

Is the population turnover of patchy-distributed annuals determined by dormancy dynamics or dispersal processes?

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In species with fragmented distribution, regional turnover dynamics is given by the processes of local population extinction and patch (re)colonization by migrants spreading from neighboring occupied patches. In plants with dormant stages (e.g. seeds) and limited dispersal capacity, regional dynamics based on dispersal processes can be overridden by pseudo-turnover determined by signals inducing or breaking dormancy (e.g. due to changes in habitat quality) resulting in a low importance of habitat configuration and size.

In this study, I investigated the turnover dynamics of 5 annual plant species growing on ant mounds of *Lasius flavus* over three years. I analyzed whether the grassland-scale dynamics of these annuals is influenced by dispersal processes, or alternatively, by pseudo-turnover of soil seed populations. For that purpose I 1) searched for populations formed from soil seeds only, 2) compared the relative contribution of the soil seed bank and seed rain for population restoration after disappearance from the vegetation and 3) investigated whether colonization and extinction events are affected by patch isolation. I assumed if population turnover was rather a result of the soil seed bank dynamics then spatial effects would be hard to detect.

In spite of the presence of populations formed from soil seed and the relatively more important soil seed bank for potential population reestablishment, turnover dynamics followed the predictions of metapopulation theory. Population appearance was more probable in larger and less isolated patches. Probability of disappearance increased with decrease of population size that was negatively influenced by the patch size and its isolation. These findings indicate dispersal processes to be important in the turnover dynamics and only limited contribution of soil seed populations. Their small effectiveness is probably related to the low chance of recurrent disturbance on the mound surface.

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Patchy distributions of plants are very common. Due to habitat specialization or weak competition ability many plant species are restricted to fragments differing, for instance, in soil properties or successional status, from the surrounding matrix of inhospitable habitats (Eriksson and Ehrlén 2001). The metapopulation concept assumes that the regional persistence of species with fragmented distributions depends on the balance between local extinction and (re)colonization events (Hanski 2000). Local extinctions are the result of demographic, enviro-

mental or genetic stochasticity and may wipe out the population from the habitat (Harrison 1991). (Re)colonization processes are governed by the dispersal capacity of the colonizing species and parameters of suitable fragments such as number, size and isolation. The dispersal of propagules in a metapopulation system may rescue declining populations, or allow colonization of vacant, but suitable sites (Harrison et al. 2000). Nevertheless some habitats remain uncolonized, even if they are suitable to host focal species, because of dispersal limitation.

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Most animal populations can only rely on migrants arriving from neighboring populations during recolonization (Gilpin and Hanski 1991, Hanski and Gilpin 1997). In plants, after a population disappears from vegetation, the same event can be achieved from dormant seeds present in the habitat (Alvarez-Buylla and Martinez-Ramos 1990, Fischer and Matthies 1998, Kalamees and Zobel 2002). In contrast to vegetative or generative life phases, dormant life stages like seeds or tubers are more resistant to habitat deterioration (Milberg 1992, Poschold 1993, Bakker et al. 1996, Bekker et al. 1997) and thus they may secure the population continuum until the site quality improves (a special case of remnant populations in the terms of metapopulation theory, Eriksson 1996). The importance of the seed bank during population reestablishment in vacant patches increases with low dispersal of plant propagules (Verkaar et al. 1983, Husband and Barrett 1996, Freckleton and Watkinson 2002, Soons and Heil 2002 but Bullock and Clarke 2000, Cain et al. 2000), but rarely have both sources been compared in their contribution to plant regional dynamics (but Alvarez-Buylla and Martinez-Ramos 1990, Kadmon and Shmida 1990, Valverde and Silvertown 1995). In extreme cases, when events of extinction and colonization are in fact pseudo-turnover driven by signals inducing or breaking dormancy, dispersal processes and habitat isolation are of little importance for regional dynamics.

The amount of empirical studies on animal metapopulation dynamics significantly outnumbers an array of studies dealing with plants (Freckleton and Watkinson 2002). The key elements of the metapopulation approach are interpopulation migration and local population extinction, and the regional distribution of suitable habitat as discrete patches within a larger matrix of unsuitable habitat. In plants it is often difficult to meet the above assumptions; plants are characterized by immobility, with only limited seed dispersal, and have long life-spans, in many species exceeding substantially the life-span of the observer and hence preventing observation of turnover dynamics in the field. Moreover, populations of some plant species occupy large, non-fragmented areas, or, if they are restricted to patchy habitats, their suitability is problematic to define a priori (but Münzbergová and Herben 2004). To overcome the above complications, the regional dynamics of plants with spatially-structured populations can be investigated using short-lived species in simpler, small-scale systems.

In this study, I explored the population turnover of 5 plant annual species (*Arenaria serpyllifolia*, *Androsace elongata*, *Myosotis ramosissima*, *Saxifraga tridactylites* and *Veronica arvensis*) confined to the mounds of *Lasius flavus* in temperate perennial grassland. Since these grasslands were abandoned and grazing discontinued 50 yr ago, ants are the only source of disturbance in this system; therefore the distribution of annuals follows the

patchy distribution of ant nests and their local population dynamics is closely linked to ant soil-heaping activity (Dostál unpubl.). However, all of above taxa are known to build persistent seed bank (Thompson et al. 1997). This trait prevents vacant or vacated patches, here ant mounds, being unequivocally defined as empty. Equally, species reappearance in vacated habitats cannot be explained only by diaspores arriving in the seed rain. It is therefore unclear whether apparent dynamics is a result of pseudo-turnover based on the dormancy or non-dormancy states of present seeds, or is due to spatial processes based on the seed dispersal and habitat configuration in the grassland. By surveying both possible seed sources and through the analysis of metapopulation dynamics I intended to evaluate whether the regional dynamics of these annuals is governed by dispersal processes, or by dormancy dynamics of soil seeds.

