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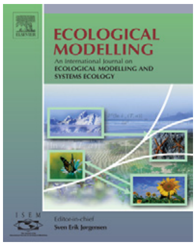

Metapopulation dynamics of a perennial plant, *Succisa pratensis*, in an agricultural landscape

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ABSTRACT

Most metapopulation models neglect the local dynamics, and systems characterized by slow population turnover, time lags and non-equilibrium, are only rarely examined within a metapopulation context. In this study we used a realistic, spatially explicit, dynamic metapopulation model of a long-lived grassland plant, *Succisa pratensis*, to examine the relative importance of local population dynamics, and short and long-distance dispersal of seeds.

Using both vegetation composition and sowing experiments we identified 94 occupied and 43 unoccupied, but suitable, habitat patches in a 7-km^2 landscape. Local population dynamics were studied in permanent plots in five populations. Simulation results showed that the colonization and extinction dynamics of *S. pratensis* were slow with about one colonization or extinction per year and the time frame for the population system to attain equilibrium in a constant landscape was several thousands of years. Sensitivity analyses demonstrated that occasional long-distance dispersal had a large influence on population turnover rates whereas regular short-distance dispersal had little effect. Our model also allowed us to assess how demographic processes affect not only local population growth but also regional dynamics. Fecundity was more important, compared with growth and survival, in a metapopulation context than when considered only within populations. The effect of landscape development was examined through different land-use scenarios and suggested that *S. pratensis* only very slowly colonizes new habitats that are made available. Our results with *S. pratensis* in an agricultural landscape show that long-distance dispersal and colonization dynamics play an important role for the regional distribution in long-lived plants but that time lags, and thus the effect of landscape history, are also very important.

1. Introduction

Regional distributions of animals and plants in landscapes may be conceived as the outcome of local population dynamics within habitat patches and dispersal among patches. The dynamics and extinction risks of local populations are strongly influenced by abiotic conditions and biotic interactions, such as competition, herbivory and predation. Dispersal may result in establishment of new populations or augmentation of existing populations. Metapopulation theory explains distributions as determined by the balance between extinctions and colonizations (Levins, 1969; Hanski,

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1994), and has generated an increased interest in large-scale spatial dynamics and landscape processes, such as habitat fragmentation. Insights from theoretical metapopulation models suggest that conservation efforts should focus as much on dispersal processes as on local habitat conditions, for example by preserving patches not yet occupied by the target species and facilitating dispersal between patches.

Metapopulation theory has most often been applied to mobile organisms that have high population turnover rates and relatively well defined habitat requirements, such as butterflies (cf. Hanski et al., 1996; Hanski, 1999; Gutiérrez et al., 1999). The application of the metapopulation concept to the regional dynamics of plant species, however, is difficult (Husband and Barret, 1996; Eriksson, 1996; Freckleton and Watkinson, 2002; Ehrlén and Eriksson, 2003; Ouborg and Eriksson, 2004). This is because many plants are long-lived, in the vegetative phase or as seeds in the seed bank. Moreover, seeds are usually dispersed only over relatively short distances. As a consequence, extinctions and colonizations occur at a low rate compared to landscape changes.

Still an increasing number of studies have demonstrated that regional processes do play a role. They showed that plant distributions cannot be explained only by regular dispersal over short to moderate distances, but that also occasional long-distance dispersal is important (Higgins and Richardson, 1999; Cain et al., 1998; Bullock et al., 2002; Vellend, 2003; Higgins et al., 2003). Moreover, the regional distributions of many plant species show that larger and more connected habitat fragments are more often occupied than small and isolated fragments (Quintana-Ascencio and Menges, 1996; Bastin and Thomas, 1999; Dupré and Ehrlén, 2002). This suggests that regional colonizations depend on isolation of patches or that local extinctions depend on habitat patch size. Thus, the metapopulation framework may be appropriate also for examining plant distributions.

Existing metapopulation models, such as incidence function models (IFM, Hanski, 1994), have been used to assess relationships between regional population dynamics and the spatial configuration of the habitat. For parameterization of these models, it is often assumed that the system is in equilibrium, i.e. that extinction rates are balanced by similar rates of colonization. However, in modern agricultural landscapes, many species are likely not to be in equilibrium because habitats are rapidly fragmenting and regional dynamics of plants is slow (Freckleton and Watkinson, 2002; Ouborg and Eriksson, 2004). Here, land use has a decisive influence on habitat availability and distributions of plant species (Bruun et al., 2001; Cousins and Eriksson, 2001, 2002). The modernization of agriculture during the 19th and 20th century in Western Europe has had dramatic effects on land use and landscape structure. For example, a lowered intensity of grazing has strong effects on the quality of grassland habitats. Moreover, the total abandonment of many hay-meadows and pastures has resulted in severe fragmentation of remaining grasslands.

The present distribution of many plants is therefore largely the result of past processes, and metapopulation models based on current conditions, such as incidence function models, are of little use to capture species' dynamics. In contrast, dynamic metapopulation models can account for non-equilibrium dynamics and time lags, but their usefulness can also be questioned because they require more parameters which weakens their predictive power (Keymer et al., 2000; Johst et al., 2002; Doebeli and Killingback, 2003). It is thus crucial to examine if dynamic models can explain distribution patterns for as realistic parameter settings as possible.

Further, in a dynamic metapopulation model it is also possible to increase realism by including empirical information on local processes, and thus to assess the sensitivity to variation both in demographic parameters and dispersal (cf. Caswell et al., 2003). This type of analysis is critical to understand the relative importance of local and regional processes to the performance of population systems in real landscapes.

The aim of this study was to explore to what extent the regional distribution of a perennial grassland herb, *Succisa pratensis*, could be understood as the outcome of colonization–extinction dynamics using a realistic dynamic simulation model that integrates landscape structure, in terms of suitable and non-suitable habitat, local population dynamics, and short- and long-distance dispersal (see also Münzbergová et al., 2005). Specifically, we asked how important occasional long-distance dispersal, by adhesion to animals, is relative to regular short-distance dispersal, by wind or unassisted, for metapopulation performance, in terms of total population size, patch occupancy and population turnover rate, and if demographic parameters are differentially important for local and regional population dynamics. We also asked how long it takes for the regional population to attain equilibrium and examined the long-term equilibrium distribution of *S. pratensis* in this landscape. Lastly we asked how different land-use scenarios affect the dynamics of *S. pratensis*. Landscape structure was described through a field survey of all potentially suitable habitat patches. Local population dynamics was investigated through demographic studies in permanent plots in five *S. pratensis* populations.

