reduce net reproductive rate of the Dyje populations, leading to a regressive population stage structure and increased extinction risk in the long run (Oostermeijer et al. 1994).

A number of plant species from semi-natural habitats have a dynamic population stage structure, i.e. a high proportion of seedlings and juveniles, in response to high habitat quality (Jensen & Meyer 2001; Colling et al. 2002), and especially regular land-use such as grazing or mowing (Oostermeijer et al. 1994; Bühler & Schmid 2001; Lennartsson & Oostermeijer 2001; Bissels et al. 2004), while populations under suboptimal conditions show a regressive stage structure, i.e. a high proportion of adult plants and no or only a few seedlings (Endels et al. 2002). Especially increased competition for light has negative effects on growth, flowering, seed production and seedling recruitment of other violet species from semi-natural habitats (Jensen & Meyer 2001; Moora et al. 2003). *Viola stagnina* showed the largest variation in life-cycle between regions, which may indicate that this species would profit most from regular management (Pullin & Woodell 1987) and soil disturbance through flooding and animal activity, which may enhance germination of dormant seeds from the soil seed bank (Croft & Preston 1996).

Elasticity analysis revealed that despite some differences between regions, small vegetative and small and large generative plants contributed most to λ in *V. elatior*, whereas all four adult stages contributed roughly equally to λ in *V. pumila*. In contrast, the contribution of different stages and vital rates varied strongly between regions in *V. stagnina*. In growing populations, the contributions of growth and fecundity increased, which has also been confirmed for *Gentiana pneumonanthe* (Oostermeijer et al. 1996), and for *Cirsium vulgare* and *Pedicularis furbishiae* (Silvertown et al. 1996). Elasticities of vital rates varied between years and populations in *Agrimonia eupatoria* and *Geum rivale* (Kiviniemi 2002) and *Primula vulgaris* (Valverde & Silvertown 1998), whereas they were relatively constant in three species of *Pinguicula* (Svensson et al. 1993). The fact that matrix transitions are not independent of each other and that elasticity varies with population growth rate (Oostermeijer et al. 1996; Silvertown et al. 1996; Caswell 2001) makes it difficult to identify unique stages or vital rates as sensitive phases or processes for conservation or management. Additionally, since elasticity is calculated as sensitivity multiplied by the quotient of the transition value (a_{ij}) and λ (de Kroon et al. 1986; Caswell 2001), common transitions will often also have a high elasticity, whereas rare transitions may be better targets for conservation or recovery plans. For example, fecundity in *V. stagnina* from the Dyje floodplains was already very low owing to low habitat quality (missing or infrequent management), which, in turn, led to elasticities close to zero, indicating that this transition (and the seedling stage) did not contribute significantly to λ. However, the populations will probably not resume positive growth unless reproduction and germination are enhanced through changes in management or disturbances improving conditions for the germination of seeds from the seed rain or the persistent seed bank.

Studies on the pollination biology and population genetic structure of the study species showed that owing to their chasmogamous-cleistogamous mating system, the three floodplain violets are not pollen limited, and there are no signs of inbreeding depression (Eckstein & Otte 2005). Additionally, despite strong genetic divergence between populations of all species and the loss of some genetic markers in marginal populations of *V. stagnina*, there was no statistically significant relationship between genetic diversity and population size (Eckstein, unpubl.) or isolation, and no equilibrium between genetic drift and gene flow (Eckstein et al. 2006b). Therefore, demographic stochasticity (this study), environmental stochasticity (Eckstein et al. 2004), pollen limitation and inbreeding depression (Eckstein & Otte 2005) as well as genetic stochasticity (Eckstein et al. 2006b) are unlikely to present a major threat to population viability and persistence as compared to deterministic processes.

However, as in many other species, the presence of a persistent seed bank probably is an efficient buffer against environmental variation and successional change (e.g., Solbrig et al. 1988; McCue & Holtsford 1998; Cabin & Marshall 2000; Adams et al. 2005). Consequently, the floodplain violets may show strong extension and contraction of population size along successional trajectories, starting with a burst of germination after a major disturbance. With the density of adults increasing, germination and seedling survival decrease, and population size slowly decreases with time until populations only persist as seeds in the soil seed bank. This has been described as remnant regional population dynamics (Eriksson 1996).

