A Metapopulation Model for Primula Vulgaris, A Temperate Forest Understorey Herb

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Summary

1 We suggest that *Primula vulgaris* in woodland habitats may form metapopulations: colonization is associated with the opening of canopy gaps and local populations become extinct as the canopy closes. The metapopulation is seen as a permanently changing system in which colonizations and extinctions are constantly occurring, coupled with forest canopy dynamics.

2 To describe metapopulation dynamics we use a Markovian model that incorporates the different stages through which local populations pass; we calculate the transition probabilities among those stages and estimate colonization and extinction rates. We combine empirical information on the demography of local populations and the dynamics of the forest mosaic in the model and use it to explore the effect of seed dispersal, f_d (i.e. the fraction of seeds dispersing out of populations) and forest disturbance rate, k, on metapopulation growth rate, λ_M (i.e. the rate at which the number of populations in the metapopulation increases or decreases).

3 Increasing either f_d or k has a positive effect on the projected metapopulation growth rate: higher disturbance rates increase the frequency of newly opened gaps in the environment and higher seed dispersal levels increase the probability of gap colonization.

4 Metapopulation growth rate is also affected by a number of other variables. It declines when time to local population extinction decreases and when fecundity is lower. The latter emphasizes that sufficient seeds must be available for dispersal to ensure gap colonization.

5 Stable patch/population-type distributions given different parameter values were obtained as the right eigen-vectors of metapopulation matrices. The proportion of forest patches occupied by *P. vulgaris* populations at equilibrium would be expected to be negligible under low k and f_d values.

6 Metapopulation structure may break down under high disturbance rates because *P. vulgaris* local populations may never go extinct and thus seed dispersal would not play a major role in local population re-establishment.

Keywords: colonization, extinction, forest dynamics, seed dispersal

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Introduction

Some populations do not function as spatially isolated units, but instead form groups or arrays of populations. Such systems of local populations which are

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connected together by dispersing individuals are known as metapopulations (Levins 1970). The idea of a metapopulation is an abstraction of the population concept at a higher level, in which a different spatial and temporal scale are considered (Hanski & Gilpin 1991; Husband & Barrett 1996): at a local scale, *populations* are groups of interacting individuals of the same species, whereas at a larger scale, *metapopulations* arise as dynamic systems of such local populations (Hanski 1989; Hanski & Gilpin 1991). At the population level, birth and death rates (as well

as migration) determine the temporal changes in the number of individuals, thus describing population dynamics. At the metapopulation level, it is colonizations and extinctions of local populations (analogous to birth and death processes at the local scale) that account for metapopulation dynamics. Thus, the analysis of metapopulation dynamics involves, among other things, the study of colonizations and extinctions and the conditions under which these two processes are in balance (Hanski 1991).

Many plant species show a spatially discontinuous distribution in which occupied patches are scattered in the habitat. Frequently, this distribution pattern is related to the patchy nature of most natural environments (Pickett & White 1985). The spatial structure of the plant populations occupying these kind of habitats may be characterized as either (a) *patchy populations* in which a group of patches functions as a single, large, extinction-resistant population (Harrison 1991), or (b) *metapopulations* in which occupied patches are rather independent local populations, interconnected through seed dispersal (Levins 1970; Hanski 1991). Whether a particular system should be regarded as a metapopulation depends on the degree of interconnection among patches, the extent to which seed dispersal determines the foundation of new local populations, and the importance of local populations extinction (Harrison 1991; Silvertown & Lovett Doust 1993).

In a study published elsewhere (Valverde 1995) we developed a patch-specific demography and canopy dynamics model for the forest understorey herb, *Primula vulgaris* Huds., in which we assumed that this species forms *patchy populations*; the dynamics of this system were explained in terms of the change in the *number of individuals* within the forest as a whole (Horvitz & Schemske 1986; Cipollini *et al.* 1993). In this paper we estimate rates of colonization and extinction to explore the possibility that *P. vulgaris* may form true *metapopulations*; thus, in this case, the dynamics of the system is described through the change in the *number of populations* through time. This aspect is important because few convincing examples of metapopulation structure in plants have so far been demonstrated (Husband & Barrett 1996), and because both the ecological and evolutionary significance of long-distance seed dispersal may vary depending on the system's spatial structure (Cohen & Levin 1991; Olivieri *et al.* 1995).

Within a particular forest, *P. vulgaris* shows a patchy distribution; here we regard each occupied patch as a local population. This distribution pattern appears to be a result of its limited dispersal ability and the fact that the establishment of populations is often associated with the opening of canopy gaps, as is the case for many other forest herbs (Collins *et al.* 1985). Presumably, the arrival of seeds at newly opened gaps allows the establishment of new populations, whereas gradual canopy closure may cause

population decline and eventual extinction. The metapopulation as a whole is thus conceived as a permanently changing system in which colonizations and extinctions are constantly occurring, coupled with the dynamics of the forest canopy.

The existence of real metapopulations in nature has been questioned due to the uncertainty regarding the level of interconnection between local populations and the actual importance of population extinction (Harrison 1991, 1994). In the case of the *P. vulgaris* system, two empirical observations support our assumption that it conforms to a metapopulation structure. First, most *P. vulgaris* seeds do not remain viable in the soil for long periods of time (Valverde & Silvertown 1995); thus, the colonization of newly opened gaps must occur from seeds dispersing into them rather than from a long-term buried seed pool. This implies that, although long-distance seed dispersal appears to be limited, it might play an important role in connecting local populations together and allowing the colonization of newly opened gaps. Little is known about seed dispersal in this species (see Methods), but the model we propose here will allow us to test the effect of this variable on metapopulation dynamics. Secondly, local populations of *P. vulgaris* in dark patches may show negative growth rates (Valverde 1995), which suggest that they eventually go extinct after prolonged periods under a full canopy cover. Thus, the time to local population extinction, as well as the rate of canopy gap formation (i.e. the disturbance rate), must play an important role in determining metapopulation dynamics. Again, by incorporating these variables into the model it will be possible to test their effect on metapopulation growth rate.

The use of projection matrices as a tool for analysis (Caswell 1989) has proved fruitful in the development of population ecology. These models recognize the existence of differences between the demographic fate of individuals in a population in relation to their age, size and/or other state-related variables. Analogous models at the metapopulation level may help to elucidate the variables that affect the system as a whole. Local populations within a metapopulation are not identical, as the original metapopulation model by Levins (1970) assumed; they differ in fundamental aspects such as their likelihood of extinction depending on their size, age or degree of isolation (Hastings & Wolin 1989; Gilpin 1991; Gotelli 1991; Hanski 1991; Lande 1993; Olivieri *et al.* 1995). These differences should be incorporated into metapopulation models as they significantly affect their structure and dynamics.

Local populations of *P. vulgaris* differ in many demographic features (e.g. fecundity, survival, mortality), and consequently in their extinction probability, according to the canopy conditions of the specific forest patch they occupy (Valverde 1995; Valverde & Silvertown 1995). In this case, metapopulation processes (i.e. extinctions and colon-

izations) are directly affected by the successional processes of the system in which the metapopulation is embedded. Forest patches advance through different stages of the forest regeneration cycle as the canopy closes, thus providing a natural framework to recognize 'population stages' within the metapopulation. In this paper we describe the metapopulation dynamics of *P. vulgaris* using a Markovian model that incorporates local population stages in different forest patches, as well as population extinction and colonization rates. To build the model, we used information about ecological processes at two different spatial scales: (1) the demography of local populations across a range of woodland conditions, and (2) the dynamics of the forest mosaic given by the canopy regeneration cycle; then, we used the model to explore the effect of other ecological processes, in particular seed dispersal and forest disturbance rate, on metapopulation growth rate. Additionally, we modelled the effect of different times to local population extinction and different values of forest initial occupancy by *P. vulgaris* populations on metapopulation dynamics.

Methods

THE STUDY SPECIES

P. vulgaris is a perennial herb characteristic of moist, shaded habitats, with a North Atlantic and Mediterranean distribution. It forms basal rosettes which, in Britain, start flowering in late winter. Flowers are distylous and vegetative spread occurs only within very short distances through the production of lateral rosettes. Seed dispersal occurs when capsules ripen around the middle of June. Seeds have an elaiosome which is attractive to ants and small mammals. These animals actively harvest seeds and may act as seed dispersers (Richards 1993; Valverde & Silvertown 1995).

STUDY SITES

Data on both *P. vulgaris* demography and forest canopy dynamics were collected at Dancers End Nature Reserve, in Buckinghamshire, UK (National Grid Reference SP 902 096). This area is mainly a *Fagus sylvatica* (beech) and *Fraxinus excelsior* (ash) forest on a chalky soil (National Vegetation Classification: W8, *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland, with some stands closer to W12, *Fagus sylvatica-Mercurialis perennis* woodland — Rodwell 1991). It has traditionally been managed through coppice cycles of 5–10 years, the coppiced species being mainly *Corylus avellana* (hazel) and *Crataegus monogyna* (hawthorn). Six *P. vulgaris* populations in different light conditions were studied in this forest. Two additional populations were also considered: one in Woburn Wood, a *Quercus robur* (oak) and *Castanea sativa* (chestnut) forest in

Bedfordshire (National Grid Reference SP 927 325), and another one in Salcey Forest, a *Quercus robur* and *Fraxinus excelsior* forest in Northamptonshire (National Grid Reference SP 814 508).

