POPULATION VIABILITY AND REINTRODUCTION STRATEGIES: A SPATIALLY EXPLICIT LANDSCAPE-LEVEL APPROACH

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Abstract. The effect of habitat destruction on the likelihood of species survival is often estimated based on the assumption that colonization and extinctions are in balance. This assumption is not sustainable in species where the dynamics of colonization and extinctions is slow in relation to landscape changes, such as in most plants.

Here we use an alternative approach, a realistic, dynamic landscape-level model that does not rely on this assumption. It enables estimation of the effect of habitat destruction using field data on the biology of a species and on real landscape structure. Because our approach relies on direct comparisons of changes in population size and survival probability due to habitat changes, it can be easily extended to other conservation questions, such as assessing the effects of events causing the extinction of populations but allowing for re-colonization, or identifying optimal reintroduction strategies.

We applied this method to a perennial herb, *Succisa pratensis*, that is a typical grassland species. We combined detailed demographic data with information on the spatial distribution of suitable habitats to model species dynamics in the landscape under different scenarios. The results show that habitat destruction alone has little effect on regional survival. However, the effect of habitat destruction increases when combined with factors causing extinctions of the existing populations that are expected to play a significant role in the study system. Our results further show that an optimal reintroduction strategy at the landscape level depends on the number of available seeds.

The approach presented here was designed for studying systems where species colonization–extinction dynamics is slow compared with landscape changes. Such time lags and nonequilibrium dynamics have been suggested to be important features of many ecosystems and life forms, and this approach is thus likely to be useful for a wide range of future studies. The approach also allows the estimation of short-term effects of habitat destruction, i.e., situations that are nonequilibrium by definition. This is never possible with equilibrium models, giving the model a wide applicability for all types of organisms.

Key words: extinction threshold; habitat fragmentation; metapopulation capacity; plants; population viability analysis; reintroduction; Succisa pratensis; *survival probability.*

INTRODUCTION

Understanding the factors affecting survival of species in fragmented landscapes is among the central issues in species conservation (van Groenendael et al. 1998). The simplest way of doing this is to perform population viability analysis at the level of the local population by examining total species demography (Morris and Doak 2002). With the recent development of metapopulation theory (Hanski 1989), it has been recognized that regional-scale processes are also important for long-term survival of species in the landscape (e.g., Carroll et al. 2003*a*, du Toit et al. 2004). In such cases population viability analysis has to be performed at regional scale and should take into account both the present distribution of the species in the

landscape and the number and distribution of patches that are potentially available for recolonization. Performing such studies is a major challenge for species conservation, and we are still lacking a general approach that would allow us to do this without restrictions to specific groups of organisms.

Fragmented landscapes present difficulties also for species reintroductions. For a single site, it is sufficient to assess the local conditions that maximize the probability of species survival (Schemske et al. 1994, Hodder and Bullock 1997, van Groenendael et al. 1998, Smulders et al. 2000, Kauffman et al. 2003). However, in a fragmented landscape it is also necessary to evaluate the success of a reintroduction by the ability of species to spread and survive at the landscape scale (Eriksson 2000*a*, Carroll et al. 2003*b*). The reintroduction strategy thus has to take into account the spatial structure of the landscape, in terms of the arrangement of suitable habitat patches around the habitat patch

where the species was reintroduced and the capacity of the species to reach them.

Recently several theoretical models have been developed to assess species survival probabilities at the landscape level (e.g., Lahaye et al. 1994, Gustafson and Gardner 1996, With et al. 1997, Hanski and Ovaskainen 2000, Casagrandi and Gatto 2002*a*, Dreschler et al. 2003). Most of these models assume that the current distribution of species in habitat patches is the result of equilibrium between colonization and extinctions (but see Lahaye et al. 1994). Under this assumption, the present distribution of the species can be used to estimate the expected threshold number of habitat patches needed to ensure metapopulation survival (Hanski and Ovaskainen 2000).

The critical point in such approaches is the assumption that colonization/extinction dynamics operate fast enough to keep the current distribution close to equilibrium. This assumption is rather difficult to test directly as the necessary long-term data on immigration and extinction rates are rarely available (Hanski et al. 1994). The assumption of equilibrium is likely to be met in short-lived, highly dispersible organisms, which is the case with many insects (Hanski et al. 1994, Baguette 2003, Purse et al. 2003). However, it is much less likely to hold in sessile organisms, such as many plants, that are known to have very low extinction and immigration probabilities (Eriksson 1996, Freckleton and Watkinson 2002). Consequently, the expected time to reach equilibrium is so long that it is extremely unlikely that it will be reached in time frames over which the external environment may be assumed to be constant. Models based on the assumption of equilibrium are therefore of little use in plants. This has been used as an argument that studying the dynamics of plants in a metapopulation framework does not make sense (Freckleton and Watkinson 2002). Unfortunately, plants, precisely due to their limited migration capacities, are directly threatened by habitat destruction, and predictions of the effects on their landscape dynamics are badly needed (Eriksson and Kiviniemi 1999).