Pseudo-turnover occurs when populations recruit from seeds present in habitats identified as empty during a vegetation survey. Therefore I first searched for such populations, and attempted to identify what determines their frequency among habitats considered to be empty, i.e. I searched what determines the magnitude of the error in the classification of habitat occupancy. It can be hypothesized that species with higher seed persistence and/or higher dispersability will be present more frequently in soil seed populations. Alternatively, frequency of soil seed populations will be determined by species frequency in active populations (i.e. populations established in vegetation). Secondly, I attempted to evaluate the relative contribution of persistent seeds, in comparison with propagules arriving in seed rain, to population restoration after disappearance from vegetation. And finally, I collected data on changes in habitat occupancy during three years of observation and investigated whether colonization and extinction events are affected by patch isolation, i.e. dependent on dispersal processes.

To answer these questions, during the period 2000–2002 I inspected ca 300 soil nests of *L. flavus* occurring in dry grassland in northern Bohemia, Czech Republic, and recorded population presence and abundance of all of 5 annuals. Presence of soil seed populations was investigated by soil sampling in 2002 in patches without active populations during the above period.

The relative contribution of persistent seeds and seed rain to potential population restoration was assessed indirectly, using information on seed reserves after population disappearance and seeds arriving from neighboring populations, estimated by modelling.

Finally, the effect of isolation on population appearance and disappearance was considered to be an evidence for dispersal processes during turnover dynamics. Failure to prove any spatial pattern in above dynamics would indicate overriding influence of the soil seed bank dynamics. Soil seed populations were assumed

not to be spatially related to active populations and thus they were expected to create “noise” in the spatial pattern of population turnover (Harrison et al. 2000). Isolation was expressed by two indices – distance to the nearest neighboring population and species isolation index (Moilanen and Nieminen 2002). I measured seed persistence in an artificial burial experiment and dispersal capacity in a seed dispersal experiment.

The existence of isolation effects on the presence and abundance of a population does not have to be a result of limited dispersal capacity, but could be due to an aggregated distribution of suitable habitats (Souza and Martins 2004). To distinguish the effect of isolation from the effect of such clumped patterns of environmental conditions, I carried out an autocorrelation analysis examining the relationship between habitat quality and increasing distance classes up to 15 m from the mound centers. As a habitat quality parameter I selected the area of bare soil that has been proved to positively influence population growth rate of all 5 species (Dostál unpubl.).

Methods

Study site and species

The field part of this study was conducted on the Boreč hill in NW Czechia (446 m a. s. l.; 50°31'N, 13°59'E), in a dry grassland enclave with an area of 600 m² on the northern side of the hill. Since 1950 when grazing was abandoned, no management has been undertaken at this site. At present, the grassland character is shaped by ant-hills of *L. flavus*, with a density of ca one mound 2 m⁻².

Metapopulation dynamics was investigated in five annual species that are restricted in the studied grassland to ant mounds: *Arenaria serpyllifolia* (Caryophyllaceae), *Androsace elongata* (Primulaceae), *Myosotis ramosissima* (Boraginaceae), *Saxifraga tridactylites* (Saxifragaceae) and *Veronica arvensis* (Scrophulariaceae; number of populations is shown in Table 2). For simplicity, species are referred to their generic names further in the text. All are winter annuals with similar ecology; they start to germinate at the end of summer or early autumn (August–September) and terminate their life cycle after fruiting in July. Whereas vegetative phases are rather ephemeral, seeds can persist for a much longer period in the soil (Thompson et al. 1997). None of the study species is adapted for myrmecochory; moreover, *L. flavus* is not involved in this type of dispersal (Woodell and King 1991).

Lasius flavus (Formicidae) is widespread and can be found 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 are formed by one queen and 8000–25 000 workers (Walloff and Blackith 1962).

The ants live mostly underground in the soil mound and feed on the honeydew and young instars of root aphids (Pontin 1978). The mound can be continuously occupied, one fertilized queen taking over from another. The size of the mounds increases over time, depending on the colony, territory size and the frequency of wet weather that is favorable for building (King 1981).

Dispersal capacity

For each annual species I measured distance-dependent seed dispersal. The design of the dispersal experiment followed the set-up of Bullock and Clarke (2000). Clumps of plants of each species were carefully dug out in the grassland enclave adjacent to the study site and planted in the middle of artificially prepared mound (diameter = 0.5 m, height = 0.3 m) in the experimental garden of the Inst. of Botany in Pruhonice. Plants were transplanted during the flowering period of all studied species and grown until the seeds were shed. On the day of transplantation (20 May, 2001), seed traps were installed along transects in eight directions from the artificial mound – N, E, W, S and NE, SE, NW, SW. Traps were placed 20 cm, 40 cm, 80 cm, 160 cm and 320 cm away from the plants in a density of 4, 8, 16, 32 and 32 in respective distance. Seed traps consisted of two telescoped plastic pots (both diameter = 9 cm) with inserted nylon mesh (mesh size = 0.2 mm) that replaced the removed bottom of the upper pot (for more details Bullock and Clarke 2000). The experimental plot was weeded regularly. *Veronica arvensis* is common in the experimental garden; contamination was prevented by removing all plants found up to distance 15 m from the experimental plot.

The traps, each trap touching its neighbors, were placed along the circumference of circles with radii corresponding to the above distances. During the experiment, traps were checked for the presence of insects that were regularly removed.

On 8 August, 2001 the content of the traps was sieved through 2 mm mesh to remove trapped litter and the rest was spread on Petri dishes. The number of seeds that were trapped in the pots was estimated by germination in the room temperature. Seedlings of target species were removed after they were identified. After 2 months, germination of viable, but dormant seeds was promoted by spraying the dishes with 100-p. p. m. gibberellic acid. After 4 months, germination was terminated.

