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Biological control of Scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores

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Summary

1. Simulation and analytical models are developed for the European shrub Scotch broom *Cytisus scoparius* Link (Fabaceae). The simulation model is spatially explicit and allows us to explore not only changes in population size but also the proportion of ground covered by the weed. The simulation model incorporates spatially local density-dependent competition, asymmetric competition between seedlings and established plants, a seed bank, local seed dispersal and an age-structured established plant population. This model is designed to incorporate much of the known population biology of broom. The analytical models are simple approximations of the simulation.
2. The basic model contains nine parameters: the probability a site is disturbed, p_{dis} ; the probability a seed becomes a seedling, g ; the probability a seedling survives the first year, s ; the probability a seed is lost from the seed bank, d ; the minimum age for reproduction, A_{min} ; maximum plant age, A_{max} ; seed production per site, F ; the probability a seed is retained in the parental site, f_h ; and the probability a site becomes suitable for colonization after broom senesces, p_{so} .
3. We review published data on the demography of broom from studies around the world, and also present some previously unpublished data. These data suggest that broom in some exotic habitats can achieve higher fecundities and live longer than in its native range.
4. Analytical approximations provide a good description of the simulation results over a wide range of biologically reasonable parameter values. Specifically, the analytical models work well when plants are long-lived or highly fecund.
5. Analysis of the models indicates that when broom colonizes all suitable sites with probability one, that the fraction of sites occupied by broom is determined by only three parameters: the probability of disturbance, p_{dis} ; the probability a site becomes suitable for colonization following plant senescence, p_{so} ; and maximum longevity, A_{max} . In exotic habitats, where individual broom plants can produce several thousand seeds, differences in these parameters are the most likely reason why broom populations are more weedy than in the native range.
6. The impact of insect herbivores, which reduce plant fecundity, on broom abundance is explored for several environmental scenarios. This analysis suggests that potential biological control agents are most likely to have a substantial impact if the disturbance rate is high, plant fecundity is low, and seedling survival is low. Even herbivores that reduce seed production by only 75% can have a dramatic impact on broom abundance, in contrast to several published predictions.
7. Extensions to the models to allow for arbitrary patterns of age-dependent senescence, and site-specific probabilities of disturbance are presented.

Key-words: age-structure, coupled map lattice, mean field approximation, spatial modelling, stage-structure.

Introduction

The European shrub Scotch broom *Cytisus scoparius* Link (Fabaceae), which is only occasionally a minor weed in Europe (e.g. Rousseau & Loiseau 1982), has been introduced into several countries around the world where it has become a serious weed of pasture, native bushland and forestry (Parsons & Cuthbertson 1992). In New Zealand and Australia, Scotch broom is the subject of a biological control programme and, as a part of this programme, experiments studying its population dynamics have been set up in habitats both where the plant is native and where it is exotic (Memmott *et al.* 1993; Fowler *et al.* 1996). These experiments will investigate why broom is more weedy in exotic habitats; for example, the seed production by Scotch broom can be higher in exotic environments (Paynter *et al.* 1996).

In order to understand how population parameters interact to make broom an invasive weed, a modelling approach is needed. Models of plant population dynamics have been used in the past to predict the effect of introduced biological control agents on the population size of the target weed (e.g. Lonsdale, Farrell & Wilson 1995). In this paper we present a spatial model which allows us to explore not only changes in population size but also the area covered by the weed. Two types of model are presented. The first is a complex simulation model which is spatially explicit and incorporates spatially local density-dependent competition, asymmetric competition between seedlings and established plants, a seed bank, local seed dispersal and an age-structured established plant population. This model incorporates much of the known population biology of broom, see below. The second type of model is an analytical approximation of the simulation. Analytical approximations are developed in order to allow the simulation model to be interpreted and to illuminate inter-relationships between parameters.

First, we introduce the basic population biology of broom, we then develop a series of models, and use these to explore the factors influencing the proportion of sites occupied by broom. The potential impact of seed feeders on the proportion of sites occupied by broom is then calculated under a range of different environmental scenarios. The implications of these results for the management of broom populations are discussed.

The population biology of Scotch broom

Scotch broom is a polycarpic perennial plant that is native to Europe, ranging within an area bounded by the Azores, Spain and Portugal in the south-west, north to the British Isles, east to southern Sweden and the west-central Ukraine, and south to northern and central Italy (Tutin *et al.* 1968).

SEED PRODUCTION, DISPERSAL AND SURVIVAL

Scotch broom normally flowers in its third year (Smith & Harlen 1991), and produces large numbers of seeds (Table 1) that mostly fall within 1 m of the parent plants (Smith & Harlen 1991; Paynter *et al.* 1996; Table 2) when the pods dehisce, leading to a slow rate of spread in exotic habitats along an advancing front (Smith 1994; Paynter *et al.* 1996). Seeds may be dispersed up to *c.* 5 m further by ants (Bossard 1990) and a variety of other seed vectors may occasionally disperse an unknown, but small proportion of seeds over much greater distances (Smith & Waterhouse 1988; Smith & Harlen 1991). In the models, described later, one parameter that is used to describe the dispersal of seeds is the probability a seed fails to disperse beyond the parental canopy, termed f_h . This was estimated from data presented in Hinz (1992) and Smith & Harlen (1991) by dividing the number of seeds

Table 1. Yearly seed production by broom in exotic and native ranges (seeds per plant, unless otherwise stated). For references 1 and 5 the number of seeds per plant was calculated by multiplying the mean number of pods per plant by the mean number of seeds per pod recorded in the respective studies

Seed production	Site	Country	Reference
Exotic habitats			
Up to 14212	Lincoln	New Zealand	1
9700	California	USA	2
28–356 seeds m ⁻²	Under Eucalyptus forest, Barrington Tops	Australia	3
107 seeds m ⁻²	Under Eucalyptus forest, Deua National Park	Australia	
8885 seeds m ⁻²	Open pasture, Deua National Park	Australia	4
Native habitats			
5600	Silwood Park, Berkshire	UK	5
72–728	Under Castanea forest, Gard	France	6
1061–5649	Abandoned terraces, Gard	France	6

1, Williams (1981); 2, Bossard & Rejmánek (1994); 3, Smith & Harlen (1991); 4, Hosking, Smith & Sheppard (1996); 5, Waloff & Richards (1977); 6, Mazay (1993).

Table 2. The yearly probability that a seed is lost from the seed bank, d , and the probability a seed is retained in the parental site, f_h

Country	Probability of seed loss, d	Reference
Native habitats		
France	≈ 0.50	1
Exotic habitats		
USA	≈ 0.65	2
Probability a seed stays in parental site, f_h		
Native habitats		
UK	≈ 0.55	3
Exotic habitats		
Australia	≈ 0.73	4

1, Q. Paynter (unpublished data); 2, Bossard (1993); 3, Hinz (1992); 4, Smith & Harlen (1991).

caught in seed traps within the canopy by the total seed production (Table 2).

Broom seeds are hard-coated and may not germinate for years (e.g. Smith & Harlen 1991; Bossard 1993), so that, typically, only a small proportion of the seed bank emerges as seedlings each year (Williams 1981; Smith & Waterhouse 1988; Memmott *et al.* 1993; Paynter *et al.* 1996) and large seed banks accumulate beneath stands (Tables 2, 3 & 4). It is not clear how long broom seed banks persist: Hosking, Smith & Sheppard (1996) note that more than 80% of seeds buried in nylon mesh bags were still alive and dormant after 45 months. However, Bossard (1993) found that only 7% of seed remained ungerminated when buried for 3 years at a depth of 4 cm. Paynter *et al.* (1996) found that vertebrate seed predation was extremely high for seeds on the soil surface in both native and exotic habitats, so that the persistence of broom in an area may not be simply related to the

size of the seed bank, but to the number of seeds that are incorporated in the soil seed bank.

SEEDLING ESTABLISHMENT

In Europe, the occasional weediness of broom has been linked to major disturbances, such as fire, that create microsites for germination and subsequent seedling survival (Rousseau & Loiseau 1982). In Australia, establishment of broom can occur in the absence of any substantial disturbance (Smith 1994) although establishment has been noted to occur more quickly in disturbed sites (e.g. Smith & Waterhouse 1988). Little work on seedling survival has been published, but Smith & Waterhouse (1988) and Memmott *et al.* (1993) present preliminary data showing that seedling mortality is negligible in the absence of a closed broom canopy (Table 4). However, Bossard & Rejmánek (1994) record seedling densities from such a site in California declining from 235 m⁻² to c. 11 m⁻² in 2 years (probability of survival 0.05). Some studies, however, have noted that seedling survival under existing broom stands is typically very low indeed (e.g. Waterhouse 1988; Smith 1994; Fowler *et al.* 1996). Preliminary data regarding the proportion of seedlings surviving for 2 years in cultivated plots are given in Paynter *et al.* (1996).

SENESCENCE, MORTALITY AND REGENERATION

There is evidence that plants live longer in exotic habitats: Scotch broom has an average life expectancy of 10–12 years in the UK (Waloff & Richards 1977) and was not found to live more than 12 years in France (Rousseau & Loiseau 1982), but stands can live for more than 20 years in Australia (Table 5). Smith (1994) noted that rotting of heartwood in very old plants makes them difficult to age by counting growth

Table 3. Seed banks beneath broom stands in exotic and native ranges (seeds m⁻²)

Seed bank	Site	Country	Reference
Exotic habitats			
400–3000	North and South Islands	New Zealand	1
190–2700	Adelaide Hills	Australia	2
1100–5300	Barrington Tops	Australia	3, 4, 5
16675	Armidale	Australia	4
4630–27000	Braidwood	Australia	6
Native habitats			
Up to 10000	Silwood Park, Berkshire	UK	7
3392–6733	County Wicklow	Eire	3
1612–9320	Gard	France	8
460–1405	Gard	France	9
595	Vinuesa	Spain	9

1, Allen, Williams & Lee (1995); 2, Steele (1993); 3, Smith & Harlen (1991); 4, Mihe (1992); 5, Hosking *et al.* (1996); 6, A.W. Sheppard & P. Hodge (unpublished data); 7, Memmott *et al.* (1993); 8, Q. Paynter (unpublished data); 9, Hosking (1995).