Moreover, even if the equilibrium assumption holds, the fact that the above-mentioned models are designed only to assess the effect of habitat destruction constitutes another important limitation. Habitat destruction can interact with other processes such as insect outbreaks, fires, and short-term change in management practices (Casagrandi and Gatto 2002*b*), which may wipe out the population while leaving the habitat essentially unchanged and ready for recolonization. We refer to these events as population destructions. Such events may be especially important in perennial plants, which are able to survive for a long time even in a single habitat patch if not wiped out (Eriksson 2000*b*). Not including population destruction in models of such systems would thus lead to unrealistic conclusions.

To study the prospect of species survival in fragmented landscapes and the possibilities for species reintroduction, it is thus important to use an approach that can represent both transient and equilibrium phases of local population development and of species regional distribution. This can be attained using a spatially explicit dynamic landscape-level model. Such a model can work with realistic data on landscape structure, and take into account actual species distribution in the landscape and data on local population dynamics. This approach does not rely on the equilibrium assumption and enables incorporation of much more site-specific information. It can be used to extrapolate changes in population sizes over time under different landscape scenarios both in transient and equilibrium phases. This has direct relevance for conservation, as it enables assessment of the consequences of expected landscape changes for species over different time frames. The same approach can be used both for a population viability analysis and for designing an optimal strategy to reintroduce a species into a landscape consisting of several suitable habitat patches.

The aims of this paper are twofold. First, we want to demonstrate the usability of a dynamic model to perform viability analysis and to design optimal reintroduction strategies. Specifically, we attempt to assess the effect of habitat destruction and population destruction, and their interaction, on species survival, and to design an optimal reintroduction strategy if the species has gone extinct at the regional scale. Second, we want to address specific conservation concerns for a group of plant species that are restricted to low-productivity grasslands, which often decline under current landscape management. Many of these species are long-lived perennials with restricted clonal growth and low dispersal; an assumption of equilibrium is unlikely to be tenable for their populations, especially at the regional scale. We therefore use *Succisa pratensis*, a long-lived perennial plant with rather slow dynamics, as the model species. This species is a typical representative of a rare grassland species in an agricultural landscape in southern Sweden. It has recently been extensively studied (M. Mildén, Z. Münzbergová, T. Herben, and J. Ehrlén, *unpublished manuscript*), and we can rely on the wealth of landscape and population biology information that has been collected for it.

Methods

Study species and system

Succisa pratensis is a perennial, polycarpic, rosette herb with a life span of at least 25 years (Hooftman et al. 2003). In August to September it produces one to several, 20–80 cm high, flowering stems with one to several pale violet flower heads. The flowers are self-compatible, but crossing enhances the seed set considerably (Vergeer et al. 2003). Inbreeding may affect small and isolated populations negatively (Vergeer et al. 2003). Clonal propagation sometimes occurs through side rosettes. In Sweden, *Succisa pratensis* is

most commonly found in dry to wet seminatural grasslands. It benefits from grazing, and the present distribution in the landscape largely depends on the management history, i.e., is closely positively correlated with previous grazing and mowing. After management of a site is abandoned, populations of *Succisa pratensis* can survive for a long time (M. Mildén, Z. Münzbergová, T. Herben, and J. Ehrlén, *unpublished manuscript*).

We collected the field data in the northern part of the Nynäs nature reserve, 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 a landscape fragment of 3.1 × 2.3 km (7.1 km²) containing managed agricultural land, and surrounded by coniferous forests that were considered unsuitable for *Succisa pratensis*. The oldest grasslands were probably already well above sea level 4000 years ago. Since the establishment of two villages in the area around 1500 yr BP, management has 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 early 19th century to 1945, a large proportion of grasslands was converted to arable field 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 a proportion of former fields have been turned into pastures. At present, grasslands constitute 18% of the study area, of which almost half are >200 years old.

Landscape data collection

From 2000 to 2002, we carefully inventoried the area and recorded the size, shape, and position of all habitat patches potentially suitable for *Succisa pratensis*. We recorded whether these patches were occupied and the population sizes (number of flowering and vegetative individuals) within each occupied patch. We assessed the suitability of unoccupied habitat patches both by comparing the floristic composition of unoccupied patches with that of occupied ones, and by using seed-sowing experiments in 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 the Beals index that express the probability of species occurrence in a patch using number of joint occurrences with other species (Beals 1984, Münzbergová and Herben 2004). The likelihood that *Succisa pratensis* would occur in an unoccupied patch was estimated using the frequency distribution of Beals index values in the occupied patches. An unoccupied patch having Beals index value equal to 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 about half of the unoccupied patches 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 the three 10 × 10 cm plots, with three unsown plots used as controls. All plots were recorded in early June and mid-September each year. The results of the seed-sowing experiment were well correlated with the Beals index values, thus further supporting our classification (M. Mildén, Z. Münzbergová, T. Herben, and J. Ehrlén, *unpublished manuscript*).