Seed persistence

I evaluated species' capacity to build persistent soil seed banks using an artificial burial experiment. In August 1999, seeds of all 5 annuals were buried in mounds in the grassland enclave adjacent to the study site and retrieved

during 3 consecutive years. Seeds of *Veronica*, *Arenaria* (n = 100 seeds per packet), *Saxifraga*, *Myosotis* (n = 50 seeds per packet) and *Androsace* (n = 25 seeds per packet) were sealed to 45 nylon mesh packets per species; three packets per species were buried in each of the 15 mounds to a depth of 10 cm. In August during 2000–2002 one packet per species was exhumed from each of 15 mounds and viability of the retrieved seeds was assessed by seedling emergence. Germination lasted for a period of 4 months in a climate chamber with a temperature regime 20°C/10°C and daily photoperiod of 12 h. A seed was considered viable if a cotyledon emerged. After 8 weeks seeds that had failed to germinate were sprayed with 100-p. p. m. gibberellic acid to break dormancy. If there were still ungerminated but visibly healthy seeds, their embryos were stained (except for *Saxifraga* due to very small seed size) with a 1000-p. p. m solution of tetrazoliumchloride. In 1999, prior to the experiment establishment, seed viability was assessed; in all species it was almost 100%.

Population turnover

Approximately 300 ant-hills were checked every May during 2000–2002 for the presence of annuals in the studied grassland. Population size (number of adults) and number of capsules (except for *Arenaria*) were recorded separately for individual species on every mound if annuals were present. Total seed production per population was estimated using additional information on seed production. Every season during 2000–2002, a set of 50 capsules (or plants in *Arenaria*) of each species was harvested in the neighboring grassland and the number of seeds per capsule (plant) was counted.

In addition to demographic records, the percentage of bare soil on the mound surface was estimated. The size of the mounds was calculated according to formula (Raabová pers. comm.):

$$S = \pi \left(\frac{v^2}{25} + \left(\frac{a+b}{8} \right)^2 + 3 \left(\frac{a+b}{8} \right) \times \frac{\sqrt{\left(\frac{4v}{5} \right)^2 + \left(\frac{a+b}{8} \right)^2}}{8} \right)$$

where a is width, b length and v height of measured mounds.

Mounds were labeled with numbered metal tags and with the aid of a metal detector identified in consecutive seasons. To calculate distances among mounds, their position in the grassland was determined using a laser rangefinder (Impulse 200 LR, Laser Technology, USA) in 2000.

Seed bank – soil sampling in the field

On 10 September, 2002, soil was sampled from 35–55 ant mounds (*Androsace*: n = 55; *Arenaria*: n = 55; *Myosotis*: n = 35; *Saxifraga*: n = 52; *Veronica*: n = 50 mounds) where focus species were absent during 2000–2002 in the above-ground vegetation. Two samples per mound were removed with a soil corer (diameter = 5 cm), 10 cm deep. Seed content was analyzed by the seedling emergence method. Stones and roots were removed from samples by sieving through a mesh = 2 cm; soil was then laid out in a layer of 4 mm at maximum over filter paper in plastic trays (diameter 24 cm) and placed in the cold greenhouse and watered regularly. Seedling emergence was followed until the beginning of December 2002 and again from late February 2003 until late May 2003. In between, the samples were left in the greenhouse. Positions of the trays in the greenhouse were changed fortnightly. Seedlings were counted and removed after identification was possible. In early April 2003, trays were sprayed with 100-p. p. m. solution of gibberellic acid.

During the same occasion on 10 September, 2002, I also sampled mounds with the known 2002 above-ground population size to prepare a calibration set of the relationship between above-ground population size and seed reserves in the soil. For this purpose I sampled 17–30 mounds (*Androsace*: n = 18; *Arenaria*: n = 18; *Myosotis*: n = 30; *Saxifraga*: n = 19; *Veronica*: n = 17 mounds) and samples were processed as described above.

Comparison of persistent seeds vs seed rain for population reestablishment

For each population that disappeared from the vegetation during 2000–2001 and 2001–2002 I estimated the seed reserves present in the soil using a calibration set. The size of the seed reserves after disappearance from vegetation was recalculated to the area of mounds; it was assumed that seeds present below 10 cm composed only a negligible proportion of seed reserves.

Comparison of the importance of seed bank and seed rain for population reestablishment was estimated for a period only one year from the last occurrence in vegetation (i.e., for 2001 and 2002 respectively). The probability of population reestablishment was defined by the minimum number of seeds necessary to produce one adult plant. This threshold was calculated on the basis of demographic records collected in the field (seedling survival, seed production) and in a sowing experiment in a garden (germination; Dostál unpubl.; see Appendix). Seed reserves present in the soil were calculated using initial seed abundance and the persistence rate measured in a burial experiment. Seed arrival to habitats vacated during 2000–2001 and 2001–2002,

respectively, was simulated using the distribution of neighboring populations recorded in the field in 2001 and 2002, respectively. Prior to the simulation, the whole simulation area was divided into i cells. Number of seeds arriving at each cell i was calculated as:

$$n_i = \frac{1}{T} \sum_k \sum_j I_{jk} \frac{x_{0k}}{A_k} \exp(-\alpha d_{ij})$$

where x_{0k} is the number of seeds produced at the habitat k , A_k is the area (number of cells) of the k -habitat, α is the slope of decline in seed densities with distance, d_{ij} is the distance between cells i and j , I_{jk} is 1 if cell j lies in the habitat k , and 0 otherwise, and T is the normalization constant $[\sum_k \exp(-\alpha d_{ij})]$; j means indexing over all cells in the grid, and k summation over all habitats. Number of seeds arriving at the l -th habitat is the sum of seeds arriving at all cells belonging to the habitat, i.e., $N_l = \sum_i n_i$, summed over all cells belonging to the habitat.

Simulation of the number of seeds landing in focal habitats was repeated 50 times and averaged for each habitat. I defined four categories of population reestablishment: 1) failure, no seed source is capable to restore population, 2) seed bank, population can be restored from persistent seed bank only, 3) seed rain, population can be restored from seeds arriving to focal habitat only, 4) seed rain and seed bank, each source can provide a sufficient seed number to successfully restore population.