Table 4. Probability of a seed becoming a seedling after a disturbance, g , and the subsequent probability of survival to first flowering in New Zealand, Australia, the UK and France (see text for details)

Country	Probability of a seed becoming a seedling, g	Probability of seedling survival to reproduction	Reference
Exotic habitats			
New Zealand	Usually low, 0–0.47	–	1
Australia	0.02	0.06	2
Australia	0.006–0.04 in autumn	–	3
Australia	–	‘Negligible mortality’	4
USA	–	0.05	5
Native habitats			
UK	0.035	‘Little mortality’	6
UK	0.036	0.58	2
France	0.013	0.16	2

1, Williams (1981); 2, Paynter *et al.* (1996); 3, Hosking *et al.* (1996); 4, Smith & Waterhouse (1988); 5, Bossard & Rejmánek (1994); 6, Memmott *et al.* (1993).

Table 5. Broom longevity estimates, where a single figure is given this is the mean, figures in brackets are maxima, otherwise some description of distribution is given, which varies depending on the source

Country	Estimate (years)	Reference
Native habitats		
UK	10–12	1
UK	10 (14)	2
France	8 (12)	3
France	< 12 years	4
Exotic habitats		
Australia	> 23 years; at least 28 years	5, 6
	12 (25), 10.5 (19), 7.6 (20)	7
USA	Up to 17 years	8

1, Waloff & Richards (1977); 2, M. Rees (unpublished data); 3, Q. Paynter (unpublished data); 4, Rousseau & Loiseau (1982); 5, Smith & Harlen (1991); 6, Smith (1994); 7, M. Rees, A.W. Sheppard & J.R. Hosking (unpublished data); 8, Bossard & Rejmánek (1994).

rings, but recorded ages up to 28 years. Two preliminary studies of the age-structure of dead plants, one from Scotland and one from France, are presented in Fig. 1; for each population, age at death was estimated by counting rings. For a population in a forest clearing (Tentsmuir Point, Fife, UK, altitude sea level) average age at death was 10.2 years, and 88% of individuals had died by the end of their twelfth year. In the French population, which occurred in the understorey of a mixed larch/pine woodland (Col d'ares, Pyrenees Orientales, France, altitude \approx 1550 m), average age at death was 7.9 years and all plants were dead by the end of their twelfth year. In both populations the distribution of age at senescence was well described by a normal distribution. In collecting these data we selected areas (each \approx 1.5 \times 1.5 m²) which contained dead broom plants, and then

aged the largest dead plant. We avoided subdominant dead plants within the canopy of established stands, as mortality here would not result in any change in the area occupied. In this way the plant longevity can be equated to the length of occupation of a site. The reason for collecting data in this way is that in the model described below we were interested in the time to a site becoming open which depends on mortality of the largest plant present. A large-scale insecticide application experiment performed in the UK revealed that excluding insect herbivores led to a *c.* 50% reduction in plant mortality over a 10-year period (Waloff & Richards 1977), suggesting that absence of herbivory by specialist insect herbivores in Australia may be a major reason for the increased lifespan of broom there.

As plants senesce and die, and despite increased illumination of the ground, regeneration of broom from the seed bank has not been recorded (Smith 1994) unless disturbance creates large gaps in the broom canopy or until after the death of most broom plants in the absence of disturbance (Hosking *et al.* 1996). However, in some Australian habitats, regeneration from seed after plant senescence has been observed (A.W. Sheppard, personal communication).

Description of simulation model

The model uses a coupled map lattice formulation, which allows a simple representation of a spatially explicit population (Crawley & May 1987; Hassell, Comins & May 1991; Perry & Gonzalez-Andujar 1993; Durrett & Levin 1994). Specifically, we assume there are a large number of identical sites; each is 1.5 m \times 1.5 m, the approximate size of an adult broom plant (see Paynter *et al.* 1996). The sites are arranged in a square lattice with wrap-around margins. This means that seeds dispersed from one edge of the plot land on the opposite side; in this way all sites within the lattice are equivalent. In all numerical simulations

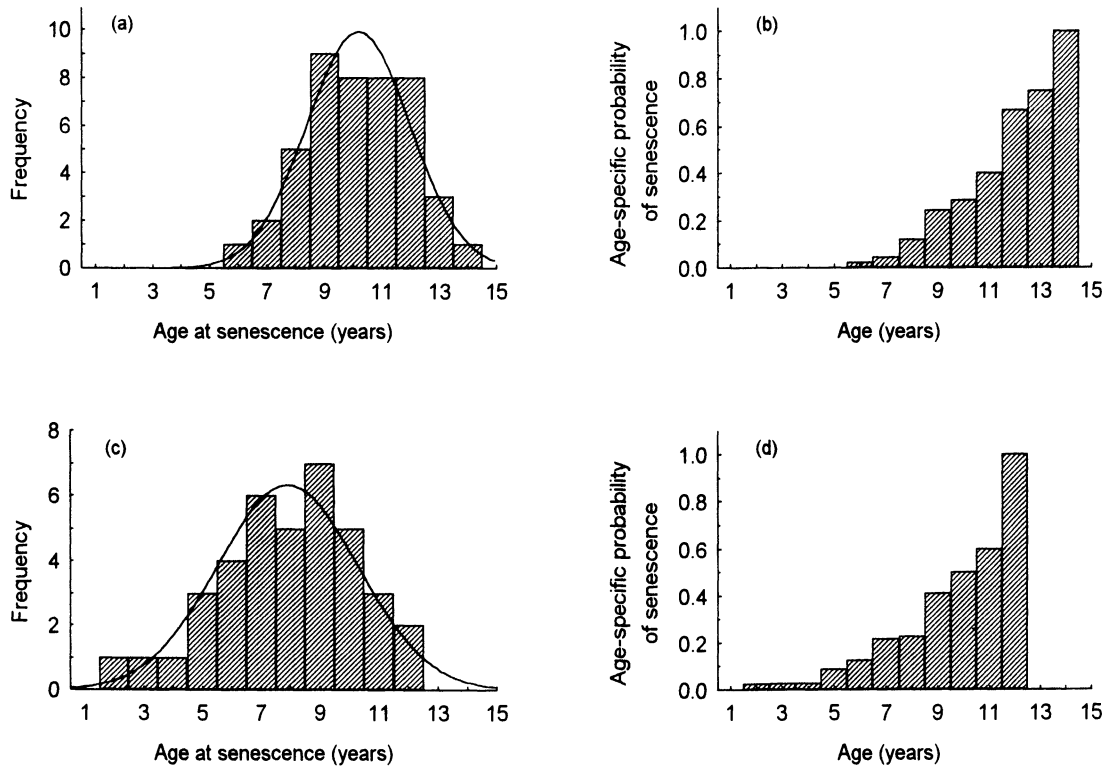


Fig. 1. Distribution of age at senescence for two broom populations. (a) Frequency distribution of age at senescence for a population from a forest clearing at Tentsmuir Point, Fife, UK; the continuous line is the fitted normal distribution, $\chi^2_3 = 4.36$, $P = 0.22$. (b) Age-specific rate of senescence calculated from (a). (c) Frequency distribution of age at senescence for a population from a forest understorey in the Pyrenees Orientales, France; the continuous line is the fitted normal distribution, $\chi^2_3 = 1.55$, $P = 0.67$. (d) Age-specific rate of senescence calculated from (c).

a grid of 75×75 sites was used. Numerical quantities estimated from the simulation model are, unless otherwise stated, arithmetic means of the last 200 years of a 500-year simulation. However, it should be noted that the model generally converged on its long-term equilibrium state within 30 years (e.g. Fig. 2). Each

site can be in one of three states, either occupied by broom, or unsuitable for colonization by broom, or open and so suitable for colonization by broom. Sites that are unsuitable for broom colonization are assumed to contain native vegetation. In each year, events occur in the following order (steps).

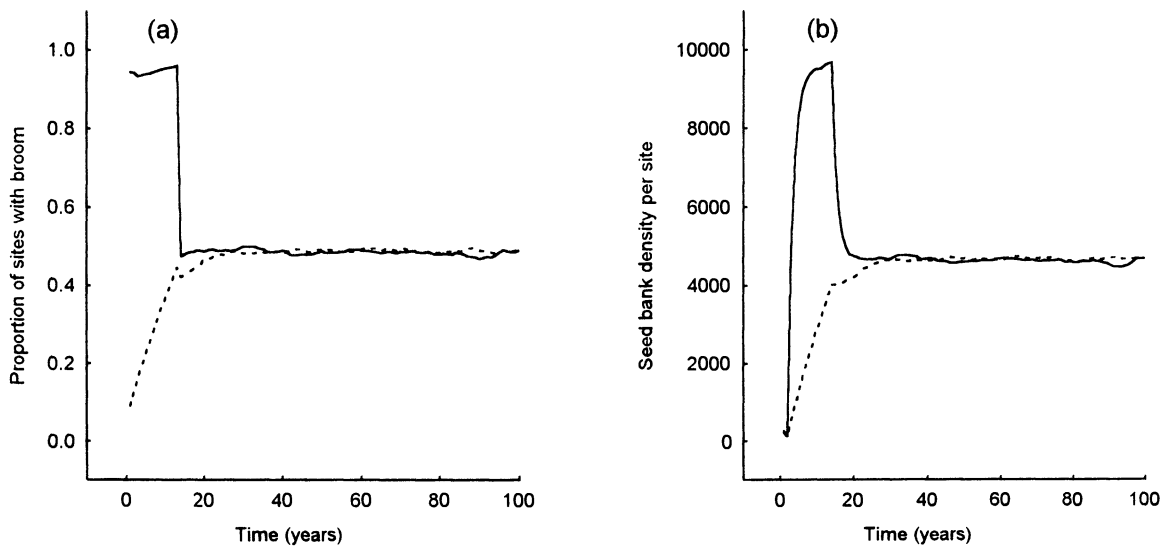


Fig. 2. Output from two runs of the simulation model for the European scenario. In one simulation only 5% of sites are initially occupied by broom (dotted line), whilst in the second 95% of sites are initially occupied (solid line). In both cases the simulation was initiated with one-year-old broom plants. Time series for (a) the proportion of sites occupied by broom for the two starting conditions and (b) the density of seeds per site. Parameter values: $F = 5600$, $d = 0.5$, $g = 0.03$, $s = 0.50$, $f_i = 0.6$, $A_{min} = 2$, $A_{max} = 12$, $p_{so} = 0.0$, $p_{dst} = 0.05$.