2. Methods

2.1. Study species and system

S. pratensis is a polycarpic herb with a maximum life span of at least 25 years (Hooftman et al., 2003). In August and September it flowers with one to six, sometimes more, flowerheads on one to three, 20–80 cm high stems. Each flowerhead contains up to 100 small pale violet flowers. The flowers are self-compatible, but outcrossing enhances seed set considerably and inbreeding may affect small and isolated populations negatively (Vergeer et al., 2003). Clonal propagation occurs rarely in the study area. In Sweden, *S. pratensis* is most commonly found in dry to mesic semi-natural grasslands. It benefits from grazing and the present distribution in the landscape largely depends on the management history, i.e. is closely correlated with former grazing and mowing (Mildén et al., unpublished data). Most seeds land close to the mother plant but long-distance dispersal by animals is likely to occur at low rates because the seed capsules of *S. pratensis* have hooks and are covered with hairs that make them easily attach to fur (Römermann et al., 2005). In the study area, there are a number of animals that could serve as dispersal vectors, e.g. cattle, roe deer, wild boars, hares and elks.

We collected the field data in the Nynäs nature reserve, ca. 100 km south of Stockholm, Sweden (58°50′N, 17°24′E). This area is a well-documented agricultural landscape with a long management history (Cousins and Eriksson, 2001). The study area was 3.1 km × 2.3 km (7.1 km^2) and contained managed agricultural land, arable fields, pastures on former fields and semi-natural grassland. The study area was surrounded by coniferous forests, unsuitable for *S. pratensis*. Since the establishment of two villages in the area around 1500 BP (inference based on the occurrence of grave fields), management has probably been continuous and slowly expanding. In the 17th and 18th century, 60% of the area was covered with grassland and 32% was arable land (Cousins and Eriksson, 2001). From the early 19th century to 1945 a large proportion of grasslands were converted to arable fields due to changing practices of producing winter fodder for livestock. Since 1945 many of the grasslands have been abandoned and are now turning into forests whereas some of the former fields have been turned into pastures. At present grasslands, of which almost half are more than 200 years old, constitute 18% of the study area, although not all of this is suitable for *S. pratensis*.

2.2. *Landscape data collection*

We carefully inventoried the area and mapped all habitat patches potentially suitable for *S. pratensis*, and recorded whether they were occupied or not. The size, shape and position of all patches were recorded in a GIS framework (ArcView 3.2 and Quantum GIS 0.6.0). Suitability of habitats was assessed in three steps. Firstly, we made a subjective classification. Occupied patches and unoccupied patches apparently within the habitat quality range of occupied habitats were classified as "suitable", and habitats that were considered outside but close to the habitat range of occupied ones as "probably suitable". All other habitats were classified as "not suitable". Secondly, we conducted a floristic survey in all "suitable" and "probably suitable" patches, and in a fraction of "not suitable" patches. Thirdly, for a random subset of each of the three categories we performed seed introduction experiments by sowing seeds into patches. Based on the results of the vegetation survey and the seed sowing experiments we made the final assessments of patch suitability (see below).

Patches were categorized according to grazing status as "grazed" or "ungrazed". If two patches that were immediately adjacent to each other differed in grazing status or other aspects of habitat quality, such as soil moisture, they were considered separately. For each occupied patch, we recorded population size, in terms of total number of flowering and vegetative individuals (excluding seedlings) during 3 years, 2000–2002. We also described population structure by counting vegetative and flowering plants in five randomly placed 0.25 m^2 plots in each occupied patch.

2.3. *Identifying unoccupied suitable habitats*

We assessed the suitability of unoccupied habitat patches both by comparing the floristic composition of unoccupied patches with that of occupied ones, and by seed sowing experiments into occupied and unoccupied patches. First, suitability of habitat patches was estimated based on presence of other plant species assembled from the floristic lists of all inventoried sites (i.e. occupied and unoccupied) using Beals index that expresses the probability of occurrence of species at a patch, using number of joint occurrences with other species (Beals, 1984; Münzbergová and Herben, 2004). The likelihood that *S. pratensis* would occur at an unoccupied patch was estimated using the frequency distribution of Beals index values at the occupied patches. An unoccupied patch having Beals index value equal or higher than the lower 10% percentile of occupied patches was categorized as suitable and all sites having lower Beals index values as unsuitable. This resulted in that about half of the unoccupied patches, preliminary categorized as suitable and potentially suitable, were being counted as suitable. Model output was qualitatively similar for threshold values corresponding to the 1–20th percentiles (results not shown). Second, we carried out seed sowings in 43 patches, 26 occupied and 17 unoccupied, in 2000 and 2001. In each patch, 50 seeds were sown into each of three 10 cm × 10 cm plots with three unsown plots used as controls. Seeds were collected when ripe, and sown as soon as possible, to create a situation as much like natural recruitment as possible. All plots were recorded in early June and mid September each year.

In order to find out how well predictions of habitat suitability based on floristic co-occurrences agreed with the results of the seed introduction experiments, we examined the relationship between Beals index value and establishment success (mean number of seedlings in the three replicates) in the sowing plots by regression.

2.4. *Demographic data collection and analysis*

After the first inventory of the study area, we selected five *S. pratensis* populations for detailed demographic studies. We chose three grazed sites and two sites where grazing was abandoned for 40–70 years ago to cover management effects. We established permanent plots of 0.25 or 1 m^2, depending on *S. pratensis* density at the site. The number of permanent plots per population varied between 6 and 14, and at least 250 plants with a minimum of 50 flowering individuals were included in each population. Individual plants were mapped, using a grid frame with mesh size of 10 cm × 10 cm. Individuals were easily found and identified in the next season. Each individual plant was recorded once each year from 2000 through 2002. At each visit seedlings were searched for, recorded and included in the study. During flowering, we measured length and width of the largest leaf and counted the number of flowers. The product of length and width of the largest leaf was used as an estimate of plant size. Seed sowing experiments were carried out at each site. At the time of seed ripening each year, 50 seeds were sown into six plots of 10 cm × 10 cm. Six control plots were also established. Plots were visited twice a year, in early June and mid September, and the numbers of new and surviving seedlings were recorded.