In addition, the number of seeds surviving in the soil (without further contribution of seeds arriving in seed rain) was projected for 10 consecutive seasons.

Statistical analysis

Dispersal capacity

Observed densities (total number of seeds/total area of the traps) of trapped seeds were described by negative exponential model (NEF):

$$S_D = a \exp(-\alpha D)$$

where S_D is density of seeds at distance D from the source and a is a constant indicating the density of seeds falling at the source and α is the slope of decline in seed densities with distance. The model was fitted by non-linear regression, using Levenberg-Marquardt algorithm.

Seed persistence

Seed depletion during 3 yr of burial was described for *Veronica* and *Androsace* using the negative exponential function model (NEF):

$$S_T = c \exp(-kT)$$

where S_T is number of seeds in time T (in days) and c is a constant indicating the number of seeds at the beginning

and k is daily decay rate determining seed dieback in time. The model was fitted by non-linear regression, using Levenberg-Marquardt algorithm.

Temporal decay of seeds of other species was not possible to successfully describe with any model (see Fig. 1). However, for simplicity I assumed constant decay rates (NEF model) and these were calculated directly from the mean number of viable seeds at the beginning and the second year of survival:

$$k = \frac{\ln N_0 - \ln N_{730}}{730}$$

where k is daily decay rate, N_0 is number of viable seeds at the beginning of the experiment and N_{730} is mean number of viable seeds the second year of burial.

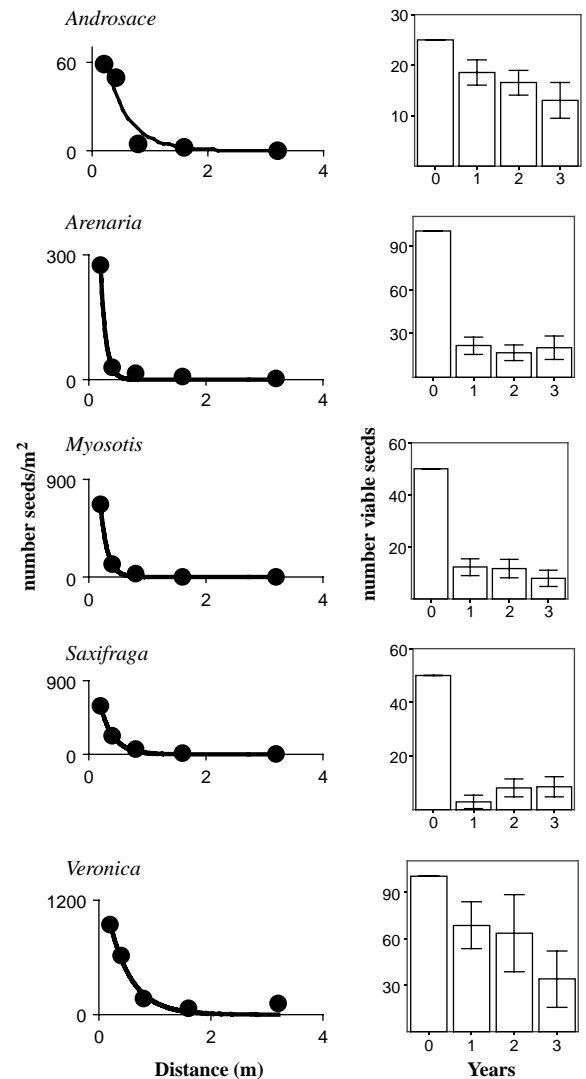


Fig. 1. Seed dispersal curves fitted with NEF model and seed persistence in soil seed bank.

Half life (the time in days taken for half of a cohort of seeds in the seed bank to die) was calculated according to the equation:

$$t_{1/2} = \frac{1}{k}$$

Population turnover

I investigated the effect of habitat size (mound surface – in cm²), habitat quality (bare soil cover – in cm²), interspecific competition (abundance of heterospecific adults) and isolation on presence, abundance, colonization and extinction of focal species. I used GLM with Binomial family and logit link except for species abundance that was analyzed by GLM, Poisson family and log link. All explanatory variables were used in the same model; isolation was used as the last term in the model to correct for other possible confounding factors.

Isolation was expressed by two isolation indices that alternated in the model: 1) distance to the nearest occupied habitat, 2) species isolation index (SII; Moilanen and Nieminen 2002):

$$S - \text{species}_i = \sum A_j \exp(-\alpha d_{ij})$$

where d_{ij} is the distance from the center of the focal habitat i to the center of each other habitat j occupied by the focal species, A is total seed production of the annual in corresponding habitat j . α is a constant describing the species' distance-dependent dispersal rate. This constant was obtained from a dispersal capacity experiment for each focal species (see above). Because of the skewed frequency distributions, values of both isolation indices were log-transformed prior to the analysis.

To analyze the spatial relationship between populations in vegetation in 2002 and populations in the soil seed bank only, I tested the effect of 1) patch size and 2) isolation (expressed by distance to the nearest popula-

tion or species isolation index) on the probability of species presence in the soil seed bank. Both explanatory variables were used in the same model with isolation as the second term.

Effect of seed persistence capacity, dispersal capacity and species frequency in the vegetation on the species frequency in the soil seed bank only was analyzed by linear regression.

Spatial autocorrelation analysis

To examine the spatial pattern of habitat quality distribution, I carried out autocorrelation analysis with the Rookcase software, an Excel Visual Basic add-in (Swada 1999). I searched for the autocorrelation of cover of bare soil along the distance gradient up to 15 m from the mound centers. I evaluated the spatial autocorrelation using the Moran's I coefficient (Moran 1950) against 15 mutually exclusive distance lags of 1 m. The Moran's I coefficient varies generally from +1 to -1 and positive values of Moran's I correspond to positive autocorrelation. Significance of Moran's I was tested by a Monte Carlo test (1000 permutations).

