Population dynamics of annuals in perennial grassland controlled by ants and environmental stochasticity

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Abstract

Questions: In a system of five annual plant species restricted to nest-mounds of the ant *Lasius flavus* in a perennial grassland: 1. Are the population dynamics influenced by ant disturbance? 2. Is the survival of the annuals at the scale of the whole grassland possible under the observed conditions of disturbance dynamics? 3. Which phases in the annuals' life cycle and patch types contribute most to population growth?
Location: Boreč hill, northern Czechia, 50°31' N, 13°59' E, 446 m a.s.l.
Methods: Local population dynamics of the annuals were analysed separately for five patch types that differed in the proportion of bare soil. Vitality rates were assessed directly in the field, but also in a garden experiment, during 2000-2001 and 2001-2002. Population dynamics at the scale of the whole grassland was analysed with a megamatrix approach, combining patch dynamics of the nest-mounds with patch-specific population dynamics. Contributions of different phases and patch types to growth rate were estimated by elasticity analysis.
Results: Nest-mounds differed in the percentage of bare soil. Increasing moss cover significantly reduced germination and seed production of all studied annuals and decreased their population growth rates (λ). Although successional processes dominated over ant disturbance, populations of all species could survive well ($\lambda \gg 1$) in the grassland according to the 2000-2001 megamatrix dynamics. Based on the dynamics from the following period, two species would not survive in a long-term perspective due to random environmental variation. Whereas the A-A transition (adult plants originating from adults of the previous year) had the highest elasticity under open conditions and 'good period' demography, the importance of persistent seeds increased under reverse conditions. This, however, differed among species.
Conclusions: Ant-disturbance was shown to be critical for the population survival of five annual species in the studied grassland. The fate of the annual populations in the grassland system also depends on random environmental variation, which may override the effect of ant activity.

Keywords: Disturbance; Dormant seed; Elasticity analysis; *Lasius flavus*; Megamatrix analysis.

Introduction

Perennial grasslands are exposed to a variety of small-scale natural disturbances (Platt 1975; Pickett & White 1985; Goldberg & Gross 1988; Dean et al. 1997; Milton et al. 1997; Wolfe-Bellin & Moloney 2000; Rogers & Hartnett 2001). Disturbances emerge through plant deaths, substrate movement or animal activity (van Tooren 1988). Although they usually affect a very small proportion of the habitat, they create environmental heterogeneity that maintains co-existence of plant species with different competitive ability (During et al. 1985; van der Meijden et al. 1992; Rees & Long 1992; Palmer 1994; Watkinson et al. 2000). Particularly annuals and biennials benefit from the presence of canopy gaps in the plant community. However, as openings are usually ephemeral, their favourability for such species declines with successional changes (Symonides 1986; van der Meijden et al. 1992; Löfgren et al. 2000; Watkinson et al. 2000).

Usually, at the scale of the whole grassland system there are gaps of different successional stages, each associated with specific population dynamics of competitively inferior species (e.g. Bullock et al. 1994; Löfgren et al. 2000). To predict their long-term perspective in such systems, single-environment demographic models may be largely inaccurate, being too unrealistic. To overcome this limitation, more complex models incorporating environmental variation have been developed (Pascarella & Horvitz 1998). Horvitz & Schemske (1986) were the first to describe population dynamics of the understorey species *Calathea ovandensis* in a tropical forest by combination of successional dynamics of the forest with habitat-specific population dynamics (so called dynamic-environment megamatrix analysis). Although this approach was used in several studies in forest ecosystems (e.g. Cipollini et al. 1994; Pascarella & Horvitz 1998), it has never been applied for the analysis of population dynamics of subordinate species from grassland ecosystems. Here, I want to use this method to analyse the dynamics of five annual species restricted to ant hills of *Lasius flavus* in temperate perennial grassland.

Permanent soil nests of *L. flavus* with a typical plant composition are well-known from temperate perennial grasslands, particularly from pastures (Grubb et al. 1969; King 1977a; van Tooren 1988; Hansell 1993; Kovář et al. 2001). A specific ant-hill flora, including several annual species, results from various ant activities such as soil-heaping. Ants bring soil particles to the mound surface to regulate temperature and moisture in the nests for optimal brood rearing, and therefore these activities are intensive in spring and summer time. This may also be affected by various external factors, such as rain or shading by surrounding vegetation (Woodell & King 1991; Blomqvist et al. 2000; Vlasáková, unpubl.). Disturbance intensity is highest in the first years after a colony is founded and drops with colony ageing (King 1977b). After the nest is abandoned, disturbance stops, but may re-appear with a new ant colony (King 1981; Kovář et al. 2001). It implies that within the same grassland system there may be large variation in the degree of disturbance caused by ant nests, and there is also significant variation between seasons.

Ants are the only important source of soil disturbance in the grassland system at the Boreč site in N Bohemia, Czech Republic. Several annual species occurring in this system are restricted to the surface of present ant-hills, but absent from nests with low or no disturbance. It is assumed that absence of disturbance limits seedling establishment, which is critical for population survival in short-lived species (e.g. Watkinson et al. 2000). Therefore, patch status as a function of ant disturbance is hypothesized to determine the demographic performance of annuals growing on the nest surface.

The primary goal of this study was to search for the effect of ant-generated patch status on the individual vital rates and population dynamics of the annuals *Androsace elongata*, *Arenaria serpyllifolia*, *Myosotis ramosissima*, *Saxifraga tridactylites* and *Veronica arvensis*. Since the local demographic performance of annuals (specifically of *Arenaria serpyllifolia*) growing on ant-hills was the subject of previous studies (e.g. King 1977c), the population performance of the study species should be estimated at the scale of a whole grassland using a megamatrix approach. Specifically, patch status dynamics (governed by ant disturbance) can be coupled to population dynamics assessed for each patch status, separately for the 2000-2001 and 2001-2002 periods. For the megamatrix constructed for each period, the population growth rate was assessed and the relative importance (elasticity) of each patch type and life history stage were calculated. As a change in population growth rate can be the result either of directional successional change or random environmental variation, both factors in the simulation were manipulated to assess their effect on above parameters. Also, the relative importance of two life-history stages was calculated for overall population growth rates obtained from simulation.