CANOPY DYNAMICS AND DEMOGRAPHY

Canopy closure and the dynamics of the forest mosaic

We used hemispherical photography to measure the degree of canopy openness (i.e. % of open sky in the hemiphoto – Chazdon & Field 1987) at each of the *P. vulgaris* populations mentioned above. By comparing photographs taken in consecutive years (i.e. summer 1992, 1993, 1994) we were able to calculate the rate of canopy closure, which occurs exponentially through time (Valverde & Silvertown, in press). Using this information we built a Markovian model of canopy dynamics in order to estimate forest structure (in terms of the number of forest patches with different levels of canopy openness). This involved the classification of forest patches into types according to percentage canopy openness (Table 1), and the calculation of the probability of each patch type advancing to the following patch type in one year's time. These probabilities were obtained from the exponential canopy closure rate measured: our data indicated that each patch type takes 3 years to become the following patch type. In the general case, if y is the time required to go from one centre of patch-type category to another, an average of $1/y$ type-x patches will become type-$(x + 1)$ each year. The probability of a type-x patch becoming a type-$(x + 1)$ patch in one year was calculated as $1/y$, and the probability of it remaining in the type-x category as $1 - (1/y)$ (shown in Fig. 1 for this case in which $y = 3$).

The probability of gap formation in closed canopy patches is given by k (i.e. the disturbance rate measured as the proportion of the forest area opened to gaps each year) (Fig. 1). As other authors have noted, gap opening may occur in any patch type (i.e. closed canopy as well as regenerating patches: Horvitz & Schemske 1986; Alvarez-Buylla & García-Barrios 1991, 1993; Cipollini et al. 1993, 1994). However, for the sake of simplicity, in this case the probability of gap formation in regenerating patches was deemed negligible; we assumed that gaps form only in closed

Table 1. Classification of forest patches into types according to their level of canopy openness

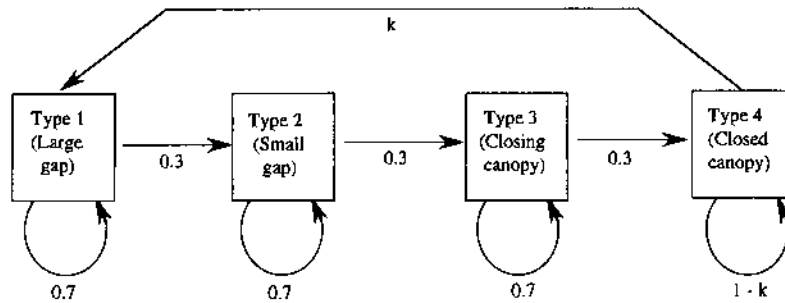| Patch type	% canopy openness	General description
1	8–16	Large gap
2	4–8	Small gap
3	2–4	Closing canopy
4	1–2	Closed canopy

Fig. 1 Canopy dynamics model. The boxes represent different forest patch types and the arrows are the transitions among patch types from one year to the next. The probability of each transition is given below each arrow. k = disturbance rate (i.e. rate of gap opening).

canopy patches, as they are by far the most frequent in the habitat.

The dynamics of the forest canopy is represented by a generalized $n \times n$ Lefkovitch matrix, P, where n is the number of forest patch-types. Each matrix entry, p_{ij}, represents the transition probability from a type-j patch to a type-i patch after one year. Let f_i be a vector representing the relative frequency of each patch type in the forest at time t. The structure of the forest after one year can be described by a vector, f_{t+1} where

$$f_{t+1} = Pf_t \tag{1}$$

The column eigen-vector of matrix P, f^*, associated with the dominant eigen-value ($\lambda = 1.00$) is proportional to the distribution of patch types in the forest at equilibrium, or 'stable patch-type distribution'. The projected forest structure at equilibrium for different k-values (spanning the range reported for other temperate forests: Runkle 1985; Runkle & Yetter 1987) is shown in Table 2. A detailed description of the canopy dynamics model and its results may be found in Valverde & Silvertown (in press).

The demography of P. vulgaris in different forest patches

An extensive demographic study was conducted in each of the eight *P. vulgaris* populations. Samples of

≈ 350 plants per population were marked and followed from 1992 to 1994, and their population dynamics were modelled using stage-based population projection matrices (see Valverde 1995 for details).

From the eight *P. vulgaris* populations sampled, there were two populations in the range of canopy openness corresponding to each of the four patch types defined in the previous section (Table 1). Thus, we pooled the demographic data for pairs of populations with similar levels of canopy openness to obtain a description of patch-specific population dynamics. In Table 3 we present some of the demographic results obtained in this way, that will be relevant in the construction of the metapopulation model. Note that local population growth rate (λ_p) decreased with increasing canopy cover as a result of lower fecundities and higher mortalities in populations under completely closed canopy conditions compared to those in relatively open patches. Population dynamics varied greatly in the two periods studied (i.e. 1992–93 and 1993–94), apparently due to weather conditions. Here we deal with the results of different periods separately in order to explore the effect of relatively 'bad' and 'good' years on metapopulation dynamics.

THE METAPOPULATION MODEL

The metapopulation graph

In the previous sections we classified *P. vulgaris* populations into four categories or types, according the level of canopy openness of the forest patch they occupy. Metapopulation dynamics may now be described by estimating the transition probabilities among different population categories in time, including new populations arising (colonization) and old populations disappearing (extinction), as illustrated in the metapopulation graph in Fig. 2. In the diagram, boxes represent the stages through which populations/patches move, whereas arrows show the possible fates that each of them may experience from one year to the next.

In Fig. 2 we represent the forest as a whole, which is composed of occupied and unoccupied patches. The

Table 2. Proportion of the forest area in each patch type at equilibrium (i.e. stable patch-type distribution, f^*) and disturbance return times for different values of disturbance rate (k). Disturbance return times (i.e. the time lapse between successive gap formations at any one point in the forest) were calculated as the reciprocal of the proportion of the forest area in gaps multiplied by 3, the time step for patch type change – Valverde & Silvertown, in press)

| Patch type | Disturbance rate | | |
	$k = 0.01$	$k = 0.03$	$k = 0.05$
1	0.029	0.075	0.108
2	0.029	0.075	0.108
3	0.029	0.075	0.108
4	0.913	0.775	0.676
Disturbance return time (years)	103.44	39.99	27.78

Table 3. Some demographic parameters for each population-type, according to their level of canopy openness. Mean ($\pm$ SD) densities of reproductives were obtained from two populations and two growth periods in each case

Pop. type	% canopy openness	Population growth rate (λ_p)		Mean fecundity		Mean density of reproductives (plants m^{-2})
		92–93	93–94	92–93	93–94	
1	8–16	1.98	1.09	17.29	2.34	30.86 $\pm$ 5.01
2	4–8	1.44	0.97	2.73	0.17	14.03 $\pm$ 0.60
3	2–4	1.04	0.94	0.11	0.10	8.45 $\pm$ 0.53
4	1–2	1.19	0.88	0.41	0.24	10.75 $\pm$ 1.74

former may be type-1 to type-4 *P. vulgaris* populations, whereas the later may be colonizable (i.e. recently opened gaps available for colonization — referred to as type-1 patches in Fig. 1) or uncolonizable forest patches (i.e. type-2, -3 and -4 patches, which we assume unsuitable for population estab-

lishment). An available gap may remain as such from one year to the next, or may become unsuitable for colonization due to canopy closure, or may turn into an 'establishing population' if enough *P. vulgaris* seeds arrive at it to produce emerging seedlings. An establishing population may either go extinct at an
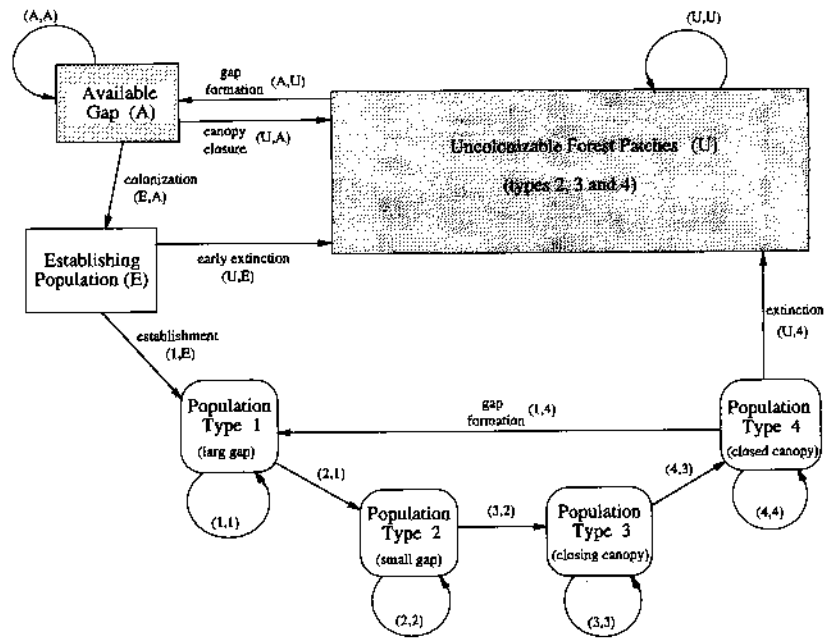
patch type at time t

		A	E	1	2	3	4	U
	A	A,A	0	0	0	0	0	A,U
	E	E,A	0	0	0	0	0	0
patch	1	0	1,E	1,1	0	0	1,4	0
type at	2	0	0	2,1	2,2	0	0	0
t+1	3	0	0	0	3,2	3,3	0	0
	4	0	0	0	0	4,3	4,4	0
	U	U,A	U,E	0	0	0	U,4	U,U

Fig. 2 *P. vulgaris* metapopulation graph. The boxes represent the different stages through which populations/patches move and the arrows show the possible contributions or transitions among stages from one year to the next. The correspondence between the metapopulation graph and the projection matrix below is shown; matrix elements, m_{ij}, correspond to the probability of a type-*j* population/patch contributing to or becoming a type-*i* population/patch in one year's time.

early stage if no seedlings are successfully recruited (by which time we assume that the patch is no longer colonizable), or may become a type-1 population if seedlings reach the reproductive stage. In this case, our model assumes that site carrying capacity is reached in a single generation (Olivieri *et al.* 1995). Once populations are established, they may remain the same or move to the following type after one year; type-4 populations may go extinct or, if a gap opens in the canopy, become type-1 populations.