All analyses except for autocorrelation analysis were performed using S-PLUS, Lucent Technologies.

Results

Dispersal capacity

In total, the number of trapped propagules was between 10 and 219 seeds depending on the species. Most seeds fell very close to the source and a very small proportion of seeds was found in the traps beyond 0.80 m. The only exception was *Veronica*; seeds found in traps 160 and 320 cm from the source formed 34% of total amount of trapped seeds (Table 1). The NEF model fitted the

Table 1. Seed dispersal a) and persistence b) capacity of five annual species. Description of dispersal pattern with NEF model and tested by non-linear regression.

a) Dispersal capacity						
Species	Total number of seeds/number of seeds >80 cm	Regression equation (linearised form)	Mean distance (m)	R ²	DF	p
<i>Androsace</i>	10/1	$\ln S_D = 4.639 - 2.462D$	0.406	0.933	1, 5	<0.001
<i>Arenaria</i>	24/4	$\ln S_D = 7.833 - 11.081D$	0.090	0.995	1, 5	<0.001
<i>Myosotis</i>	52/0	$\ln S_D = 8.218 - 8.566D$	0.117	0.998	1, 5	<0.001
<i>Saxifraga</i>	72/6	$\ln S_D = 7.273 - 4.496D$	0.222	0.996	1, 5	<0.001
<i>Veronica</i>	219/74	$\ln S_D = 7.362 - 2.493D$	0.401	0.995	1, 5	<0.001
b) Persistence capacity						
<i>Androsace</i>		$\ln N_T = 3.218 - 0.000744 T$	1344 ¹⁾	0.960	1, 2	0.001
<i>Arenaria</i>			377			
<i>Myosotis</i>			524			
<i>Saxifraga</i>			302			
<i>Veronica</i>		$\ln N_T = 4.605 - 0.000860 T$	1163	0.793	1, 2	0.028

¹⁾ Refers to half-lives (in days).

observed seed densities with coefficient of determination (R^2) larger than 0.90 in all species. According to this model, fifty per cent of seeds end up at a distance of 0.090 and 0.406 m, depending on the species (Fig. 1; Table 1).

Seed persistence

Even after 3 yr, exhumed bags contained viable seeds of all 5 species, documenting the capacity of these annuals to build persistent soil seed banks. Two types of seed survival were observed: for *Arenaria*, *Myosotis* and *Saxifraga* the number of viable seeds declined dramatically during the first season of burial and showed small changes in subsequent seasons; in contrast, in *Androsace* and *Veronica*, the decline in seed survival was gradual. Half of the present seeds are lost after 302–1344 d depending on the species (Table 1, Fig. 1).

Population turnover

During 2000–2002, the most abundant species (*Myosotis*) was present on average in 51% of available habitats in contrast to the rarest species (*Arenaria*) present in 15% of habitats only (Table 2). Appearance and disappearance events were frequent in all 5 species. In *Androsace*, *Arenaria* and *Saxifraga*, the number of disappearances exceeded the number of newly colonized habitats thus resulting in an overall decline of habitats with their presence. In *Veronica* and *Myosotis*, the number of occupied habitats remained more stable during the course of observation (Table 2).

Populations present in soil seed bank only

Soil sampling in the patches classified to be empty during 2000–2002 found some of them to be occupied by seed populations (Table 3). Linear regression did not prove any relationship between species frequency in the seed bank and species dispersal nor persistence capacity (not shown). However, species frequency in seed bank was only weakly correlated with frequency of the species in vegetation ($p = 0.10$; Fig. 2). The probability of species occurrence in the soil seed bank was not influenced by

patch size neither it was spatially related to the species presence in the vegetation (Table 3).

Comparison of importance of seed bank and seed rain for the population reestablishment

According to an estimation based on the calibration set, large seed reserves (ranging from 200 up to 7000 seeds per mound patch depending on the species) could be expected in the soil after the last seed production prior to disappearance. This is well above the minimum necessary to produce a single adult plant (Appendix). After one year from last presence of adults in vegetation the seeds in the soil were estimated to still be abundant and could reestablish 75–100% of populations. The percentage of habitats that can be recolonized by seeds arriving in seed rain, based on a modelling approach, is much smaller and was estimated to be 2–15% for respective species (Fig. 3).

If no additional seeds arrive in the seed rain and seedling recruitment is prevented, then populations could reappear in 40 and 93% of the habitats in *Androsace* and *Veronica* respectively from persistent seeds after 10 yr from the last occurrence above-ground. In *Arenaria*, *Saxifraga* and *Myosotis*, seed reserves would be depleted after 5, 6 and 9 yr respectively since the last occurrence in vegetation.

Effect of habitat parameters and isolation on species distribution and turnover dynamics

The probability of habitat occupancy was positively influenced by habitat size in all species (Table 4a) and also by the cover of bare soil on the mound surface. There was no evidence for a negative effect of heterospecifics on the presence of the focal species; on contrary, they were generally positively associated with the presence of the focal species. The same parameters had an identical effect on the abundance: population size increased with habitat size, cover of bare soil and number of heterospecifics.

Increasing isolation negatively influenced the probability of habitat occupancy (Table 4a). Expressed by the distance to the nearest neighboring population or by the

Table 2. Number of habitats ($N = 304$ mounds in total) occupied by annuals and appearance and disappearance events.

Species	Habitat occupancy			Mean occup. (%)	Disappearances		Appearances	
	2000	2001	2002		2000–2001	2001–2002	2001–2002	2001–2002
<i>Androsace</i>	60	48	33	15.5	21	24	9	6
<i>Arenaria</i>	52	46	39	15.0	14	14	8	7
<i>Myosotis</i>	155	151	157	50.8	37	28	33	34
<i>Saxifraga</i>	78	68	63	22.9	21	18	11	13
<i>Veronica</i>	70	74	76	24.1	12	16	16	18

Table 3. Habitat occupancy by soil seed populations (%; in 2002) with the absence of respective species in vegetation during 2000–2002. Results of logistic regression show effect of patch size and isolation (distance to nearest occupied patch and SII) on probability of occurrence in soil seed bank. *, $p < 0.05$; ns, not significant.