1. Sites, irrespective of their state, become disturbed with probability p_{dist} .

2. Broom seeds germinate at each site resulting in a Poisson distribution of recruits at time t in site i,j with mean

$$R_i^{t,j} = gsS_i^{t,j} \quad \text{eqn 1}$$

where g is the probability a seed becomes a seedling, s is the probability a seedling survives to the end of the first year and $S_i^{t,j}$ is the number of viable seeds in the site. We use a Poisson distribution here to model effects of demographic stochasticity (May 1974). The importance of including demographic stochasticity in spatial models was emphasized by Perry & Gonzalez-Andujar (1993).

3. The number of seeds in each site is reduced according to the decay probability, d , so:

$$S_{i+1}^{t,j} = (1-d)S_i^{t,j} \quad \text{eqn 2}$$

the parameter d subsumes all sources of loss from the seed bank (i.e. germination, loss of viability, granivory, etc.) and so d is always greater than or equal to g .

4. If a site is disturbed and the number of recruits is greater than zero then broom successfully recruits at that site. By setting the site dimensions so that it can accommodate a single adult broom plant we assume that the law of constant yield (Harper 1977) holds overall densities and so avoid having to track the number of recruits at each site. We do not distinguish between effects of density-dependent mortality or changes in plant size, and so when we refer to a broom plant this may correspond to a single broom plant in a site, or several plants that recruited simultaneously at a site. All broom recruits that occur in undisturbed sites (i.e. those already occupied by broom or unsuitable) are assumed to die in their first year.

5. Disturbed sites which have not been colonized by broom become unsuitable for colonization as the ground cover recovers from the disturbance.

6. Sites containing plants older than the minimum age for reproduction, A_{min} , produce F seeds and these are dispersed locally. Some fraction f_h of seeds produced are retained in the parental site, and the rest are dispersed equally to the eight neighbouring sites.

7. Plants older than A_{max} senesce and these sites become open and so suitable for broom recruitment with probability p_{so} , otherwise the site becomes unsuitable.

8. Plants grow older.

The computer simulation is spatially explicit, and incorporates spatially local competition, asymmetric competition between seedlings and established plants, local seed dispersal, a seed bank, and an age-structured established plant population and so is a reasonably realistic description of the known population biology of broom. Two time series from the simulation model are shown in Fig. 2 where the model was

initiated either with low or high levels of broom occupancy. When the simulation starts with a high occupancy level, the population crashes after the initial cohort of plants senesce and the resulting population undergoes small-scale fluctuations as a result of demographic stochasticity, see point 2 above. Note, that despite the presence of a long-lived adult stage and a seed bank, the model rapidly converges on the equilibrium. Before numerically exploring the simulator we derive the age-structure of the broom population and some approximations which will give an insight into the properties of the system.

Age-structure of the broom population

At equilibrium let the fraction of sites occupied by broom plants in their first year be P_0 ; it then follows that the fraction of sites with broom plants aged x will be:

$$P_x = (1-p_{dist})^x P_0 \quad \text{eqn 3}$$

In order to calculate the age-structure of broom plants we sum overall age classes, giving:

$$\sum_{x=0}^{A_{max}} P_x = \frac{P_0(1-(1-p_{dist})^{A_{max}+1})}{p_{dist}} \quad \text{eqn 4}$$

Let z_x be the fraction of broom plants aged x , then:

$$\begin{aligned} z_x &= \frac{P_x}{\sum_{i=0}^{A_{max}} P_i} \\ &= \frac{p_{dist}(1-p_{dist})^x}{1-(1-p_{dist})^{A_{max}+1}}, \end{aligned} \quad \text{eqn 5}$$

so the age-structure of broom plants follows a truncated geometric distribution. For examples of the use of this probability distribution see Rees & Long (1992, 1993). Note, in discussing the age-structure of the broom population we are assuming that the population rapidly thins to a single plant per site. If self-thinning occurs more slowly then the age structure of sites and broom plants will differ depending on the number of plants per site. In general, the average age of an occupied site will be greater than the average age of a plant. However, to avoid having to use the awkward expression 'the age structure of occupied sites' we will simply refer to the population age-structure.

Saturation approximation

Here we seek simple approximations for the proportion of sites occupied by broom, assuming that disturbed sites are colonized with probability one, providing either (i) the site contained a reproductive broom plant the previous year, or (ii) a neighbouring site contained a reproductive broom plant the previous year. In biological terms this means that local

colonization is not seed limited, although this assumption will be relaxed in the next section.

Equations describing the simulation assume that the system is censused after the senescence of plants (i.e. step 7 in the simulation model). Initially, we ignore the seed bank and describe the system using just three variables: the fraction of sites occupied by broom at time t , B_t ; the fraction of sites that are unsuitable for broom establishment, U_t ; and the fraction of open sites, O_t . To construct equations for each of these variables we need to calculate the probability that a site had no neighbouring broom plants of reproductive age the previous year. This is given by:

$$p_{nr} = (1 - B_t f_r)^8, \quad \text{eqn 6}$$

where f_r is the fraction of broom plants that are reproductive ($f_r = \sum_{x=A_{min}}^{A_{max}} Z_x$). Note that the parameter, f_r , is assumed to be constant through time (i.e. the population has reached a stationary age-structure). The '8' arises because we assume that seed dispersal occurs to the eight nearest neighbours on a square lattice. We can then derive a set of equations which ignores details of the spatial arrangement of broom plants and instead, uses the fraction of sites occupied. This is known as a mean field approximation, hence:

$$\begin{aligned} U_{t+1} &= (1 - p_{dist})[U_t + B_t z_{max}(1 - p_{so})] \\ &\quad + p_{dist} p_{nr} [U_t + B_t(1 - f_r)] \\ B_{t+1} &= (1 - p_{dist})[B_t(1 - z_{max})] + p_{dist}[B_t f_r + U_t(1 - p_{nr}) \\ &\quad + B_t(1 - f_r)(1 - p_{nr})] + O_t \\ O_{t+1} &= (1 - p_{dist})B_t z_{max} p_{so} \end{aligned} \quad \text{eqn 7}$$

where p_{dist} is the probability of disturbance, z_{max} the fraction of broom plants in the maximum age class, p_{so} the probability that a site which contained a senescent plant (i.e. one of maximum age) becomes suitable for recruitment following senescence, p_{nr} the probability that a site had no broom plants of reproductive age as nearest neighbours in the previous year, and f_r is the proportion of broom plants of reproductive age.

To see how these equations are derived, consider the equation for the fraction of unsuitable sites. This has several terms which correspond to the following events.

1. The site was not disturbed, in which case it remains unsuitable. This occurs with probability $(1 - p_{dist})U_t$.
2. The site was not disturbed and contained a broom plant that senesced resulting in an unsuitable site. This occurs with probability $(1 - p_{dist})B_t z_{max}(1 - p_{so})$.
3. The site was disturbed, not colonized and was previously either an unsuitable site or a site with a pre-reproductive broom plant. This occurs with probability $p_{dist} p_{nr} [U_t + B_t(1 - f_r)]$.

In a similar way, the equations for the proportion of sites containing broom plants or open sites can be

calculated. Hence, using just two equations (the third is redundant because $B_t + O_t + U_t = 1$), we can summarize a great deal of information about the simulator. The accuracy of the approximation will be explored later.

In general, it is not possible to solve for the equilibrium proportion of sites occupied by broom, B^* , using eqn 7. However, at the limit when all disturbed sites are colonized with probability one, regardless of whether or not they previously contained a reproductive plant or had reproductive neighbours, we obtain:

$$B^* = \frac{p_{dist}}{1 - (1 - p_{dist})[(1 - z_{max}) + (1 - p_{dist})z_{max}p_{so}]}. \quad \text{eqn 8}$$

Hence, the fraction of sites occupied by broom when all open sites are colonized is set by the probability of disturbance, p_{dist} , the probability a site becomes suitable for colonization after senescence, p_{so} , and maximum plant longevity, A_{max} . As maximum longevity becomes larger so z_{max} becomes smaller and B^* tends to unity. Note, even when all open sites can be colonized, the proportion of sites occupied at equilibrium is still less than one, providing plants have finite longevity. This equation provides a useful upper bound on the proportion of sites occupied by broom. Assuming $p_{so} = 0$ we can simplify eqn 8 to give:

$$B^* = \frac{1}{1 - z_{max} + z_{max}/p_{dist}}. \quad \text{eqn 9}$$

If $p_{dist} = 0.05$ and $A_{max} = 12$ then $B^* = 0.49$, which is a surprising result as we have assumed that all disturbed sites are colonized with probability one! So, even if broom had a very long-lived seed bank and widely dispersed seeds, it would occupy less than 50% of the habitat. The reason for this is that the levels of occupancy are set by the probabilities of sites being captured by broom, which depends of the probability of disturbance, or becoming unsuitable. Assuming $p_{so} = 1$ we simplify eqn 8 giving:

$$B^* = \frac{1}{1 + z_{max}(1 - p_{dist})}, \quad \text{eqn 10}$$

which is less than one because of the presence of open sites, O_t ; note however, if $z_{max} = 0$ then, as expected, $B^* = 1$.

In order to determine if broom will invade a habitat, we consider the initial stages of an invasion. When broom is introduced into a habitat, virtually all sites will be unsuitable because we have assumed that open sites that are not colonized by broom become unsuitable for colonization (step 5 in the simulation model), hence $U_t \approx 1$ and so the equation for B_{t+1} simplifies giving:

$$\begin{aligned} B_{t+1} &= (1 - p_{dist})[B_t(1 - z_{max})] + p_{dist}[B_t f_r + (1 - p_{nr}) \\ &\quad + B_t(1 - f_r)(1 - p_{nr})] + O_t \end{aligned} \quad \text{eqn 11}$$

Differentiating B_{t+1} with respect to B_t and setting $B_t = 0$ in the resulting equation, we obtain the condition for broom to invade a habitat. The resulting mathematical condition is:

$$9f_r p_{dist} + (1 - p_{dist})[1 - z_{max}(1 - p_{so})] > 1 \quad \text{eqn 12}$$

This equation has a straightforward interpretation; $9f_r p_{dist}$ is the average number of new sites colonized by a reproductive broom plant in one year, made up of the eight neighbouring sites plus the parental site, and $(1 - p_{dist}) [1 - z_{max}(1 - p_{so})]$ is the fraction of broom plants that survive from one year to the next plus those that senesce and are subsequently colonized by broom. Therefore, if we imagine a single broom plant invading a habitat then, providing the invasion condition holds, there will be more broom plants the following year and so an invasion will succeed. In contrast if this condition is not met, each plant will replace itself with, on average, less than one plant and so the population will go extinct. When considering this equation it is important to remember that both f_r and z_{max} are functions of p_{dist} , so if one wishes to calculate the critical probability of disturbance, one must substitute for these expressions. In constructing the saturation approximation we have assumed the broom population is at the equilibrium age-structure, which explains the presence of the z_{max} term in the invasion condition (eqn 12). Other invasion conditions can be constructed looking at the fate of seeds or pre-reproductive plants. If the year to year changes in these stages are considered one gets the nonsensical result that all invasions fail or, conversely, if one considers the introduction of a single reproductive plant then the population increases providing $p_{dist} > 0$ (R. Freckleton, personal communication). For this reason we have used an invasion condition averaged over the age-structure which produces results in agreement with the simulation model.