To build a matrix model of the dynamics of the different populations, *S. pratensis* individuals were assigned to one of five stages: (1) seeds in the seed bank, (2) seedlings, (3) small vegetative individuals (estimated area of the largest leaf 30–449 mm^2), (4) large vegetative individuals (estimated area of the largest leaf more than 449 mm^2) and (5) flowering individuals. The size limit between small and large vegetative individuals corresponded to the size threshold below which almost no individual flowers. The number of flower heads was counted in individuals in permanent plots and the number of seeds per flower head was estimated by examination of 30 flower heads collected outside the permanent plots in each year and population. The proportion of seeds germinating in their first year was estimated from the seed sowing experiments in 2000 and 2001. Based on the assumption that seeds that survived in the soil to the second year after sowing had a germination rate that was equal to the germination rate the first year after sowing, survival in the soil seed bank was calculated as the ratio between the number of new seedlings that emerged in the second year after sowing and the number that emerged the first year after sowing. Seedling survival was estimated from seedlings in the seed sowing experiments. For survival of seeds in the soil and seedling survival we used the value for the transition interval 2000–2001 also for 2001–2002.

2.5. *The model*

To build a simulation model of the real landscape, the geographical information from patches was transferred to a model grid. Habitat patches were thus explicitly located on a simulation plane representing a rectangular area of 7.1 km^2. The sizes and shapes of patches were taken from the field inventory. The patches were represented as sets of contiguous cells (cell size 5 m × 5 m) with explicit positions in the simulation plane. Each patch was assigned a habitat quality (grazed or ungrazed) based on the field data. Absorbing boundaries (i.e. diaspores passing over the boundary are lost) were used at the simulation plane since forests largely surround the modeled region and no significant outside import of diaspores is conceivable.

Local population dynamics of *S. pratensis* were simulated at the level of patches. Each patch was assigned a population vector that contained numbers of individuals in each size class. Population growth at the *k*th patch was modeled as

$$\mathbf{x}'_k(t+1) = \mathbf{A}_{Q(k)}.\mathbf{x}_{k(t)}, \qquad (1)$$

where elements of $\mathbf{A}_{Q(k)}$ are stage-specific transition probabilities at the habitat quality state $Q(k)$ (grazed or ungrazed). One-year transition intervals were used.

Modelling density-dependent population growth (i.e. due to patches being of finite sizes) was constrained by the fact that we did not have any data to model a transition-specific density-dependence. Therefore we used a simple logistic model replacing growth rate by the dominant eigenvalue of the transition matrix. We therefore lowered the number of individuals in each stage using the difference between total population size and maximum population size at the patch as the logistic term. The population vector resulting from the matrix multiplication was thus replaced by

$$\mathbf{x}''_k(t+1) = \mathbf{x}'_k(t+1)\frac{1}{\lambda}\left[1+(\lambda-1)\left(1-\frac{N(t)}{K}\right)\right] \qquad (2)$$

where λ is the dominant eigenvalue of the matrix $\mathbf{A}_{Q(k)}$, $N(t)$ the total population size (sum of all stages) at the time t (before the matrix multiplication), and K is the maximum number of individuals at the patch of the given size. This affects all stages of the life cycle equally; this is not very realistic for plant populations, where often some transitions are more density-dependent than other. Still it is the most parsimonious type of density dependence given the data available; further, type of density dependence does not have qualitative effects on the behaviour of the model (Herben et al., unpublished data).

Finally, to simulate demographic stochasticity, each vector element was replaced by a Poisson-distributed deviate with the mean of x_i. This yields the $\mathbf{x}_k(t+1)$ population vector of each patch passed to the next simulation step. Environmental stochasticity was simulated by using several matrices for one habitat quality. At each step, one matrix was drawn from this set at random with specific probabilities assigned to each matrix.

Two types of dispersal were simulated: distance-dependent (primarily unassisted and wind dispersal) and distance-independent (primarily adhesive dispersal by animals). Distance-dependent dispersal was assumed to affect most of the seeds, while distance-independent dispersal was used to model rare dispersal events (see below for the estimates of these values). For distance-dependent dispersal, seeds produced at each patch were divided among the cells that comprise that patch and dispersed from these cells (the grid size corresponded to the size of the grid used to represent patches). Seed source was located in the cell centre. Number of seeds arriving at the cell *i* by distance-dependent dispersal is therefore defined as

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

where p is the proportion of seeds spread independently of distance, x_{0k} the number of seeds produced at the habitat k, A_k the area (number of cells) of the kth habitat, α the dispersal constant, d_{ij} 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 $[\sum_j \exp(-\alpha d_{1j})]$; j means indexing over all cells in the grid, and k is summation over all habitats. Number of seeds arriving at the lth habitat is the sum of seeds arriving at all cells belonging to that habitat, i.e.

$$N_{dd\,l} = \sum_i n_i,$$

summed over all cells belonging to that habitat. Number of seeds arriving at the lth habitat by distance-independent dispersal is proportional to the area of that habitat as follows:

$$N_{di\,l} = p\frac{A_l}{A}\sum_k x_{0k},$$

where A is the total area of the simulation plane. Total number of seeds arriving at a habitat is the sum of N_{dil} and N_{ddl}.

In each step, the simulated processes were performed in the following order: (1) transitions within patches, including density-dependence, yielding a seed crop, (2) dispersal, both distance-dependent and -independent. The random number generator *ran2* (Press et al., 1992) was used.

2.6. *Parameter estimation*

To simulate local population dynamics we used matrices from two transition intervals and five populations. Six matrices were thus from grazed sites (3 populations × 2 transition intervals) and four matrices were from ungrazed sites (2 populations × 2 transition intervals). To represent environmental stochasticity, all demographic matrices collected at all plots of one habitat quality (grazed and ungrazed) in both intervals were pooled. In this way we pooled spatial environmental variation within one habitat quality (grazed or ungrazed) with the temporal variation obtained by recording demography over two transition intervals.

For density-dependent simulations, maximum population size (*K*) was estimated as a product of the third highest density of *S. pratensis* found in the field (two extreme outlier densities in unusual habitat patches were excluded), and patch size. The results were similar when the fourth highest population density value was used.