Conclusions and management recommendations

The results of the present demographic study together with information from other published papers on different aspects of the ecology of the study species suggest that deterministic processes present the strongest threat for the viability and persistence of populations of the three floodplain violets (Korneck et al. 1998; Eckstein et al. 2006 a). These processes comprise reduced management of the non-intensively used sub-continental floodplain meadows, the succession from open forest fringes and paths to closed mature alluvial forests (concerning especially *V. elatior*), habitat destruction, and reduced disturbance through flooding. These processes decrease habitat quality through litter accumulation, bryophyte encroachment and colonization by shrubs and trees. Consequently, seed germination is reduced and population size decreases. The persistent seed bank of the species presents a buffer against environmental variation and a reservoir for the recovery of populations after resumption of suitable management.

Together with information from other studies on the floodplain violets (Hölzel 2003; Eckstein et al. 2004; Eckstein & Otte 2005; Hölzel et al. 2006; Eckstein et al. 2006a, b), results of the current study suggest that the most suitable management of the meadow species *V. pumila* and *V. stagnina* consists of regular mowing. Depending on the weather and on local conditions, meadows with these species should be mown once (May/June) or twice (May/June; July/August) per year. Mowing should not be done too late to efficiently suppress competitors and to allow regrowth and seed development of the violets. Management as meadow pastures, e.g. aftermath grazing with sheep or non-intensive pasture use, also appears to be suitable. However, short-duration grazing seems to be preferable to permanent pastures. Regular mowing or grazing will keep the stands open and reduced competition will improve recruitment and increase the proportion of seedlings in these two species (Eckstein et al. 2004; this study). Unlike some other species-rich grasslands with low productivity such as Mesobromion communities, extensively managed temperate floodplain meadows of the alliances Arrhenaterion and Cnidion at the Upper Rhine are characterised by annual yields of between 350 and 470 g m^{-2} (Donath et al. 2004). Regarding fodder quality, hay from these stands is well suited as basic ration for feeding systems with cattle and horses (Donath et al. 2004).

Viola elatior has a lower mowing compatibility and thus avoids early or regularly mown meadows (Hölzel 2003). However, also this species will profit from regular meadow management, which includes the occasional mowing of the ecotonal fringe between hay meadows and alluvial forests, and thus prevents the expansion of shrubs and trees. Owing to a more suitable light regime and rotation times of 30–40 years traditional simple coppice or coppice-with-standards management appears to be more suitable than the common timber forest use with long rotation times (120 years).

As the current study shows, regular management is crucial for the violet species. Suitable land use on the other hand will enable the conservation of viable population of these endangered plant species even at the margin of the distribution range.

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References

Adams V.M., Marsh D.M. & Knox J.S. 2005. Importance of the seed bank for population viability and population monitoring in a threatened wetland herb. Biol. Cons. **124:** 425–436.

Bissels S., Hölzel N. & Otte A. 2004. Population structure of the threatened perennial *Serratula tinctoria* in relation to vegetation and management. Appl. Veg. Sci. **7:** 267–274.

Bühler C. & Schmid B. 2001. The influence of management regime and altitude on the population structure of *Succisa pratensis*: implications for vegetation monitoring. J. Appl. Ecol. **38:** 689–698.

Burkart M. 2001. River corridor plants (Stromtalpflanzen) in Central European lowlands: a review of a poorly understood plant distribution pattern. Global Ecol. Biogeogr. **10:** 449–468.

Brys R., Jacquemyn H., Endels P., DeBlust G. & Hermy M. 2005. Effect of habitat deterioration on population dynamics and extinction risks in a previously common perennial. Cons. Biol. **19:** 1633–1643.

Cabin R.J. & Marshall D.L. 2000. The demographic role of soil seed banks. I. Spatial and temporal comparison of below- and above-ground populations of the desert mustard *Lesquerella fendleri*. J. Ecol. **88:** 283–292.

Caswell H. 1996. Analysis of life table response experiments II. Alternative parameterizations for size- and stage-structured models. Ecol. Model. **88:** 73–82.

Caswell H. 2001. Matrix population models. Construction, analysis and interpretation. 2nd ed. Sinauer, Sunderland, 722 pp.

Chapin F.S. III, Walker B.H., Hobbs R.J., Hooper D.U., Lawton J.H., Sala O.E. & Tilman D. 1997. Biotic control over the functioning of ecosystems. Science **277:** 500–504.

Colling G., Matthies D. & Reckinger C. 2002. Population structure and establishment of the threatened long-lived perennial *Scorzonera humilis* in relation to environment. J. Appl. Ecol. **39:** 310–320.

Croft J.M. & Preston C.D. 1996. Species recovery programme: Fen Violet (*Viola persicifolia* Schreber). 3rd Progress Report, Institute of Terrestrial Ecology.

de Kroon H., Plaisir A., van Groenendael J. & Caswell H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology **67:** 1427–1431.