If disturbed sites, which are suitable for broom colonization, persist for several years this would make invasion easier, as the average number of new sites colonized by an initial invader would be increased because more sites are suitable for colonization. The dynamics of disturbed sites will depend on the native vegetation. In many European habitats, disturbances are rapidly colonized by perennial grasses which prevent subsequent broom colonization. However, in some habitats, such as braided rivers in New Zealand, native plants may be rare and so most sites will be permanently suitable for colonization.

Non-saturation approximation

In the previous section, an approximation was derived which assumed that local colonization processes are saturated and there was no seed bank. Here, we relax these assumptions and derive a more complex approximation of the system. When colonization saturation does not occur, the probability of colonization

depends on the number of seeds produced in the local environment plus those from the seed bank. In this case, assuming a site that was occupied by a reproductive broom plant in the previous year and had n reproductive neighbours was disturbed, we can calculate the probability of successful recruitment. This is simply one minus the probability of getting no recruits. This gives:

$$1 - \exp \left[-gs \left(f_h F + \frac{(1-f_h)}{8} F n + (S_t - F f_r B_t) \right) \right], \quad \text{eqn 13}$$

where the first term in the exponential represents seeds produced by the plant at the site the previous year, the second is seed input from neighbouring reproductive broom plants, and the third term is the seed bank excluding the current year's seed production; S_t being the average number of seeds in the seed bank at a site. In order to calculate the average value of this expression we assume broom plants occupy sites in the lattice independently at random, hence the number of reproductive broom neighbours around a site follows a binomial distribution, so we have:

$$\begin{aligned} p_{bc} &= \sum_{n=0}^8 \binom{8}{n} (f_r B_t)^n (1 - f_r B_t)^{8-n} \\ &\times \left[1 - \exp \left(-gs \left(f_g F + \frac{(1-f_h)}{8} F n + (S_t - F f_r B_t) \right) \right) \right] \\ &= 1 - \exp \left(-gs (f_h F + (S_t - F f_r B_t)) \right) \\ &\times \left[f_r B_t \exp \left(-gs \frac{(1-f_h)}{8} F \right) + 1 - f_r B_t \right]^8, \quad \text{eqn 14} \end{aligned}$$

where p_{bc} is the probability that a site that previously contained a reproductive broom plant and was disturbed, is colonized. Arguing in exactly the same way, we can derive the probability a disturbed site is colonized if it did not previously contain a reproductive broom plant p_{nbc} , this gives:

$$\begin{aligned} p_{nbc} &= \sum_{n=0}^8 \binom{8}{n} (f_r B_t)^n (1 - f_r B_t)^{8-n} \\ &\times \left[1 - \exp \left(-gs \left(\frac{(1-f_h)}{8} F n + (S_t - F f_r B_t) \right) \right) \right] \\ &= 1 - \exp \left(-gs (S_t - F f_r B_t) \right) \\ &\times \left[f_r B_t \exp \left(-gs \frac{(1-f_h)}{8} F \right) + 1 - f_r B_t \right]^8, \quad \text{eqn 15} \end{aligned}$$

We then modify the previous set of equations derived assuming local colonization saturates, to allow for probabilities of colonization less than unity. Hence:

$$\begin{aligned}
U_{t+1} &= (1-p_{dist})[U_t + B_t z_{max}(1-p_{so})] \\
&\quad + p_{dist}(1-p_{nbc})[U_t + B_t(1-f_r)] \\
&\quad + p_{dist}B_t f_r(1-p_{bc}) + O_t(1-p_{bc}) \\
B_{t+1} &= (1-p_{dist})B_t(1-z_{max}) + p_{dist}[B_t f_r p_{bc} \\
&\quad + B_t(1-f_r)p_{nbc} + U_t p_{nbc}] + O_t p_{bc} \\
O_{t+1} &= (1-p_{dist})B_t z_{max} p_{so} \\
S_{t+1} &= (1-d)S_t + FB_t f_r.
\end{aligned}
\tag{eqn 16}$$

Although it is not possible to obtain an analytical expression for the equilibrium proportion of sites occupied by broom, this can be calculated numerically or an upper bound can be obtained using eqn 8. Once the equilibrium proportion of sites occupied by broom, B^* , has been calculated, the equilibrium seed bank, S^* , can be determined using:

$$S^* = \frac{FB^* f_r}{d}. \tag{eqn 17}$$

Calculating the condition for invasion for this new system leads to a complex expression that is not readily interpretable. However, when there is no seed bank ($d = 1$) a calculation similar to that presented in the previous section leads to the following invasion condition:

$$\begin{aligned}
p_{dist} f_r \left[9 - 8 \exp\left(-\frac{gsF(1-f_h)}{8}\right) - \exp(-Ff_h gs) \right] \\
+ (1-p_{dist})[1 - z_{max}(1 - (1 - \exp(-Ff_h gs))p_{so})] > 1.
\end{aligned}
\tag{eqn 18}$$

As the parameter combination gsF becomes large, this condition converges on the invasion condition for the saturation approximation, eqn 12, as expected. All the parameters and variables used in the simulation and the approximation schemes are listed and defined in Table 6.

The equilibrium proportion of sites occupied by broom

Demographic parameters for broom are available from a wide range of countries (Tables 1–5). For European populations we assumed the following baseline parameter set, $F = 5600$, $d = 0.5$, $g = 0.03$, $s = 0.50$, $f_h = 0.6$, $A_{min} = 2$, $A_{max} = 12$, $p_{so} = 0.0$, $p_{dist} = 0.05$ (as used in Fig. 2). The influence of each of these parameters on the proportion of sites occupied by broom is explored in this section. For each of the parameters we estimate the proportion of sites occupied at equilibrium using the simulation model and the two approximation schemes. Using this parameter set and eqn 8 we find the maximum level of site occupancy is 0.49.

The impact of the parameters, g , s , d and f_h on the proportion of sites occupied by broom is presented in Fig. 3. Surprisingly, none of these variables has any appreciable impact on the proportion of sites occupied by broom because plant fecundity is large, which means that local colonization processes tend to saturate and so all disturbed sites are almost certainly colonized by broom. When plant fecundity is lower these parameters become important (cf. Figs 6–8). In

Table 6. Parameters and variables used in the simulation model and the approximation schemes

Symbol	Meaning
p_{dist}	Probability a site is disturbed
g	Probability a seed becomes a seedling
s	Probability a seedling survives to end of first year
$S_i^{t,j}$	Number of viable seeds in site i,j at time t
S_i	Average number of viable seeds in a site
$R_i^{t,j}$	Number of recruits in site i,j at time t
d	Probability a seed is lost from the seed bank
A_{min}	Minimum age for reproduction (years)
A_{max}	Maximum plant age (years)
F	Per site seed production
f_h	Probability a seed is retained in parental site
p_{so}	Probability a site which contained a senescent broom plant becomes suitable for colonization
P_x	Fraction of sites that contain a broom plant x years old
z_x	Fraction of broom plants x years old
z_{max}	Fraction of broom plants in the maximum age class
B_t	Fraction of sites occupied by broom
U_t	Fraction of sites unsuitable for broom colonization
O_t	Fraction of sites suitable for broom colonization
p_{nbc}	Probability of having no reproductive broom neighbours
f_r	Fraction of broom plants of reproductive age
p_{bc}	Probability a site which previously contained a reproductive broom plant is colonized
p_{nbc}	Probability a site which previously did not contain a reproductive broom plant is colonized
p_{distU}	Probability an unsuitable site is disturbed
ρ	Probability a broom plant senesces, averaged over the stationary age-structure