Mean dispersal distance was estimated as the product of plant height and wind speed divided by the terminal velocity [Soons, personal communication, see also Soons and Heil, 2002]. Given the variation in terminal velocity (1.7–3.1 m/s, data from Soons and Heil, 2002), variation of wind speed at the locality (4.3–7.8 m/s, data from Landsort Meteorological Station 1991–1995), and variation in height of seed release in *S. pratensis* (0.25–0.60 m), the values obtained ranged from 0.35 to 2.77 m. In the simulations we used values from 0.46 to 2.35 m; this corresponds to 99.9% dispersal tails of 2.5–22.5 m (0–4 cells used in the model). The data from Landsort Meteorological Station probably give an overestimation of the wind strength in the study area, but were used without correction, as preliminary simulations showed quite small effects of this distance dependent dispersal. Since we lacked an estimate of the proportion of seeds dispersing independently of distance, simulations (except the sensitivity analysis) were run with several values (0, 10^{-8} to 10^{-1}), covering the most likely range.

2.7. *Initial conditions for simulations*

We used two types of initial conditions for the simulations: First we used actual patch occupancy, population sizes and stage distributions in the year 2002. Since the field data did not contain numbers of seeds and seedlings these were calculated from the numbers of adult individuals assuming that the actual distribution was equal to the projected stable stage structure. Second, we used 10 randomly selected occupied patches, each with 100 individuals, assigned to stages according to the projected stable stage structure.

2.8. *Sensitivity analysis*

We investigated the sensitivity to model parameters for: (i) number of patches occupied, (ii) local population growth rate, (iii) total population size summed over all patches, and (iv) number of colonizations and extinctions events. The following parameters were varied in these sensitivity analyses: (i) short-distance dispersal (mean dispersal distance), (ii) long-distance dispersal (proportion of seeds dispersed independent of distance), and (iii) individual demographic transition rates. The simulations for sensitivity calculations were run for 20 years in 100 realizations and without density-dependence, since effects of density were negligible during this interval. One of the parameter combinations was used as a baseline for comparisons (mean dispersal distance: 1.37 m and proportion of seeds dispersed with long-distance dispersal: 10^{-4}). The dispersal parameters were changed one by one, investigating several different values for each type of dispersal, using actual patch occupancy for initial conditions. To examine sensitivity to demographic transition rates we grouped transitions into those related to survival in the same or a smaller stage, fecundity and growth to a larger stage (Silvertown et al., 1993). Each matrix element was increased by 10% (Caswell, 2001). This change was done concurrently in all matrices in the pool of matrices from which sampling was done. We used both types of initial conditions for analyses of sensitivity to demographic transitions. The sensitivity of the response variable to the parameter was expressed as proportional sensitivity (elasticity). Lastly, we calculated elasticities of the underlying matrices. This was done using stochastic simulations separately for grazed and ungrazed set of matrices, and calculated following Caswell (2001).

2.9. *Simulations and scenarios*

To predict patch occupancy and population sizes under different scenarios of landscape development, we used the simulation model calibrated with the field data and made different assumptions of future management, and hence suitability, of habitats. These assumptions were based on the knowledge of past and current management in the study area. Currently, there are essentially two kinds of suitable habitat patches, differing in management history, for *S. pratensis*: pastures of old, unfertilized and species-rich grazed grasslands, and pastures of former fields that were left abandoned between 30 and 70 years ago and have been grazed since then. We ran six scenarios corresponding to different combinations of assumptions for old pastures and former fields. We assumed old pastures to be all grazed, all ungrazed, or grazed and ungrazed according to the current management state. For former fields, we assumed them either to be grazed or unsuitable, i.e. abandoned or used for crops.

These scenarios were assumed to represent possible combinations of past, present and future land use. For example, the scenario where former fields are used for crops and thus not suitable for *S. pratensis*, while the pastures are grazed, mimics the conditions up to the mid 20th century landscape. Grazing of all former fields and the pastures is close to the present management situation in the landscape. The scenario where former fields, but not old pastures, are grazed, represent a probable future management, where grazing has been moved to the most productive grasslands. To simulate population dynamics at grazed fields, the ‘grazed’ set of matrices were used. Abandoned or cultivated fields were assumed to be unsuitable. For grazed and ungrazed pastures, we used the grazed and ungrazed set of matrices, respectively. The simulations of the landscape were run with the density-dependent version of the model, for 100 years in 100 realizations. Only the actual occupancy was used as the initial conditions.

3. Results

3.1. Landscape inventory and assessments of patch suitability

Within the study area we identified and made vegetation surveys in a total of 171 patches that were considered to be at least potentially suitable to S. *pratensis*. Ninety-four of these were occupied. Forty-three unoccupied patches had a Beals index value equal or higher than that of the lower 10% percentile of all Beals index values at occupied patches, and were assumed to be suitable and the 34 unoccupied patches with lower Beals index were considered unsuitable. This left us with a total of 137 suitable patches for S. *pratensis* in the target area (Fig. 1). Mean recruitment rate in the first year was 16% in the first seed sowing experiment (2000–2001) and 7% in the second (2001–2002). Mean proportion of seeds surviving as seedlings after 2 years (2000–2002) was 9% in the first seed sowing experiment. There was a significant, positive relationship between the Beals index value and seedling germination and seedling survival in the seed sowing experiment (Table 1, Fig. 2, Beals index versus germination and survival to June 2001 of seeds sown in 2000: $F_{1,39} = 20.6$, $P < 0.001$, $R^2 = 0.37$; survival to June 2002 of seeds sown in 2000: $F_{1,39} = 12.2$, $P = 0.001$, $R^2 = 0.15$; germination and survival to June 2002 of seeds sown