Methods

Study site

The field part of this study was conducted on Boreč Hill (50°31' N, 13°59' E; 446 m a.s.l.), which is part of the Protected Landscape Area 'České středohoří' in the north of the Czech Republic. The vegetation of Boreč, growing on phonolite bedrock, is a mosaic of dry grasslands, scree slope vegetation and ravine and thermophilic oak forests covering ca. 20 ha. The study of the annuals/ant-hill system was undertaken in a grassland enclave with an area of 600 m^2 on the northern side of the hill. This grassland, dominated by *Bromus erectus* and *Arrhenatherum elatius*, was maintained until 1950 by grazing, which favours the establishment of ant colonies in grasslands (Woodell & King 1991). Despite the abandonment of grazing, ca. 300 ant-hills of *L. flavus* were still present at the study site and shrubs (*Rosa* spec., *Prunus spinosa*) covered less than 1 % of the grassland during the 1999-2002 study period. Ant-hills of *L. flavus* covered 19 % of the meadow area. The proportion of disturbed plant cover was much smaller: during 2000-2002, exposed soil covered 1.7-2.7 % of the meadow surface. Besides *L. flavus*, there is no other important source of disturbance in this grassland.

Study species

Ant species

Lasius flavus (Fabricius) (*Formicidae*) is common in temperate regions of Europe, Asia and North America, from lowlands to the mountains. It prefers open habitats like marshes, abandoned arable fields and grasslands. Colonies (consisting of 8000-25 000 workers) live in soil nests that are on average 40 cm deep, 30 cm high and 50 cm in diameter (Wallof & Blackith 1962). Ants maintain their nest by constantly bringing soil particles onto the mound top. One colony may bring on average 1.04 l/a of fresh soil onto the mound surface (King 1981). Workers of *L. flavus* live mostly underground in the mound and feed on the honeydew and young instars of root aphids (Pontin 1978). The mounds can be continuously occupied, one fertilized queen taking over from another. Soil structures may cover up to 12 % of the grassland area (Elmes 1991).

Plant species

Arenaria serpyllifolia (*Caryophyllaceae*), *Androsace elongata* (*Primulaceae*), *Myosotis ramosissima*

(*Boraginaceae*), *Saxifraga tridactylites* (*Saxifragaceae*) and *Veronica arvensis* (*Scrophulariaceae*) are all winter annuals with similar ecology; all of them are weak competitors, and therefore restricted to disturbed habitats such as road verges, rock outcrops, arable fields or, as in this study, ant-hills. Their life cycle starts with germination in August-September and seedling emergence continues until winter; in the spring, a new cohort of seedlings may germinate (as recorded for *V. arvensis* by Baskin & Baskin 1983 and Boutin & Harper 1991), but its contribution to the seedling population is negligible (Dostál unpubl.). They flower from April and set fruit in May. Adults usually die before the end of July (except for *A. serpyllifolia* which may live until late summer or even until the next season; King 1977b). In contrast to the vegetative phase that lasts for some months, seeds can persist in the soil for years (Thompson et al. 1997). This strategy helps to bridge periods of unfavourable conditions.

None of the study species is adapted for myrmecochory; *L. flavus* is not involved in this type of dispersal (Woodell & King 1991).

Matrix model construction: Patch dynamics

Each of the ca. 300 mounds in the grassland was checked in May during three consecutive seasons (2000-2002) and the percentages of exposed soil, moss and vascular plant cover were estimated. Mounds were assigned to one of five patch types on the basis of percentage of bare soil (Type 1: ≥ 40 % ; Type 2: 25.1-39.9 %; Type 3: 10.1-25 %; Type 4: 5.1-10 %; Type 5: 0-5 %). Each mound was labeled on the first occasion in 2000 with a metal tag, in order to identify mound position in the following seasons with a metal detector. Changes in habitat type were described by a patch-transition matrix, separately for each period (2000-2001, 2001-2002). Stable patch-type distribution (right eigenvector) was calculated for each matrix (both with the dominant eigenvalue $\lambda = 1.00$).

Matrix model construction: population dynamics within patch types

To describe the population dynamics within each patch type, a time-invariant population projection matrix model (Caswell 2001) was prepared for each plant species, separately for each of the 2000-2001 and 2001-2002 seasons:

$$n(t+1) = An(t), \qquad (1)$$

where $n(t)$ is a vector of k stage/age classes, and A is a square matrix of dimension k. The dominant eigenvalue

of A, λ, the population growth rate, was calculated. Further the demographical importance of individual elements was assessed, namely of A-A and S-S transitions (for explanation see further) using elasticity analysis (de Kroon et al. 1986):

$$e_{ij} = \delta(\ln\lambda) / d(\ln A_{ij}) = (A_{ij} / \lambda)(\delta\lambda / dA_{ij}), \qquad (2)$$

that gives proportional change in growth rate l resulting from a proportional change in matrix element A_{ij}.

Projection matrices were constructed as described by Kalisz & McPeek (1992). Individuals of all five species were assigned to one of two life stages, adult plants and dormant seeds in the seed bank. Adult plants bearing seeds may become adults again in the next season (by direct germination of seeds produced; A-A) or may contribute to the pool of dormant seeds (A-S). These may emerge to adult plants (S-A) or stay dormant in the coming season (S-S). Fate of dormant seeds was analysed without respect to their age, i.e. demographic matrices consisted of four matrix elements. The transition period was one year (approximately from May of year t to May of t+1).