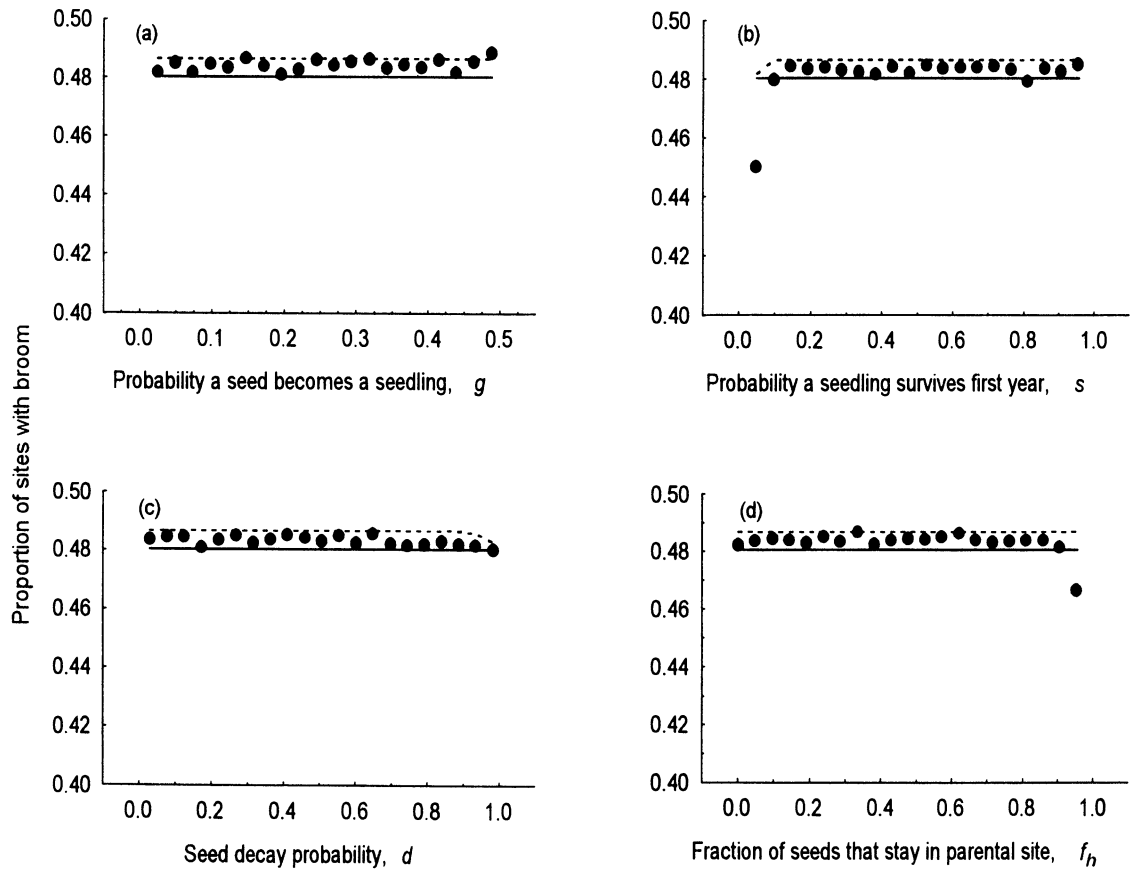


Fig. 3. Proportion of sites occupied by broom for the European scenario, varying (a) the probability a seed becomes a seedling, g , note g must be less than d ; (b) the probability a seedling survives the first year, s ; (c) the probability of seed decay, d , note d must be greater than g ; and (d) the fraction of seeds retained in the parental site, f_h . Other parameter values unless varied: $F = 5600$, $d = 0.5$, $g = 0.03$, $s = 0.50$, $f_h = 0.6$, $A_{min} = 2$, $A_{max} = 12$, $p_{so} = 0.0$, $p_{dist} = 0.05$. Solid line is the saturation approximation, dashed line the non-saturation approximation, and the dots are from a spatially explicit simulation model, see text for details.

each case the analytical results provide an excellent description of the simulation. The agreement with the maximum level of site occupancy, in this case 0.49, set by eqn 8, is excellent in all cases.

In sharp contrast, changing maximum longevity or the minimum age for reproduction has a dramatic effect on the proportion of sites occupied (Fig. 4).

Increasing maximum adult longevity increases the proportion of sites occupied. The agreement between the analytical results for the non-saturation approximation and the simulation is excellent over the entire range. The saturation approximation tends to underestimate the proportion of sites occupied at low maximum longevitys, Fig. 4a. This is a direct result

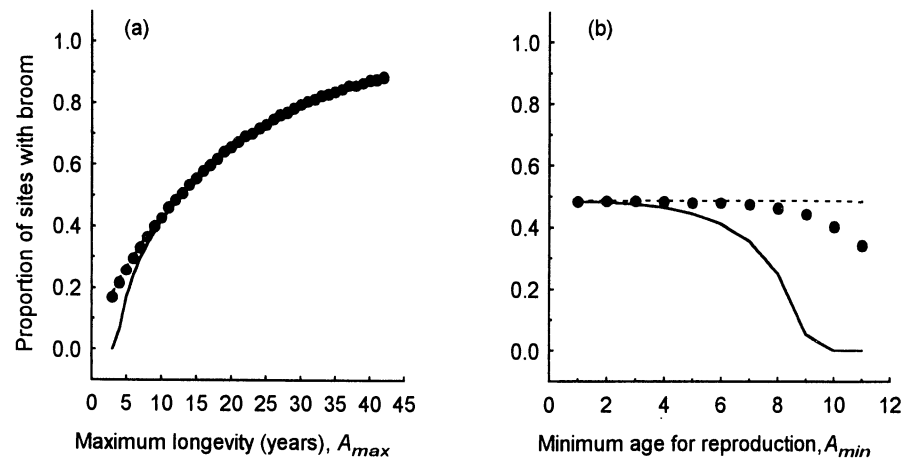


Fig. 4. Proportion of sites occupied by broom for the European scenario, varying (a) maximum plant longevity, A_{max} ; and (b) the minimum age for reproduction, A_{min} . Other parameter values unless varied: $F = 5600$, $d = 0.5$, $g = 0.03$, $s = 0.50$, $f_h = 0.6$, $A_{min} = 2$, $A_{max} = 12$, $p_{so} = 0.0$, $p_{dist} = 0.05$. Solid line is the saturation approximation, dashed line the non-saturation approximation, and the dots are from a spatially explicit simulation model, see text for details.

of not modelling the seed bank in this approximation. Increasing the minimum age for reproduction decreases the proportion of sites occupied, as more plants are in the non-reproduction category and so the population's colonization potential is reduced. The fit between the analytical models and the simulation results is less satisfactory in this case; the non-saturation approximation overestimates the proportion of sites occupied, whereas the saturation approximation gives an underestimate, Fig. 4b.

The effects of the final three parameters, seed production, F , the probability a site becomes suitable for colonization after senescence, p_{so} , and the probability of disturbance, p_{dist} , on the proportion of sites occupied are illustrated in Fig. 5. Increasing seed production increased the proportion of sites occupied as expected, but increases in seed production over 1000 seeds per site have little effect on the proportion of sites occupied and over this range the approximation schemes accurately describe the simulation results, Fig. 5a. The upper bound on the proportion of sites occupied is set by eqn 8, which in this case gives $B^* = 0.49$, in close agreement with the simulation results. Below a seed production of about 1000 seeds per site the non-saturation approximation overestimates the proportion of sites occupied; this is largely a result of the assumption that the spatial distribution of the seed bank can be described by a Poisson distribution. In the saturation approximation all open sites which previously contained reproductive plants or had reproductive neighbours are always

colonized, hence there is no dependence on the per site seed production.

Increasing the probability that a site becomes suitable for colonization after senescence increases the proportion of sites occupied, and in this case both analytical approximations provide an excellent description of the simulation results, Fig. 5b. The relationship between the proportion of sites occupied and the probability of disturbance is humped, with occupancy maximized at intermediate disturbance levels (Fig. 5c); at low probabilities of disturbance most sites are unsuitable for colonization and the population goes extinct; at high rates of disturbance no plants survive to reproductive age and so again the population goes extinct. At intermediate levels of disturbance the population is persistent. For probabilities of disturbance less than about 0.5 both analytical approximations provide an accurate description of the simulation results. Above this value the saturation approximation underestimates the simulation results, whereas the non-saturation approximation gives an overestimate.

Impact of seed feeders on British broom populations

In a now classic study, Waloff & Richards (1977) looked at the impact of the insect fauna on growth, mortality and seed production of broom. Using chemical exclusion methods they found that, over the lifespan of a bush, insects reduced seed production by

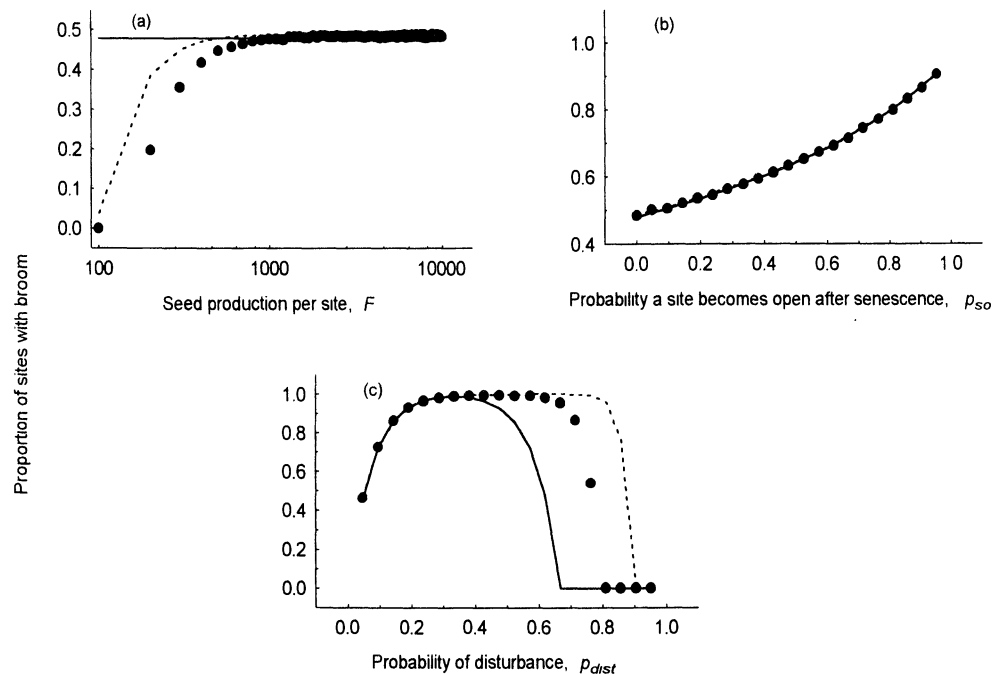


Fig. 5. Proportion of sites occupied by broom for the European scenario, varying (a) the seed production per site, F ; (b) the probability a site becomes suitable for colonization after senescence, p_{so} ; and (c) the probability of disturbance, p_{dist} . Other parameter values, unless varied: $F = 5600$, $d = 0.5$, $g = 0.03$, $s = 0.50$, $f_n = 0.6$, $A_{min} = 2$, $A_{max} = 12$, $p_{so} = 0.0$, $p_{dist} = 0.05$. Solid line is the saturation approximation, dashed line the non-saturation approximation, and the dots are from a spatially explicit simulation model, see text for details.

75%. This would mean that seed production per bush would have increased from 5600 to 22400 seeds per year. In order to explore the impact of this level of herbivory on the proportion of sites occupied by broom, we ran the simulation model with: (i) two values of seed production per bush, $F = 5600$ and $F = 22400$; (ii) three different levels of seedling survival, $s = 0.01$, $s = 0.5$ and $s = 0.9$; and (iii) the probability of disturbance, p_{dist} , varying over the interval 0–1.

The results of the simulations are illustrated in Fig. 6. In each of the graphs it is clear that insect herbivores have a greater impact on the proportion of sites occupied by broom at higher disturbance levels. At low levels of disturbance insect herbivores only have an appreciable impact when the probability of seedling survival is low ($s = 0.01$), compare Fig. 6a with Fig. 6c.