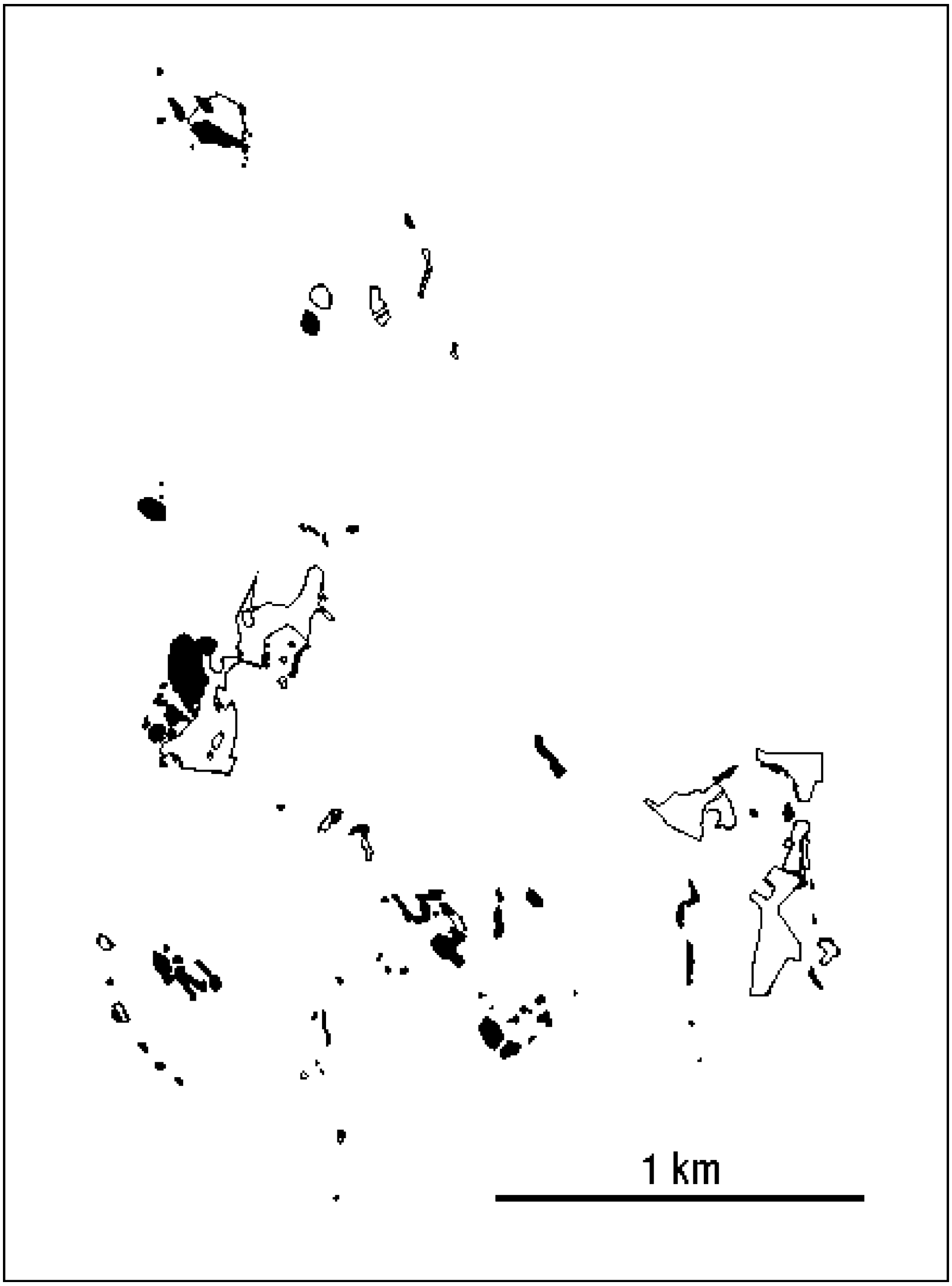

Fig. 1 – Overview map of the distribution of patches suitable for *Succisa pratensis* in a Swedish agricultural landscape. Contour lines indicate suitable patches, black patches indicates occupied patches.

Table 1 – Seedling recruitment and Beals index value for different patch types in a seed sowing experiment of *Succisa pratensis* in an agricultural landscape of Sweden

	Mean value of Beals index	Number of seedlings		
		From seeds sown in 2000, at the 2001 monitoring	From seeds sown in 2000, at the 2002 monitoring	From seeds sown in 2001, at the 2002 monitoring
Occupied patches	0.59	8.3 (7.6)	3.5 (4.4)	4.2 (5.5)
Unoccupied patches	0.59	7.0 (7.5)	3.6 (6.2)	4.6 (6.2)
Suitable	0.60	8.4 (8.1)	4.5 (6.8)	5.3 (6.8)
Unsuitable	0.54	3.1 (3.4)	1.0 (1.8)	2.1 (1.8)

Recruitment values are mean number of surviving seedlings out of 50 seeds sown into 10 cm × 10 cm plots. Standard deviations are given in brackets.

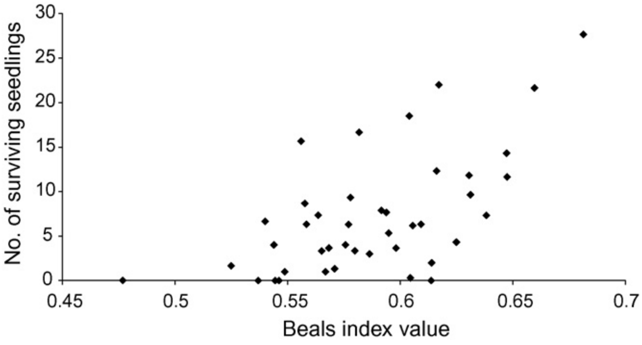

Fig. 2 – Relationship between Beals index value and seedling recruitment after experimental sowing for *Succisa pratensis* in 41 habitat patches in a Swedish agricultural landscape. Recruitment was measured as the proportion of seeds sown in 2000 that survived as seedlings in June 2001.

in 2001: $F_{1,39} = 9.59$, $P = 0.004$, $R^2 = 0.24$). Similarly, the subjective classification provided a good fit with both seed sowing estimates of habitat suitability as well as Beals index values (not shown).

3.2. *Demographic study*

Growth rates of the five populations with different managements ranged from 0.90 to 1.34 (Table 2). Mean growth rate of grazed sites was 1.10, while abandoned sites had a mean population growth rate of 1.08. The probability for a seed to survive more than 1 year in the seed bank ranged from 0.4 to 3%, and the probability for survival in the seed bank longer than 5 years was ranged from 8×10^{-7} to 2×10^{-4}.