Species	Occupancy (%)	Residual DF	Residual deviance	Size		Isolation (LOG MINDIST)		Isolation (LOG (SII+1))	
				DF	Deviance	DF	Deviance	DF	Deviance
<i>Androsace</i>	12.7	54	41.93	1	2.05 ns	1	0.06 ns	1	0.33 ns
<i>Arenaria</i>	18.2	54	52.15	1	0.09 ns	1	0.39 ns	1	0.40 ns
<i>Myosotis</i>	65.7	34	45.00	1	1.29 ns	1	0.42 ns	1	5.92 *
<i>Saxifraga</i>	19.2	51	50.91	1	0.12 ns	1	0.17 ns	1	0.25 ns
<i>Veronica</i>	58.0	49	68.02	1	1.10 ns	1	0.66 ns	1	0.00 ns

species isolation index, populations were less likely to be present on more remote soil nests. For instance, in the case of *Androsace*, occupied mounds were on average 1.64 m from the nearest population and the distance of empty nests to the nearest *Androsace* individuals was on average 1.96 m. The negative effect of isolation on species abundance was consistent with the use of both indices in *Arenaria*, *Myosotis* and *Veronica* (Table 4a). In *Androsace* and *Saxifraga*, no effect of isolation on population size was recorded using distance to the nearest neighbor, but it was negative if expressed by log SII (Fig. 4).

Disappearance events were mainly determined by the previous season's population size (and seed production respectively); small-sized populations were more prone to be missing in the consecutive season except for *Myosotis* (Table 4b). Extinction risk also increased with the ongoing process of habitat deterioration due to decreased disturbance activity. Isolation per se

increased the probability of population disappearance in *Myosotis* and *Veronica* (consistent for both isolation indexes). Effect of size and abundance of heterospecifics on the probability of disappearance varied between focal species (Table 4b).

Appearance was more likely to occur in large and less isolated habitats (consistent for both indices), except for *Saxifraga* (Fig. 5). Other parameters did not influence the probability of population appearance except for cover of bare soil in *Androsace* (Table 4b).

Spatial autocorrelation analysis revealed that cover of bare soil was positively autocorrelated at distances up to ca 9 m, which is well beyond the scale of the annuals' distribution and colonization processes (Fig. 6).

Discussion

Distribution and turnover dynamics of the annuals in studied grassland

The incidence probability of the studied annuals was primarily determined by habitat quality, specifically by the area of bare soil cover on the mound surface. Recruitment and early life stages of plants are critically

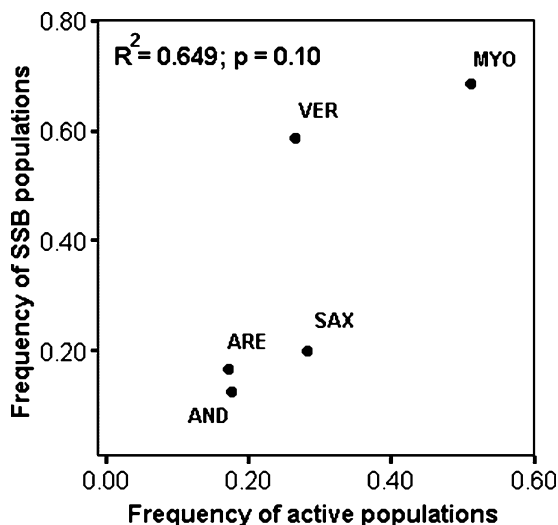


Fig. 2. The relationship between frequency of soil seed bank (SSB) populations (based on the soil sampling in 2002) and frequency of active populations (mean of the period 2000–2002). AND, *Androsace*; ARE, *Arenaria*; MYO, *Myosotis*; SAX, *Saxifraga*; VER, *Veronica*.

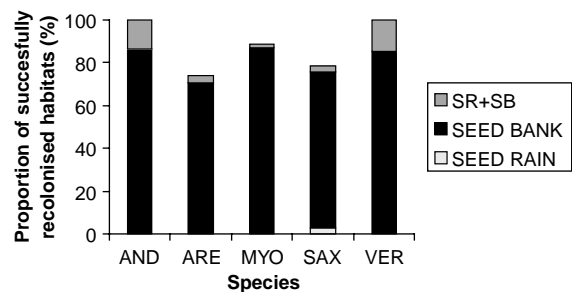


Fig. 3. Contribution of soil seed bank and seed dispersal to successful population reestablishment immediately after its disappearance from vegetation (1 yr since last occurrence in vegetation). Successful reestablishment indicates that size of respective seed source equaled or was larger than number of seeds necessary for production of 1 adult (see Appendix). SR + SB indicates that both sources may contribute to population reestablishment. For species abbreviations see Fig. 2.

Table 4a. Analysis of deviance on the effect of habitat size, its quality (percentage of bare soil), abundance of other species, and isolation (expressed by 2 indexes) on the species presence and abundance on the ant-hills. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, not significant. Sign indicates direction of the effect. For species abbreviations see Fig. 2.