The proportion of sites occupied by broom gives little insight into the potential impact of insect herbivores. For example, in Fig. 6c if the probability of disturbance is ≈ 0.4 then there is almost complete cover by broom and insect herbivores have little impact on the proportion of sites occupied. However, in Fig. 6a when the probability of disturbance is about 0.4, again there is almost complete cover of broom,

but here insect herbivory drives the population extinct. The cover of a weed seems to give little insight into how easily it might be controlled.

Will herbivores that reduce fecundity have any impact on exotic broom populations?

We addressed this question by calculating the potential impact of an insect biological control agent on the proportion of sites occupied assuming that it reduces seed production by 75%. This is, of course, a gross simplification of the population dynamics of insect herbivores, and if appropriate data were available more complex models could be constructed (see, for example, Caughley & Lawton 1981; Crawley 1983). Three Australian scenarios were explored. In all scenarios broom was assumed to have a maximum longevity of 20 years; other parameters other than F and A_{max} were as for the European scenario. Fecundities per site were calculated by multiplying the seed production per metre squared, given in Table 1, by 2.25 (each site is 2.25 m²). In the first scenario we have a population with low fecundity under a eucalyptus forest; fecundity in the absence of herbivores is assumed to be 240 seeds per site, in their presence 60 seeds per plant. In this situation broom can only per-

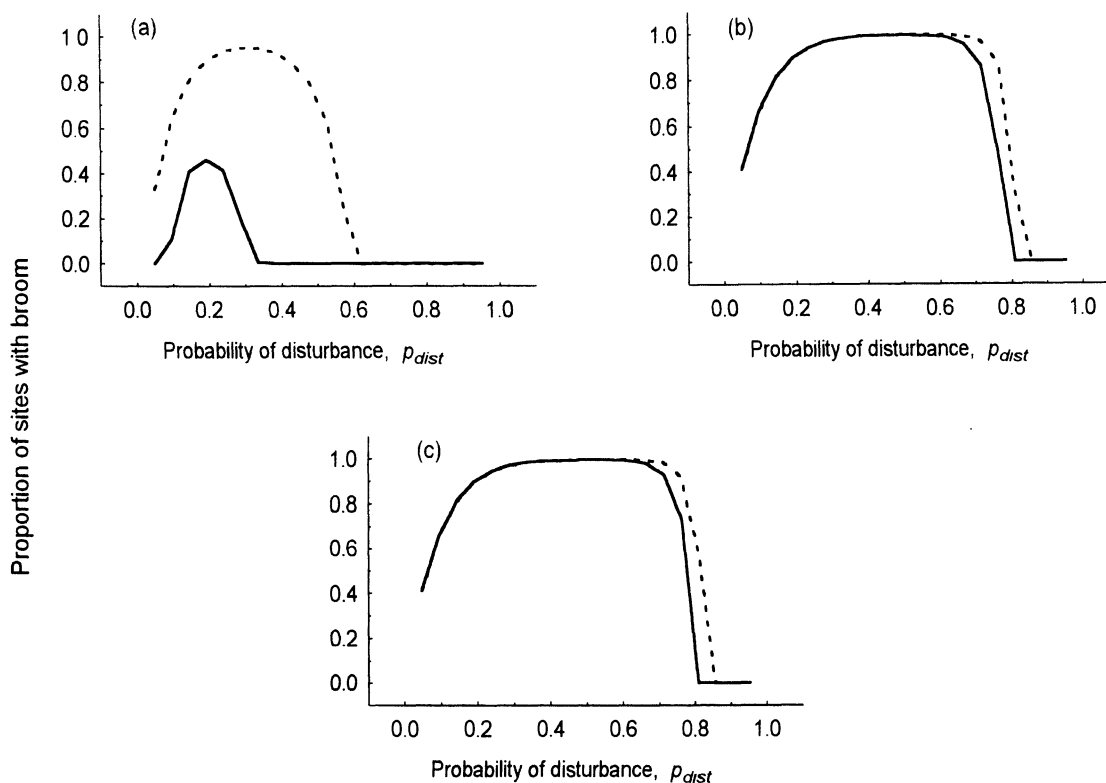


Fig. 6. Impact of insect herbivores on the proportion of sites occupied by broom for the European scenario. In each graph the solid line was calculated from the simulation model assuming a fecundity of 5600 seeds per plant, the dashed line is from the same model but with no insect herbivory resulting in a fecundity of 22400 seeds per plant, levels of herbivory from Waloff & Richards (1977), assuming three levels of seedling survival; (a) $s = 0.01$ (b) $s = 0.5$ and (c) $s = 0.9$. Other parameter values: $d = 0.5$, $g = 0.03$, $f_h = 0.6$, $A_{min} = 2$, $A_{max} = 12$ and $p_{vo} = 0.0$.

sist if seedling survival is reasonably high, and the probability of disturbance, p_{dist} , less than about 0.6, Fig. 7. Over a wide range of parameter values insect herbivores can have a dramatic effect on the proportion of sites occupied and in many cases drive a population extinct.

In the second scenario we assume a broom fecundity of 430 in the absence of insect herbivores and 110 in their presence (Fig. 8). As expected this reduces the impact of the control agent, but even in habitats where the probability of seedling survival is high ($s = 0.9$), biological control agents can have dramatic effects, Fig. 8c. As the probability of seedling survival increases so the range of disturbance regimes where a biological control agent would have any impact decreases, compare Fig. 8b with 8c.

In the final scenario we look at a broom population in a pasture with per site fecundity of 1991 seeds in the absence of a biological control agent and a fecundity of 4998 seeds per site in its presence. Here control is difficult to achieve except with high probabilities of disturbance, $p_{dist} > 0.7$, Fig. 9. Therefore, a biological control agent that reduces seed production by 75% would be unlikely to have any impact on the proportion of sites with broom. In evaluating the potential impact of a biological control agent we have deliberately not calculated eradication thresholds as these will depend critically on the details of the demographic parameters chosen and the disturbance regime.

Extensions to the basic models

Here we describe how the basic models, described above, can be modified to include (i) more realistic patterns of age-dependent senescence, and (ii) site-specific disturbance regimes. Specifically we will assume that senescence is the only form of plant mortality, and that only unsuitable sites can be disturbed;

this type of disturbance regime mimics the actions of wild boar which often root around established broom plants disrupting the ground cover whilst leaving the broom untouched.

If we assume that we have some schedule of age-specific senescence, such as that shown in Fig. 1b,d, where the probability of a broom plant aged x senesces is $p_{s,x}$, it is then a straightforward procedure to modify the simulation model. This involves changing step 1 so that only unsuitable sites are disturbed, and step 7 so that plants are killed with age-specific probabilities. However, the construction of the analytical approximations is rather more complicated. We start, as before, by deriving the equilibrium age-structure of the population. Specifically, let P_0 be the equilibrium fraction of sites occupied by broom plants in their first year, then it follows that the fraction of sites with plants aged x will be:

$$P_x = \prod_{t=0}^{x-1} (1 - p_{s,t}) P_0, \quad x = 1, 2, \dots, A_{max}. \quad \text{eqn 19}$$

Let z_x be the fraction of broom plants aged x , then using the same argument as used in the construction of eqn 5 we obtain:

$$z_x = \begin{cases} \frac{1}{1 + \sum_{j=1}^{A_{max}} \prod_{t=0}^{j-1} (1 - p_{s,t})} & x = 0 \\ \frac{\prod_{t=0}^{x-1} (1 - p_{s,t})}{1 + \sum_{j=1}^{A_{max}} \prod_{t=0}^{j-1} (1 - p_{s,t})} & x = 1, 2, \dots, A_{max} \end{cases} \quad \text{eqn 20}$$

We then use eqn 20 to calculate the probability that a randomly chosen broom plant senesces, which is denoted ρ , and defined by:

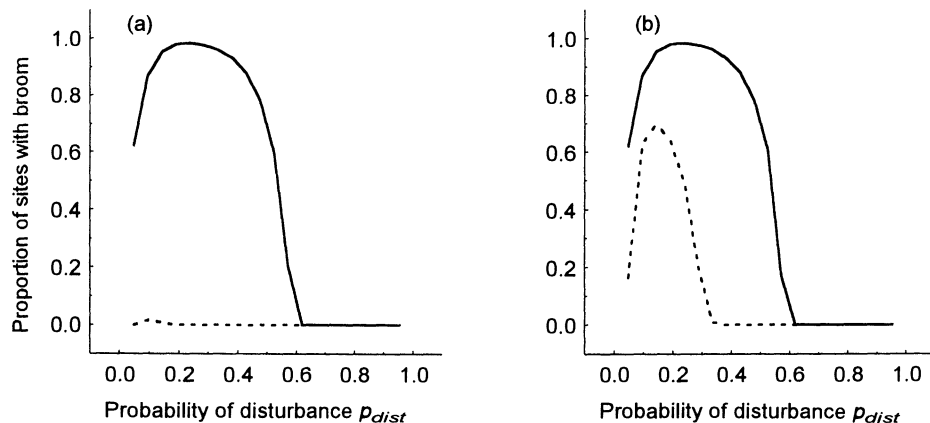


Fig. 7. Impact of insect herbivores on the proportion of sites occupied by broom for the first Australian scenario (under Eucalypt cover). In each graph the dashed line was calculated from the simulation model assuming a fecundity of 60 seeds per plant, the solid line from the same model but with no insect herbivory resulting in a fecundity of 240 seeds per plant, assuming two levels of seedling survival; (a) $s = 0.5$ and (b) $s = 0.9$. Other parameter values: $d = 0.5$, $g = 0.03$, $f_h = 0.6$, $A_{min} = 2$, $A_{max} = 20$ and $p_{so} = 0.0$.