Demographic data collection and analysis

Demographic data were collected at three grazed and two non-grazed sites. In each population we recorded at least 250 plants with a minimum of 50 flowering individuals. Individual plants were mapped using a grid frame with mesh size of 10 cm × 10 cm. Each individual plant was recorded once a year and followed from 2000 through 2002. At each visit emerged seedlings were searched for, recorded, and included in the study. Following this protocol, seedlings that emerged and died the same field season before recording were not included in the study. Because we model population dynamics at one-year steps, this does not affect our results. During flowering, we measured length and width of the largest leaf and flower number. The product of length and width of the largest leaf was used as an estimate of plant size. The number of seeds per flower head was estimated by examining 30 flower heads outside the permanent plots in each year and population. Seed germination experiments were carried out at each site. At the time of seed ripening each year, 50 seeds were sown into six plots of 10 × 10 cm. The sowing plots were visited twice a year, in early June and mid-September, and the number of new and surviving seedlings was recorded.

To build a matrix model of the dynamics of the different populations, *Succisa 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 mm²); (4) large vegetative individuals (estimated area of the largest leaf >449 mm²); and (5) flowering individuals. We then used this division to calculate transition probability of individuals of each stage in one year to each stage in the next year. First-year germination rates were estimated from the seed-sowing experiments in 2000 and 2001 as the proportion of sown seeds that germinated. Germination rates of seeds in the second and subsequent year after sowing were assumed to be equal to germination in the first year. Survival in the soil seed bank was calculated from the number of seedlings that emerged in the second year after sowing based on the assumption of constant germination rates. Seedling sur-

vival was estimated from seedlings in the seed-sowing experiments. For both the survival of seeds in the soil and of seedlings we used the estimate for the 2000–2001 transition also for the 2001–2002 transition.

The model

The model simulates a set of habitat patches explicitly located on the simulation plane. In our example, the simulation plane represented a rectangle of an area of 7.13 km², which covers the entire habitat surveyed in the field study. Absorbing boundaries (i.e., diaspores passing over the boundary are lost) were used because forests largely surround the region modeled. The sizes and shapes of patches were taken from the field inventory. The patches were represented as sets of contiguous cells (cell size 5×5 m) with explicit positions in the simulation plane. Each patch was assigned a habitat quality (grazed or ungrazed) based on the field data.

Local population dynamics 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 kth patch was modeled as

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

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

Density dependence within habitats was modeled using a logistic growth equation. We used 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 then replaced by the following term:

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

where λ is the dominant eigenvalue of the matrix $\mathbf{A}_{Q(k)}$, $N_k(t)$ is the total population size (sum of all stages) at the time t (before the matrix multiplication), and K is the maximum number of individuals in the patch of the given size calculated as a product of habitat size and maximum density. This equation affects the results only when population size is close to carrying capacity, and was considered the best solution given that we do not know the exact shape of the relationship. Finally, each vector element was replaced by a Poisson-distributed deviate with the mean of x_{ik} to represent demographic stochasticity. These numbers were combined to produce a new population vector $\mathbf{x}_k(t + 1)$. In our case, maximum population size was estimated as a product of the third highest density of *Succisa pratensis* found in the field (the two most extreme densities were excluded because they resulted in very high population sizes) and patch size. Using the highest density did not, however, quantitatively affect our results (data not shown).

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 (see *Parameter estimation and initial conditions*). Environmental stochasticity was assumed to be uncorrelated over space and time.

Following Tackenberg et al. (2003), two components of dispersal were modeled: distance dependent (unassisted and wind dispersed) and distance independent (adhesive dispersal by animals). Distance-dependent (dd) dispersal was assumed to affect most of the seeds, while distance-independent (di) dispersal was used to model rare dispersal events (see the following paragraphs 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). Number of seeds arriving at the cell i by distance-dependent dispersal is therefore defined as

$$n_i = \frac{1 - p}{T} \sum_k \sum_j I_{jk} \frac{x_{0k}}{A_k}\exp(-\alpha d_{ij}) \qquad (3)$$

where p is the proportion of seeds spread independent of distance, x_{0k} is the number of seeds produced at the habitat k, A_k is the area (number of cells) of the kth habitat, α determines the effect of distance on the number of seeds dispersed, 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 $[\Sigma_j\exp(-\alpha d_{1j})]$; j means indexing over all cells in the grid, and k 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.,

$$N_{ddl} = \sum_i n_i \qquad (4)$$

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:

$$N_{dil} = p\frac{A_l}{A} \sum_k x_{0k} \qquad (5)$$

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}.