Dixon P.M. 1993. The bootstrap and the jackknife: Describing the precision of ecological indices, pp. 290–318. In: Scheiner S.M. & Gurevitch J. (eds), Design and Analysis of Ecological Experiments. Chapman & Hall, New York.

Donath T.W., Hölzel N., Bissels S. & Otte A. 2004. Perspectives for incorporating biomass from non-intensively managed temperate flood-meadows into farming systems. Agric. Ecosyst. Environ. **104:** 439–451.

Durka W. 1999. Genetic diversity in peripheral and subcentral populations of *Corrigiola litoralis* L. (Illecebraceae). Heredity **83:** 476–484.

Eckstein R.L., Danihelka J., Hölzel N. & Otte A. 2004. The effects of management and environmental variation on population stage structure in three river-corridor violets. Acta Oecol. **25:** 83–91.

Eckstein R.L. & Donath T.W. 2005. Interactions between litter and water availability affect seedling emergence in four familial pairs of floodplain species. J. Ecol. **93:** 807–816.

Eckstein R.L., Hölzel N. & Danihelka J. 2006a. Biological Flora of Central Europe: *Viola elatior*, *V. pumila*, and *V. stagnina*. Perspect. Plant Ecol. Evol. Syst. **8:** 45–66.

Eckstein R.L., O'Neill R., Danihelka J., Otte A. & Köhler W. 2006b. Genetic structure among and within peripheral and central populations of three endangered floodplain violets. Mol. Ecol. **15:** 2367–2379.

Eckstein R.L. & Otte A. 2005. Effects of cleistogamy and pollen source on seed production and offspring performance in three endangered violets. Basic Appl. Ecol. **6:** 339–350.

Endels P., Jacquemyn H., Brys R., Hermy M. & De Blust G. 2002. Temporal changes (1986–1999) in populations of primrose (*Primula vulgaris* Huds.) in an agricultural landscape and implications for conservation. Biol. Cons. **105:** 11–25.

Eriksson O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos **77:** 248–258.

Eriksson O., Cousins S.A.O. & Bruun H.H. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. J. Veg. Sci. **13:** 743–748.

Facelli J.M. & Pickett S.T.A. 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. **57:** 1–32.

Gaston K.J. & Kunin W.E. 1997. Concluding comments, pp. 262–272. In: Kunin W.E. & Gaston K.J. (eds.), The Biology of Rarity. Causes and Consequences of Rare-common Differences. Chapman & Hall, London.

Grime J.P. 2002. Plant Strategies, Vegetation Processes, and Ecosystems Properties. Wiley, Chichester, 417 pp.

Hölzel N. 2003. Re-assessing the ecology of rare flood-meadow violets (*Viola elatior*, *V. pumila* and *V. persicifolia*) with large phytosociological data sets. Folia Geobot. **38:** 281–298.

Hölzel N., Bissels S., Donath T.W., Handke K., Harnisch M. & Otte A. 2006. Renaturierung von Stromtalwiesen am hessischen Oberrhein. Naturschutz und biologische Vielfalt **31:** 1–263.

Hölzel N. & Otte A. 2004. Assessing the soil seed bank persistence in flood-meadows: The search for reliable traits. J. Veg. Sci. **15:** 93–100.

Honnay O., Jacquemyn H., Bossuyt B. & Hermy M. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytol. **166:** 723–736.

Hood G.M. 2005. PopTools version 2.6.7. http://www.cse.csiro.au/poptools (accessed 15.03.2005).

Huenneke L.F. 1991. Ecological implications of genetic variation in plant populations, pp. 31–44. In: Falk D.A. & Holsinger K.E. (eds), Genetics and Conservation of Rare Plants. Oxford University Press, New York.

Hultén E. & Fries M. 1986. Atlas of North European Vascular Plants (North of the Tropic of Cancer). Koeltz Scientific Books, Koenigstein, 1172 pp.

Jacquemyn H., Brys R. & Hermy M. 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. Biol. Cons. **111:** 137–147.

Jensen K. & Meyer C. 2001. Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. Plant Ecol. **155:** 169–181.

Jongejans E. & de Kroon H. 2005. Space versus time variation in the population dynamics of three co-occurring perennial herbs. J. Ecol. **93:** 681–692.

Kiviniemi K. 2002. Population dynamics of *Agrimonia eupatoria* and *Geum rivale*, two perennial grassland species. Plant Ecol. **159:** 153–169.

Kluth C. & Bruelheide H. 2005. Central and peripheral *Hornungia petraea* populations: patterns and processes. J. Ecol. **93:** 584–595.