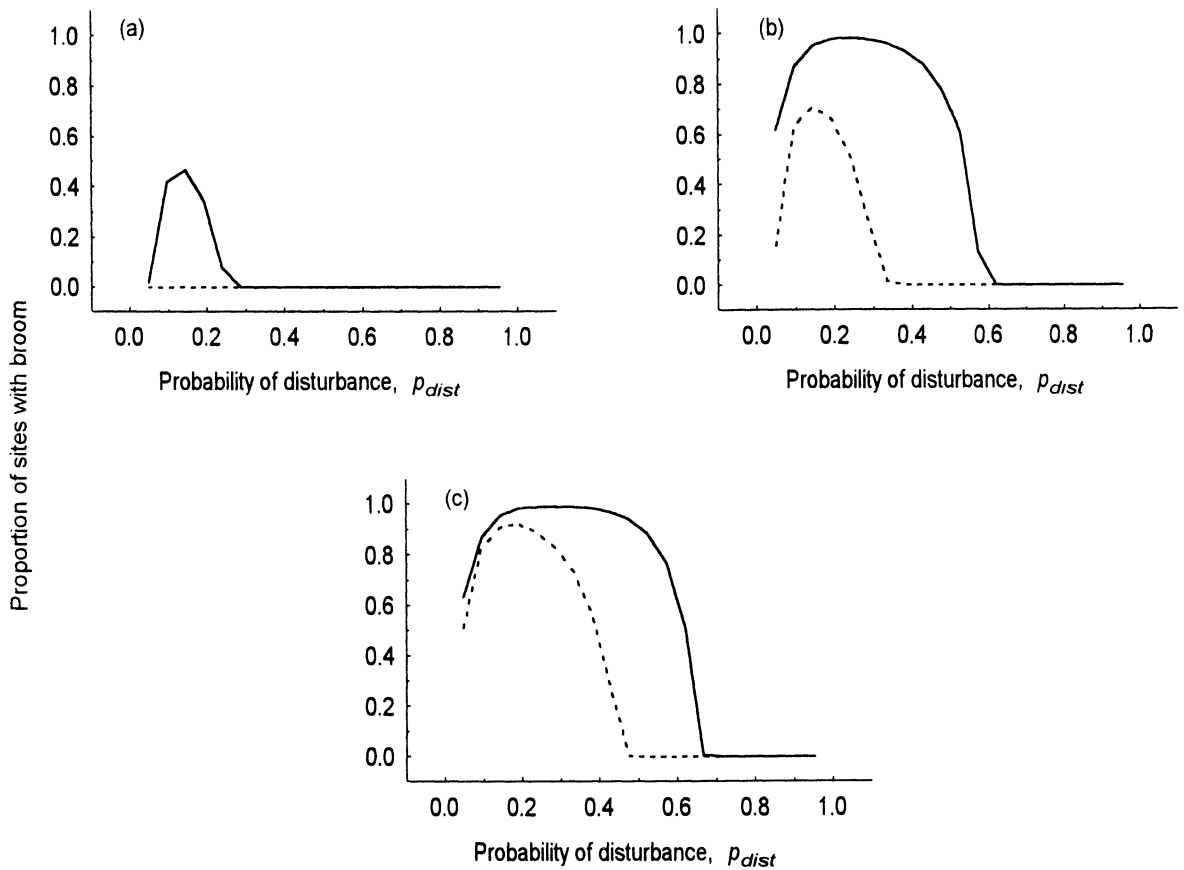


Fig. 8. Impact of insect herbivores on the proportion of sites occupied by broom for the second Australian scenario (under Eucalypt cover). In each graph the dashed line was calculated from the simulation model assuming a fecundity of 110 seeds per plant, the solid line from the same model but with no insect herbivory resulting in a fecundity of 430 seeds per plant, assuming three levels of seedling survival; (a) $s = 0.1$ (b) $s = 0.5$ and (c) $s = 0.9$. Other parameter values: $d = 0.5$, $g = 0.03$, $f_h = 0.6$, $A_{min} = 2$, $A_{max} = 20$ and $p_{so} = 0.0$.

$$\rho = \sum_{i=0}^{A_{max}} z_i p_{s,i} \tag{eqn 21}$$

Here we have used the equilibrium age structure to calculate the average probability of senescence. We use this equation in the development of a saturation approximation; before doing this it is necessary to define a new parameter, which is the probability an unsuitable site is disturbed, p_{distU} . We can then write down a system of equations similar to eqn 7 which incorporates the new assumptions, this gives:

$$\begin{aligned} U_{t+1} &= (1 - p_{distU})U_t + \rho(1 - p_{so})B_t \\ &\quad + p_m[p_{distU}U_t + (1 - f_i)O_t] \\ B_{t+1} &= (1 - \rho)B_t + p_{distU}U_t(1 - p_m) \\ &\quad + O_t[f_i + (1 - f_r)(1 - p_m)] \\ O_{t+1} &= \rho p_{so}B_t \end{aligned} \tag{eqn 22}$$

Calculation of the invasion condition, as in the previous models, leads to the following condition:

$$8f_r p_{distU} + 1 - \rho(1 - f_r p_{so}) > 1. \tag{eqn 23}$$

Again, this has a straightforward interpretation: the $8f_r p_{distU}$ is the average number of unsuitable sites that

are disturbed and colonized, and $1 - \rho(1 - f_r p_{so})$ is the proportion of plants that do not senesce plus those that do senesce, become open sites and are colonized. As with eqn 7 it is not possible to solve for the equilibrium proportion of sites occupied by broom. However, if we assume that all disturbed sites are colonized with probability one, we can solve for B^* which gives:

$$B^* = \frac{p_{distU}}{p_{distU} + \rho[1 - p_{so}(1 - p_{distU})]} \tag{eqn 24}$$

As in the models in the main body of the paper the maximum occupancy is set by just three parameters: the probability an unsuitable site is disturbed, p_{distU} ; the probability a broom plant senesces evaluated at the stationary age-structure, ρ ; and the probability a site becomes open following senescence, p_{so} . If $p_{so} = 0$ then eqn 24 simplifies to give:

$$B^* = \frac{1}{1 + \rho/p_{distU}}, \tag{eqn 25}$$

a result similar to eqn 9, although derived assuming a very different disturbance regime (i.e. only unsuitable sites are disturbed) and an arbitrary pattern of age-specific senescence. If all sites become suitable for

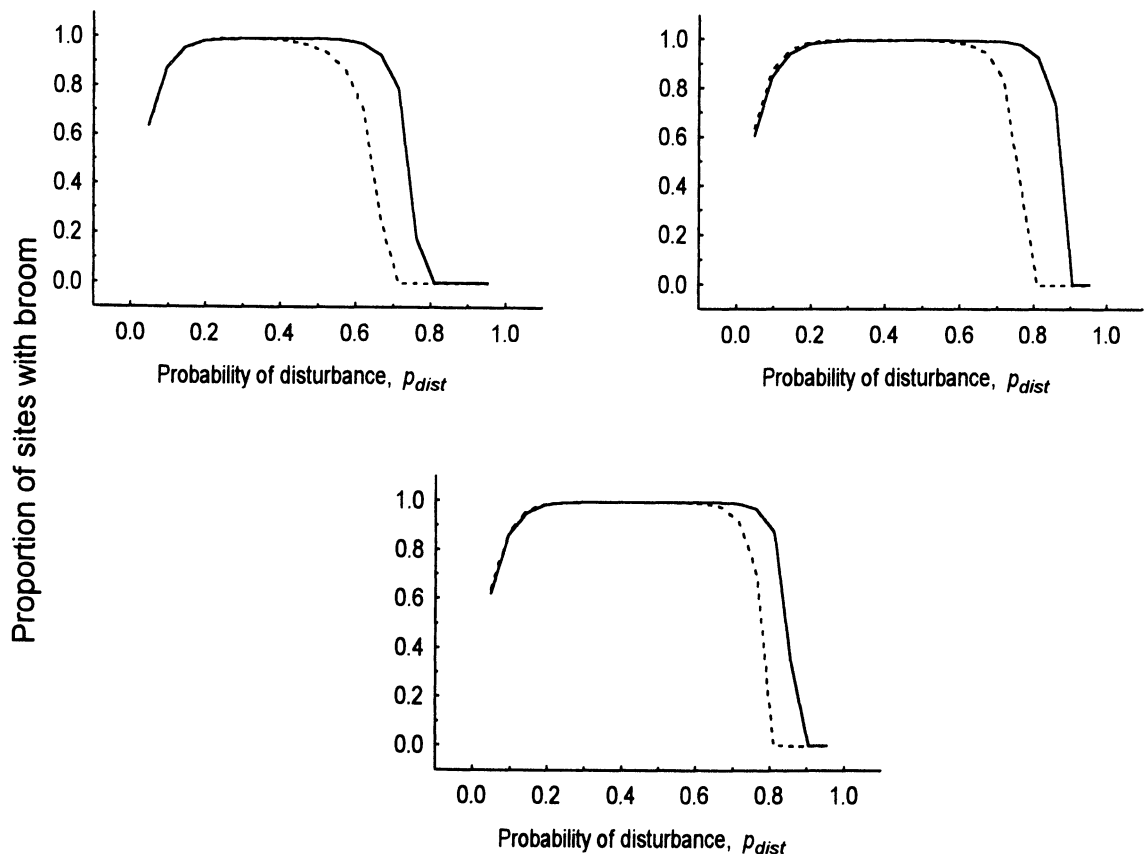


Fig. 9. Impact of insect herbivores on the proportion of sites occupied by broom for the third Australian scenario (in pasture). In each graph the dashed line was calculated from the simulation model assuming a fecundity of 4998 seeds per plant, the solid line from the same model but with no insect herbivores reducing seed production resulting in a fecundity of 19991 seeds per plant, assuming three levels of seedling survival; (a) $s = 0.1$ (b) $s = 0.5$ and (c) $s = 0.9$. Other parameter values: $d = 0.5$, $g = 0.03$, $f_h = 0.6$, $A_{min} = 2$, $A_{max} = 20$ and $p_{so} = 0.0$.

broom colonization after senescence, $p_{so} = 1$, then B^* simplifies to give:

$$B^* = \frac{1}{1 + \rho} \quad \text{eqn 26}$$

which is similar in form to eqn 10, where $z_{max}(1 - p_{dist})$ is the probability a broom plant senesces multiplied by the probability a site is not disturbed, which is analogous to the parameter ρ in the current model. These results illustrate how the models presented in the main body of this paper can be modified to account for details of the demography of populations in particular environments.

Output from the simulation model is compared with the analytical results in Fig. 10. In this comparison we have used the age-specific rates given in Fig. 1b,d in the simulation model, and calculated the equilibrium proportion of sites occupied by numerically solving eqn 22. For both data sets the fit between simulation results and the analytical model is excellent over the entire range, and the error in using eqn 24, rather than numerically solving eqn 22 is negligible. Rather surprisingly the calculation indicates that quite different patterns of age-specific senescence can give similar patterns of broom occupancy. Note, that when disturbances only create germination microsites, as

opposed to killing plants and creating germination microsites, then the proportion of sites occupied by broom is an increasing function of the probability of disturbance, compare Fig. 5c and Fig. 10. This illustrates the importance of understanding the process of disturbance, and the dynamics of open sites.