Due to the persistent soil seed bank of the study plants, proportions of germinated and dormant seeds in the year t+1 cannot be assessed directly in the field from the seed production of year t. To estimate these rates, an experiment in a garden of the Institute in Průhonice was set up, considering variation in habitat type. In June 2000, mound soil and seeds of annuals were obtained from the field site (but outside the study system). Soil was autoclaved for 24 h to kill seeds of study species that might be present, and then spread in a 5 m × 5 m plot prepared by removing the top soil (10 cm) in the experimental garden.

Seeds were sown in plastic-covered wire baskets (15 cm × 15 cm) placed in the plot with autoclaved mound soil. The seeds were sown on a nylon mesh (mesh size = 0.2 mm) fixed to the wire baskets (n = 48 per species) to prevent downward seed movement, and covered with a 2 mm layer of mound soil. In total 200 seeds (100 seeds in the case of *Myosotis*) were sown in each basket. To simulate successional changes of mound surface, half of the baskets were covered with a 3 cm layer of the pleurocarpous moss *Pleurozium schreberi*. Germination was monitored biweekly from September 2000 till May 2001; on each check, emerged seedlings were counted and removed from the baskets by clipping. Baskets were harvested in June 2001 and the remaining seeds were extracted. Seed viability was tested by germination on filter paper in 9-cm Petri dishes. Germination was carried out in climate chambers with a temperature regime 20 °C/day and 10 °C/night, and a 12 h photoperiod for two months. Seeds were considered to be viable if cotyledons

emerged. After six weeks, seeds that failed to germinate were sprayed with a 100 p.p.m. solution of giberellic acid to break dormancy. If there were still non-germinated but visibly healthy seeds, their embryos were stained with a 1000 p.p.m solution of tetrazoliumchloride. Seeds of *Saxifraga* are too tiny to be fully extracted from the soil and therefore the number of viable seeds was assessed by the germination method only.

In June 2001, the experiment was repeated with a new seed cohort (*n* = 32 baskets). Germination was followed until May 2002 and the remaining seeds were processed as described for the 2000 cohort.

Prior to sowing, the viability of both cohorts was tested by germination at room temperature (dormant seeds were stimulated by a 100 p.p.m. solution of gib-erellic acid); the viability was very close to 100 %, for both cohorts and all five species. Baskets were randomly placed in tetrads in the plot; new baskets from 2001, also in tetrads, were placed in gaps that resulted from the harvest of part of the 2000 baskets. The effect of moss treatment on proportions of germinated and persisting seeds was analysed with GLM with a Poisson distribution.

Data on further demographic transitions (seedling survival to adult stage and seed production) were obtained in the field, also with respect to variation in habitat type. For this purpose 11 mounds were selected in 1999; they were chosen on the basis of (1) presence of at least one annual species: *Androsace*: *n* = 6 mounds; *Arenaria*: *n* = 7; *Myosotis*: *n* = 10; *Saxifraga*: *n* = 4 ; *Veronica*: *n* = 8; some mounds had more than one annual species; and (2) of their locations representing S-N and W-E gradients of the grassland enclave. The area of each mound was divided into a grid of cells that could be monitored repeatedly. Cells were delimited on each census event by a device similar to a point-quadrat frame.

Censuses were undertaken during (1999) 2000-2002 twice a year in May and November. Numbers of juveniles (in November) and numbers of fruiting plants and capsules (in May; in *Arenaria* number of fruiting adults only) were recorded for all cells of each mound. Besides demographic records, the percentage of exposed soil and acrocarpous mosses was recorded in each cell. Number of seeds per capsule was measured in a set of 50 capsules per species harvested during the record period in the adjacent grassland enclave.

The effect of variation in habitat type on seedling abundance and seed production was analysed by GLM with a Poisson distribution; mound ID, cell size, percentage of bare soil and number of heterospecific neighbours were used as independent variables in the model. Effects of the same factors on seedling survival was tested by GLM with a binomial distribution.

For each species and period, i.e. 2000-2001 and

2001-2002, two baseline matrices were constructed for the most open (Type 1) and closed patches (Type 5). For the remaining three intermediate habitat types, corresponding projection matrices were calculated by linear interpolation from the baseline matrices above on the basis of percentage of bare soil.

Megamatrix model construction and analysis

A detailed description of the construction of mega-matrix models is given in Pascarella & Horvitz (1998). The dimensions of a megamatrix is given by the product of the number of life history stages and the number of patch types. In the present case this is a 10×10 matrix, a product of a 2×2 plant population projection matrix and 5×5 matrix of patch-type transitions. As the order of multiplication does matter in matrix processes, it is necessary to carefully consider the relationship between plant phenology and timing of disturbance, in this case of ant soil-heaping (Pascarella & Horvitz 1998). Disturbance intensity is highest during April and May and declines during the rest of the year. All five species start to flower around April and set seeds by June. However, other events of the annual life cycle, such as germination and survival to adult stage, precede the peak in soil disturbance at time *t*+1, and thus follow the rules of patch type at time *t*. Thus, processes related to plant population dynamics must be modeled first, followed by patch dynamics.

A time-invariant megamatrix model (Caswell 2001) was prepared for each species, separately for the 2000-2001 and 2001-2002 seasons:

$$n\,(t+1) = \boldsymbol{M}\,n\,(t), \tag{3}$$

where $\boldsymbol{M}$ is the 10×10 matrix, in which each entry gives the probability that an individual in a given patch type and stage class at time *t* will contribute to or enter another stage class in the same or another patch type by time *t*+1. For each megamatrix the dominant eigenvalue l_m, was calculated as well as patch and summed stage-class elasticity. Patch elasticity gives the importance of life history events within one patch type relative to the importance of life history events in other patch types. Summed stage-class elasticity yields the importance of a given stage across all patch types relative to the other life history stages.