Parameter estimation and initial conditions

There were 6 matrices from grazed sites (3 populations $\times$ 2 transition periods) and 4 matrices from ungrazed sites (2 populations $\times$ 2 transition periods). To represent environmental stochasticity, demographic matrices collected at all populations of one habitat quality (grazed and ungrazed) in both transition periods were pooled. In this way we pooled spatial environmental variation (data from three and two different

sites, respectively) separately for each habitat quality (grazed or ungrazed) with the temporal variation obtained by recording demography over two transition periods. For the simulation, matrices were drawn from the pool of matrices of the given habitat quality in proportions derived from the field data on occurrence of these habitat types. Effect of the quality of our local demography information on the results was estimated by bootstrapping the original data used to construct demography matrices and performing the simulations with matrices based on these bootstrapped data (see Appendix: Fig. A2). Since the results based on the bootstrapped matrices did not significantly differ from those based on the original matrices, we present results only from the latter.

Dispersal distance was estimated as the product of plant height and wind speed divided by the terminal velocity, using the formula in 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 *Succisa pratensis* (0.25–0.60 m), the estimated dispersal distances ranged from 0.35 to 2.77 m. We first tested several values from this range. Because results were similar for different values, we show only the results for one value, 0.94 m. No good estimation of the proportion of seeds dispersing independently of distance was available. We therefore ran simulations with several values (0.00001 to 0.001), values that we considered to cover the range where the true value of this parameter would fall. The results for different values were similar, and thus only simulations assuming that 0.0001 of seeds were dispersing independently of distance are shown. The sensitivity of our results to estimates of species population dynamics and dispersal is shown in the Appendix: Figs. A3–A6.

Habitat and population destruction

To assess the prospect of species survival after future landscape changes we studied effects of two different kinds of changes that are likely to be associated with ongoing habitat fragmentation and deterioration. First, we examined the effects of habitat destruction, i.e., of permanent removal of some suitable habitat patches from the system. Second, we investigated the effects of population destruction, i.e., of single removal of the population from a habitat patch while keeping the habitat essentially intact and ready for recolonization. Habitat destruction mimics situations where available habitats disappear from the landscape because they are converted to arable fields, become unsuitable due to successional changes, or are destroyed due to construction activities. Assessing the proportion of habitats that can be destroyed without affecting species survival probability at a landscape level is essentially the same as finding the threshold value in metapopulation capacity models. In contrast, population destruction brings in another dimension, that is, the assumption that a population may be wiped out of its habitat without essentially affecting the habitat. Population destruction mimics large-scale noncorrelated events, such as insect outbreak, burning, or intensive trampling that result in sudden disappearance of local populations.

The effects of habitat destruction were assessed by randomly removing a fraction, ranging from 10% to 90%, of all habitat patches from the system. Effects of population destruction were simulated by removing all individuals (including seeds) from a given habitat patch; this was attained by drawing a zero transition matrix for a habitat patch with a specified probability. This probability was set so that population destruction (per habitat patch) occurred on average once every 20, 30, 40, or 50 years. We also investigated combined effects of population destruction and habitat destruction. The effects of population and habitat destruction were assessed using the parameter combination without any population and habitat destruction as a reference.

In all simulations of effects of population destruction and habitat destruction, we used actual patch occupancy and population sizes in 2002 as initial conditions. Since the field data did not contain numbers of seeds and seedlings, these were calculated from the number of adult individuals assuming a stable stage structure. To examine the effects of this assumption we performed the analysis assuming that no seeds and seedlings were present initially. Differences in the initial setting had no major effect on the results (see the Appendix: Fig. A1).

In all cases, the response variables (total population size, proportion of occupied habitat patches, and probability of extinction at the landscape level) were evaluated after 100 years. We used the averages of 100 runs for each parameter combination.