	Presence					
	DF	AND	ARE	MYO	SAX	VER
Size (cm ²)	1	+52.2***	+70.9***	+49.9***	+42.1***	+73.1***
Bare soil (cm ²)	1	+14.5***	+8.7**	+24.0***	+15.8***	+3.9*
Heterospecific neighbors	1	+21.4***	+6.4*	+10.3**	+4.6*	0.0 ns
Isolation (LOG MINDISTANCE)	1	-6.2*	-35.3***	-66.5***	-6.6*	-32.8***
Isolation (LOG (SII+1))	1	-25.6***	-14.1***	-31.9***	-4.9*	-47.6***
Residual deviance		785.4	771.7	1264.1	981.8	1007.7
Residual DF		911	911	911	911	911

	Abundance					
	DF	AND	ARE	MYO	SAX	VER
Size (cm ²)	1	+4887.1***	+3653.2***	+1288.7***	+1947.3***	+610.1***
Bare soil (cm ²)	1	+112.1***	+82.0***	+271.7***	+1661.3***	+152.0***
Heterospecific neighbors	1	+209.9***	+788.5***	+270.4***	+1179.5***	+16.2***
Isolation (LOG MINDISTANCE)	1	2.1 ns	-188.6***	-291.7***	0.0 ns	-746.2***
Isolation (LOG (SII+1))	1	-102.7***	-31.6***	-257.1***	-126.7***	-1180***
Residual deviance		16137.2	16066.8	11555.3	26355.8	11411.2
Residual DF		911	911	911	911	911

Table 4b. Analysis of deviance on the effect of habitat size, its quality (percentage of bare soil), abundance of other species, and isolation (expressed by 2 indexes) on species appearance and disappearance events. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, not significant. Sign indicates direction of the effect. For species abbreviations see Fig. 2.

	Disappearances					
	DF	AND	ARE	MYO	SAX	VER
Bare soil (cm ²)	1	2.7 ns	-4.3*	-4.5*	-10.8***	2.6 ns
Heterospecific neighbors	1	1.1 ns	0.6 ns	2.5 ns	-11.6***	1.2 ns
Seed production in year t-1	1	-51.3***	-7.2**	1.0 ns	-15.4***	-6.4*
Isolation (LOG MINDISTANCE)	1	2.5 ns	0.0 ns	+3.9*	0.1 ns	+3.4*
Isolation (LOG (SII+1))	1	1.6 ns	0.2 ns	+5.2*	2.6 ns	+8.7**
Residual deviance		147.2	117.3	316.5	169.5	138.9
Residual DF		110	97	305	145	143

	Appearances					
	DF	AND	ARE	MYO	SAX	VER
Size (cm ²)	1	+4.6**	+5.8*	+6.4*	+6.1*	+8.9**
Bare soil (cm ²)	1	+6.7**	0.1 ns	2.3 ns	2.3 ns	0.4 ns
Heterospecific neighbors	1	1.9 ns	1.8 ns	1.6 ns	1.2 ns	0.2 ns
Isolation (LOG MINDISTANCE)	1	-3.8*	-20.6***	-22.7***	1.5 ns	-4.5*
Isolation (LOG (SII+1))	1	-5.4***	-13.8***	-14.3***	2.6 ns	-5.0*
Residual deviance		134.6	135.3	319.7	188.7	243.1
Residual DF		496	509	301	461	463

dependent on open microsites (Grub 1977) in the studied grassland these emerge through the soil heaping activity of ants. When ant colonies stop mounding, habitat quality declines due to the succession of mosses and vascular plants, and the mound patch becomes unsuitable for the annuals (Dostál unpubl.). However, in addition to habitat quality, occupancy was determined by habitat isolation and size, which is consistent with the assumptions of the metapopulation models (Hanski 2000). Incidence was less probable with decreasing patch size and increasing habitat isolation.

Both parameters also significantly influenced population size in the patch and consequently the probability of extinction. Smaller patches were occupied by smaller populations, which in turn increased the probability of their disappearance (cf. Pimm et al. 1988, Matthies et al. 2004). Isolation per se influenced the disappearance of most species indirectly, by its negative effect on population size in the patch (cf. Fahrig and Paloheimo 1988). Species appearance probability increased with the size of the patch and smaller habitat isolation (in 4 out of 5 species).

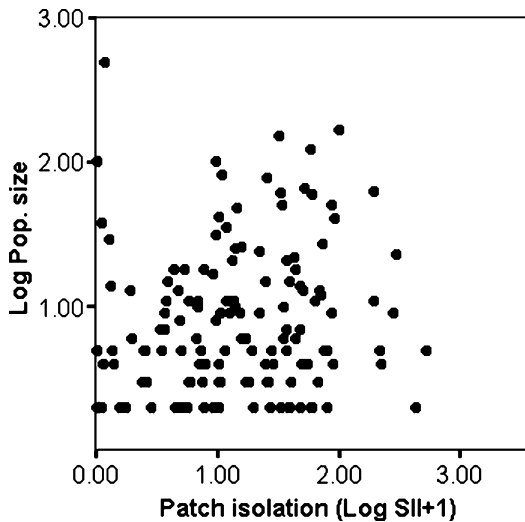


Fig. 4. Effect of isolation (expressed by $\log(SII+1)$) on population size of *Androsace*. Increasing SII indicates decrease in isolation. Graph shows records merged from 2000, 2001 and 2002 years.

In spite of the presence of soil seed populations and short distance-dependent dispersal of studied species, the significant effect of habitat configuration (isolation) on population distribution and turnover dynamics is evidence for the ongoing dispersal processes and limited contribution of the pseudo-turnover to the observed dynamics.

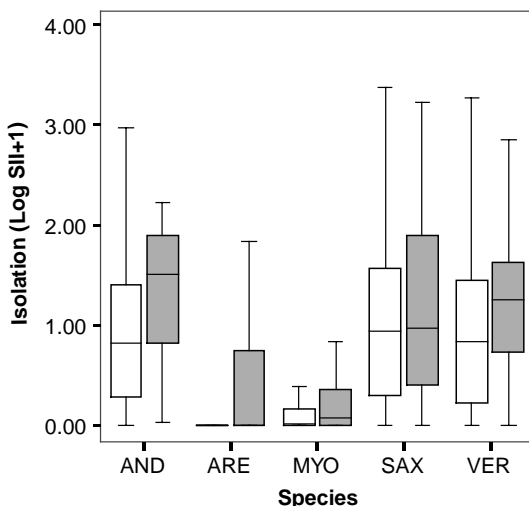


Fig. 5. Effect of isolation on probability of population appearance. White boxes refer to mounds that were found without population of focal species whereas grey boxes indicate mounds that were colonized in 2001 (2002) by focal species missing in 2000 (2001). Increasing SII indicates decrease in isolation. Median, 25 and 75 percentiles, and minimum and maximum values are shown. Based on the data collected in the field. For species abbreviations see Fig. 2.