Korneck D., Schnittler M. & Vollmer I. 1996. Rote Liste der Farn- und Blütenpflanzen (Pteridophyta et Spermatophyta) Deutschlands. Schriftenreihe Vegetationsk. **28:** 21–187.

Korneck D., Schnittler M., Klingenstein F., Ludwig G., Takla M., Bohn U. & May R. 1998. Warum verarmt unser Flora? Auswertung der Roten Listen der Farn- und Blütenpflanzen Deutschlands. Schriftenreihe Vegetationsk. **29:** 299–444.

Lammi A., Siikamäki P. & Mustajärvi K. 1999. Genetic diversity, population size, and fitness in central and peripheral populations of a rare plant *Lychnis viscaria*. Cons. Biol. **13:** 1069–1078.

Lawton J.H. 1993. Range, population abundance and conservation. Trends Ecol. Evol. **8:** 409–413.

Lennartsson T. & Oostermeijer G.B. 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. J. Ecol. **89:** 451–463.

Lepš J. 1999. Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow copy. J. Veg. Sci. **10:** 219–230.

Lesica P. & Allendorf F.W. 1995. When are peripheral populations valuable for conservation? Cons. Biol. **9:** 753–760.

Lindborg R., Cousins S.A.O., Eriksson O. 2005. Plant response to land use change – *Campanula rotundifolia*, *Primula veris* and *Rhinantus minor*. Ecography **28:** 29–36.

Manly B.F.J. 2001. Randomization and Monte Carlo Methods in Biology. Chapman & Hall, London, 399 pp.

McCue K.A. & Holtsford T.P. 1998. Seed bank influences on genetic diversity in the rare annual *Clarkia springvillensis* (Onagraceae). Am. J. Bot. **85:** 30–36.

McPeek M.A. & Kalisz S. 1993. Population sampling and bootstrapping in complex designs: demographic analysis, pp. 232–252. In: Scheiner S.M. & Gurevitch J. (eds), Design and Analysis of Ecological Experiments. Chapman & Hall, New York.

Menges E.S. 2000. Population viability analyses in plants: challenges and opportunities. Trends Ecol. Evol. **15:** 51–56.

Moora M., Sõber V. & Zobel M. 2003. Responses of a rare (*Viola elatior*) and a common (*Viola mirabilis*) congeneric species to different management conditions in grassland – is different light competition ability responsible for different abundances? Acta Oecol. **24:** 169–174.

Morris W.F. & Doak D.F. 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer, Sunderland, 480 pp.

Newell S.J., Solbrig O.T. & Kincaid D.T. 1981. Studies on the population biology of the genus *Viola*. III. The demography of *Viola blanda* and *Viola pallens*. J. Ecol. **69:** 997–1016.

Nicolè F., Brzosko E. & Till-Bottraud I. 2005. Population viability analysis of *Cypripedium calceolus* in a protected area: longevity, stability and persistence. J. Ecol. **93:** 716–726.

Oostermeijer J.G.B., Brugman M.L., de Boer E.R. & den Nijs H.C.M. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. J. Ecol. **84:** 153–166.

Oostermeijer J.G.B., van't Veer R. & den Nijs J.C.M. 1994. Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. J. Appl. Ecol. **31:** 428–438.

Pullin A.S. & Woodell S.R.J. 1987. Response of the fen violet, *Viola persicifolia* Schreber, to different management regimes at Woodwalton Fen National Nature Reserve, Cambridgeshire, England. Biol. Cons. **41:** 203–217.

Quinn G.P. & Keough M.J. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, 537 pp.

Reger B., Otte A. & Waldhardt R. 2007. Identifying patterns of land-cover change and their physical attributes in a marginal European landscape. Landsc. Urban Plan. **81:** 104–113.

Sagarin R.D. & Gaines S.D. 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? Ecol. Lett. **5:** 137–147.

Sala O.E., Chapin F.S. III, Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., LeRoy Poff N., Sykes M.T., Walker B.H., Walker M.