Reintroduction strategies

To examine the efficiency of reintroduction strategies we used the same model of species dynamics and the same realistic landscape as above and assumed that the species had gone extinct. We investigated the effect of sowing a fixed number of seeds and distributing them in different ways over an unoccupied landscape. We studied introductions of either 1000, 10 000 or 100 000 seeds into the landscape. This roughly corresponds to seed production of 1, 10, and 100 flowering individuals, respectively. Five reintroduction strategies were evaluated: (1) introducing an equal number of seeds into each habitat patch, (2) introducing an equal number of seeds into 10 habitat patches systematically distributed over the landscape, (3) introducing an equal number of seeds into the 10 largest habitat patches, (4) introducing equal numbers of seeds into the three largest habitat patches, and (5) introducing all the seeds into the largest habitat patch only. Further, we combined these strategies with population destructions occurring on average once every 20 or 50 years. This mimicked large-
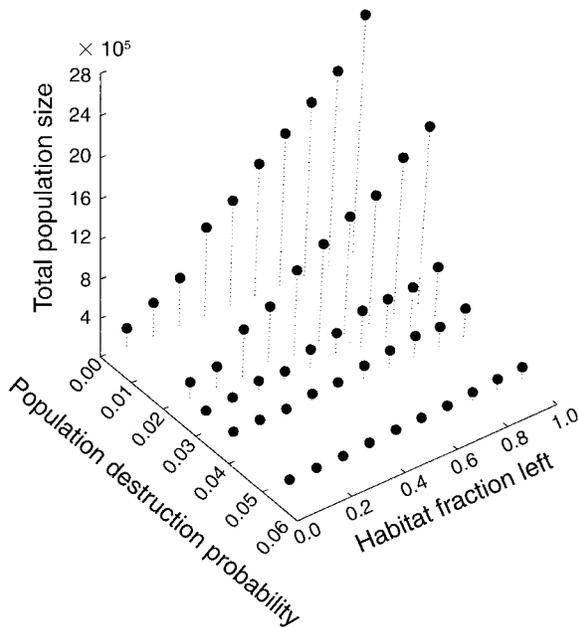
FIG. 1. Effect of population destruction probability and fraction of the habitat left on total population size of *Succisa pratensis* after 100 years. The points are means of 100 simulations. After population destruction, no living individual remains in the habitat patch. In all simulations, the proportion of seeds dispersing independently of distance was 0.0001.
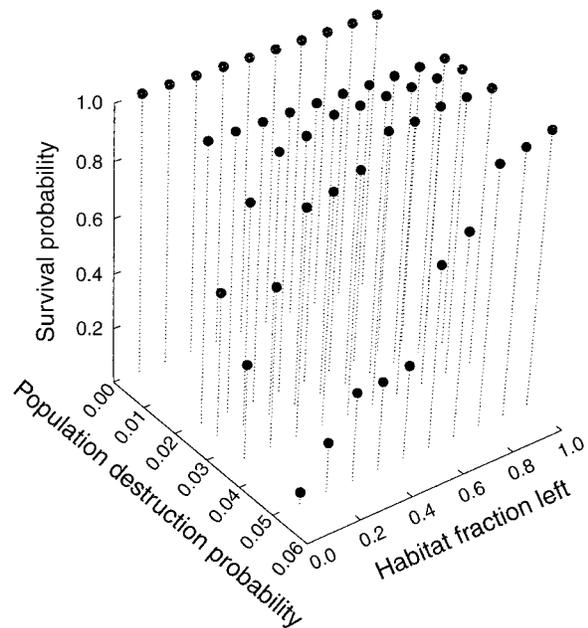
FIG. 2. Effect of population destruction probability and habitat fraction left on survival probability of the whole metapopulation; the vertical axis indicates the proportion of realizations (out of 100) where *Succisa pratensis* persisted after 100 years. After population destruction, no living individual remains in the habitat patch. In all simulations, the proportion of seeds dispersing independently of distance was 0.0001.

scale noncorrelated population destructions that could interfere with the reintroduction attempts. The response variables (total population size, number of occupied habitat patches) were evaluated after 20 and 100 years. Results were evaluated using the same response variables as for the effects of habitat destruction and population destruction discussed in the previous section.

RESULTS

Habitat and population destruction

Total population size declined strongly with both increased habitat and population destruction (Fig. 1). In the case of habitat destruction, this was simply the effect of a lower carrying capacity of the environment. The species had a 100% survival probability even if only 20% of the habitat patches remained (Fig. 2), suggesting that habitat destruction alone does not affect species survival over 100 years. Also patch occupancy was little affected by habitat destruction only (Fig. 3).

In contrast to the small effect of habitat destruction, population destruction occurring every 20 years resulted in a very high probability of extinction even in intact habitat patch networks (Fig. 2).

