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Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: linking dynamical modelling with historical maps

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Summary

1 We attempt to explain the current distribution of a long-lived perennial plant, *Succisa pratensis*, in a rural landscape in southern Sweden by linking its population biology with documented changes in the landscape, using a dynamical, spatially explicit model incorporating population dynamics and spatial spreading of the plant. Changes in the landscape were inferred from historical maps (1850 and 1900) and aerial photographs (1945 and 2001).

2 We tested whether predictions for the current species distribution are affected by assumptions about its early 19th century distribution, to determine whether recent history and current processes are dominant, and how past landscape changes determine current distributions.

3 Initial conditions influence predictions of current distribution, suggesting that the current distribution still partly reflects the distribution of the species in the early 19th century. A period of 150 years is too short for *Succisa* to have spread extensively if dispersal parameters are given realistic values.

4 Simulations in which present-day land-use patterns were imposed at earlier dates showed that changes in landscape structure over the past 175 years also had a strong effect on the present-day habitat occupancy and population sizes of *Succisa*.

5 The dominant process for *Succisa* now is extinction from marginal habitats. It is therefore likely that the (relatively) high present-day occupation patterns are still due to much larger areas having been available in the past rather than to successful dispersal. Although the species has responded to landscape changes, there is little evidence of population sizes reaching equilibrium.

6 Our approach shows that the wealth of landscape information available from historical maps can be linked with data on population biology by means of dynamical models that can make predictions about species dynamics.

Key-words: equilibrium, extinction debt, landscape manipulation experiments, land-use change, metapopulation dynamics, population biology, southern Sweden, transient dynamics

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Introduction

Whether the distribution of a plant species (at any scale) is at equilibrium with its environment or whether it is in a transient state has major consequences for its ecology (Williams *et al*. 2004). At equilibrium, the observed patterns are primarily due to present-day processes, such as tolerance to environmental factors or species interactions; these processes can, at least in principle, be studied and linked to the patterns. By contrast, the transient behaviour of a non-equilibrium system is largely determined by its history, and an understanding of the system is therefore impossible without reference to its past. Whether a plant distribution is in equilibrium is

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primarily determined by the rate of spread of the species relative to the rate of change in the spatial structure of available habitats.

It has been shown that patterns of plant species distribution and abundance are influenced by landscape history (cf. Peterken & Game 1984; Foster 1993, 2002; de Blois *et al.* 2002; Eriksson *et al.* 2002). Historical effects often reflect a delayed response to landscape changes, either due to local populations resisting extinction or due to slow colonization when new habitat patches become available. If the time from habitat deterioration to local extinction of a species is long, habitat patches that have become unsuitable for long-term persistence may continue harbouring the species for some time (e.g. Koerner *et al.* 1997; Motzkin *et al.* 1999; Bossuyt & Hermy 2001; Dupouey *et al.* 2002). Imminent local extinctions may be expected at such sites (leading to an extinction debt; see Tilman *et al.* 1994; Hanski & Ovaskainen 2002). Many species are dispersal-limited (e.g. Primack & Miao 1992; Eriksson 1998; Ehrlén & Eriksson 2000; Turnbull *et al.* 2000) and slow colonization may lead to low occupancy at younger sites (i.e. where the present habitat conditions have occurred for a relatively short time). As a consequence, there may also be historical 'pattern effects', i.e. changes in landscape connectivity in time that underlie differences in the present-day distribution of species (Bellemare *et al.* 2002; Vellend 2003; Lindborg & Eriksson 2004).

Such effects are particularly important in agricultural landscapes, where land-use practices have continued to change. Legacies from historical land use are commonly inferred in habitats such as hay meadows and pastures (e.g. Austrheim *et al.* 1999; Norderhaug *et al.* 2000; Cousins & Eriksson 2002), or forests that have developed after abandonment of management (e.g. Bellemare *et al.* 2002), but may also be present in seemingly pristine habitats (Willis 1993; Hermy *et al.* 1999; Hellberg *et al.* 2003; van Gemerden *et al.* 2003; Vellend 2003). Human effects on species composition have usually been suggested to persist for decades or centuries (Bossuyt & Hermy 2001; Eriksson & Ehrlén 2001), but may last for up to one or several millennia (Eriksson 1998; Dupouey *et al.* 2002).

Strictly spatial phenomena, such as area and isolation effects, have received more attention, but comparatively few studies have examined the relative importance of land-use history on regional population dynamics (but see Motzkin *et al.* 1999, 2002; Bruun *et al.* 2001; Cousins & Eriksson 2001; Aragón & Morales 2003). Historical effects are inherently difficult to generalize and are often difficult to quantify. Their use as predictors requires site-specific and quantitative information on the history of the particular landscape, which is not easily dealt with by most general-purpose modelling frameworks.

The advent of geographical information systems has, however, made it possible to quantify historical changes in the landscape by analysing historical maps. Such maps, often drawn up for taxation purposes, are available for many parts of Europe (particularly Sweden) from the late 17th century onwards. The spatial detail on land-use patterns can permit analysis of plant distributions over the past two or even three centuries. Furthermore, population dynamics of plants in fragmented landscapes are now beginning to be better understood. In particular, modelling studies have shown that parameters relating to dispersal (particularly long-distance dispersal) are most critical for plant distribution in a landscape and its dynamics (Mildén *et al.* 2005). Although such parameters are difficult to estimate, recent research has provided much more accurate data on dispersal both by wind and by other vectors (Soons & Heil 2002; Tackenberg *et al.* 2003). An ability to interpret historical maps in terms of habitat availability for the species would allow us to model the dynamics of species-spread in a quantitative fashion. The predictions could then be compared with present-day distributions to determine the role of landscape history.

We used a long-lived perennial plant, *Succisa pratensis*, in an agricultural landscape in south-east Sweden to study the link between the population biology of a species, its present-day distribution and historical changes in the landscape. This species is a typical representative of grassland species in a rural landscape, and much information about its population biology is available (Soons & Heil 2002; Hooftman *et al.* 2003; Vergeer *et al.* 2003; Mildén *et al.* 2005). Landscape changes, which are documented in cadastral maps from the 19th and 20th centuries (Cousins 2001), were used in a dynamic, spatially explicit model that has been developed and tested for this species (Mildén *et al.* 2005). Assumptions regarding the species distribution in the landscape in the early 19th century allow predictions about its current distribution, which can be compared with present-day observations.