The probability of each of these potential fates occurring from one year to the next can be calculated and incorporated into a metapopulation projection matrix, M, where each individual entry, m_{ij}, represents the probability of a type-j patch/population becoming a type-i patch/population in one year's time. The correspondence between the arrows in the metapopulation graph and the transition probabilities in matrix M is also shown in Fig. 2.

Let s_t be a vector representing the relative frequency of each patch/population-type in the forest at time t. The structure of the system after one year can be described by a vector, s_{t+1}, where

$$s_{t+1} = Ms_t \qquad (2)$$

Each of the columns of M sums to unity; thus, its dominant eigen-value also equals unity. We chose an initial vector, s_t, representing forest structure at time t, and we obtained s_{t+1}. By multiplying matrix M with the resulting vector each time, we obtained $s_{t+2}, s_{t+3}, \ldots s_{t+15}$. The analysis of these vectors allowed us to describe the transient dynamics of the metapopulation matrix: from each resulting vector we could calculate the proportion of the forest occupied by *P. vulgaris* populations at each point and look at the projected change in this proportion through time. In this way we were able to calculate 'metapopulation growth rate' (λ_M), in terms of the net change in the number of *P. vulgaris* populations in the forest from one year to the next (see eqn 11 for details).

Model parameter estimation

Formation of available colonizable gaps. Uncolonizable forest patches (types 2, 3 and 4) can become available type-1 patches following the opening of a gap in the canopy. The probability of any forest patch becoming an available gap (entry A,U in Fig. 2), is given by the disturbance rate (k). It follows that the probability of uncolonizable forest patches remaining as such (entry U,U in Fig. 2) is given by $1 - k$.

Transitions among population types. The probability of any *P. vulgaris* population remaining in the same category or moving to the following category over the period of one year is given by the probability of forest patches changing types in that same period, which is determined by canopy closure. Thus, recalling the

canopy dynamics model presented in a previous section (Fig. 1), the probability of any population type becoming the next type after one year is 0.3 (i.e. entries 2,1, 3,2 and 4,3 in Fig. 2), whereas the probability of populations remaining in the same category is 0.7 (i.e. entries 1,1, 2,2 and 3,3 in Fig. 2).

The probability of a type-4 population becoming a type-1 population (1,4 in Fig. 2) is equivalent to the probability of a gap opening in any closed canopy patch in the forest, which is given by the disturbance rate, k. Thus, the probability of a type-4 population remaining as such from one year to the next (4,4 in Fig. 2) is $1 - k$, minus the probability of the population going extinct (see below).

Extinction rate. We estimated the extinction probability of a population under closed canopy conditions by calculating its expected time to extinction as follows:

the intrinsic rate of natural increase of a population is defined as

$$r = \ln \lambda_p \qquad (3)$$

where λ_p is the population growth rate. Population size (n) at time $t + x$ can be calculated as

$$n_{t+x} = n_{to}e^{rx} \qquad (4)$$

Let $x = t_e$, the expected time to extinction. Thus, combining eqns 3 and 4,

$$t_e = \frac{\ln \dfrac{n_{t+te}}{n_{to}}}{\ln \lambda_p} \qquad (5)$$

We regard a population as virtually extinct when its number of individuals drops to 5% of initial population size:

$$\frac{n_{t+te}}{n_{to}} = 0.05 \qquad (6)$$

Assuming that local population growth rate under completely closed canopy conditions is $\lambda_p = 0.88$ (i.e. the lowest λ_p value obtained empirically for a population under a full canopy – Table 3), the time to extinction is given by

$$t_e = \frac{\ln(0.05)}{\ln(0.88)} = 23.4 \text{ years}$$

As λ_p approaches unity, the time to extinction (t_e) increases exponentially (Fig. 3a).

Following the same logic explained in previous sections, if a type-4 population takes 23.4 years to go extinct, the extinction probability (p_e) of any type-4 population from one year to the next is 0.043 (i.e. 1/23.4); this corresponds to the probability of type-4 populations contributing to the 'uncolonizable forest patches' category, given by entry U,4 in the matrix in Fig. 2. As the λ_p of type-4 populations increases, their probability of extinction decreases (Fig. 3b).
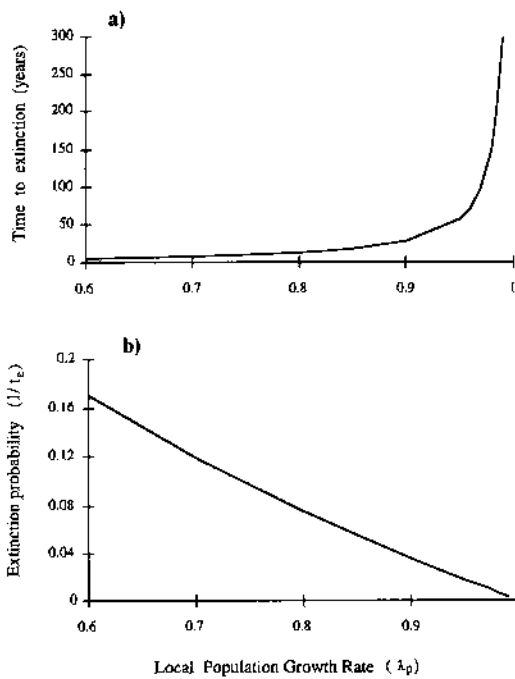
Fig. 3 (a) Time to local population extinction, and (b) population extinction probability, as a function of local population growth rate (λ_p).

Colonization parameter. Colonization is defined here as the successful establishment of *P. vulgaris* seedlings in an available gap, described in terms of the colonization parameter, C. This is a function of the number of seeds arriving at available gaps via the seed rain, which is in turn given by (1) the total number of *P. vulgaris* populations present in the forest, (2) the amount of seeds produced in those populations (i.e. fecundity), and (3) the fraction of seeds being dispersed out of their original populations, f_d, to form the 'migrant pool', as described below. The later variable, f_d, is an unknown and was assumed to be constant for all populations; its effect on metapopulation dynamics was tested by giving it different arbitrary values.

Thus, consider a theoretical forest composed of 10 000 patches. Each patch is 10 m × 10 m. Let a certain proportion, I_o, of forest patches be occupied by *P. vulgaris* populations. This initial occupancy, I_o, was assumed to be the same for all patch types. Thus, the number of *P. vulgaris* populations of each type in our hypothetical forest is

$$T_x = 10\,000 \times f_x^* I_o \qquad (7)$$

where T_x is the number of type-x populations and f_x^* is the proportion of the forest area composed of type-x patches, given by the x-th element of vector f^* (Table 2). We may now calculate the total number of seeds being dispersed out of populations to form the migrant seed pool, i, as

$$i = \sum_{x=1}^{x=4} (R_x \times \phi_x \times T_x \times f_d) \qquad (8)$$

where R_x is the number of reproductive individuals in a 10-m × 10-m type-x population (calculated from the density of reproductives — Table 3), ϕ_x is the mean fecundity in a type-x population (Table 3), T_x is the number of type-x populations in the forest, and f_d is the fraction of seeds dispersed out of populations. We assumed that the migrant seed pool is equally distributed over all forest patches and each patch gets $i/10\,000$ seeds via the seed rain. An example of these calculations is given in Table 4.

Finally, we calculated the colonization parameter, C, as a function of the number of seeds arriving at each available gap (i.e. the number of seeds arriving at *any* forest patch — see Table 4). According to our field data, 17.2% of the seeds shed into the soil of a type-1 patch became seedlings (Valverde & Silvertown 1995). Thus, the probability of one seed *not* emerging as a seedling is $n_e = 1 - 0.172 = 0.828$. The probability of two seeds *not* emerging as seedlings is $n_e \times n_e = 0.685$, and the probability of z seeds *not* emerging as seedling is $(n_e)^z$. Thus, the colonization parameter is given by

$$C = 1 - (n_e)^z \qquad (9)$$

where z is the total number of seeds arriving at each available gap (see Table 4). The relationship between the number of seeds arriving at a gap and its probability of being colonized is shown in Fig. 4a.