There was a strong effect of the interaction between habitat destruction and population destruction, and a higher number of habitat patches was needed to maintain the species in landscapes with a higher frequency of population destructions (Fig. 2).
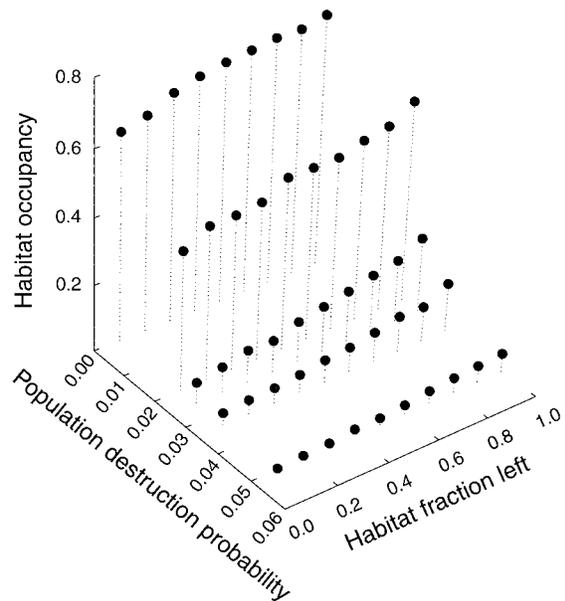
FIG. 3. Effect of population destruction probability and habitat fraction left on relative habitat occupancy (proportion of all existing habitats) of *Succisa pratensis* after 100 years. The points are means of 100 simulations. After population destruction, no living individual remains in the habitat patch. In all simulations, the proportion of seeds dispersing independently of distance was 0.0001.

FIG. 4. Total population size of *Succisa pratensis* 100 years after reintroduction. Reintroduction is based on three amounts of seeds available (no. seeds); these are distributed using five different strategies, i.e., ways in which the seeds were distributed over the landscape. ''All'' means that seeds were distributed evenly among all habitats, ''10 regular'' means 10 habitats regularly distributed over the landscape, ''10 largest'' means 10 largest habitats, ''3 largest'' means three largest habitats, and ''1 largest'' means one largest habitat. Results are based on 100 simulation runs. In all simulations, the proportion of seeds dispersing independently of distance was 0.0001. For the ''box and whisker'' plots, the horizontal center line is the median, the box covers the interquartile range, and the whiskers indicate maximum and minimum values.
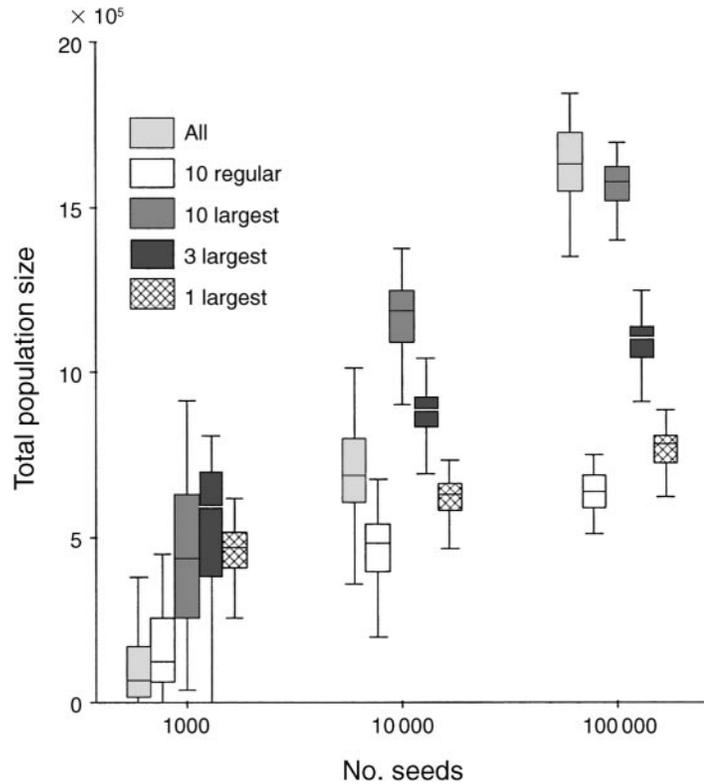
Reintroduction strategies

The optimal reintroduction strategy to maximize total population size and the number of occupied habitats was dependent on initial seed number (Figs. 4 and 5). The results after 20 and 100 years were similar, and the frequency of population destructions had little effect (not shown).

Introducing the species into the three largest habitat patches was the best strategy to maximize population size if only 1000 seeds were available. If 10 000 seeds were available, then introducing them into the 10 largest habitat patches was the best strategy. Introduction to all habitat patches was the best strategy if 100 000 seeds were available (Fig. 4).

Introducing seeds into the 10 largest habitat patches was the best strategy to maximize the number of occupied habitats if only 1000 seeds were available. If at least 10 000 seeds were available, then introducing seeds to all habitat patches was the best strategy (Fig. 5).