Stochastic megamatrix model

The effects of two different sources of variation on population dynamics were investigated. First the effect of variation in soil-heaping activity on the population dynamics in the grassland system was investigated. For that purpose seven new patch-type transition matrices were constructed, based on the matrix recorded for the 2001-2002 period. This was done by manipulation of the bare soil percentage recorded in 2002 by multiplication with a factor of 0.4, 0.6, 0.8, 1.0, 1.2, 1.4 or 1.6. New patch dynamics matrices were crossed with patch-specific projection matrices of *Androsace* and *Myosotis*, of 2000-2001 and 2001-2002 demography. Thus, for each species, 14 time-invariant megamatrices were obtained and the dominant eigenvalue λ_m, patch and summed stage-class elasticity were calculated, specifically of the A-A and S-S transitions. By selecting these two species, differences in response to disturbance could be demonstrated in a strong (*Androsace*) and a weak seed banker (*Myosotis*; see Results). Further, the effect of random environmental variation was investigated by manipulation of the frequency of 2000-2001 and 2001-2002 demography. Within each disturbance scenario, the annual population for a period of 100 years was projected and the probability of selecting the 2000-2001 megamatrix ($P = 0.1, 0.3, 0.5, 0.7$ and 0.9) varied. It is worth remarking that this period was demographically more favourable than the period that followed. From each simulation the dominant eigenvalue l_m was calculated and the stage-class elasticity was summarized as a mean of 10 realizations per parameter combination.

All simulations were implemented with Matlab, ver. 5.3.1. (The MathWorks Inc). All other analyses were carried out with S-PLUS 6 for WINDOWS (Lucent Technologies, Inc.).

Results

Patch dynamics

Within-season changes in patch status followed the periodicity of ant soil-heaping activity and successional processes. There was a significant dominance of bare soil cover over cover of acrocarpous mosses during May, and a reverse pattern during November (Fig. 1).

Patch openness (expressed by bare soil percentage on the mounds) at time t was positively correlated with the openness at time *t*+1 during both 2000-2001 and 2001-2002 periods; successional processes, however, prevailed over ant disturbance activity as slopes of regression lines were below 1 (for 2000 vs. 2001, $r^2 = 0.437$, $p < 0.001$, $k = 0.738$, $m = 0.093$; for 2001 vs. 2002, $r^2 = 0.738$, $p <$
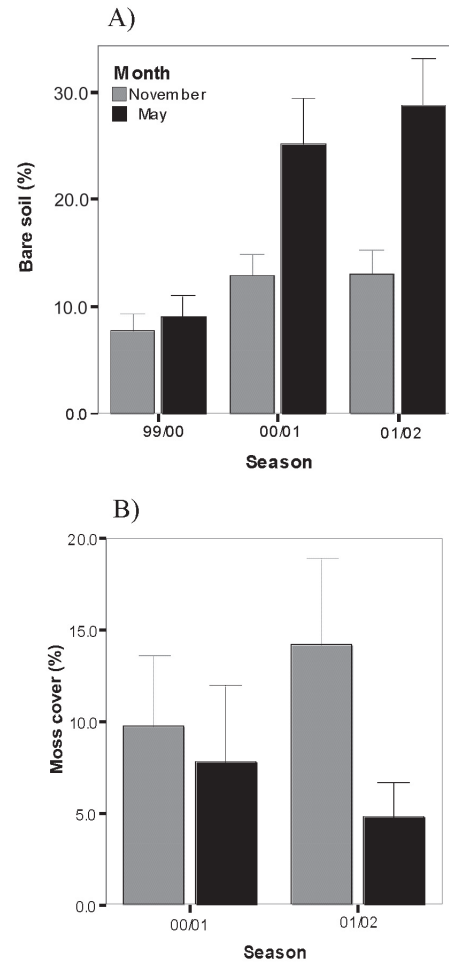

Fig. 1. Mean percentage (+ SE) of bare soil (**A**) and acrocarpous mosses (**B**) recorded in 11 mounds during (1999) 2000 - 2002. Month of observation had significant or marginally significant effect respectively on both parameters (Bare soil: $p < 0.001$; Moss $p = 0.093$).

0.001, $k = 0.915$, $m = 0.055$; where k and m are the slope and the y intercept, respectively). Disturbance activity in the latter period was significantly higher according to a comparison of the slopes of regression lines ($F_{1, 591} = 8.43$, $p = 0.004$).

After classification of each mound to one of five patch types, 2 patch transition matrices were constructed (Table 1). The stable patch type distribution predicts undisturbed patches to dominate in the system during the first period (Fig. 2). The latter period is characterized by a substantial increase in the proportion of most disturbed patches (Type 1 and Type 2): whereas their proportion was predicted to be 16 % during 2000-2001, in 2001-2002 it was 48% (Fig. 2).

Table 1. Patch-transition matrices constructed separately for the periods 2000-2001 (**A**) and 2001-2002 (**B**), based on the observation of ca. 300 ant nests.