Discussion

The modelling results indicate that, although several parameters affect local colonization (e.g. F , g , s , f_h and d), because broom produces many seeds, local colonization processes rapidly saturate and the proportion of sites occupied then depends on just three factors: the disturbance regime, the probability of senescence and the probability of re-colonization of sites after senescence. This highlights the importance of understanding these processes. The decoupling of population parameters that influence local colonization from those that set the global level of occupancy allows a complex simulation model to be summarized, over a biologically reasonable range of parameter values, with simple equations (e.g. eqns 8 and 24).

Characterizing the disturbance regime is clearly important. However, quantifying the term p_{dist} will, in

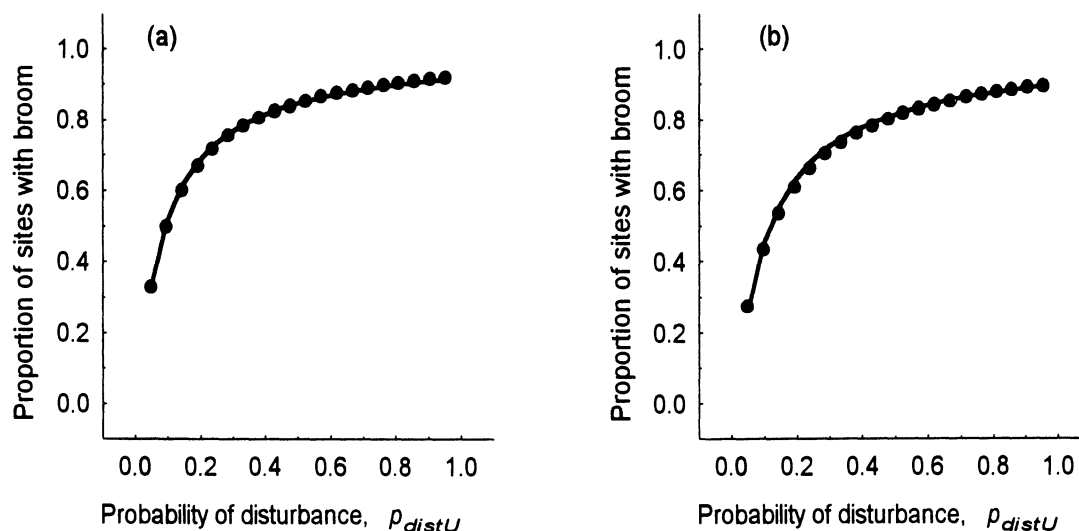


Fig. 10. Comparison of the equilibrium proportion of sites occupied by broom estimated from the simulation model with age-specific senescence and disturbances acting only on unsuitable sites with the analytical model, eqn 22. (a) Using the age-specific probabilities of senescence from a Scottish site, see Fig. 1b, and (b) using the age-specific probabilities of senescence from the French site, see Fig. 1d. Other model parameters: $F = 5600$, $d = 0.5$, $g = 0.03$, $s = 0.50$, $f_h = 0.6$ and $p_{so} = 0.0$.

general, be complicated because of the wide range of processes that are summarized in this single parameter. It represents losses caused by fire, landslide, flooding, grazing and trampling by horses and feral pigs, and grazing by smaller herbivores; we have also assumed that the net effect of these processes does not vary from year to year. However, as illustrated in the previous section, it is possible to modify the equations to incorporate different probabilities of disturbance in sites occupied by broom and in unoccupied sites. This allows types of disturbance that cause broom mortality to be separated from those which only create suitable germination microsites. Useful information on the rates of disturbance, which cause broom mortality, can be obtained from the age-structure of established plant populations, and also from studies that follow the fates of individual plants. For example, easily collected information on the ratio of pre-reproductive to reproductive plants would allow simple estimates of the probability of disturbance to be derived. Disturbances that create germination microsites are best studied using seed sowing experiments, and also observational studies that quantify the proportion of bare ground in a habitat.

The interaction between the disturbance regime and the potential impact of seed-feeding biological control agents is a direct result of disturbances causing plant mortality which changes the proportions of pre-reproductive and reproductive plants. High rates of disturbances, that cause plant mortality, result in populations dominated by young pre-reproductive plants (eqn 5); these populations are seed limited and so insect herbivores that affect plant reproduction can have potentially substantial effects on plant abundance (Figs 6–9). This suggests that using seed-feeders for the biological control of broom will be most likely to succeed in habitats, such as braided rivers in New

Zealand, which are inherently highly disturbed (Fowler *et al.* 1996). It also points to the possibility of combining biological control with mechanical control, for example, by using a roller for crushing mature plants, while minimizing the disruption of the ground flora.

Broom senescence is not well understood. In Europe many large plants which have good illumination are often killed by apparently generalist plant pathogens such as *Phomopsis* and *Fusarium* sp. (Fowler *et al.* 1996; S. Hasan, personal communication). However, insect exclusion experiments resulted in a 50% reduction in plant mortality (Waloff & Richards 1977). Interactions between levels of insect and pathogen attack have been described for gorse and broom in New Zealand (Johnson, Parkes & Broadhurst 1995). Why broom generally fails to recruit under senescent adults is also not well understood, but again plant pathogens and insect herbivores from neighbouring plants could be important (Fowler *et al.* 1996). For example, Denton (1994) has shown that seedling damage levels decline substantially as the distance from established plants increases.

Encouraging interspecific competition may also form an important tool for broom management (e.g. by reducing p_{so} , the probability a site which contained a senescent broom plant becomes suitable for colonization): Rousseau & Loiseau (1982) noted that sowing seeds of the perennial grass *Dactylis* reduced the population density of broom seedlings in pasture 2 years after mechanical clearing. The importance of the interaction between natural enemies and interspecific plant competition for the biological control of weeds has recently been reviewed by Sheppard (1996).

Assessment of the impact of a potential biological control agent assumed that plant fecundity was reduced by 75%. However, some agents have an even

greater impact on seed production: *Exapion fuscirostre* regularly destroyed enormous numbers of seeds in the United States – an average of 85% in Oregon (Andres, Hawkes & Rizza 1967; Andres & Coombs 1992) which makes the model predictions rather conservative. Also we have not considered the impact of a biological control agent that reduces plant longevity. Changes in longevity can have profound effects on the proportion of sites occupied (see Fig. 4a).

MODIFICATIONS TO THE MODEL

In many plant species the probability of germination depends on the environment (Rees & Long 1992). This means that the probability of germination in open sites and unsuitable ones will be different. If seeds have higher germination probabilities in open sites compared with sites that are unsuitable, or contain broom, this will promote persistence and make biological control more difficult to achieve (Rees & Long 1992). The model framework presented here can easily be modified to incorporate this type of seed germination behaviour.

By assuming that fecundity per site is constant, regardless of the number of plants in a site, we have avoided having to follow the number of plants in each site. This approximation allows the development of relatively simple models. It would be possible to modify the simulation model to allow seed production to depend on the number or age of recruits present (see, for example, Perry & Gonzalez-Andujar 1993). However, whenever seed production or survival in the seed bank is high these effects will be small and the simple approximations we have developed will suffice. As always in modelling studies we face a conflict between producing relatively simple models, with parameters that can be estimated from the literature, and constructing more realistic models, which require dedicated observational or experimental studies to obtain parameter estimates. The models presented here were designed to allow published demographic data to be incorporated into a model framework, whilst being sufficiently flexible to allow new information on demographic processes to be incorporated as it becomes available.

Selecting the most appropriate site size represents a trade-off between describing average plant size and obtaining a simple representation of local seed dispersal. Changing the site size will alter several of the model parameters. For example, the probability a site is disturbed could be dependent on its area and this dependence can be described with a variety of probability models (e.g. Poisson, negative binomial, etc.). However, the qualitative results of the models presented do not depend on the precise site size chosen.

In constructing the simulation model we assumed that seeds were only dispersed into neighbouring sites; how would the incorporation of occasional long-range

dispersal affect the proportion of sites occupied? This can be assessed by comparing the results of the simulation model with (i) the maximum level of site occupancy, set by eqn 8, and (ii) the results of the non-saturation approximation. In the non-saturation approximation we assumed the spatial distribution of the seed bank could be described by a Poisson distribution. This assumption is only valid when seeds are dispersed over large areas (see Pacala & Silander (1985) for a mathematical discussion of this point). From Figs 4 and 5 we see that occasional long-range seed dispersal would only be important when: (i) fecundity is low; (ii) the probability of disturbance high; or (iii) the minimum age for reproduction is high. Under these circumstances long-range dispersal increases colonization ability which allows populations to persist. However, over a wide range of realistic parameter values, inclusion of long-range dispersal would have little impact on the proportion of sites occupied by broom (Figs 3, 4 & 5). Of course, this is not to say that long-range dispersal would not have dramatic effects on other aspects of population behaviour, for example the pattern and rate of spatial spread (Harper 1977; Shigesada, Kawasaki & Takeda 1995).

CONCLUSIONS

To summarize, in habitats where individual plants produce thousands of seeds the proportion of sites occupied is largely determined by disturbance rates, patterns of plant senescence and what happens to sites after broom senesces. The true significance of each of these factors is still not clear, emphasizing the importance of the population dynamics studies currently underway (see Fowler *et al.* 1996). Our current knowledge suggests that integrating the following approaches is most likely to succeed.

1. Identification and the removal of sources of disturbance that create opportunities for broom to colonize (such as feral pigs at Barrington Tops (Smith & Waterhouse 1988)).
2. Reducing the probability of recolonization of broom following control by encouraging interspecific competition by sowing pasture plants.
3. Introducing biological control agents, or other management techniques that reduce broom longevity, particularly in conjunction with seed-feeders.

Understanding the impact of biological control agents is complicated because once recruitment becomes seed-limited, germination biology, seedling survival and many other processes are important, in addition to details of the agent's population biology. However, in contrast to previously published results (e.g. Andersen 1989; Cloutier & Watson 1990; Myers *et al.* 1988; Paynter *et al.* 1996), the models presented here suggest that even with a 75% reduction in seed production, biological control agents could have sig-

nificant effects particularly in disturbed habitats where the population is dominated by young plants. These results highlight the importance of detailed, comparative demographic studies, in a wide range of countries, for understanding the determinants of abundance, and also the potential for biological control, even of perennial species with seed banks.

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