Going back to the metapopulation matrix, the probability of an available gap becoming an establishing population in one year's time (entry E,A in Fig. 2), is given by the colonization parameter multiplied by the probability of a type-1 patch remaining as such over that period of time (i.e. $C \times 0.7$). It follows that the probability of an available type-1 patch remaining unoccupied (A,A in Fig. 2) is $(1 - C) \times 0.7$.

Establishment probability. Here we considered a population as 'established' if at least one seedling is recruited; at this point we assume that this colonized patch turns into an established type-1 population, with its full carrying capacity (Olivieri *et al.* 1995). The probability of seedlings reaching the reproductive stage is given by two demographic transitions: the probability of seedlings becoming juveniles, times the probability of juveniles becoming reproductives. These transitions were actually calculated as part of the extensive demographic study carried out in the field (Valverde 1995): for type-1 populations, in the 1992–93 period these probabilities were 0.58 and 0.45, respectively, whereas in 1993–94 they were 0.34 and 0.22, respectively. Thus, the probability of a seedling becoming a reproductive was 0.26 in 1992–93 and 0.07 in 1993–94.

Following the same logic as in the previous section, in 1992–93 an establishing population with *one* seedling would have $1 - 0.26 = 0.74$ probabilities of early extinction, e_c. If the population in question consists

Table 4. An example of the calculation of the migrant seed pool and the total number of seeds arriving at each forest patch, considering a theoretical forest of 10000 10 × 10 m patches, using the fecundity data obtained in 93, and assuming that $k = 0.01$, $I_o = 10\%$, and $f_d = 0.1$. These assumptions are indicated in parenthesis where relevant, as well as the use of data in other columns to calculate the figures shown

Patch type	(a) Frequency in the habitat (if $k = 0.01$)	(b) No. of *P. vulgaris* pops. of each type (if $I_o = 10\%$)	(c) Density of reproductives (plants m^{-2})	(d) Total no. of reprods. in 10 × 10 patches (c × 100)	(f) Fecundity (for 92–93)	(g) No. of seeds per pop. (d × f)	(h) Total no. of seeds in the forest (b × g)
1	0.029	29	30.86	3086	17.29	53 356.94	1 547 351.3
2	0.029	29	14.03	1403	2.73	3830.19	111 075.5
3	0.029	29	8.45	845	0.11	92.95	2695.5
4	0.913	913	10.75	1075	0.41	440.75	402 404.7
Total							2 063 527.0

Note: According to the data in the table, the total number of seeds in the migrant pool (when $f_d = 0.1$) would be 206 352.7, and the number of seeds arriving at each forest patch would be 20.63.

of *two* seedlings, its probability of early extinctions would be $e_e \times e_e = 0.55$; and with z seedlings its probabilities of extinction would be $(e_e)^z$. In contrast, the probability of an establishing population becoming a type-1 population (i.e. entry 1,E in Fig. 2), is $1 - (e_e)^z$, where z is the number of seedlings present in the patch. The probability of population establishment, E, as a function of the number of seedlings present is illustrated in Fig. 4. In 1993–94 (Fig. 4c), a higher number of seedlings is needed to achieve a high population establishment probability compared to 1992–93 (Fig. 4b), because of the difference in the probability of seedlings becoming reproductives between the two periods.

Metapopulation matrix

We calculated the initial structure of our 10 000-patch theoretical forest, in terms of the number of patches/populations of each type, considering different values of I_o (i.e. initial occupancy) and k (i.e. disturbance rate) (Table 5). For the sake of simplicity, the number of establishing populations was initially set to zero; the number of populations of each type was given by eqn 7; the number of available gaps, A, was calculated as

$$A = (\text{type-1 patches}) - (\text{type-1 populations})$$

(10)

The number of uncolonizable forest patches was calculated as 10 000 minus the sum of all the rest (Table 5). The forest structures obtained in this way were used as the initial vectors, s_o, to iterate the metapopulation matrix.

The structure of the metapopulation matrix, M, is illustrated in Table 6. Note that it has only four parameters:

1 the disturbance rate, k, which was given three values (0.01, 0.03 and 0.05) according to what has been reported for other temperate forests (Runkle 1985; Runkle & Yetter 1987);

2 the probability of type-4 populations going extinct, p_e, which is a function of local population growth rate, λ_n, in patches under a full canopy cover;

3 the colonization parameter, C, which is a function of the number of seeds arriving at available gaps (defined by local densities and fecundities), by the initial number of populations of each type (i.e. initial occupancy, I_o, which was given the values of 10% and 30%), and by the fraction of seeds dispersing out of population, f_d (which was given values of 0.01, 0.1, 0.2 and 0.3);

4 the population establishment probability, E, which is a function of the number of seedlings present at colonized gaps.

The metapopulation matrix, M, was first multiplied by the vectors representing the initial forest composition, s_t (Table 5) and iterated 15 times by multiplying M by the resulting vector each time (standardizing each vector to add up to 10 000). From the vectors resulting from each iteration we obtained the total number of forest patches occupied by *P. vulgaris* populations of each type. We plotted the way in which the projected number of *P. vulgaris* populations changed throughout time (see Results, Fig. 5) and obtained a value for the 'metapopulation growth rate', λ_M (i.e. the rate of change in the number of *P. vulgaris* populations from one year to the next), as the geometric mean of n_{t+1}/n_t (where n_t is the total number of *P. vulgaris* population in the forest at time t) over the last 13 matrix iterations as follows:

$$\lambda_M = \sqrt[13]{\prod_{t=3}^{t=15} \frac{n_{t+1}}{n_t}}$$

(11)

Each time unit (i.e. a year) is represented by a matrix iteration. Calculating λ_M in this way gave a description of the transient dynamics of the model, projecting the behaviour of the metapopulation over the first few years. We arbitrarily decided to use the last 13 matrix iterations for this purpose, leaving out the first two iterations as they were not representative of the sub-
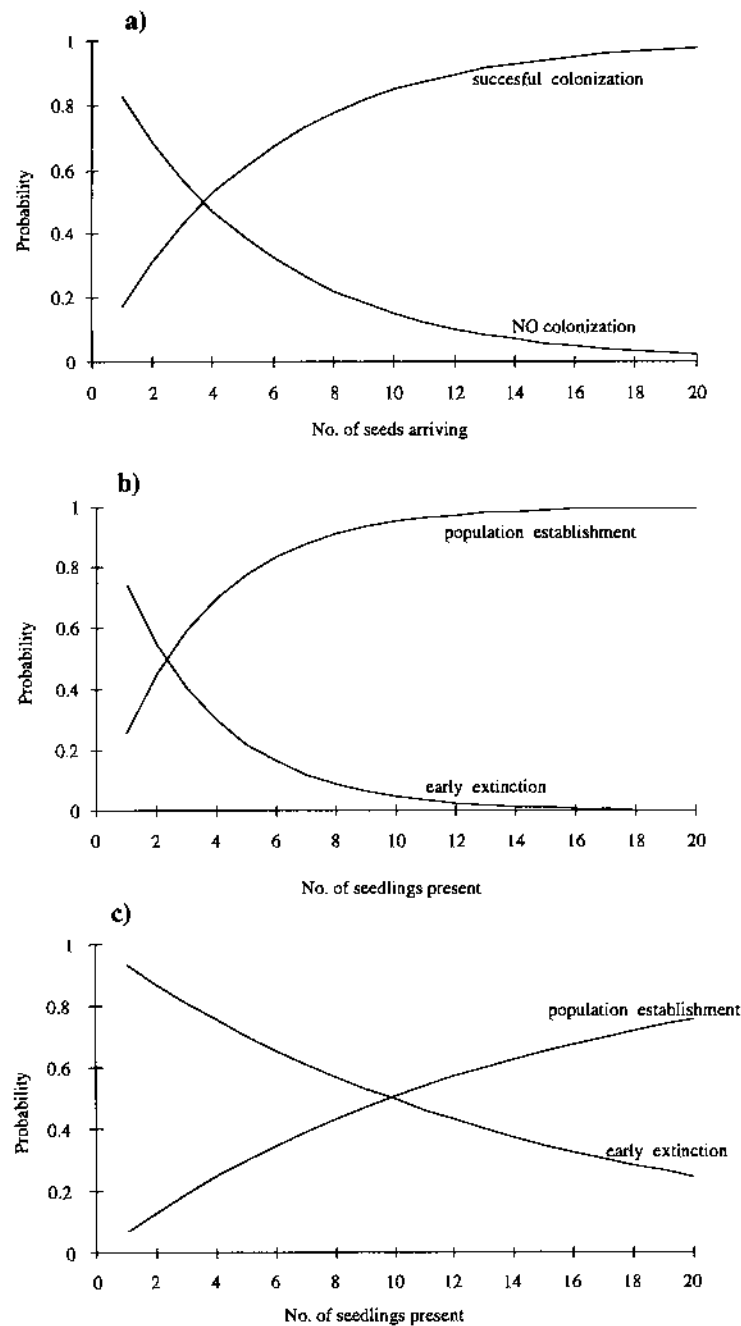
Fig. 4 (a) Probability of successful colonization of available gaps in relation to the number of seeds arriving at them; (b) and (c) show the probability of population establishment in a colonized gap as a function of the number of seedlings present in it considering the 1992–93 (b) and the 1993–94 (c) fecundities and seedling recruitment probabilities.

sequent behaviour of the model (see Results, Fig. 5 and 6). However, note that, as λ_M is estimated in terms of the relative change in the structure of resulting vectors, its value will eventually fall to zero as the stable patch-type distribution is reached, i.e. a balance between colonizations and extinctions is achieved at equilibrium. Thus, we also analysed the structure of the right eigen-vectors of metapopulation matrices (i.e. the stable patch/population-type distribution) given different values of disturbance rate, k (0.001–0.05) and seed dispersal, f_d (0.01–0.1) and looked for the combination of these parameters that resulted in the presence or absence of *P. vulgaris* populations in

the forest at the projected equilibrium. In this case we tried only low k and f_d values in order to approach the threshold figures under which, according to the model's projections, a metapopulation would no longer be viable.