We examined how the present-day distribution of the species predicted by the model depended on different assumptions about its distribution in the early 19th century (for a given set of other assumptions on dispersal and population biology of the species). If these assumptions, rather than recent history and current processes, are dominant, we may assume that the current distribution still partly reflects the historical distribution. Because plant dispersal is a critical, but rarely evaluated, parameter driving plant distributions, we examined how different assumptions about dispersal affect the prediction of the model and its fit to the present-day distribution of the species. We also investigated the time frame needed to attain an equilibrium distribution of this species in the landscape given the assumptions on dispersal, and compared this with the documented rates of landscape changes. We also examined how the particular course of landscape changes in the past 200 years has determined the current distribution of *S. pratensis*, assuming different histories of the landscape and assessing the sensitivity of the predictions to these assumptions. In addition to these main questions, we tested the validity of our use of historical maps by examining how different interpretations of one weak assumption (availability of outland, i.e. the extensively grazed areas outside the fenced meadows and fields around the farms, which usually were grazed until the beginning of the 20th century) affect model output.

Methods

STUDY SPECIES AND SYSTEM

Succisa pratensis Moench. (Dipsacaceae) is a perennial polycarpic herb with a maximum life span of at least 25 years (Hooftman *et al*. 2003). In August and September it produces 1–3 flowering stems, each 20–80 cm high, usually carrying a total of up to six, but occasionally more, flowerheads with up to 100 small, pale violet flowers. The flowers are self-compatible, but outcrossing enhances seed set considerably (Vergeer *et al*. 2003). In Sweden, *S. pratensis* is most commonly found in dry to mesic semi-natural grasslands. The species benefits from animal grazing and is able to resprout after mowing, which does not affect seed set (M. Mildén, personal observation). Most seeds land close to the mother plant, but long-distance dispersal by animals is likely to occur because the seed capsules are covered with hairs that easily attach to fur.

We collected the field data in the Nynäs nature reserve, *c*. 100 km south of Stockholm, Sweden (58°50′ N, 17°24′ E), a well-documented agricultural landscape with a long management history (Cousins 2001). The study area (2 × 2.5 km) consisted of managed agricultural land, arable fields, pastures on former fields and semi-natural grassland, surrounded by coniferous forests. This area corresponds to the oldest available historical map, and management has probably been continuous and slowly expanding since the establishment of two villages around 1500 BP (inference based on the occurrence of gravefields, cf. Cousins & Eriksson 2002). In the 17th and 18th centuries, 60% of the area was covered with grassland and 32% was arable land (Cousins 2001). Up until the late 19th century the study area was covered with infields (i.e. semi-natural grasslands, mainly used for hay-making, and arable fields) and areas used for outland grazing. From the late 19th century many meadows were transformed to arable fields, along with an increasing use of ley production, i.e. winter fodder for the livestock produced on cultivated fields. During the 20th century many semi-natural grasslands on poor soils were abandoned and outland grazing was banned; most semi-natural grasslands thus developed into forest, although some were still used for grazing. By contrast, a sizeable proportion of ploughed fields were converted to grasslands in the second half of the 20th century. At present, semi-natural grasslands constitute *c*. 18% of the study area, but not all of them are considered available for *S. pratensis* (see below).

PRESENT-DAY 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). Habitat suitability was assessed by subjectively excluding sites that we considered to be obviously unsuitable (e.g. fields used for crops) and then dividing the remaining patches into good- and poor-quality patches. The inventory of *S. pratensis* was used to indicate vegetation structure, soil moisture and management history likely to be associated with suitable habitat. Because we did not want a potentially biased set of prejudged factors, our definition of poor patches was very inclusive. For habitats classified as good and poor, we then used floristic inventories (see Münzbergová & Herben 2004) and, for a subset of 43 habitats, direct sowing tests to assess directly the patch's suitability for *S. pratensis*. As a result, the current landscape was translated into a set of polygons that were either suitable (good or poor) or unsuitable for *S. pratensis*. For each occupied patch, we recorded population size, in terms of total number of flowering and vegetative individuals (excluding seedlings) in 2000. The suitability assessed in the present-day survey was used to aid interpretation of the historical maps.

HISTORICAL LAND COVER MODEL AND ITS INTERPRETATION

The history of the landscape was based on a model of land cover change in four time layers, 1850, 1900, 1945 and 2001, using data from cadastral maps from the 18th and 19th centuries, aerial photographs from 1945 (black and white) and 2001 (infra-red), and present-day field inventories. A detailed description of sources of information and land-use history of the study area are given in Cousins (2001), Cousins *et al*. (2002) and Cousins & Eriksson (2001, 2002).

We modelled local population dynamics for both good (i.e. those that had been grazed continuously, or with short interruptions) and poor habitats (those where management had been abandoned and which were gradually becoming unsuitable for *S. pratensis*). The land cover model thus aims to represent the spatial distribution of good, poor and unsuitable habitat for the different time layers. For the first time layer (1850) we assumed that grasslands (part of the infields) were suitable (good) habitat. As there is considerable uncertainty about how suitable grazed outlands are for *S. pratensis*, we started by testing all three possible interpretations (good, poor and unsuitable), but the differences were negligible, and we therefore assumed that all grazed outlands were 'good', apart from areas on exposed bedrock.

The second time layer, representing the year 1900, was constructed based on land cover information from the 1850s and 1940s. Our knowledge of rural landscape development in the area led us to assume that patches that were grasslands in 1850 but were arable fields in 1945 became cultivated, and therefore unsuitable, by 1900 and that patches that became forest had become poor habitat by 1900. The time layer of 1900 thus represented a transition stage between the 'traditional' landscape of 1850 and the 'modern' landscape of 1945, which accurately reflected patterns seen in a small-scale regional map from 1904.

For the third (1945) and fourth (2001) time layers, suitability classes were both assigned according to the cover type seen on aerial photographs. For 1945, areas within villages, midfield islets and grasslands with > 50% tree cover were classified as 'poor'. For 2001, areas that were grassland in 1945 but had been transformed to forest by 2001 were classified as 'poor', whereas areas within villages and midfield islets were considered unsuitable and grazed grassland derived from previously arable fields were considered as good habitats.

DEMOGRAPHIC DATA COLLECTION AND ANALYSIS

We selected five *S. pratensis* populations from good habitats, three at grazed and two at ungrazed sites. Ungrazed sites were included to allow for the fact that grazing has often been interrupted in some years, but these sites were only lightly overgrown and *S. pratensis* populations had population growth rates very close to those at the grazed sites (Mildén *et al.* 2005). We recorded at least 250 plants with a minimum of 50 flowering individuals in each population. All plants, including seedlings, were recorded once each year and followed from 2000 through 2002. The product of length and width of the largest leaf was used as an estimate of plant size and the number of flower heads was counted in flowering individuals. At the time of seed ripening in 2000 and 2001, 50 seeds were sown into six plots, each 10 × 10 cm, in undisturbed vegetation and allowed to establish under natural conditions. The 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 > 449 mm^2) and (5) flowering individuals. The transition between small and large vegetative individuals corresponded to the size below which there were almost no individual flowers. The number of seeds per flower head was estimated by examination of 30 flower heads collected outside the permanent plots in each year and for each population. The proportion of seeds germinating in their first year, seed survival in the soil seed bank and seedling survival up to the third year were estimated from the seed sowing experiments.