A. Patch at time $t+1$	Patch at time t				
	Type1	Type2	Type3	Type4	Type5
Type1	0.400	0	0.170	0.036	0
Type2	0.333	0.167	0.151	0.086	0
Type3	0.200	0.333	0.377	0.230	0.038
Type4	0.067	0.250	0.264	0.482	0.163
Type5	0	0.250	0.038	0.165	0.800

B. Patch at time $t+1$	Patch at time t				
	Type1	Type2	Type3	Type4	Type5
Type1	0.550	0.185	0.226	0.021	0
Type2	0.350	0.519	0.161	0.082	0
Type3	0.100	0.259	0.403	0.206	0.078
Type4	0	0.037	0.177	0.526	0.089
Type5	0	0	0.032	0.165	0.833

Patch status and demographic transitions

Germination and seed persistence – garden experiment

In the garden experiment, moss cover significantly reduced the number of seedlings (in all species $p < 0.001$; Fig. 3A). The reverse relationship was recorded for the proportion of dormant seeds persisting in the soil (Fig. 3B). In analogy with the garden experiment, there was a positive relationship in the field between percentage of exposed soil in the cells and presence and abundance of seedlings presence (analyses not shown).
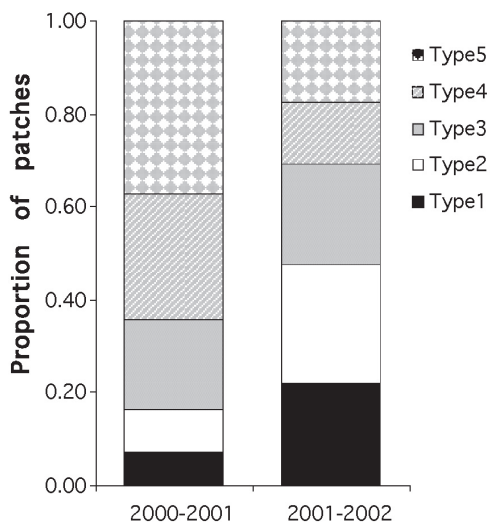

Fig. 2. Distribution of stable patch types based on disturbance dynamics during 2000 vs. 2001 and 2001 vs. 2002. Mounds (patches) were assigned to one of five types on the basis of percentage of bare soil (Type 1: ≥ 40 %; Type 2: 25.1-39.9 %; Type 3: 10.1-25 %; Type 4: 5.1-10 %; Type 5: 0-5 %).

Survival – field observations

In contrast to germination, there was a negative relationship between proportion of bare soil and seedling survival to adult stage in *Androsace* and *Arenaria* (Table 2A). In the other three species no effect of habitat quality was detected. Survival was also affected by other factors: it was positively influenced by the density of heterospecifics in *Androsace*, *Arenaria* and *Saxifraga*. Increasing density of conspecifics, in contrast, decreased the probability of survival in *Veronica*, *Arenaria* and *Myosotis*.
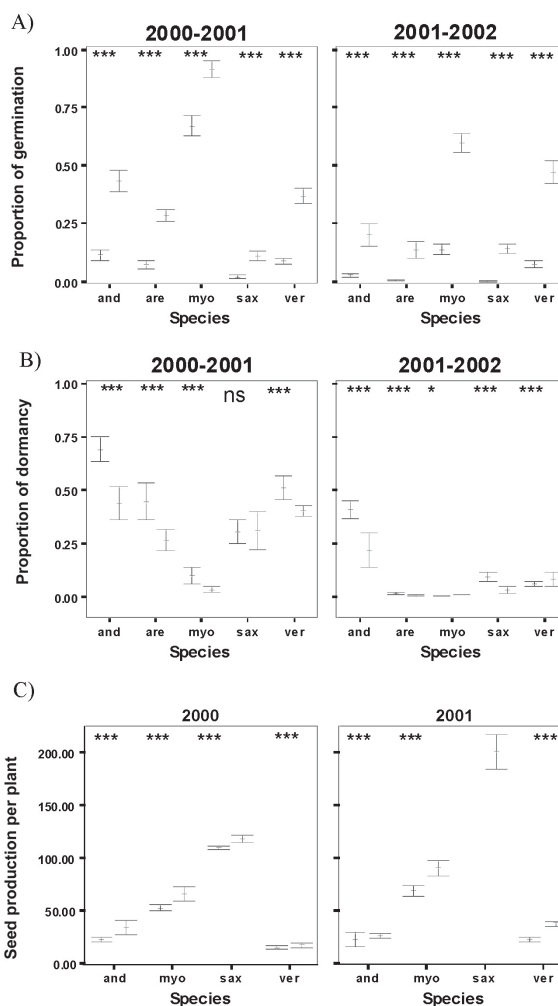

Fig. 3. Proportion of seeds germinated (**A**) and those remaining dormant (**B**) from the garden experiment if covered by moss (left whiskers) or left uncovered (right whiskers). The experiment was carried out during 2000-2001 and 2001-2002 respectively. (**C**) Effect of mound disturbance on seed production as found in the field. Open circles refer to bare soil percentage ≥ 20 %, closed squares to < 20 % (there was an insufficient number of replicates for bare soil < 20 % in case of *Saxifraga* in 2001). See Methods for details. Mean (± SE) is shown. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant; and = *Androsace*, are = *Arenaria*, myo = *Myosotis*, sax = *Saxifraga*, ver = *Veronica*.

Table 2. Analysis of deviance of the effects of mound identity, cell size, cell state (percentage of bare soil), and of the abundance of heterospecifics and conspecifics on **(A)** seedling survival (pooled for the 2000-2001 and 2001-2002 periods) and **(B)** per plant seed production (pooled for 2000 and 2001). Species differed in number of mounds sampled (see df for individual species and analyses). *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant. Values in Tables show deviance related to each source of variation (Variable) and residual deviance. Sign indicates the direction of the effect. For species abbreviations see Fig. 4.