Results

After each iteration of the metapopulation matrix, the resulting vector was divided into three parts: (1) available forest gaps, (2) *P. vulgaris* populations (i.e. type-1, -2, -3, -4 and establishing populations), and (3) uncolonizable forest patches. Figure 5 shows the

Table 5. Initial forest composition for different values of disturbance rate (k) and percentage of initial occupancy (I_o). The table shows the total number of available gaps (A), establishing populations (E), *P. vulgaris* populations (types 1, 2, 3 and 4) and uncolonizable forest patches (U) under the conditions specified in a hypothetical forest of 10 000 patches. These figures were used as the initial vectors, s_{to}, to iterate the metapopulation matrix (see text)

		A	E	1	2	3	4	U
k = 0.01								
$I_o <$	10%	261	0	29	29	29	913	8739
	30%	203	0	87	87	87	2739	6797
k = 0.03								
$I_o <$	10%	675	0	75	75	75	775	8325
	30%	525	0	225	225	225	2325	6475
k = 0.05								
$I_o <$	10%	972	0	108	108	108	676	8028
	30%	756	0	324	324	324	2028	6244

Table 6. Structure of the metapopulation projection matrix. C = colonization parameter; E = establishment probability; p_e = extinction probability $(1/t_e)$; k = disturbance rate

	A	E	1	2	3	4	U
A	$(1-C) \times 0.7$	0	0	0	0	0	k
E	$C \times 0.7$	0	0	0	0	0	0
1	0	E	0.7	0	0	k	0
2	0	0	0.3	0.7	0	0	0
3	0	0	0	0.3	0.7	0	0
4	0	0	0	0	0.3	$(1-k)-p_e$	0
U	0.3	$1-E$	0	0	0	p_e	$1-k$

A, available gaps; E, establishing populations; 1, 2, 3 and 4, *P. vulgaris* population types; U, uncolonizable forest patches.

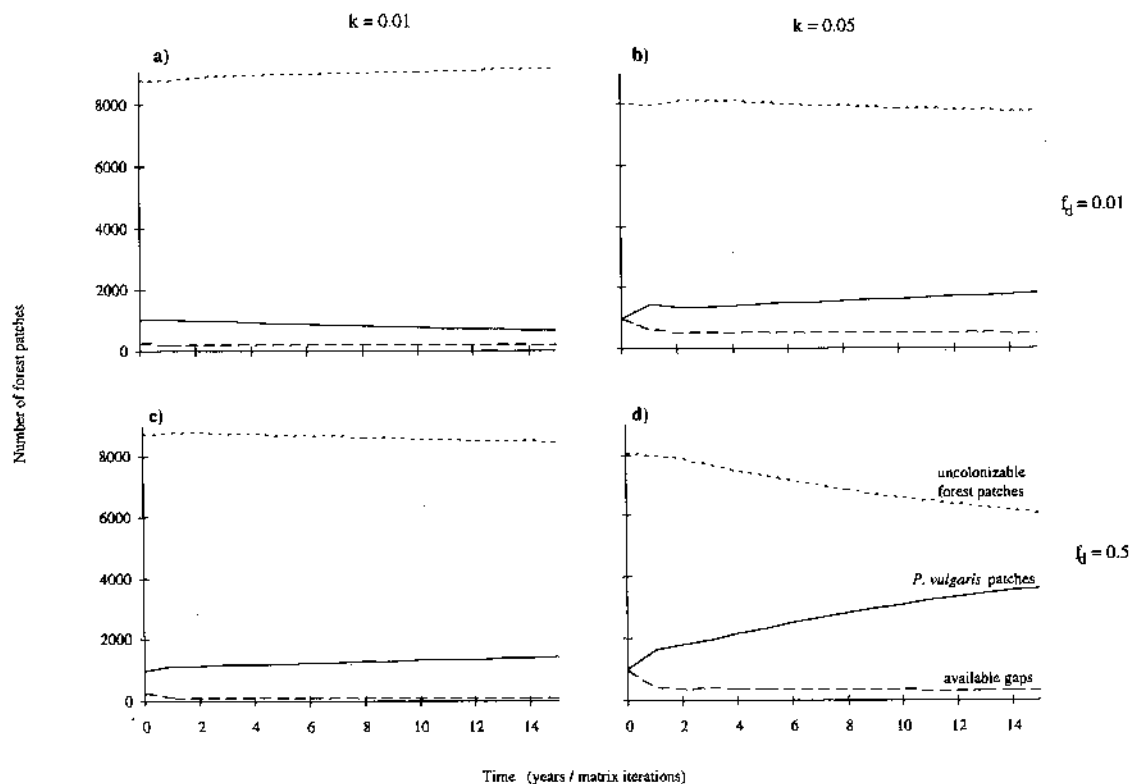Time (years / matrix iterations)

Fig. 5 Projected change in the number of forest patches of each type (i.e. dotted line = uncolonizable forest patches; continuous line = *P. vulgaris* populations; broken line = available gaps) through time, given by matrix iterations when (a) $k = 0.01$ and $f_d = 0.01$; (b) $k = 0.05$ and $f_d = 0.01$; (c) $k = 0.01$ and $f_d = 0.5$; and (d) $k = 0.05$ and $f_d = 0.5$ (for the 1992–93 conditions and assuming $I_o = 10\%$).
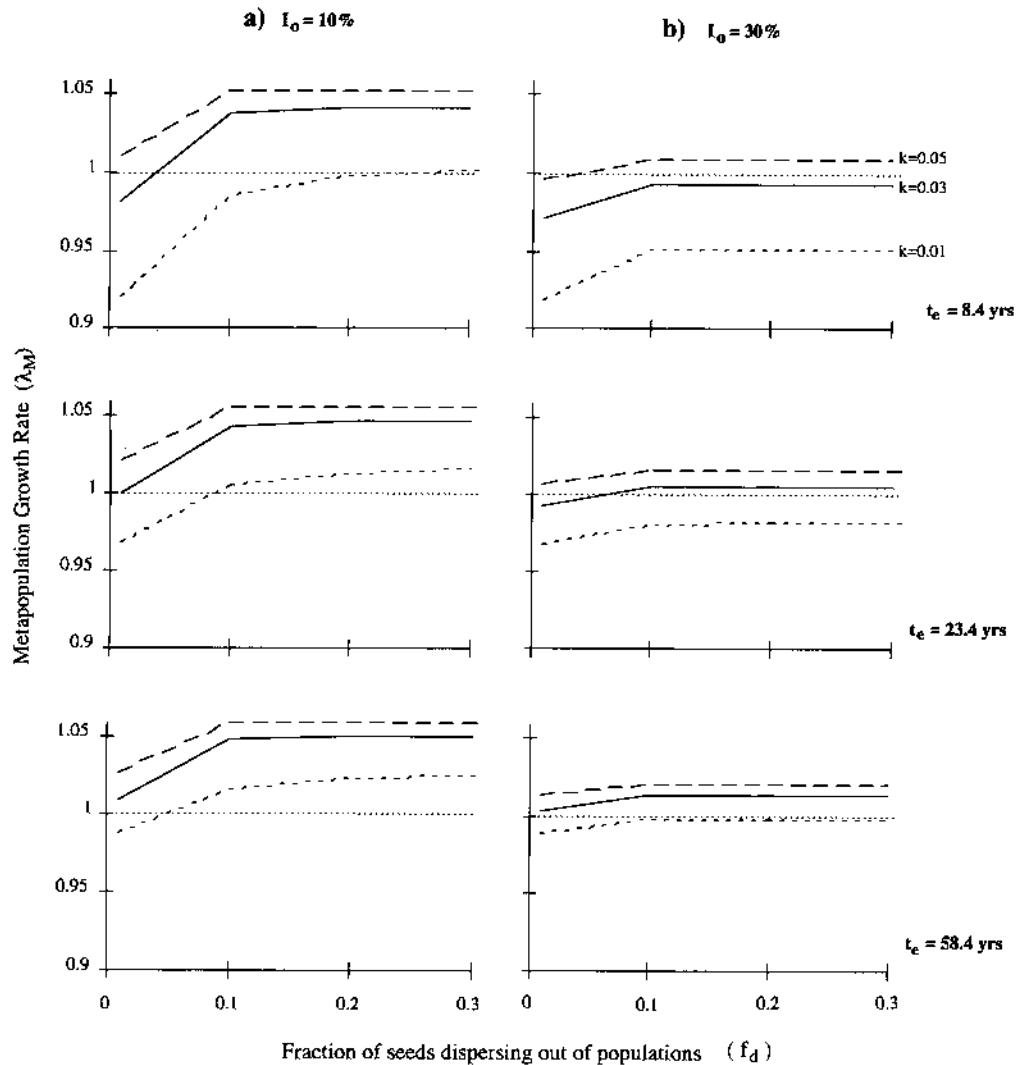
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J. Silvertown

a) $I_o = 10\%$ **b)** $I_o = 30\%$

Fraction of seeds dispersing out of populations (f_d)