Estimation of population parameters in poor habitats is more difficult. Populations that had been ungrazed for a long period of time or where successional changes were more extensive were often very small and sparse, although our field observations suggest they consist of seemingly healthy, large individuals with no obvious decrease in seed production, without any small vegetative individuals or seedlings. We therefore assumed that differences in the earlier phases of the life cycle are most important for differences in population performance between good and poor habitats. We adjusted the four matrices (2 populations × 2 years) for good but ungrazed habitats, leaving the performance of large vegetative and flowering individuals unaltered, but deriving the other transition probabilities, from three replicate seed sowing experiments (as above) at each of six sites in late-successional habitats. The transition from flowering to seedlings for poor habitats was calculated as the number of seeds produced per flowering individual in permanent plots in the two ungrazed habitats each year multiplied by the probability that a seed would germinate and survive up to the next summer in sowing plots in late-successional habitats.

THE MODEL

To simulate dynamics of the species in the landscape, we used a simulation model of Münzbergová *et al.* (2005). In the model, habitat patches were explicitly located on a simulation plane representing a rectangular area of 2 × 2.5 km^2. The spatial resolution (i.e. grid cell size) in all maps (historical and present-day land-cover distribution) is 5 × 5 m; separate grid-layers were used to represent each particular temporal layer. Therefore, no habitat could be smaller than one cell. We assumed absorbing boundaries (i.e. diaspores passing over the boundary are lost) given that forests largely surround the region modelled 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 modelled as

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

where elements of $\mathbf{A}_{Q(k)}$ are stage-specific transition probabilities of the habitat quality state $Q(k)$ (grazed or ungrazed). One-year transition intervals were used. To incorporate the fact that patches were of finite sizes, we used a form of the logistic equation (with intrinsic growth rate determined by the dominant eigenvalue of the matrix) with 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 the following term

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

where λ is the dominant eigenvalue of the matrix $\mathbf{A}_{Q(k)}$, $N(t)$ is the total population size (sum of all stages) at time t (before the matrix multiplication) and K is the maximum number of individuals at the patch of the given size. K was calculated as the product of patch size and the maximum *S. pratensis* density at a patch. To simulate demographic stochasticity, each vector element was replaced by a Poisson-distributed deviate with the mean of x_i. These numbers were combined to produce a new population vector $\mathbf{x}_k(t + 1)$. Environmental stochasticity was simulated by using several matrices for each habitat quality. At each step, one matrix was drawn from this set at random with equal probability assigned to each matrix. Environmental stochasticity was assumed to be uncorrelated over space and time.

The model simulated both distance-dependent (unassisted and by wind) and distance-independent dispersal (adhesive dispersal by animals). Distance-independent dispersal was assumed to affect only a small proportion of the seeds and was modelled by removing a fraction of seeds at each step from each patch and redistributing them randomly over the whole simulation plane. For distance-dependent dispersal, seeds produced at each patch were divided equally among the 5 × 5 m cells that comprised that patch and dispersed from these cells according to a negative exponential relationship with the distance between the source and target cells. The seeds arriving at all cells within a patch were summed to yield the seed input to that patch. Seeds that fell into the space between patches were considered lost.

At each step, transitions within patches, including density-dependence, were simulated to yield a seed crop before dispersal, both distance-dependent and distance-independent, was modelled. The random number generator *ran2* (Press *et al.* 1992) was used.

When one landscape structure (map) was replaced by another, the population at each patch was divided equally (retaining the stage structure) among all cells comprising that patch and these cells were projected onto the new landscape structure. Population size at a patch in the new landscape structure was the sum of population sizes at cells that fell on this habitat patch rounded to the nearest integer; plants at cells that fell into uninhabitable areas (not belonging to any patch) were discarded. A patch in the new landscape structure remained empty if no cell belonging to a patch occupied at the old landscape structure fell onto it.

PARAMETER ESTIMATION

To simulate local population dynamics we used 10 matrices (5 populations × 2 transition intervals) for good habitats and 4 (2 populations × 2 intervals) for poor habitats. To represent environmental stochasticity, all demographic matrices in both intervals were pooled. In this way we pooled spatial environmental variation within both good and poor habitats with the temporal variation obtained by recording demography over two transition intervals. This may be assumed to represent well the variation in demography in the past, when livestock densities varied and many patches might have experienced shifts in grazing regime.

Maximum population density (to model density-dependence) was estimated as the product of the mean density of *S. pratensis* found in the field (4.65 individuals m^{-2}) and patch size. We used mean density to allow for spatial heterogeneity within habitats: under favourable conditions, *S. pratensis* can attain much higher densities at a small scale, but we believe that these densities are not representative of the normal densities that thriving populations can attain in a realistic landscape at a realistic temporal scale. Mean dispersal distance, estimated as the product of plant height and wind speed divided by the terminal velocity (Soons & Heil 2002), ranged from 0.35 to 2.77 m and we used either 0.94 or 2.35 m in the simulations (Mildén *et al.* 2005). Because we lacked an estimate of the proportion of seeds dispersing independently of distance, we used two values (10^{-4} and 10^{-3}) that fall into the range of likely values. We worked with four different dispersal assumptions: low distance-independent dispersal/low short-dispersal distance (10^{-4}/0.94), low distance-independent dispersal/high short-dispersal distance (10^{-4}/2.35), high distance-independent dispersal/low short-dispersal distance (10^{-3}/0.94), and high distance-independent dispersal/high short-dispersal distance (10^{-3}/2.35). Analysis of sensitivity of the model to the parameters of local population dynamics (transition matrices) and to parameters of dispersal showed that dispersal is the major parameter determining dynamics of the model (Mildén *et al.* 2005). Mean dispersal distance up to values of several metres has little effect on the overall dynamics of the model. By contrast, distance-independent dispersal has the potential to affect the dynamics strongly if its values are above 0.1% (Mildén *et al.* 2005).

SIMULATION EXPERIMENTS

We used the simulation model calibrated with the field data to predict patch occupancy and population sizes in the calendar year 2000 from different assumptions on the initial patch occupancy, different landscape structures and different assumptions on dispersal. We assumed that the landscape structure, as documented by the individual maps, represents an average value over a symmetric interval so that the 1850 map represents landscape structure from 1825 to 1874, the 1900 map from 1875 to 1921, and the 1945 map from 1922 to 1971. An asymmetric interval (1972–2001) was used for the 2001 map to enable comparison with the present-day distribution. Because the data on the present-day distribution of *S. pratensis* come from 2000, the simulations were always run for 175 years beginning with 1825 to give predicted habitat occupancy and population sizes in 2000.