Table 2 – Population growth rates from deterministic matrix models of five populations of *Succisa pratensis* in habitats with different land-use

	Management	$\lambda_{00\text{-}01}$	$\lambda_{01\text{-}02}$
Population 1	Grazed	0.98	1.08
Population 2	Grazed	1.19	0.95
Population 3	Abandoned	0.90	1.05
Population 4	Abandoned	1.34	1.02
Population 5	Grazed	1.27	1.14

3.3. *Sensitivity to dispersal*

Compared to long-distance dispersal, short-distance dispersal had a weak effect on metapopulation dynamics. The number of occupied patches after 20 years was little affected by short-distance dispersal (Fig. 3A). Short-distance dispersal did, however, result in a reduced population growth rate due to seed loss, and this reduction was larger for smaller patch sizes (not shown).

Long-distance dispersal had strong effects on the number of occupied patches. The effects were detectable already when one seed out of 10,000 was dispersed independent of distance,

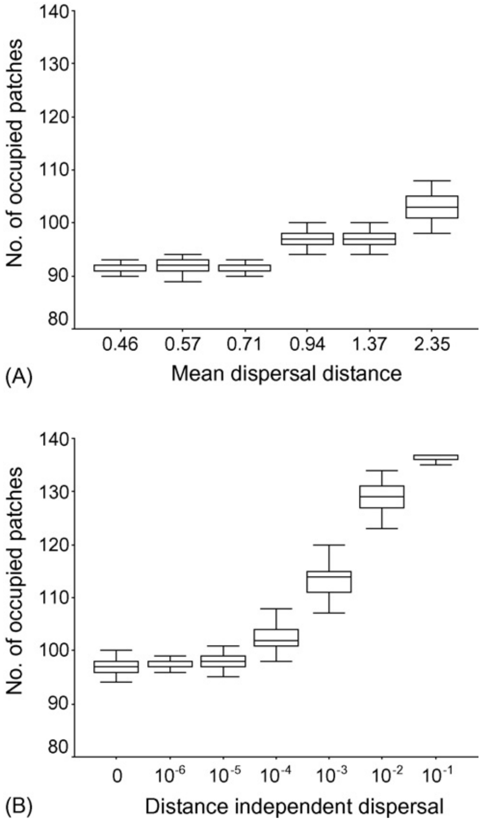

Fig. 3 – Effects of (A) short-distance and (B) long-distance dispersal on the number of occupied patches in a model of metapopulation dynamics of *Succisa pratensis*, a perennial grassland plant after 20 years. There were 137 patches in total and actual occupancy in the field (94 habitats occupied) was used as the initial occupancy in the simulations.

Table 3 – Sensitivity of a model of metapopulation dynamics of *Succisa pratensis*, a perennial grassland plant, to changes in fecundity, survival and growth transitions of demography matrices

	Elasticities of local population growth		Total population size		Number of occupied habitats		Number of transitions	
	Grazed	Ungrazed	Actual	10	Actual	10	Actual	10
Fecundity	0.10	0.12	0.16	0.14	0.10	0.58	0.72	0.45
Survival	0.53	0.49	0.47	0.43	0.33	2.05	2.05	1.99
Growth	0.37	0.39	0.39	0.36	0.30	1.18	1.54	0.09

The first two columns provide non-spatial elasticity values calculated by combining all the matrices of each type (grazed or ungrazed) using stochastic simulations. In the other columns, sensitivity is expressed as change in total population size, number of occupied patches and number of transitions (colonisations and extinctions). These values are expressed as proportional changes (elasticities) of the parameters over 20 years. The simulation started either with actual habitat occupancy or with only 10 occupied patches. The results are averages of 100 replicates.

i.e. "long distance" (Fig. 3B). Within the range of values used (up to 10% of total seed production), the proportion of seeds dispersed independent of distance had negligible effect on within-habitat population dynamics (not shown).

3.4. *Sensitivity to demographic parameters*

The relative importance of fecundity, growth and survival differed between the different response variables (Table 3). The effects of fecundity were larger on metapopulation performance than on local population growth rate, whereas the effects of survival were smaller in a metapopulation context. However, survival was still the most critical life stage transition for local population size, as well as for number of occupied patches and total population size.

3.5. *Long-term dynamics of the system*

The long-term dynamics of the system were very slow (Fig. 4). The time to equilibrium ranged from 1000 years (from present day occupation) to 9000 years (from 10 random patches occupied). Even with only 10^{-5} of all seeds long-distance dispersed, the number of occupied patches converged to an equilibrium state with about 90% (to be compared with 69% occupancy in the current landscape) of the patches occupied, independently of initial patch occupancy (Fig. 4). At equilibrium, approximately one colonization or extinction occurred per year. Most of the turnover took place in small and isolated patches (Fig. 5), and extinction occurred mostly soon after colonization. Without long-distance dispersal, patch occupancy was markedly affected by initial conditions and the system failed to reach the same high level of occupancy as with long-distance dispersal. There was very little variation within a certain parameter combination in the number of occupied patches at the end of simulations with long-distance dispersal (range of S.D. 0.74–2.74 patches). However, there was a considerable variation in the time needed to reach the equilibrium (range of S.D. 10.7–897.4 years). All patches were colonized at least once during the simulation period.

3.6. *Landscape management scenarios and predicted dynamics of S. pratensis populations*

The scenario with former fields unsuitable and pastures grazed resulted in stable levels of patch occupancies that where close to, or lower than, the present-day habitat occupancy (Fig. 6). This distribution of *S. pratensis* largely corresponds to the equilibrium distribution in the landscape many decades ago when the fields were still unsuitable habitat. For scenarios with fields assumed to be grazed and suitable as they currently are, the predicted number of occupied patches as well as total population size was higher than the observed level. In contrast, there was no clear difference between scenarios when pastures were grazed or ungrazed (Fig. 6).

4. Discussion

4.1. *Model parameterisation*

We used a dynamic metapopulation model to examine the dynamics of a perennial grassland herb, *S. pratensis*, in a real landscape, and based, as far as possible, the parameterization of the model on real data. In particular, we used extensive demographic data to describe local dynamics in detail, seed sowing experiment to estimate probability of colonization rates, and several methods to assess the suitability of unoccupied habitat.