A)

Variable	df	Survival				
		and	are	myo	sax	ver
Mound ID		42.6 *** (6)	54.6 *** (7)	172.0 *** (10)	247.9 *** (4)	89.9 *** (8)
Cell size	1	1.0 ns	− 25.8 ***	3.1 ns	+ 16.6***	0.5 ns
Bare soil[1]	1	− 5.6 *	− 85.2 ***	3.2 ns	0.0 ns	0.3 ns
Conspecific neighbors[2]	1	+ 5.7 *	− 8.7 **	− 55.6 ***	1.0 ns	− 12.1 ***
Heterospecific neighbors[2]	1	+ 5.8*	+ 393.2***	1.0 ns	+ 16.3 ***	0.2 ns
Residual deviance		622.3	1576.1	1280.0	939.1	420.8
Residual d. f.		147	233	432	80	139

B)

Variable	df	Seed production			
		and	myo	sax	ver
Mound ID		411.1 *** (6)	164.0 *** (8)	557.4 *** (2)	104.9*** (5)
Cell size	1	0.2 ns	- 32.9 ***	− 51.8 ***	− 30.9***
Bare soil[1]	1	+ 59.5 ***	+ 781.9 ***	+ 157.1 ***	+ 272.7***
Conspecific neighbors[2]	1	0.6 ns	+ 42.4 ***	− 236.9 ***	1.2 ns
Heterospecific neighbors[2]	1	+ 111.2 ***	1.9 ns	− 142.7 ***	− 15.4 ***
Residual deviance		1484.2	4224.7	5020.1	1564.1
Residual d. f.		139	175	80	145

[1] refers to area of bare soil (cm^2) recorded in November of year t–1 (Survival) and to area of bare soil (cm^2) in May of year t (Seed production);
[2] refers to number of juveniles (Survival) and adult plants (Seed production).

Table 3. A. Population growth rates (λ) and elasticities (e) of the most important life-history component in open (Type1) and closed patches (Type5). **B.** The same parameters for megamatrices. Periods 2000-2001 and 2001-2002 are shown separately.

A

Species	2000-2001						2001-2002					
	Type1			Type5			Type1			Type5		
	λ		e	λ		e	λ		e	λ		e
Androsace	5.748	A-A	0.845	1.906	A-A	0.408	0.674	A-A	0.372	0.460	S-S	0.771
Arenaria	3.509	A-A	0.828	2.003	A-A	0.607	0.840	A-A	0.985	0.088	A-A	0.706
Myosotis	7.682	A-A	0.988	5.162	A-A	0.964	3.829	A-A	0.999	0.955	A-A	1.000
Saxifraga	2.946	A-A	0.806	0.876	A-A	0.431	2.564	A-A	0.963	0.117	S-S	0.607
Veronica	1.925	A-A	0.609	0.906	S-S	0.313	2.085	A-A	0.935	0.381	A-A	0.732

B

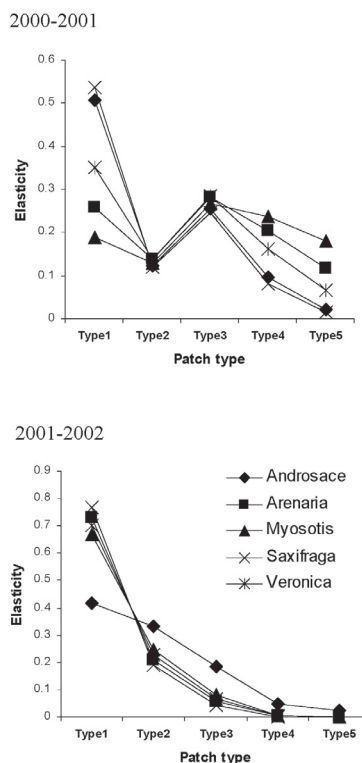| Species	2000-2001			2001-2002		
	λ		e	λ		e
Androsace	3.134	A-A	0.734	0.536	S-S	0.473
Arenaria	2.389	A-A	0.707	0.566	A-A	0.967
Myosotis	5.744	A-A	0.973	2.707	A-A	0.973
Saxifraga	1.578	A-A	0.716	1.689	A-A	0.938
Veronica	1.187	A-A	0.417	1.439	A-A	0.919

2000-2001

2001-2002

Fig. 4. Patch elasticity of the megamatrix based on the 2000-2001 and 2001-2002 dynamics.

Seed production – field observations

Fecundity was higher in disturbed cells (Fig. 3C) and this was consistent for all four species (number of capsules of *Arenaria* was not counted). Increasing density of conspecifics and heterospecifics decreased seed production of *Saxifraga*. Heterospecifics had the same effect on the seed production of *Veronica* (Table 2B).

Within-patch population dynamics – matrix model

The population dynamics of the annuals was influenced by habitat type, as well as by inter-seasonal variation in vital attributes. Population growth rate in the most open patches (Type 1) was far above 1 in all five species during 2000-2001. During the same period, *Androsace*, *Arenaria* and *Myosotis* could survive well in the undisturbed patches (Type 5), whereas *Saxifraga* and *Veronica* could not. Based on the projection matrices of the following period, two out five species would eventually go extinct even in the most open patches; in closed patches, populations of none of the species can survive (Table 3A). The A-A transition made the highest contribution to population growth in Type 1 patches in both seasons and all species. In the closed patches, A-A was the most important matrix element in 4 of the species during 2000-2001; in *Veronica* it was S-S transition. In closed patches in the following period, S-S had

the highest elasticity in *Androsace* and *Saxifraga*, in the other species it was the A-A transition (Table 3A).