In the first set of simulations (to address the question of dependence on initial occupancy), we combined, in a factorial design, six different 1825 occupancy scenarios

Table 1 Scenarios for landscape experiments in the third set of simulations. Columns refer to successive temporal layers while the cells indicate which map was applied for the given period

Scenario	First layer 1825–1874	Second layer 1875–1922	Third layer 1923–1971	Fourth layer 1972–2000
S0	1850	1900	1945	2000
S1	1850	1850	1850	1850
S2	1850	1850	1850	2000
S3	1850	1850	1900	2000
S4	1850	1850	1945	2000
S5	1850	1850	2000	2000
S6	1850	1900	1900	2000
S7	1850	1900	2000	2000
S8	1850	1945	1945	2000
S9	1850	1945	2000	2000
S10	1850	2000	2000	2000
S11	2000	2000	2000	2000

with four different assumptions on dispersal (as above) and three different interpretations of the outland (as good, poor or unsuitable for *S. pratensis*). The initial (1825) occupation patterns were as follows.

1. One patch occupied. To separate variation due to stochasticity in the realizations and stochasticity in initial patch selection, 10 different patches were selected randomly, and 100 realizations were run with each of them initially occupied. An initial density of 500 plants was used (pilot experiments showed that changing initial density had little effect on the dynamics of the system). To initialize the size structure, the numbers of plants were recalculated to the long-term average of the stage structure assuming stochastic matrix dynamics with all matrices of the good patches included with the same probability (Caswell 2001).

2. Ten patches occupied. Twelve variants were used: 10 random arrangements of 10 occupied patches over the landscape, together with 10 westernmost patches and 10 easternmost patches occupied. An initial density of 500 plants with stable stage structure was again used.

3. Half of the patches occupied. Twelve variants were used: 10 random arrangements of 50% occupied patches over the landscape, together with the westernmost half of the patches and easternmost half of the patches occupied. An initial density of 500 plants with stable stage structure was used.

4. All patches occupied with an initial density of 500 plants with stable stage structure.

5. Mean equilibrium patch occupation. The mean equilibrium patch occupation was approximated by running the model with the 1850 landscape structure for 5000 years, assuming low dispersal. This amount of time is sufficient to generate an equilibrium landscape structure for most of the parameter settings (Mildén *et al*. 2005). One hundred realizations were run; the patches occupied in more than 50 runs were defined as occupied if the density was equal to the mean density over all the runs; the patches occupied in fewer than 50 runs were defined as unoccupied. Stage structure at each patch was also taken as an average over all the realizations.

6. Projection of the 2000 occupation to the landscape structure of the oldest landscape (1850 map), using the same rules as when one map was replaced by another (see above).

In the second set of simulations (to address questions about the importance of dispersal), we started with two initial landscape patterns in 1925 (10 habitats and projection of the 2000 pattern, i.e. scenarios 2 and 4 above) and combined them with a range of values for each dispersal parameter (proportion of seeds dispersed independently of distance and mean dispersal distance).

In the third set of simulations (to address the impact of land-use changes), we shifted different map layers in time and skipped some maps while retaining the temporal sequence (see Table 1). Two of these scenarios are taken as reference 'null' history scenarios, i.e. 175 years with the present-day landscape only, and equilibrium distribution in the present-day landscape. All 12 scenarios were combined with two different assumptions on dispersal (low and high distance-independent dispersal, combined with long short-distance dispersal). Two different initial conditions were used: 2000 distribution projected to 1850 and 1850 equilibrium distribution; the latter was obtained after running the model with the 1850 map layer for 5000 years with low dispersal assumption (scenarios 5 and 6 above). For the only scenario that does not begin with the map layer of 1850 (S11, Table 1), the actual distribution in 2000 and the 1850 equilibrium distribution projected to the 2000 map layer were used instead.

To determine the time to attain equilibrium for each map layer separately, we ran 100 realizations over 10 000 years for each landscape structure, starting with an initial habitat occupancy of 10 habitats and a population size 100 individuals at each habitat. We calculated mean habitat occupancy for each year (averaged over all realizations) and took the time to attain equilibrium as the time interval required for the yearly mean habitat occupancy to exceed its average calculated over the last 100 years (9900–10 000).

Each parameter combination was run in 100 realizations. The predictions of habitat occupancy and population sizes at individual habitats were compared both over different model parameter settings and with the actual data on habitat occupancy and population sizes in the calendar year 2000. The Jaccard coefficient was used to measure the qualitative fit (fit in habitat occupancy). It is defined as $a/(a + b + c)$, where a is the number of habitats that are both predicted to be occupied and are occupied in the field, b are habitats occupied in the field but predicted to be unoccupied by the model, and c are unoccupied habitats that are predicted to be occupied. The quantitative fit (difference in relative population sizes) was measured by Euclidean distance (further called relative Euclidean distance), defined as

$$\sqrt{\sum\left(\frac{n_{\mathrm{obs}\,i}}{N_{\mathrm{obs}}}-\frac{n_{\mathrm{pred}\,i}}{N_{\mathrm{pred}}}\right)^2}$$

where $n_{\mathrm{obs}\,i}$ is the observed population size at habitat i, $n_{\mathrm{pred}\,i}$ is the predicted population size at habitat i, and N_{obs} and N_{pred} are observed and predicted total population sizes summed over all habitats.

Results

Analysis of historical maps showed pronounced changes in the number and size of habitat patches available for *S. pratensis* over time. The number of patches and the fraction of the landscape available for *S. pratensis* decreased consistently (Table 2, Fig. 1), with an almost fivefold decrease in the area available between 1850 and 2000. In addition, considerable fragmentation occurred between 1850 and 1900, with an increase in the total number of habitats but a decrease in their relative and even absolute sizes. Only 3.6% of the area has remained suitable for the entire 150-year period. There was a threefold decrease in mean habitat size from 1850 to 2000. Time to equilibrium for *S. pratensis* is well correlated with landscape fragmentation: in 1850 the maximum was several hundred years, particularly when outlands are included as available habitat, contrasting with the very long time estimated for the present-day (2000) landscape structure under all dispersal assumptions.

Simulations show that landscape changes are likely to have had a strong effect on habitat occupancy patterns

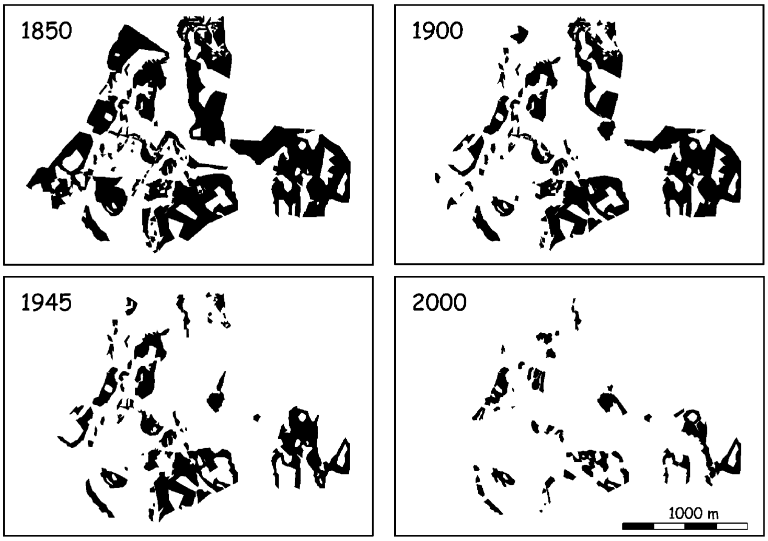

Fig. 1 Distribution of habitats suitable for *Succisa* in the four map layers. Outlands (i.e. the areas outside the fenced meadows and fields) are not included.