DISCUSSION

In this study we demonstrate an approach to estimate the prospect of species survival at the landscape level that does not assume that the target species is currently in equilibrium between colonization and extinctions. Nonequilibriums may arise because colonization and extinction rates are slow compared with the rate of landscape change. Several recent studies suggest that time lags and nonequilibrium dynamics are important features of many ecosystems and plant life forms. For forest ecosystems, it has been shown that new forests are colonized by forest herbs only very slowly, and mainly from adjacent older forests (Matlack 1994, Brunet et al. 2000, Gerhardt and Foster 2002, Wulf 2003, Verheyen and Hermy 2004). Similarly in agricultural landscapes, it has been shown that past landscape structure is a better determinant of species distribution than the present landscape structure (e.g., Lindborg and Eriksson 2004). Moreover, Eriksson (1996) suggested that populations of many species might persist for several decades after the conditions have become unfavorable, in the sense that they can no longer complete their entire life cycle. Although such delays in time to extinction may be most pronounced in long-lived plants, slow colonization rates seem to be common in many plants (Eriksson and Ehrlén 1992, Turnbull et al. 2000). Approaches such as the one used in the current study are thus likely to be useful for a wide range of ecosystems and plant life forms. Furthermore, this approach allows for estimation of short-term effects of habitat and population destruction, i.e., effects causing a nonequilibrium state by definition. This is not possible with equilibrium models, giving this model a wide applicability for all types of organisms.

Population viability

Population destruction strongly interacts with habitat destruction in our system. This suggests that incor-
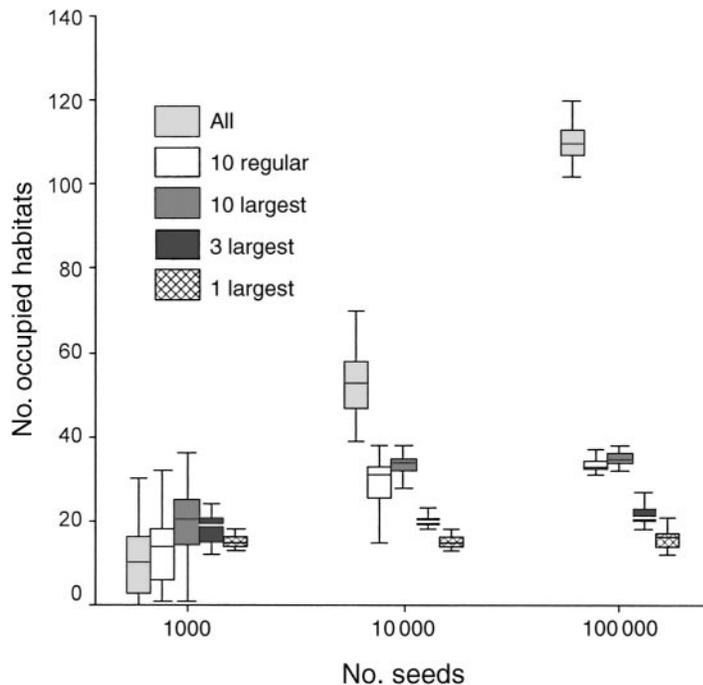
Fig. 5. Number of occupied habitats 100 years after reintroduction. Reintroduction is based on three amounts of seeds available (no. seeds), distributed using five different strategies, as defined in Fig. 4. Results are based on 100 simulation runs. In all simulations proportion of seeds dispersing independently of distance was 0.0001. For the ''box and whisker'' plots, the horizontal center line is the median, the box covers the interquartile range, and the whiskers indicate maximum and minimum values.

porating population destruction into models estimating the prospect of species survival at a landscape level is important. Since population destruction is a factor causing nonequilibrium, the necessity to incorporate it supports the need for nonequilibrium models. These results correspond well with the biology of *Succisa pratensis*, which is a long-lived, slowly growing perennial with seeds that lack any specific adaptation to wind dispersal (Grime et al. 1989). It has rather low colonization ability and is strongly affected by demographic stochasticity in early stages of population development, but is highly persistent in a habitat patch once the population becomes established. If there are no population destructions and local conditions remain the same, then the species is capable of surviving even if only one population is left.

In reality, however, population destructions do occur and have to be taken into account when assessing species survival in the landscape. A methodological difficulty here is that population destructions occur at different temporal and spatial scales. Large-scale population destruction that has the strongest effect is often so rare that realistic estimates of their frequency are seldom available. In the course of our study, two population destructions due to construction work that resulted in total disappearance of a local population were observed (M. Mildén, *personal observation*). Both of these events wiped out the populations while leaving the habitats essentially intact; vegetation recovered very fast, indicating that the habitats remained suitable. Therefore we believe that population destructions need to be taken into account when assessing the risks for long-term survival of *Succisa pratensis*. The data pre-

sented indeed show that for a slow-growing plant with low rate of spreading, rate of population destruction is important and determines whether the species will be able to survive. The effect of habitat destruction thus has to be assessed in interaction with population destruction.