Fig. 6 Metapopulation growth rate (λ_M) for the 1992–93 conditions, as a function of the fraction of seeds dispersing out of populations (f_d) for different disturbance rate values (i.e. broken lines, $k = 0.05$; continuous lines, $k = 0.03$; dotted lines, $k = 0.01$). Graphs in column (a) were obtained assuming that 10% of the forest was originally occupied by *P. vulgaris* populations, whereas those in column (b) were obtained assuming 30% initial occupancy. The three different rows correspond to different times to population extinction (t_e).

projected change in the number of these patches/ populations in time for the 1992–93 conditions (considering an initial occupancy of 10%). Only four graphs are presented, showing the effect of extreme values of both disturbance rate ($k = 0.01$ and 0.05) and fraction of seeds dispersing out of populations ($f_d = 0.01$ and 0.5).

The effect of disturbance rate on forest composition can be seen by comparing graphs in different columns in the Fig. 5 (a vs. b and c vs. d). Increasing disturbance rate resulted in a higher proportion of forest patches occupied by *P. vulgaris* populations and a lower proportion of empty uncolonizable forest patches. This was because higher disturbance rates produce greater availability of gaps for colonization. The effect of different levels of seed dispersal can be analysed by comparing graphs in different rows in Fig. 5 (a vs. c and b vs. d). Higher seed dispersal resulted in available gaps being occupied more readily; thus, the number of *P. vulgaris* populations increased

at a faster rate when a larger proportion of seeds was dispersed away from populations.

Both disturbance rate and seed dispersal had a dramatic effect on the projected behaviour of the metapopulation: when these variables were given low values, the number of *P. vulgaris* populations in the forest decreased, as indicated by the negative slope of the solid line in Fig. 5a (i.e. $\lambda_M < 1$). By either increasing disturbance rate (Fig. 5b), or the level of seed dispersal (Fig. 5c), or both (Fig. 5d), positive metapopulation growth rates (i.e. positive slopes indicating that $\lambda_M > 1$) were achieved. The effect of increased levels of seed dispersal can be seen in the reduction in the number of available gaps as a result of an increase in f_d (i.e. in Fig. 5 compare graphs a vs. c and graphs b vs. d). This is because gaps are more efficiently colonized when a higher proportion of seeds is dispersed.

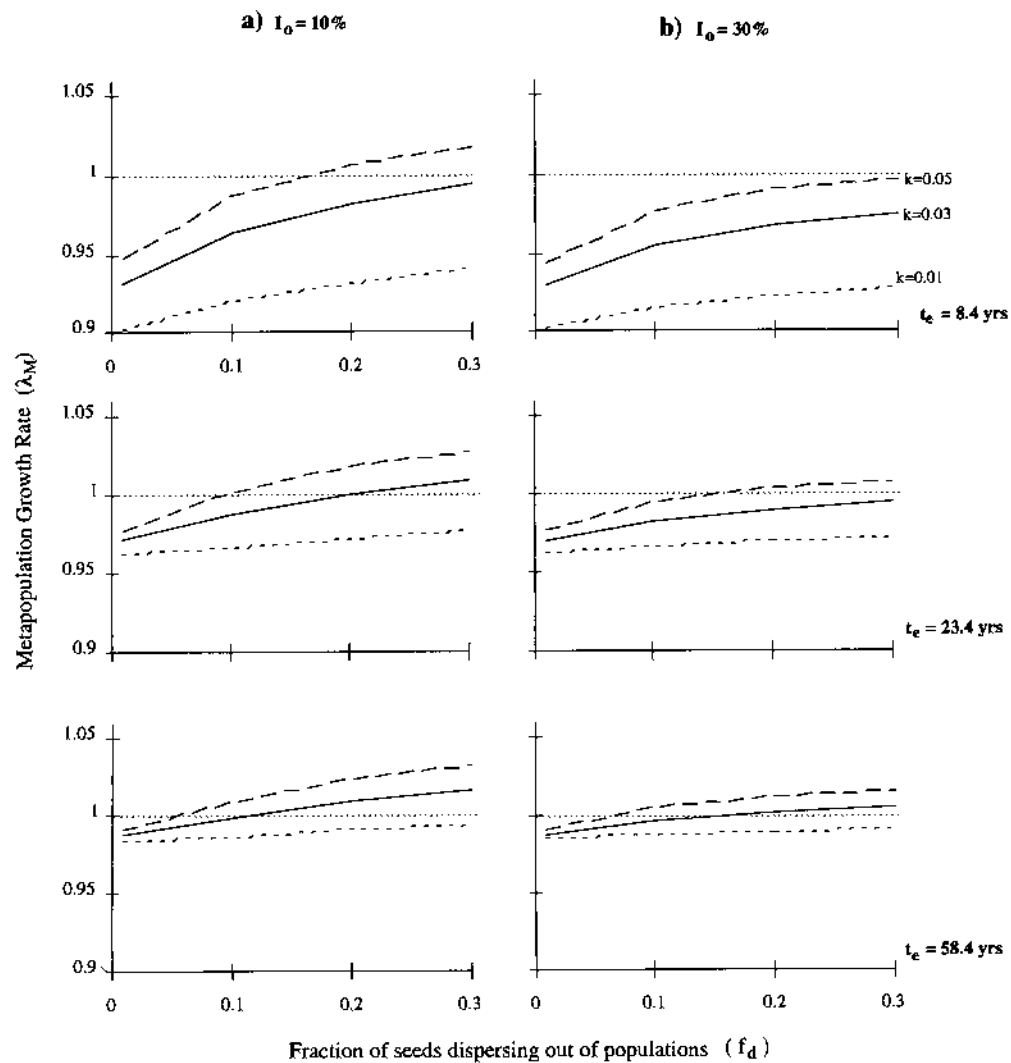The results presented in Fig. 5 considered only the 1992–93 conditions, and assumed that (1) type-4

a) $I_0 = 10\%$

b) $I_0 = 30\%$

Fraction of seeds dispersing out of populations (f_d)

Fig. 7 Metapopulation growth rate (λ_M) for the 1993–94 conditions, as a function of the fraction of seeds dispersing out of populations (f_d) for different disturbance rate values (i.e. broken lines, $k = 0.05$; continuous lines, $k = 0.03$; dotted lines, $k = 0.01$). Graphs in column (a) were obtained assuming that 10% of the forest was originally occupied by *P. vulgaris* populations, whereas those in column (b) were obtained assuming 30% initial occupancy. The three different rows correspond to different times to population extinction (t_e).

populations take 23.4 years to go extinct (i.e. $\lambda_p = 0.88$ under closed canopy conditions), and (2) initial forest occupancy, I_o, was 10%. We now relax these assumptions and explore their effect on metapopulation growth rate.

Figures 6 and 7 show the projected metapopulation growth rate under a range of conditions for 1992–93 and 1993–94, respectively. The difference between the two periods is given by lower fecundities and lower probabilities of seedlings becoming reproductives in 1993–94 compared to 1992–93. In each individual graph, higher disturbance rate ($k = 0.05$, broken lines) and higher dispersal levels always resulted in higher metapopulation growth rate. Furthermore, seed dispersal and disturbance rate had a synergistic effect on metapopulation growth rate: disturbance rate had a greater effect on λ_M at high dispersal levels than at low dispersal levels. This was because higher disturbance rates produced a higher frequency of colonizable patches in the forest, and high dispersal

values increased the probability of those patches being colonized.

These trends were apparent in both periods. However, in 1992–93 metapopulation growth rate reached a plateau and did not maintain the increasing tendency as seed dispersal increased (Fig. 6). In this period, high fecundities resulted in a large number of patches being colonized due to high seed availability. Additionally, a larger number of establishing populations became type-1 populations, as the probability of seedlings becoming reproductives was relatively high. Thus, beyond a certain level of dispersal, *all* gaps were colonized and *all* populations became established; at this point, the only factor that limited metapopulation growth rate was the disturbance rate, i.e. the rate at which gaps became available. This plateau was never reached when the 1993–94 conditions were considered. Increasing the level of seed dispersal always resulted in an increase in λ_M (Fig. 7). Also, metapopulation growth rate values were always

lower in this period compared to the previous year (i.e. compare Fig. 6a vs. 7a, 6b vs. 7b, and so on). This is an example of the way in which metapopulation dynamics may be affected by the change in the demography of local populations — in this case given by the yearly variation in fecundity and mortality of early plant stages. Note that this results imply that the positive effect of long-distance seed dispersal can be reduced when plant fecundities are high because all gaps become colonized and all populations become established.