Table 2 Basic landscape parameters of individual map layers. I: with outlands (i.e. the areas outside the fenced meadows and fields) included, E: with outlands excluded. Dispersal assumptions: low/low – dispersal distance 1.37 m, proportion of seeds dispersed independently of distance 0.0001; low/high – dispersal distance 1.37 m, proportion of seeds dispersed independently of distance 0.001; high/low – dispersal distance 2.35 m, proportion of seeds dispersed independently of distance 0.0001; high/high – dispersal distance 2.35 m, proportion of seeds dispersed independently of distance 0.001

Time layer	No. of suitable habitats	Fraction of the landscape covered by suitable habitats (%)	Overlap with previous layer (% of the total area)	Mean area of one habitat (% of the total landscape area)	Time to equilibrium (years) under different dispersal assumptions			
					low/low	low/high	high/low	high/high
1850-I	122	22.0		0.180	534	188	377	93
1850-E	115	17.0		0.147	582	224	525	95
1900	140	14.9	12.9	0.107	1911	337	1160	96
1945	89	9.8	8.3	0.110	1954	357	1311	105
2000	67	4.5	3.6	0.067	7861	1311	6368	205

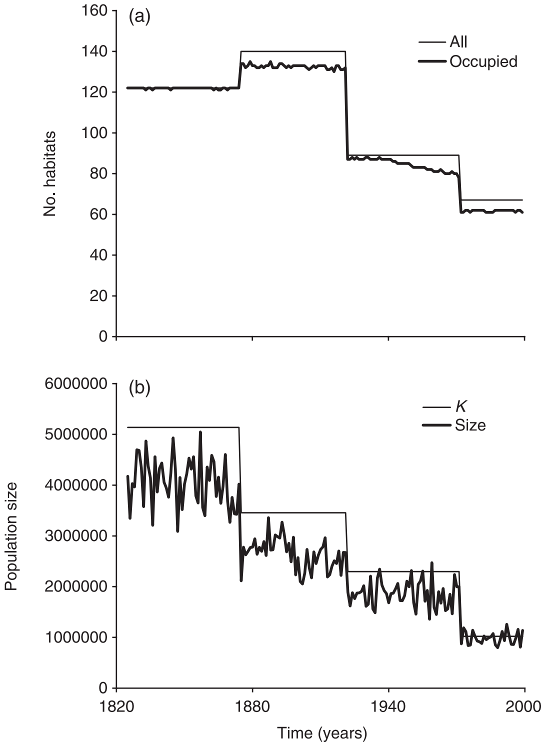

Fig. 2 Simulation of number of occupied habitats (a) and total population size (b) from 1825 to 2000. In (a) All indicates the total number of habitats and Occupied the number occupied; in (b) *K* indicates the population size (number of individuals) if all habitats were occupied at maximum density and Size the actual value. The simulation started with equilibrium habitat occupancy in the 1850 landscape and makes the low dispersal assumption and that outlands are suitable habitat.

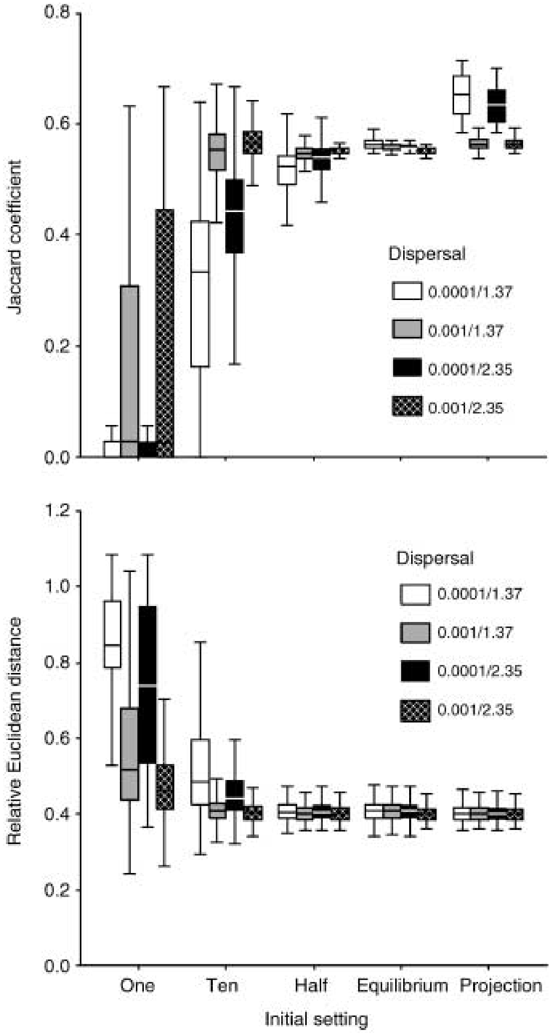

Fig. 3 Effects of different assumptions on occupancy patterns in 1825 on the fit between the distribution predicted for 2000 and field data for habitat occupancy (Jaccard coefficient) and relative population sizes (relative Euclidean distance). Four different types of dispersal are used. Dispersal scenarios are defined by the proportion of seeds dispersed independently of distance/mean dispersal distance (m) (open boxes 0.0001/1.37; grey boxes 0.001/1.37; black boxes 0.0001/2.35; patterned boxes 0.001/2.35). Habitat occupancy scenarios are described in the text and range from 1 (average of 10 different spatial configurations) to 10 (average of 12 different spatial configurations) and half (average of 4 different spatial configurations) to equilibrium and the observed occupancy in 2000 projected back to 1825. One hundred realizations were performed for each parameter combination. Boxes cover interquartile ranges, with horizontal lines showing median values.

and population sizes of *S. pratensis* over the past 175 years (see Fig. 2 for an example) under realistic assumptions on dispersal. The initial distribution of *S. pratensis* within the landscape had a major effect on the outcome of the simulations both in qualitative and in quantitative terms (Fig. 3). In general, the higher the habitat occupancy assumed for 1825, the better the simulation fit with the present-day distribution of *S. pratensis* (lowest when only one habitat was occupied in 1825 but much better when half, all or equilibrium habitat occupancy was assumed). In addition, if the simulation started with low occupancy (1 or 10 habitats), there was high variation in the fit between runs differing in actual spatial arrangement at the beginning (Fig. 4). The best fit (particularly in terms of number of habitats occupied) for all four major dispersal assumptions tested was produced by starting with the present distribution projected back to 1825.