Megamatrix analysis

According to the megamatrix model of the 2000-2001 period, population growth rates of individual species were between 1.18 (*Veronica*) and 5.74 (*Myosotis*), indicating the capacity of each species to survive well and expand within ant-maintained patch systems. In the consecutive period, however, growth rates dropped dramatically in *Androsace* and *Arenaria*, indicating eventual extinction of these species. Population growth rates of the other three species also differed from the previous period, but were significantly above 1 (Table 3B). The A-A transition had the highest elasticity in all five species during 2000-2001. The same transition was most important in four of the species in the consecutive period; in *Androsace* it was the S-S transition. Concerning the relative contribution of specific patch type to population growth, during 2000-2001, Type 1 had the highest elasticity in *Androsace*, *Saxifraga*, and *Veronica*. In *Arenaria* and *Myosotis* all patch types had similar elasticities. During the second period, Type 1 had invariantly the highest elasticity and the importance of other patch types declined steeply, in *Androsace* gradually (Fig. 4).

Stochastic megamatrix model

Increasing both the frequency of 'good periods' (i.e. of 2000-2001) and the disturbance activity increased population growth rates, but the pattern differed between *Androsace* and *Myosotis*. The effect of disturbance activity on growth rate in *Androsace* was important only if the frequency of the 'good period' was high; in *Myosotis* more disturbance contributed to higher λ irrespective of the sampling probability of 'good period' (Fig. 5A). In both species, disturbance activity increased the importance of A-A and decreased the importance of S-S. In *Androsace* elasticity of A-A and S-S, respectively, was positively and negatively influenced by a higher frequency of 'good period'. Elasticity of A-A in *Myosotis* was under all conditions very close to 1, indicating negligible importance of the other life history events (Fig. 5B, C). It was also found that the elasticity of different patch types changed with the intensity of disturbance. Whereas importance of closed patches declined with higher disturbance, the opposite trend was observed in the most open patches. Both species, however, differed in patch elasticities within a given disturbance scenario. In *Myosotis*, the use of 'bad period' demography resulted in a greater importance of Type 1 patches relative to the use of 'good period' demography. The opposite pattern was observed in *Androsace* (Fig. 5D).
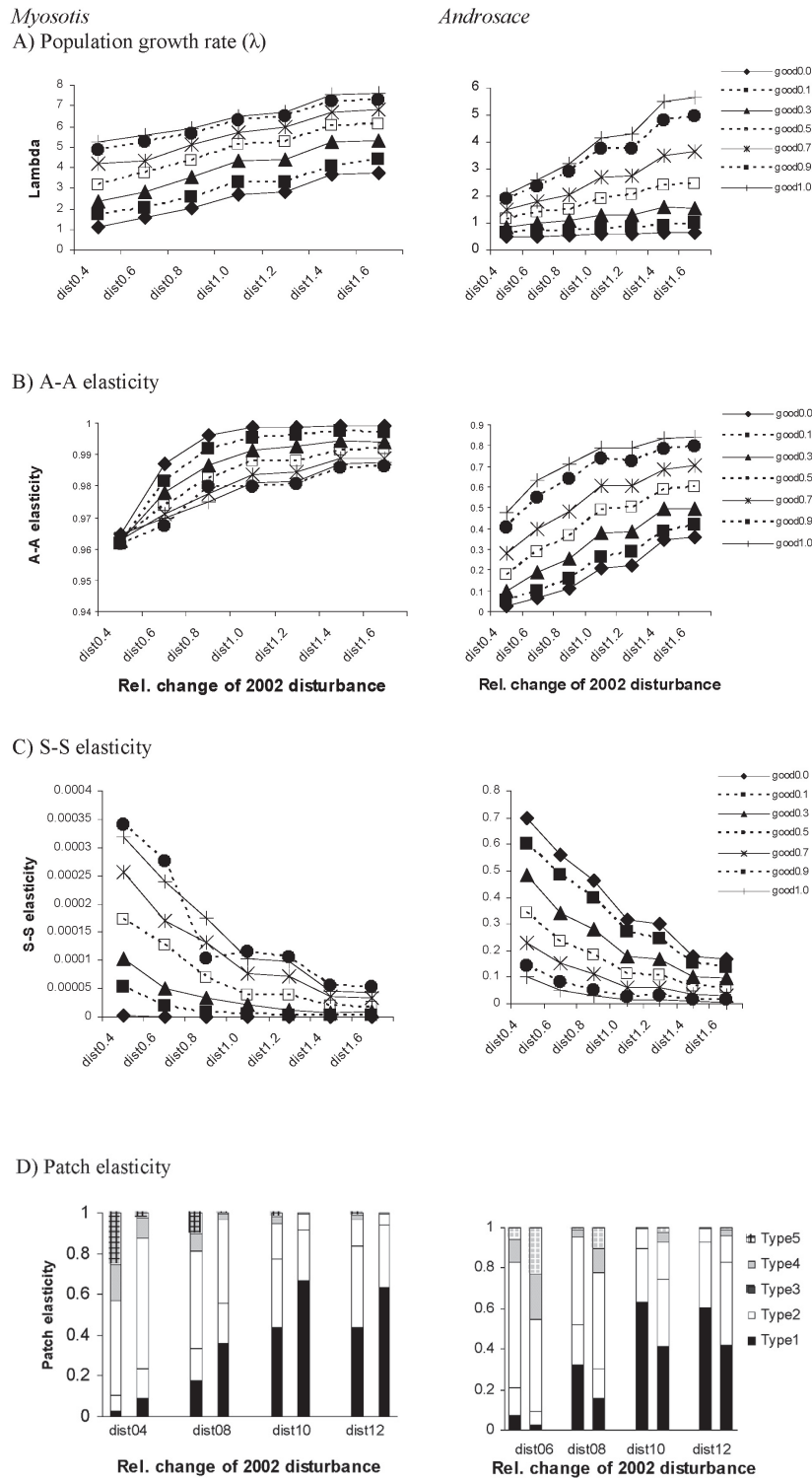
Myosotis

Androsace

A) Population growth rate (λ)

B) A-A elasticity

C) S-S elasticity

D) Patch elasticity

Fig. 5. Effect of relative change in bare soil percentage observed in the field in 2002 and frequency of 2000-2001 demography ('good period') on (**A**) population growth rate, (**B**) A-A elasticity (adult plants originating from adults of previous year), (**C**) S-S elasticity (seeds persisting in the soil) and (**D**) patch type elasticity in *Myosotis* (left column) and *Androsace* (right column). In case of patch elasticity, left bars refer to frequency of 2000-2001 demography = 1; right bars to frequency = 0.