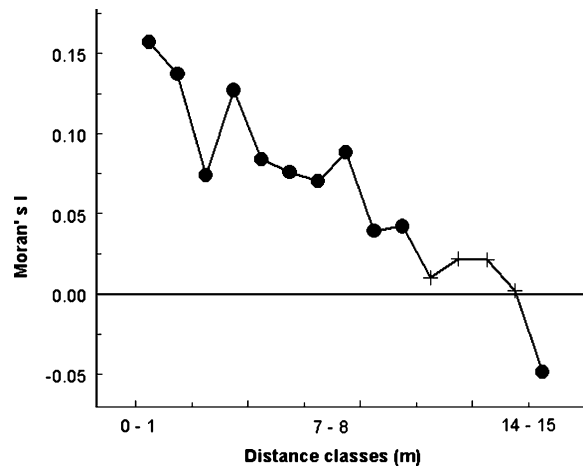


Fig. 6. Correlogram of bare soil cover. Round symbols indicate significant values at the $\alpha=0.05$ level, crosses indicate non-significant values.

Soil seed bank vs seed dispersal in regional population dynamics

The presence of soil seed populations in patches, in the absence of reproductive plants, confirmed the limitations of the definition of population extinction and patch occupancy in plants (discussed by Husband and Barrett 1996 and Freckleton and Watkinson 2002) which is a central aspect of most metapopulation models (Harrison 1991). Habitat occupancy by the soil seed bank results from a higher tolerance of seeds to habitat deterioration and the capacity of seeds to persist for long periods in the soil. For instance, in *Veronica*, it has been estimated that after 10 yr since disappearance from the vegetation, only a very small proportion of patches (7%) were without seeds capable of restoring active populations.

Differences between species in the frequency of soil seed populations are not, however, directly related to species-specific seed persistence nor to their dispersal capacity. Instead, soil seed population frequency was weakly correlated with the frequency of active populations. Since there was no spatial relationship between both types of populations, this pattern cannot be directly linked to the process of seed accumulation in unsuitable patches spreading from active populations. It can, however, be assumed that soil seed populations reflect active populations from the past, that differed in configuration but not in the frequency from the active populations at present.

Soil seed populations were found to be of even greater significance for potential population restoration than seed rain. The relative contribution of this seed source is expected to decline with increasing time-span. However, it is hard to predict the relative contribution of seeds

arriving from neighboring populations beyond the observation period. As the distribution and abundance of active populations will change in time, accordingly the abundance of seeds arriving to target patches will vary and therefore I restricted the comparison of both seed sources to the period consecutive to population disappearance.

In spite of the presence of soil seed populations and their higher estimated importance for the restoration of active populations, the significant effect of isolation on the turnover dynamics indicated only limited contribution of pseudo-turnover from soil seed bank. And soil seed populations were very likely to create “noise” in the spatial effects of population turnover since their distribution was not related to the distribution of active populations. Limited contribution of soil seed populations can be probably accounted for ants’ soil heaping activity. Mounding is responsible for the balance between the proportion of disturbed cover and moss encroachment. If mosses start to dominate, seedling emergence is reduced and seeds become dormant. The dormancy is broken again if ants start to redisturb the moss cover, as proved by experimental manipulation of the moss cushion (Dostál unpubl.). However, mounds with >90% cover of mosses have an approximate probability of 0.06 to be transformed into disturbed mounds with >50% cover of bare soil. Consequently seed reserves become effectively dead without significant contribution to active populations. However, it can be hypothesized that under different disturbance scenarios, the influence of soil seed bank on metapopulation dynamics could increase.

Conclusions

It could be argued that the complication of dormant seeds for the analysis of species regional dynamics concerns mostly short-lived species, in perennials similar constraints can be, however, posed due to formation of the storage organs that can persist in dormancy (Neeser et al. 1997, Ehrlén 2000, Foley 2002). Also in animals, dormant stages are found in several groups such as copepods or rotifers (Cáceres 1998). In all these organisms dormant stages may generate a more complicated picture of regional turnover dynamics than in biota without such adaptations. This study showed that presence of dormant stages have only a negligible influence on the spatial effects of metapopulation dynamics, under the specific settings of this studied system.

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Appendix. Size of seed reserves present in habitats prior to the disappearance event. Using regression equation, seed density was assessed from the last size of population present in vegetation (y = seed density in 0–10 cm, x = number of adults). Number of seeds necessary for production of 1 adult was obtained from demographic measurements presented elsewhere (Dostál unpubl.).

Species	Regression of number of plants in vegetation and seed density (0–10 cm)		n	Seed reserves after last occurrence in vegetation	Number of seeds necessary for production of 1 adult
	Regression equation	Significance		Number of seeds mean (SE)	
<i>Androsace</i>	$y = 8.16 + 0.036x$	$R^2_{(1, 16)} = 0.623^{***}$	45	209.0 (43.8)	10
<i>Arenaria</i>	$y = 8.745 + 0.008x$	$R^2_{(1, 16)} = 0.358^{**}$	28	577.2 (180.1)	42
<i>Myosotis</i>	$y = 11.368 + 0.007x$	$R^2_{(1, 28)} = 0.170^*$	65	288.9 (100.4)	10
<i>Saxifraga</i>	$y = 12.330 + 0.005x$	$R^2_{(1, 17)} = 0.681^{***}$	39	500.3 (117.9)	38
<i>Veronica</i>	$y = -3.403 + 0.293x$	$R^2_{(1, 15)} = 0.443^{**}$	28	6687 (2532.7)	9