The second set of simulations showed that different assumptions on dispersal had quite strong effects on the outcome, particularly at low initial occupancy and for the qualitative measure of fit (Jaccard coefficient) (Fig. 5). If distance-independent dispersal affected more than 1% of all seeds, the spatial dynamics of *S. pratensis* were fast enough to compensate for landscape changes. Dispersal distance had little effect below 1 m and even greater distances had less effect than distance-independent dispersal. In general, both qualitative and quantitative fit were improved by assuming better dispersal (either long-distance or short-distance). However, high dispersal decreased (qualitative) fit if projected 2000 occupation was used.

By contrast, interpretation of outland in terms of its availability for *S. pratensis* had little effect on the outcome of the simulations (Fig. 6) except when the simulation started with only one habitat occupied in

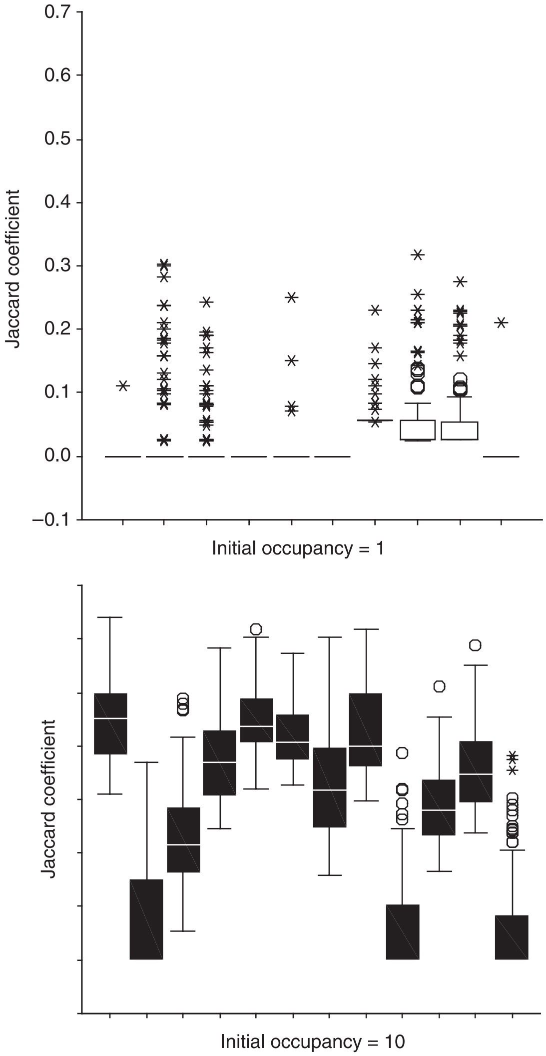

Fig. 4 Effects of different spatial arrangements of initially occupied patches in 1825 on the qualitative fit (Jaccard coefficient) between the distribution predicted for 2000 and field data. The variation between runs with identical initial spatial arrangement is shown for each arrangement tested for each of two occupancy levels. Low dispersal assumptions are used (distance-independent dispersal 10^{-4}, dispersal distance 0.94) and 100 realizations were performed for each parameter combination. Results are displayed as in Fig. 3 except that outlying values closer than three times the interquartile range are shown as circles and the remaining outlying values as stars.

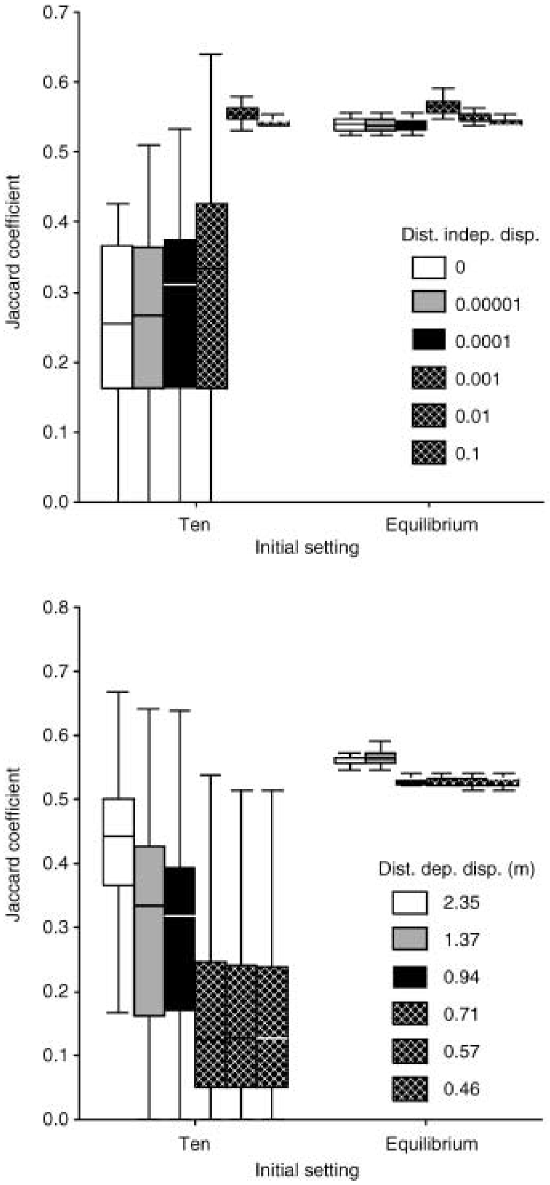

Fig. 5 Effects of the two dispersal parameters on the fit between the distribution predicted for 2000 and field data. (a) Distance-independent dispersal (fraction of the seeds dispersed independently of distance, assuming dispersal distance = 1.37 m) 0, 0.00001, 0.0001, 0.001, 0.01, 0.1, 2.35 (from left to right). (b) Distance-dependent dispersal [mean dispersal distance (m), assuming 0.01% of all seeds undergo distance-independent dispersal] 2.35, 1.37, 0.94, 0.71, 0.57, 0.46 m (from left to right). Data presented as in Fig. 3.

1825 (outlands available for *S. pratensis* produced better fit than outlands unavailable or poor – data not shown).

Comparison of sets of simulations that were identical apart from considering the documented landscape changes (i.e. vs. S11 in Table 1) showed that the fit between the predicted occupancy and the actual *S. pratensis* distribution is enhanced by the inclusion of the historical information (Fig. 7). This is true particularly for simulations starting with initially low occupation, where the plant was able to benefit from easier spread in the much less fragmented 19th century landscape.