Discussion

Vital rates of annuals and ant disturbance

This study shows that vital rates, specifically germination and seed production, of annuals are severely reduced in the absence of open microsites. It stands in line with the findings of other studies dealing with the effect of habitat characteristics on the early stages of plant life cycle (King 1975; During & van Tooren 1990; Kitajima & Tilman 1996; Špačková et al. 1998; Zamfir 2000; Zobel et al. 2000). A 'regeneration niche', i.e. a competition-free environment, is necessary for seedling recruitment and establishment for species with diverse life-history tactics (Grubb 1977). However, in contrast to perennials that also reproduce vegetatively, low and irregular recruitment in annual plants may have fatal consequences for the population (Watkinson 1990; Watkinson et al. 2000). In this respect, workers of *Lasius flavus* and their disturbance activity appear to be a critical factor maintaining safe microsites for seedling establishment of annuals in grasslands. On the other hand, negative aspects of soil-heaping should also be taken into account. King (1977c) found that soil-heaping may be one of the principal sources of density-independent mortality of juveniles in annuals. Soil heaping may also bury seeds too deep for successful emergence (Grubb et al. 1969; Dostál 2005a). In spite of these possible demographic losses, disturbance is considered to have a positive effect on local population persistence, as suggested by higher growth rates of annuals in open patches than in closed ones.

Patch status dynamics

The patch status did not stay constant but changed according to the balance between moss succession and mound construction moving the successional clock backwards. Based on the dynamics observed in the field during both periods, successional processes dominated over disturbance activity. According to the 2000-2001 dynamics (with $k = 0.738$), a typical Type 1 patch (mean percentage of bare soil = 70 %) would transform to a typical Type 5 patch (mean percentage of bare soil = 2.5 %) in 10.9 years, and according to 2001-2002 dynamics (with $k = 0.915$) in 37.5 years (calculated as time = ln $(\alpha/\alpha_0)/c$, where α is the percentage of bare soil at time t, i. e. 2.5 %, and α_0 is proportion at time $t–1$, i. e. 70 %; c is a constant, given by ln(k); Valverde & Silvertown 1997). Although mounds with very small or no disturbance activity were largely represented in the system, it did not imply their abandonment. A careful check of moss-covered nests always revealed workers of *L. flavus*, indicating the possibility of recurrent disturbance (as it

can be seen from the patch transition matrix – see Table 1). However, based on a three-year study it is hard to identify factors that would trigger the re-appearance of ant activity.

Megamatrix dynamics – population projection at grassland scale

Regarding the state of mounds changing through time, the use of a megamatrix approach for demographic projection at the scale of whole grassland seems appropriate (Pascarella & Horvitz 1998). According to this model, the time-invariant population growth rate of all study species during 2000-2001 was substantially greater than 1, indicating the capacity of observed patch-dynamics to maintain annuals in the grassland. Based on the model for the following period, two species, *Androsace* and *Arenaria*, could not survive in a long-term perspective. This result was obtained in spite of a significant increase in disturbance activity. As pointed out by Valverde & Silvertown (1998) and others, the demography of understorey species varies due to directional changes in habitat openness (here determined by nest-construction activities of the ants), but also due to random environmental variation in time and space. This source of variation in plant demography is rather the rule than the exception (e.g. de Jong & Klinkhamer 1988; Kalisz & McPeek 1992; Horvitz & Schemske 1995; Lennartsson & Oostermeijer 2001). In the present study, the reduction in demographic performance during 2001-2002 reflected primarily lower recruitment (Fig. 3) and decreased seedling survival (not shown).

Changes in population dynamics, either due to variation in patch dynamics or to random environmental variation, were also associated with the changes in major determinants of population growth rates. Both field observations and matrix simulations showed that elasticity of A-A ('true annual pathway'; Kalisz & McPeek 1992) was highest in open patches and under conditions of 'good period' demography (in case of *Androsace*). Importance of the S-S transition increased under 'bad period' conditions, indicating its buffer function in harsh environments (Cohen 1966; Venable & Brown 1988; Kadmon & Shmida 1990; Kalisz & McPeek 1993). Although all five species build persistent soil seed banks (Thompson et al. 1997; Dostál 2005b), the relative importance of dormant seeds for population growth rates differed considerably among them. The importance of S-S in *Myosotis* differed more than by three orders from that in *Androsace*. This can be explained by a higher proportion of seeds remaining dormant in *Androsace*, but also by the differences among species in other vital rates (fecundity, seedling survival) that must be taken into account when assessing the relative importance of

S-S for population growth rates.

Changes in disturbance activity and random environmental variation also influenced the relative importance of different patch types. According to the simulations, the most open patches increased their elasticities in both *Myosotis* and *Androsace* with the increase of disturbance activity. However, differences were observed between the species in relative importance of open patches under 'good and bad period' conditions. The smaller importance of this patch type in 'bad period' demography in *Androsace* is probably related to low importance of the A-A transition in such conditions. Instead, dormant seeds associated with closing or closed habitats are much more important for population dynamics, and thus diminish the importance of open patches. In *Myosotis*, in which S-S contributes very little to population growth rate, the only way to improve population performance in demographically poor periods is to increase the proportion of strongly disturbed patches.

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