While interpreting these results it should be kept in mind that the predictions are based on the assumption that local demography is stable over time. This is clearly a weak point of the model, since it does not incorporate possible negative effects of lower population size, greater isolation, and habitat deterioration on vital rates. Such effects have been repeatedly shown to play an important role in many species (e.g., Lienert et al. 2002, Paschke et al. 2002, Vergeer et al. 2003). Incorporating these effects is feasible; however, we do not yet have any realistic estimates of such effects for *Succisa pratensis*.

Optimal reintroduction strategy

Using our model, we were able to design optimal reintroduction strategies for the study species. From the modeling perspective, reintroduction is essentially identical to viability analysis of existing populations; only the initial conditions differ. It again requires following the species' local population dynamics and its spread between habitat patches over time. Once the model is parameterized for the species, it can thus be used for studying both the effects of habitat and population destruction and the optimal reintroduction strategy. In a manner similar to the analysis of the effect of population destruction, designing optimal reintroduction strategy also involves answering a question

regarding nonequilibrium behavior, and would thus also not be feasible with any equilibrium model.

Assessment of an optimal reintroduction strategy in a fragmented landscape depends on which parameter (total population size or number of occupied habitat patches) one wants to maximize. However, the optimal strategy also depends on the number of seeds available. If a sufficiently large number of seeds are available, then distributing seeds equally among all habitat patches maximizes the number of occupied habitat patches. If only few seeds are available, this strategy leads to a very high probability of initial local population extinctions due to demographic stochasticity, and it is much better to introduce the seeds to only the 10 largest habitat patches. A similar pattern holds for local population size, where introducing seeds to 10 or all habitats proved to be the best strategy, depending on the number of seeds available.

It should also be noted that the conclusions on optimal strategy did not differ much when evaluated after 20 and 100 years. This is clearly the result of slow dynamics of the species, since it is far from equilibrium even after 100 years. Detailed analysis of the model predictions shows that the species can attain equilibrium in the landscape only at a time frame of several thousand years (M. Mildén, Z. Münzbergová, T. Herben, and J. Ehrlén, *unpublished data*).

The decision on the parameter to be maximized (total population size or number of occupied habitats) depends on whether there is a need to spread the risk between many habitat patches. This, in turn, largely depends on the probability of population destruction as shown by simulations of species survival. If the frequency of such events is high, then the reintroduction strategy should be designed to maximize the number of habitat patches occupied. While the results on optimal reintroduction strategy did not qualitatively depend on whether or not population destructions were introduced in the system, the results clearly confirm that habitat occupancy is a less sensitive measure than total population size.

The difference between the conclusions on the optimal reintroduction strategy based on the parameter to be maximized alone is intuitive. Its interaction with the number of available seeds, however, is not straightforward and shows that this kind of simulation experiment is helpful in developing reintroduction strategies at a landscape level. In combination with considerations on optimal reintroduction strategy at a local level (e.g., Schemske et al. 1994, Hodder and Bullock 1997, van Groenendael et al. 1998, Smulders et al. 2000, Kauffman et al. 2003), this approach is likely to improve the design of future reintroduction plans.

Conclusions

Compared to most other methods, the approach presented here makes the estimation of the effect of habitat destruction possible, irrespective of whether the species distribution is in a transient stage or in equilibrium. For this reason, it also enables the inclusion of other processes such as population destruction that played a key role for the survival of *Succisa pratensis*.

A further strength of this approach is its ability to incorporate a whole range of landscape and species-specific information and evaluate the outcome over any time frame. The same feature, however, makes this approach data intensive. It requires information on the explicit position of all available habitat patches, the present distribution of the species, the magnitude of dispersal, and on local population dynamics. Therefore, the results are more difficult to obtain, and are necessarily more context-dependent and more difficult to generalize. However given the slow dynamics of *Succisa pratensis*, as well as of many similar long-lived perennial plants, only a dynamic model such as the one presented here makes it fully possible to perform population viability analysis for the species in fragmented landscapes and to design the most appropriate reintroduction strategy.

While the data available in this study were rather detailed, more easily obtained information from aerial photographs and rough estimates of species demography should be sufficient for many systems. Even with rough estimates, the information gained using this approach, compared to traditional approaches, is expected to be much more accurate and reliable. Sensitivity analyses, which demonstrate that the conclusions of our model are not affected by changing the model's parameters (provided that they stay within a reasonable range) support such a conclusion.

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APPENDIX

Figures showing sensitivity of the results of simulations to estimates of population size, local population dynamics, and dispersal are available in ESA's Electronic Data Archive: *Ecological Archives* A015-038-A1.