The third set of simulations also showed that the duration and sequence of use of maps from different time periods had a strong effect on the final frequency of occupied habitats, but less so for total population size (Fig. 8). In particular, there was a strong negative relationship between the time over which the 2000 map was applied and the frequency of *S. pratensis*. This indicates increased loss of populations from this fragmented landscape where there are fewer and small habitats compared with earlier maps. The predicted population sizes of *S. pratensis* for 2000 are never in equilibrium (running the 2000 landscape for 5000 years

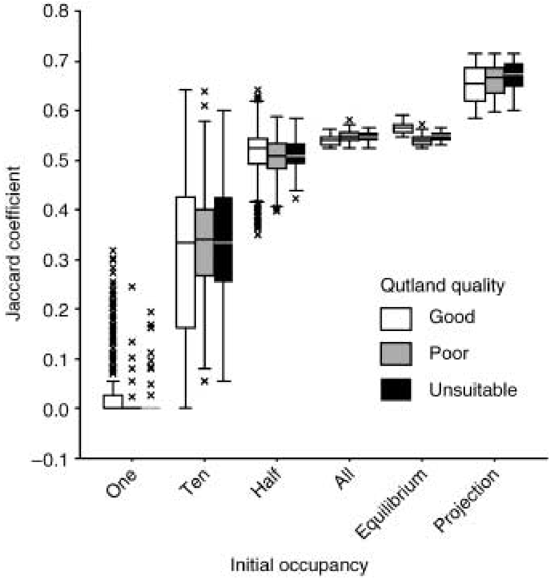

Fig. 6 Effects of different interpretations of outland (i.e. the areas outside the fenced meadows and fields) on the fit between the distribution predicted for 2000 and field data. Open boxes: outland interpreted as good quality; grey boxes: outland interpreted as poor quality; black boxes: outland interpreted as unsuitable. Low dispersal assumptions are used (distance-independent dispersal 10^{-4}, dispersal distance 0.94). One hundred realizations were performed for each parameter combination. Boxes cover interquartile ranges, lines within boxes are medians, and crosses show outlying values.

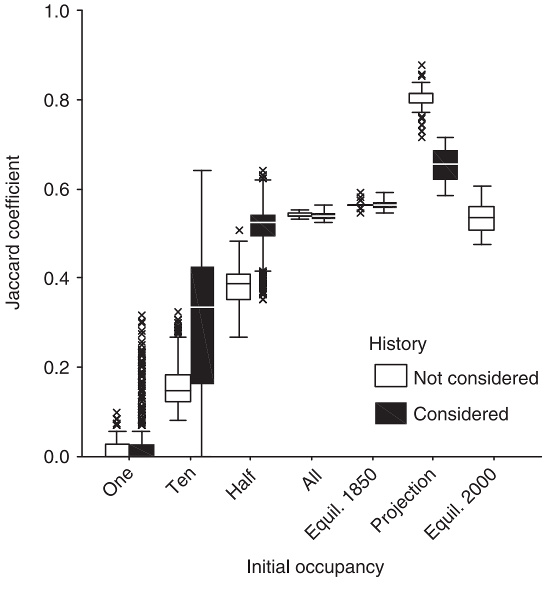

Fig. 7 Effect of using historical information on the quality of the prediction of the present-day pattern. Simulations not considering history (open bars) use the 2000 landscape over the whole time, rather than switching between the four map layers over time (filled bars). Data for habitat occupancy levels (see Fig. 3) are compared with an equilibrium distribution derived for the 2000 landscape over 10 000 years (Equil. 2000). Low dispersal assumptions are used (distance-independent dispersal 10^{-4}, dispersal distance 0.94 m).

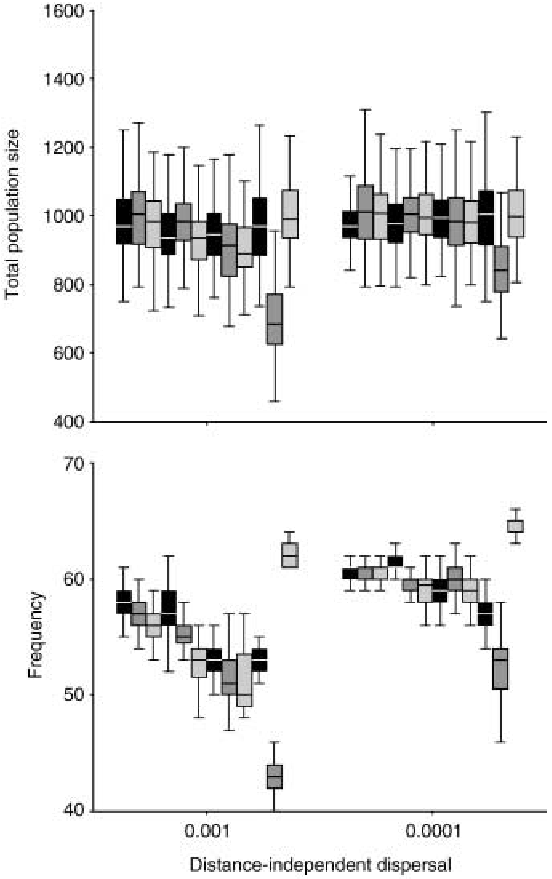

Fig. 8 Effects of manipulation of landscape development scenario on number of occupied habitats (frequency) and total population size of *Succisa pratensis* under two proportions of distance-independent dispersal. Predictions under one of the 12 individual landscape manipulation scenarios are shown in the same order as they are listed in Table 1. Distance-dependent dispersal was assumed to be 1.37 m, and occupancy in 2000 projected back to 1825 was used as the initial condition.

produced much higher occupancy patterns), indicating that the dominant process is now extinction from marginal habitats (thus accounting for the decrease of habitats with the duration of using the 2000 map). Colonization of new habitats will occur, but only over a much longer time scale. The results were not affected by the initial conditions (equilibrium 1825 occupation or projected 2000 occupation used – data not shown). Different dispersal assumptions had a strong effect, but did not change the qualitative picture (Fig. 8).

Discussion

USING HISTORICAL INFORMATION TO EXPLAIN PRESENT-DAY PATTERNS

The concept of history as we use it in the modelling considers the course of changes in the landscape structure that have occurred over the past 175 years. However, it also allows us to include initial conditions, i.e. the distribution of the species in 1825, which will reflect historical processes that are even older, particularly if

S. pratensis was not initially in equilibrium. For obvious reasons, only the first component can be directly tested. Comparing simulations over the known history of the landscape with two 'null' history scenarios (175 years with the present-day landscape and an equilibrium distribution for the present-day landscape) including the history of the landscape gives a better fit. This finding does not depend on initial conditions (Fig. 7): current habitat occupancy is simply too high to be due to 175 years of dispersal in a landscape with the present-day structure.