Figures 6 and 7 also explore the effect of initial occupancy, I_o, on metapopulation growth rate. Note that when we started matrix iterations by assuming that 10% of forest patches were initially occupied by *P. vulgaris* populations, we obtained higher λ_M values than when we considered an I_o value of 30% (compare columns a vs. b in both Figs 6 and 7). This difference was more apparent at high levels of seed dispersal. This results from the fact that when a high proportion of the forest was already occupied by *P. vulgaris* populations, the rate at which patches became available for colonization was necessarily lower than in the case when fewer forest patches were occupied. Thus, although the total number of populations was higher if we started with 30%, rather than 10%, of the forest occupied, the rate at which the number of populations increased was lower when I_o was given higher values. This shows that λ_M, as defined here, should be seen only as a description of the transient dynamics of the model and not as a thorough measure of the system's behaviour, unless considered over a range of initial conditions.

The effect of time to population extinction, t_e, on metapopulation dynamics was also explored. According to our empirical data, the lowest λ_p value was 0.88 for populations under completely closed canopy conditions; thus, they would go extinct after 23.4 years. But local demography also varies in time, as shown by our own results (Table 3). Thus, we asked our model how the metapopulation would behave if type-4 local populations had growth rates of say, $\lambda_p = 0.7$ ($t_e = 8.4$ years), or $\lambda_p = 0.95$ ($t_e = 54.4$ years). The results are represented by the different rows in Figs. 6 and 7. Metapopulation growth rate was higher when type-4 populations took longer to go extinct. However, the effect of t_e was more dramatic for low levels of dispersal and disturbance rate.

Finally, we analysed the structure of right eigenvectors of metapopulation projection matrices given different values for the parameters studied. The dominant right eigen-vector of the metapopulation matrix corresponds to the stable patch/population-type distribution, i.e. the structure of the forest and the metapopulation at equilibrium in terms of the relative number of patches/populations of each type. From each right eigen-vector obtained we calculated the proportion of forest patches that would be occupied by *P. vulgaris* populations (i.e. establishing, type-1,
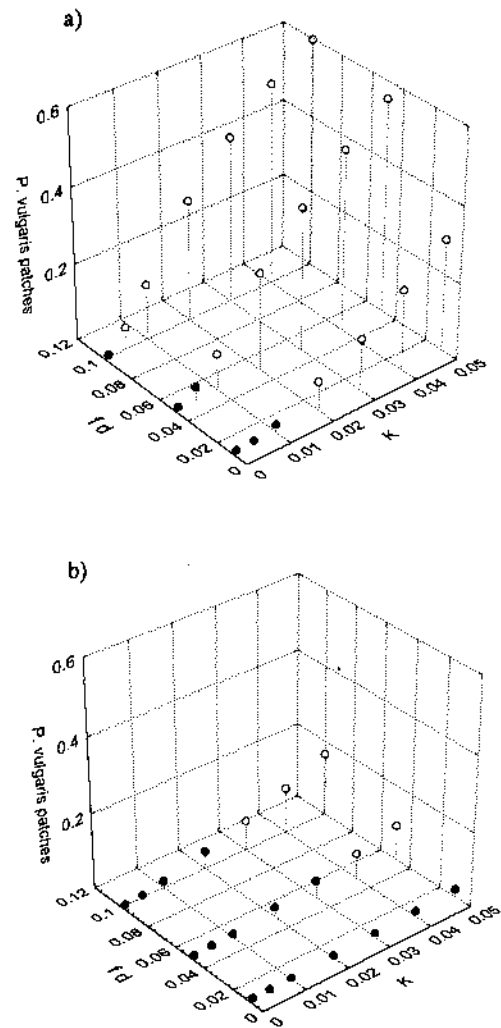
a)

b)

Fig. 8 Proportion of forest patches occupied by *P. vulgaris* populations at equilibrium given different disturbance rate (k) and seed dispersal (f_d) values for (a) the 1993–92 and (b) the 1993–94 fecundity and seedling recruitment probabilities. The metapopulation was considered nonviable when less than 5% of forest patches were occupied by *P. vulgaris* populations at the projected equilibrium; this is represented in the graphs by filled dots.

-2, -3 and -4 populations) at equilibrium. We were interested in finding the combination of values for k and f_d that would result in the permanence of the metapopulation, i.e. in the occupation, at equilibrium, of at least 5% of forest patches by *P. vulgaris* populations.

When seedling survival and fecundities were high (i.e. 1992–93 values; Fig. 8a) only very low disturbance rates ($k < 0.01$) and seed dispersal values ($f_d < 0.1$) resulted in the extinction of the metapopulation. However, when seedling survival and fecundities were low (i.e. 1993–94 values; Fig. 8b), higher k and f_d values were necessary for the metapopulation to survive.

According to the model's projections, the fate of the metapopulation is also dependent on time to local population extinction, t_e (which is a function of λ_p of
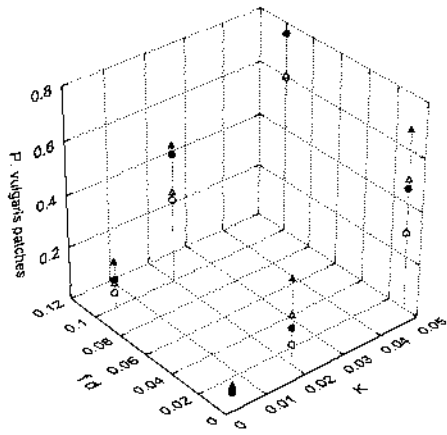
Fig. 9 Proportion of forest patches occupied by *P. vulgaris* populations at equilibrium for various disturbance rate (k) and seed dispersal (f_d) values, assuming two different times to population extinction, t_e and two initial occupancy levels, I_o. Open circles, $t_e = 23.4$ years and $I_o = 10\%$; open triangles, $t_e = 23.4$ years and $I_o = 30\%$; filled circles, $t_e = 58.4$ years and $I_o = 10\%$; filled triangles, $t_e = 58.4$ years and $I_o = 30\%$.

patches in closed canopy conditions) and forest initial occupancy, I_o — incorporated in the metapopulation matrix in the calculation of the colonization parameter, C (eqn 7, 8 and 9). Figure 9 shows, for some k and f_d values, the variation in the proportion of forest patches occupied by *P. vulgaris* populations at equilibrium for different times to local population extinction and initial occupancies. The results show that the metapopulation was composed of a larger number of *P. vulgaris* populations at equilibrium at higher values of either I_o or t_e (Fig. 9).

Discussion

Recent demographic studies on spatially structured plant populations have considered the patch-type concept, recognizing that the demography of local population differs from patch to patch in response to environmental variation (Martínez-Ramos *et al.* 1985; Olivieri & Gouyon 1985; Horvitz & Schemske 1986; Alvarez-Buylla & García-Barrios 1991, 1993; Cipollini *et al.* 1993, 1994; Alvarez-Buylla 1994; Wu & Levin 1994; Olivieri *et al.* 1995; Valverde 1995). Some metapopulation studies have used the stochastic approach to address this issue and have modelled the effect of different stochasticity sources on local population extinction (Hanski 1991; Lande 1993; Perry & González-Andujar 1993). However, the type of environmental variation that many populations experience within plant metapopulations is often the result of directional (i.e. nonstochastic) changes which are part of secondary succession processes. This is the case for *P. vulgaris*, where the variation in local population demography is determined mainly by changes in canopy cover during the forest regeneration cycle.

In this context, the patch-type concept involves the

idea of local populations passing through different consecutive stages along a successional gradient. Thus, the directionality of habitat change enables the projection of the demographic behaviour and fate of local populations within a metapopulation, provided the patterns of environmental variation can be described. In this study, knowledge of the variation in the demography of local populations and of some canopy dynamics variables, allowed us to classify local populations into types and use stage-based projection matrices to model metapopulation dynamics and address specific metapopulation processes (e.g. dispersal, colonization, extinction). The convenience of stage-structured metapopulation models of the sort introduced here is that they recognize the different role played by related local populations within metapopulations. In this case, *P. vulgaris* local populations differ in their extinction probability and seed productivity depending on their 'stage' in the canopy regeneration cycle; populations in gaps produce a much higher number of seeds and are less prone to extinction than populations under closed canopy conditions (Tables 3 and 4). Thus, the relative abundance of each population type in a forest will have an effect on metapopulation growth rate by affecting the total number of seeds available for dispersal, as well as local population extinction frequency.

The λ_M values obtained ranged approximately from 0.9 to 1.06. Figures 6, 7 and 8 can be used to determine which combinations of values for all the variables resulted in a positive (i.e. > 1) metapopulation growth rate, and therefore, in the persistence of the metapopulation. In the context of ecological conservation, this kind of analysis would be useful in evaluating the variables that should be controlled or manipulated in the short term if a species structured in metapopulations is to be preserved. In the case of *P. vulgaris*, an obvious factor to consider in conservation management plans would be the rate of gap opening, which can be manipulated through coppice cycles. The gradual loss of this traditional practice in Britain may lead to significant decline in the abundance of this and other forest herbs (Barkham 1992).