We collected detailed demographic data from permanent plots in five populations to get an accurate description of variation in local population dynamics. The demographic data showed only moderate differences between grazed and ungrazed populations. However, we assume that this difference reflects only short-term effects of grazing, and not successional changes over longer time periods. The ungrazed sites where we collected demographic data have been abandoned for 40–70 years and together with the fact that *S. pratensis* only occurs in areas formerly grazed (Mildén et al., unpublished data) show that the response of *S. pratensis* to ongoing change is very slow.

Colonization depends on establishment success of seeds arriving at new patches. Extinction rates of populations of species possessing a seed bank will also largely depend on seed bank survival. We used establishment data from a 3-year seed sowing experiment and demographic data collected in five sites with different habitat types to calculate the fate of seeds arriving in empty patches. From data collected in the seed sowing experiment we could also calculate the probable size of the seed bank and survival of seeds. The estimation of the seed bank survival seems to be in accordance with field

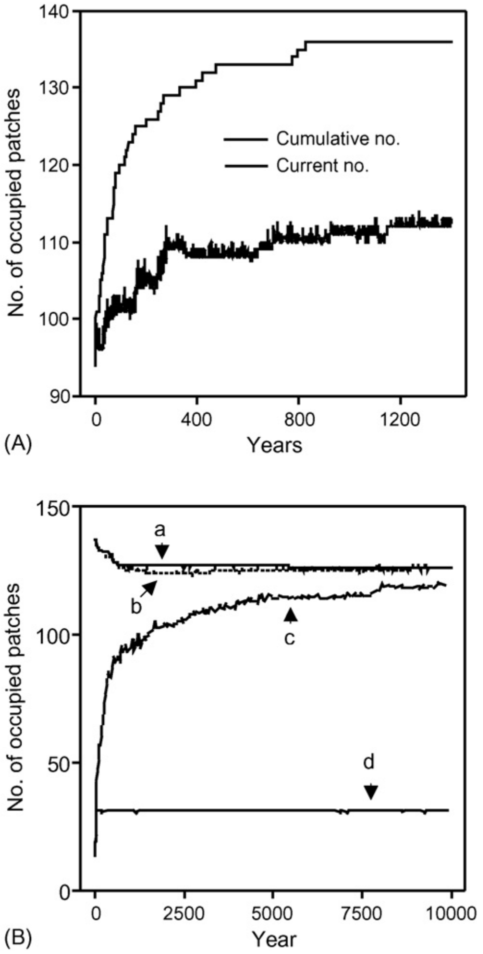

Fig. 4 – Number of patches occupied by *Succisa pratensis* against simulation time (results for a single simulation). The mean dispersal distance for the short-distance (exponential) dispersal is 1.37 m. Altogether there are 137 suitable patches in the system. (A) The simulation started with actual field occupancy (94 habitats occupied) and with actual number of individuals in each patch. Long-distance dispersal affects 0.0001 of all seeds. (B) The simulation started with full occupancy (all patches occupied, lines a and b) and with ten patches occupied having 100 individuals in stable stage distribution (lines c and d). There was either no long-distance dispersal (b and d), or long-distance dispersal affecting 0.0001 of all seeds (lines a and c).

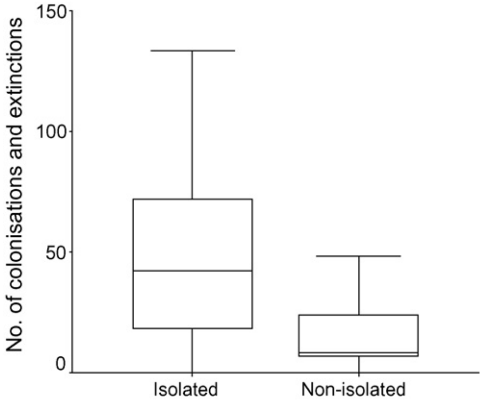

Fig. 5 – The relationship between number of colonization and extinctions over 10,000 runs and patch isolation. As isolated we regarded those patches that do not receive any seeds from surrounding habitats via exponential dispersal while those that receive seeds were regarded non-isolated. The data come from a single simulation over 10,000 years starting with real field occupancy (94 habitats occupied) and with actual number of individuals in each patch. Long-distance dispersal affects 0.0001 of all seeds. The mean dispersal distance for the short-distance (exponential) dispersal is 1.37 m.

studies presented in Thompson et al. (1997) even though the results of these studies are not fully consistent. Hence, data on establishment success and seed banks allowed us to estimate both colonization and extinction probabilities more accurately than in many previous studies.

A critical issue in all metapopulation studies is the identification of unoccupied but suitable habitat patches. It has even been argued that difficulties in assessing patch suitability may invalidate a metapopulation approach to plant regional dynamics (Freckleton and Watkinson, 2002). Such claims are understandable as previous attempts to assess habitat suitability have often been purely subjective. In this study we used a combination of subjective, correlative and experimental methods to assess patch suitability. The overlap between occupied and unoccupied patches for the Beals index was small. Moreover, recruitment after experimental seed sowing was significant and positively correlated to the Beals index values. It is important to bear in mind that these approaches to assess patch suitability are not equivalent, but rather complementary. Seed sowing experiments focus on establishment processes, while vegetation surveys incorporate several aspects of habitat quality and patch history. We believe that our approach, utilizing both correlative evidence based on floral composition and direct experimental tests,

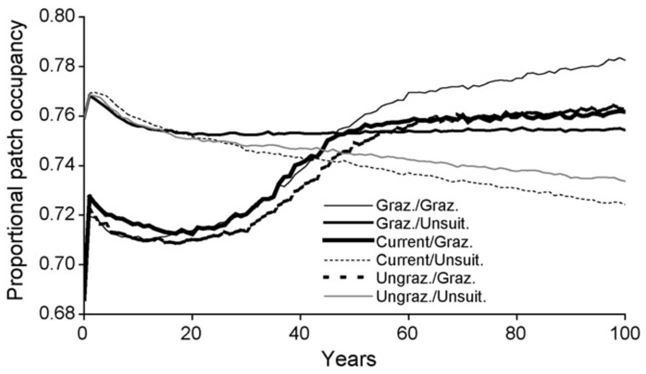

Fig. 6 – Effects of different landscape management scenarios on proportional patch occupancy. The original values are the values observed in 2002. The legend shows the status of grasslands (all grazed, all ungrazed or their current status) and of old fields (grazed or unsuitable). Results are averages of 20 realizations, each run over 100 years.

reduced the uncertainty about patch suitability and that it provided fairly accurate estimates for the S. *pratensis* system.