& Wall D.H. 2000. Global biodiversity scenarios for the year 2100. Science **287:** 1770–1774.
Schemske D.W., Husband B.C., Ruckelhaus M.H., Goodwillie C., Parker I.M. & Bishop J.G. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology **75:** 584–606.
Schnittler M. & Günther K.-F. 1999. Central European vascular plants requiring priority conservation measures – an analysis from national Red Lists and distribution maps. Biodiv. Cons. **8:** 891–925.
Silvertown J., Franco M. & Menges E. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Cons. Biol. **10:** 591–597.
Silvertown J., Franco M., Pisanty I. & Mendoza A. 1993. Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J. Ecol. **81:** 465–476.
Solbrig O.T., Curtis W.F., Kincaid D.T. & Newell S.J. 1988. The population biology of the genus *Viola*. VI. The demography of *V. fimbriatula* and *V. lanceolata*. J. Ecol. **76:** 301–319.
Solbrig O.T., Newell S.J. & Kincaid D.T. 1980. The population biology of the genus *Viola*. I. The demography of *Viola sororia*. J. Ecol.**68:** 521–546.
Svensson B.M., Carlsson B.Å., Karlsson P.S. & Nordell K.O. 1993. Comparative long-term demography of three species of *Pinguicula*. J. Ecol. **81:** 635–645.
Tolvanen A., Schroderus J. & Henry G.H.R. 2001. Demography of three dominant sedges under contrasting grazing regimes in the High Arctic. J. Veg. Sci. **12:** 659–670.
Valverde T. & Silvertown J. 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. J. Ecol. **86:** 545–562.
Vitousek P.M., Mooney H.A., Lubchenko J. & Melillo J.M. 1997. Human domination of earth's ecosystems. Science **277:** 494–499.

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Appendix 1. Mean population matrices for transitions from 2001 to 2002 of *Viola elatior*, *V. pumila* and *V. stagnina* in their main Central European regions of occurrence (Dyje, Czech Republic; Rhine, Germany). Numbers below and to the right of the stages give the number of individuals (n) observed in 2001 and 2002, respectively. Matrix elements (a_{ij}) represent probabilities for the transition between stage j in 2001 to stage i in 2002, except for the transitions a_{14} ('small generative to seedling') and a_{15}('large generative to seedling') in the first row; numbers given there express the average number of seedlings in 2002 produced per small and large flowering plant in 2001 ('anonymous reproduction', Caswell 2001). n = number of populations.

Viola elatior Rhine ($n = 6$)	2001	seedling	small vegetative	large vegetative	small generative	large generative
2002	n	103	179	65	41	43
Seedling	142	0	0	0	2.003	2.003
small vegetative	153	0.434	0.363	0.237	0.272	0.012
large vegetative	54	0	0.159	0.378	0.319	0.210
small generative	22	0.004	0.076	0.029	0.200	0.024
large generative	30	0	0.006	0.073	0.048	0.276
Viola pumila Rhine ($n = 5$)	2001	seedling	small vegetative	large vegetative	small generative	large generative
2002	n	126	85	80	40	45
Seedling	64	0	0	0	1.532	1.532
small vegetative	102	0.491	0.272	0.094	0.113	0.099
large vegetative	81	0.008	0.210	0.386	0.336	0.370
small generative	22	0	0.046	0.114	0.189	0.065
large generative	26	0	0	0.179	0.090	0.345
Viola stagnina Rhine ($n = 3$)	2001	seedling	small vegetative	large vegetative	small generative	large generative
2002	n	494	131	57	11	24
Seedling	100	0	0	0	4.021	4.021
small vegetative	152	0.338	0.246	0.075	0.067	0.048
large vegetative	42	0.005	0.109	0.216	0.111	0.158
small generative	35	0.012	0.107	0.239	0.333	0.396
large generative	27	0.022	0.052	0.190	0.244	0.268
Viola elatior Dyje ($n = 5$)	2001	seedling	small vegetative	large vegetative	small generative	large generative
2002	n	11	22	6	16	4
Seedling	20	0	0	0	0.689	0.589
small vegetative	18	0.400	0.481	0	0.117	0
large vegetative	16	0	0.079	0.150	0.383	0.333
small generative	7	0	0.267	0.200	0.283	0
large generative	4	0	0	0.050	0.217	0
Viola pumila Dyje ($n = 5$)	2001	seedling	small vegetative	large vegetative	small generative	large generative
2002	n	83	17	23	10	11
Seedling	30	0	0	0	1.373	0.973
small vegetative	44	0.603	0.261	0.167	0.040	0.000
large vegetative	25	0	0.132	0.267	0.280	0.450
small generative	8	0	0.029	0.000	0.480	0.050
large generative	10	0	0	0.167	0.200	0.300

Viola stagnina Dyje ($n = 3$)	2001	seedling	small vegetative	large vegetative	small generative	large generative
2002	n	28	63	41	21	18
Seedling	1	0	0	0	0.042	0.042
small vegetative	49	0.667	0.443	0.084	0.325	0
large vegetative	37	0	0.172	0.392	0.230	0.291
small generative	22	0	0.093	0.269	0	0.067
large generative	27	0	0.026	0.238	0.397	0.456