The effect of initial conditions (i.e. history prior to 1825) can only be studied indirectly by determining which of the potential scenarios best predicts current patterns. In addition to a range of non-specific initial distributions, we tested the use of equilibrium habitat occupancy in the 1850 landscape (conditions prior to 1825 are assumed to have been relatively constant for a sufficiently long period of time and to have been unaffected by transient dynamics) as well as a back-projection of the 2000 distribution to the 1850 landscape structure (as a non-equilibrium distribution that is, *a priori*, likely to produce a good fit to the present-day occupancy pattern). Both the latter scenarios gave good fit, but the back-projection was better – suggesting that *S. pratensis* may not have been in equilibrium, even in 1825. As a corollary, the current distribution may still carry information on the history of *S. pratensis* prior to 1825. These results indicate that the time frame available has been too short for *S. pratensis* to spread in the landscape, and that it is likely to have been present in considerable numbers in 1825.

LANDSCAPE CHANGES AND DISTRIBUTION OF *S. PRATENSIS*

The current distribution of *S. pratensis* can thus be explained either as a strong effect of the initial conditions in 1825 combined with low dispersal, or a weaker effect of the initial conditions combined with high dispersal. As the time to equilibrium in the current landscape is quite long, even under high dispersal assumptions (> 200 years; Table 2), the present-day distribution must be due to either higher dispersal rates in the past or higher connectivity of the past landscape. Although we know nothing about dispersal rates in the past (we may expect them to have been higher than today because of more animal movement), higher landscape connectivity is well documented by the maps. The two-field system, whereby fields were left fallow and grazed every other year, as well as the practice of grazing the infields after harvest, meant that connectivity was much higher in the past. The models show that the current distribution of *S. pratensis* owes a lot to the past landscape structure, irrespective of the dispersal assumptions: the (relatively) high present-day occupation patterns are due to much larger areas having previously been available for *S. pratensis*, and to populations having not yet become extinct, rather than to dispersal processes in the 2000 landscape. Current habitat occupancy or species richness unrelated to present-day connectivity has been demonstrated in other systems: for example, the site connectivity 50 and 100 years ago explained *c*. 50% of the among-site variation in species richness in semi-natural grasslands in Sweden (Lindborg & Eriksson 2004). Similar results were obtained by Bellemare *et al*. (2002) for herbaceous vegetation typical of primary forests, and by Vellend (2003) for species richness of the ground flora in forests.

Landscape manipulations suggest that the arrival of the present-day (2000) landscape structure, with high fragmentation, low cover of available habitats and, consequently, very long time to equilibrium, is the major factor constraining the distribution and spread of the species in comparison with earlier landscapes. However, running the 2000 landscape structure to equilibrium shows that the species is not currently carrying a strong extinction debt. This is due to long survival times at individual habitats provided there are no sudden population destructions by disturbance (Münzbergová *et al*. 2005). The long time to equilibrium is therefore due to low rates of immigration, which have a longer-term impact on distributions.

LIMITATIONS OF THE APPROACH

We identify the following major limitations of this type of study: (i) generally poor knowledge of species dispersal, (ii) lack of information on the population biology of the species in the past, (iii) interpretation of the maps in terms of habitat suitability and (iv) non-independence of different tests of historical effects.

Dispersal parameters are generally the driving force for this and similar kinds of model (Higgins *et al*. 2001, 2003; Fig. 5) and their estimation is rather difficult (Tackenberg *et al*. 2003). It should be noted that high values of distance-independent dispersal (> 1% of seeds dispersed independently of distance) override the historical signal completely (Fig. 3), whereas mean dispersal distance does not have this effect. However, such high values are unlikely given the shape, size and dispersal biology of *Succisa* seeds. Lower dispersal values have a large effect on model predictions (Figs 3 and 8), but the qualitative prediction (i.e. that the landscape changes are too fast relative to species dispersal) holds independently of the actual values.

Although the assumption of stable population biology over time is perhaps reasonable, dispersal rates might have undergone changes. As the dominant component of dispersal is occasional, animal-mediated, long-distance dispersal (Mildén *et al*. 2005), historical grazing patterns might have led to rather different patterns of dispersal. Although even a qualitative prediction is difficult, given the poor documentation, increased connectivity in the early 19th century may mean that short-distance dispersal (which is likely not to change over time) may have been more important in relative terms.

Any kind of dynamical modelling of the past is based on the assumption that we are able to interpret the historical maps correctly in terms of the availability of the patches for *S. pratensis*. The outlands, i.e. the areas outside the fenced meadows and fields around the village, were grazed and might (or might not) have been suitable habitats for *S. pratensis*. Indeed, at the beginning of the 20th century the outland was fairly open with no or few shrubs as a result of grazing (S. Cousins unpublished data). A different interpretation of the suitability of outlands changes the connectivity of the landscape and thus the potential of *S. pratensis* to spread. Fortunately, the model showed that the predictions do not depend to any great degree on the assumptions about this particular habitat; however, in other cases, uncertainties in map interpretation may represent a serious problem.

Finally, the effects of actual changes of the landscape over the past 175 years are not independent of the distribution of the species prior to 1825. As a result, assumptions on one have to be made in order to test the other. This is less of a problem when different initial conditions are tested, in which case the subsequent landscape change can be taken as given. However, testing the effect of the landscape change as such is strongly dependent on the initial conditions and cannot be disentangled from assumptions on them.

OTHER POSSIBLE USES OF THE APPROACH

Linking dynamical modelling based on data on the population biology of a species to interpreted historical maps enables us to perform quantitative and predictive analyses of historical effects operating on plant distributions. Although only applicable when the underlying historical information can be interpreted spatially, this approach may become more widespread as many old maps are made available through the use of GIS technologies. It is thus likely that many similar cases of patterns that can be explained by history will emerge (Lindborg & Eriksson 2004). Dynamical modelling enables us to determine the ecological effects of increased connectivity in terms of higher spread of species over realistic time scales.

A similar approach can be also used in reverse fashion, i.e. to deduce historical patterns from current species distributions. Thus, *S. pratensis* still seems to be carrying information on its 1825 distribution, despite a general decrease of available area over time. The deduction of historical patterns from current distributions can be advanced by linking them to phylogeographical information on fine-scale similarities in the genetic composition of populations. This can be done over different temporal and spatial scales, from several decades or centuries in rapidly changing agricultural landscapes to long-term changes, e.g. over the Holocene.

Considerations of land-use history provide several benefits for conservation biology. Identifying possible historical constraints (such as non-equilibrium dynamics) in species distributions and abundances and the proper time frames for dispersal limitation can help in the design of conservation strategies. For example, the present-day pattern of *S. pratensis* suggests that the effects of fragmentation are critical for conservation, whereas modelling has shown that current habitat occupancy is not related to present-day connectivity. It may also help in the identification of remnant populations, which are necessary to set criteria for choosing restoration sites. Historical analyses can also be useful in integrating biological and cultural values of landscapes, increasing public support for conservation plans and resolving conflicts between different conservation goals (e.g. wilderness vs. cultural landscapes).

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