4.2. *Sensitivity to demography and dispersal*

With the model we used, we were able to compute sensitivities not only of local population growth rate, but also of several parameters for the regional system with colonizations and extinctions. The dynamics of colonizations and extinctions and the number of occupied patches were hardly affected by increases in short-distance dispersal within a realistic range. The impact of long-distance dispersal on the number of occupied habitat patches exceeded the impact of short-distance dispersal. This result is largely the effect that for S. *pratensis* in our study system, the distance between suitable patches is in general longer that the distance that can be achieved by wind dispersal. A fraction of seeds of one out of 10,000 dispersing over long distances had a great impact on colonization rates and patch occupancy in the landscape. Caswell et al. (2003) reached a similar conclusion, when examining the effects of local processes and long- and short-distance dispersal on wave-speed in a landscape. In terms of conservation, the importance of long-distance dispersal implies that more attention should be paid to potential long-dispersal agents such as cattle and wild animals or even agricultural machinery (Fragoso et al., 2003).

The fraction of seeds dispersed over long distances thus has a critical impact on the output of regional plant population models. However, long-distance dispersal is highly problematic to parameterize from field data, and few attempts have been made to empirically estimate dispersal curve tails (cf. Tackenberg, 2003; Higgins et al., 2003). We tried to tackle this problem by running simulations using a wide range of values, assuming that they would cover the range where the true value of this parameter most likely will fall. We found important effects already when one seed out of 10,000 was dispersed independently of distance. Moreover, 98% of the seeds that were dispersed independently of distance in the modelled landscape landed in unsuitable habitat, so that only a fraction corresponding to 2×10^{-6} of seeds, dispersed independent of distance, ends up in suitable habitat. As we have no good direct estimate, it is still possible to argue that the fraction of S. *pratensis* seeds that disperse independently of distance and end up in suitable habitat, in reality is even smaller than this fraction. Still, we believe that long-distance dispersal by adhesion to wild animals, such as roe deer, wild boars, hares and elk, or domestic animals, such as cattle, occur regularly in the study area since seeds of S. *pratensis* adhere easily to fur animals (Römermann et al., 2005) and these also often serve as vectors of highly directed dispersal.

With only short-distance dispersal, the number of occupied patches in equilibrium was considerably lower than when both kinds of dispersal occurred. This is not surprising, since patches where populations have gone extinct will be recolonized to a lesser extent. Somewhat more surprising is the fact that even without long-distance dispersal, the regional population does not go extinct even in 10,000 years. The explanation for this is that extinctions in the model are caused by a combination of environmental and demographic stochasticity, and that the largest patches have a very low probability of going extinct. Long-distance dispersal is thus unnecessary as long as there is a large population that can function as a source in a mainland-island type of dynamics. Such a system only goes extinct through catastrophic events, such as plowing or other changes in management, stressing the role of catastrophes in understanding dynamics.

The relative sensitivities to different demographic processes changed when we introduced dispersal to the system, and calculated the sensitivities for a spatially explicit regional population. Fecundity, which was of minor importance for local population growth, became relatively more important regionally, in terms of effects on total population size, number of occupied patches and population turnover. In contrast, the influence of survival, which was locally important, decreased in a regional context. With dispersal, a higher fecundity enhanced colonization success by providing more seeds and thereby chances of successful colonization, while survival only kept local extinction rates low. Hence, demographic processes that are unimportant in a local population context may still be important for metapopulation performance.

4.3. *Long-term dynamics*

Trajectories from different initial conditions converged provided that long-distance dispersal occurred. One reason for the converging scenarios is that long-distance dispersal is not spatially restricted, i.e. any patch can be colonized from anywhere as long as there are enough populations to produce seeds for dispersal. However the modelled time to equilibrium was very long, 1000–9000 years. This was because the long-term dynamics of the regional population was slow (at equilibrium, only one colonization or extinction per year). Most of the extinctions occurred in small and recently colonized patches, which indicates that the dynamics of most patches in the system are even slower. Such slow dynamics must not be interpreted as if there were no metapopulation dynamics in the system. However, the low speed of the dynamics means that the system is slow to reach equilibrium and patch occupancy models that assume equilibrium conditions may not be appropriate.

Former fields may differ from old grasslands, in several respects, and may constitute a “worse” habitat from the point of view of S. *pratensis*. However, the existence of established populations in some former fields, together with successful establishment after seed sowing experiments, suggest that they constitute suitable habitat and that low occupancy may partly reflect dispersal limitation. Modelling of the different scenarios showed that the current distribution of S. *pratensis* largely reflects the equilibrium distribution in the landscape many decades ago where the fields were still unsuitable habitat, that the current distribution is in a non-equilibrium, and that the species may still be slowly increasing in the landscape after old fields were abandoned 30–70 years ago.

In the simulations of the different scenarios, time to equilibrium is far shorter than the 1000–9000 years that were achieved in earlier simulations. This is largely due to the fact that in scenarios where former fields are excluded as being unsuitable, the number of patches is lower, and therefore, the initial occupation closer to the equilibrium. In the scenarios that include former fields, the number of occupied patches is still increasing after the simulated 100 years.

It is thus likely that the investigated regional population of *S. pratensis* is not in equilibrium and time lags are important. In such systems, the full effects of changed management practices, such as opening of new habitat or habitat degeneration (ungrazed habitats), will not result in changes in the regional distribution of *S. pratensis* until after several decades. Knowledge of landscape history is therefore essential to understand species distribution as well as to direct conservation efforts.

4.4. *Concluding remarks*

Our model results for the perennial plant *S. pratensis* in an agricultural landscape suggests that metapopulation dynamics proceed at a very low pace. This is in contrast to the results for most animals investigated so far, and suggests that in long-lived species with a restricted capacity to disperse over long distances both extinctions and colonizations can be relatively infrequent. As a result, time lags in the population response to landscape changes and non-equilibrium regional distributions are important. However, long-distance dispersal and colonization–extinction dynamics still play an important role for the regional distribution, but the relevant time scale is many decades or even centuries and the impact of landscape history is strong. Metapopulation models assuming equilibrium are not well suited to examine the dynamics in such systems. Instead empirically parameterized non-equilibrium metapopulation models are needed to examine their slow dynamics.

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