Our results also illustrate the effect of 'good' or 'bad' years for the demography of local populations, at the metapopulation level. This result emphasizes that a sufficiently large number of seeds must be produced in existing local populations to generate positive metapopulation growth rates and assure the persistence of the metapopulation. When fecundities were low (i.e. in 1993–94), the number of seeds arriving at available gaps was insufficient to achieve high colonization probabilities, even when seed dispersal was high. Thus, within-population dynamics should always be considered in the study of metapopulations (Hastings & Wolin 1989).

Our model showed that increasing both the disturbance rate and the level of seed dispersal had a

positive, additive effect on metapopulation growth rate: higher disturbance rates increased the frequency of newly opened gaps in the environment, and higher seed dispersal levels increased the probability of gap colonization and population establishment (note that the assumption that established populations instantly fill up assures that increasing seed dispersal will increase metapopulation growth rate). Also, the persistence probability of type-4 populations was higher at higher disturbance rates, as their probability of becoming type-1 populations following gap creation increased with increasing k. Note that if no seeds disperse out of their original populations, available gaps cannot be colonized, which results in eventual metapopulation extinction unless type-4 populations become type-1 populations (due to gap formation) at a faster rate than they go extinct. This could occur at sufficiently high disturbance rates. However, in the absence of seed dispersal the system should be regarded as a collection of isolated populations, rather than a metapopulation. If the system is a real metapopulation, i.e. if it depends on a balance between colonization and extinction, then both extinction and dispersal must play a fundamental role.

Other theoretical and empirical studies have emphasized the importance of seed dispersal in plant metapopulations. Perry & González-Andujar (1993) modelled the behaviour of a hypothetical annual plant and found that dispersal aided metapopulation growth in a spatially heterogeneous environment. Herben *et al.* (1991) showed that spore transport was the primary factor influencing the behaviour of a metapopulation of *Orthodontium lineare*, a moss species that establishes in rotting wood. A metapopulation study on the mistletoe *Phrygilanthus sonorae* illustrated that its distribution pattern on *Bursera* trees could be explained by the patterns of long-distance (off-tree) seed dispersal by birds (Overton 1994). Additionally, Horvitz & Schemske (1986) developed a patch-and-population dynamics model, which was later applied by Cipollini *et al.* (1993, 1994), to explore the effects of seed dispersal on the overall growth rate of spatially structured plant populations.

When evaluating the benefits of long-distance seed dispersal, it should be recognized that there are conflicting forces acting at different hierarchical levels (i.e. the individual, the population and the metapopulation — Hamilton & May 1977; Olivieri *et al.* 1995). Seed dispersal often represents a cost at the individual and/or population level because, among other things, the risk of landing in unfavourable patches may be extremely high (Murray 1986; Venable & Brown 1993). In fact, Horvitz & Schemske (1986) showed that there was a negative effect of long-distance dispersal in the forest understorey herb *Calathea ovandensis* when analysed at the level of the overall population (i.e. in terms of the change in the total *number of individuals* in the system). However, for some species, long-distance seed dispersal rep-

resents an important mechanism for the colonization of ephemeral favourable sites, allowing the formation and persistence of metapopulations. The evolutionarily stable dispersal strategy from the individual point of view could be suboptimal from the population perspective (Hamilton & May 1977). Similarly, in species structured as metapopulations, the individual and population optimal rates of dispersal may be different from the 'species optimum', which would tend towards the level of dispersal yielding a maximum colonization rate of available sites (Hanski 1991).

In many cases local population extinction is unavoidable as part of the natural processes inherent to particular systems. Global persistence in such species depends on colonizations. Migration will be selected for in those systems because each particular local population will eventually go extinct and only offspring that have emigrated will be able to reproduce. Thus, two opposing selection pressures, selection for dispersal during recolonization and selection against dispersal once local populations are established, act on the dispersal rate in systems where extinctions are an important phenomenon (Olivieri *et al.* 1995). In the case of the *P. vulgaris* system, we could ask (a) to what extent is extinction a driving force, and (b) how important is dispersal in the foundation of local populations.

Little is known about seed dispersal in *P. vulgaris*. A high proportion (between 50 and 60%) of seeds are harvested, and small mammals appear to be primarily responsible for this amount of seed loss (Valverde & Silvertown 1995). Ants harvest only a low proportion of seeds (around 10%) and it is unlikely that they transport them more than a few metres from the source (Keith-Lucas 1968; Cahalan & Gliddon 1985). However, dispersal by rodents could potentially play an important role in the arrival of seeds at newly opened gaps. Some rodents from temperate habitats have been reported to store between one third and one fifth of their harvest (Price & Jenkins 1986). In this study we analysed the effect of various levels of seed dispersal by assigning f_4 different values. However, we did not include the effect of seed predation and death during the process of dispersal. The actual arrival of seeds at newly opened gaps must therefore be less frequent, and in smaller numbers, than that which we have assumed here. Thus, *P. vulgaris* metapopulations would possibly go extinct if seed dispersal was the only mechanism for population establishment following gap formation.

In natural conditions, new local populations could be founded through means other than seed dispersal. Although the buried seed bank appears to be quite sparse (Valverde & Silvertown 1995), yet it could occasionally be the source of seedlings for gap colonization. Colonization could also result from old individuals surviving in scattered isolation under closed canopy conditions. These could be individuals estab-

lished from exceptional germination under these conditions or, more likely, survivors of old populations. If a gap opens where one of these individuals is established, a new population could be founded. Thus, the 'rescue effect', described by Hanski (1982) as the process by which seed dispersal may prevent local populations from going extinct, may not be the only means by which local populations can be 'rescued' from extinction. Longevity and late reproduction may also play an important role in preventing this environmentally induced extinction; a new term, 'longevity-driven recovery', could be introduced to describe this phenomenon.

Boyd *et al.* (1990) estimated that *P. vulgaris* plants may live between 10 and 30 years. According to the results of our canopy dynamics model, disturbance return time (i.e. the time lapse between successive gap formations at any one point in the forest) should be between 113.78 (with $k = 0.01$) and 30.56 (with $k = 0.05$) years (Table 2); successive gap formations in the same forest patch could, in fact, occur within the life span of a long-lived individual, thus preventing population extinction. Type-4 populations might never go extinct given sufficiently high disturbance rates: gap formation may 'rescue' declining populations by recreating environmental conditions adequate for reproduction, germination and establishment.

Thus, the question arises as to whether the persistence of *P. vulgaris* in a forest actually depends on a balance between colonizations and extinctions, i.e. whether it forms real metapopulations or falls into some other category of spatially structured populations. Empirically, this issue could be approached from different perspectives: the proportion of closed-canopy patches that have old, potentially reproductive *P. vulgaris* individuals could be estimated; alternatively, the number of new gaps that have surviving *P. vulgaris* individuals could be determined. Thus, the relative importance of the different gap-colonization mechanisms (i.e. 'longevity-driven recovery', exogenous dispersal or buried seed pool) could be explored. In this paper we have used a modelling approach to address some of these questions and by identifying the key factors in the system's dynamics we have been able to hypothesize about the conditions under which metapopulation processes would be important.

Our results suggest that *P. vulgaris* would form metapopulations in cases in which gap opening rate was sufficiently low to allow for eventual local population extinction, and only if seed dispersal was efficient enough to assure the arrival of seeds at newly opened gaps. If local population extinction occurs (which would also be determined by their λ_p), then gap colonization would become of great importance for the persistence of the species at a site and metapopulation survival would depend upon the efficiency of seed dispersal (assuming that other gap-colon-

ization mechanisms were negligible). Alternatively, *P. vulgaris* could probably fit the category of 'non-equilibrium metapopulations', which are characterized by unstable extinction-colonization dynamics given by some forms of habitat deterioration in the context of a species' regional decline (Harrison 1991). This is consistent with the observation that, in Britain, several species requiring sunny openings in woodlands are declining due to the cessation of the traditional coppicing which generates forest clearings (Harrison 1991; Barkham 1992).

Our results appear to suggest that *P. vulgaris* metapopulations would perform better in highly disturbed habitats and when seed dispersal is maximal. However, the model does not consider other factors that may limit metapopulation growth rate under such conditions. For instance, seed dispersal must be moderate for local populations to maintain positive growth rates; their demography would be very much affected if a large number of seeds were dispersed away (Valverde 1995). Furthermore, *P. vulgaris* performs poorly in highly disturbed environments, apparently because it cannot tolerate the high levels of competition from other species that colonize more open habitats. Thus, in nature, the system must exist in a balance between the factors that enhance metapopulation growth (e.g. high seed dispersal and disturbance rates) and those which ensure the survival of individual populations (e.g. low seed dispersal and moderate disturbance rates).

The metapopulation model developed here considers only a limited number of factors, and as such, it cannot reproduce reality. However, by extracting the most important elements from real systems and examining their relevant interactions, ecological models may be successful in describing a simplified version of natural systems and assessing the role of particular variables affecting them. In this sense, our model provides a useful tool for analysing metapopulation dynamics, as well as evaluating the effect of certain ecological processes on metapopulation behaviour. By evaluating the conditions under which colonizations and extinctions may take place, the model also offers the possibility of testing whether a group of local populations may be regarded as a real metapopulation, i.e. whether it exists in a balance between colonizations and extinctions.

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