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A stochastic model of the distribution of unequal competitors between resource patches

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Abstract

We present a stochastic model of individuals' movements between two patches of resources. The population is made up of two types of individual with differing competitive abilities, and two types of movements occur, with individuals moving either to increase their intake rate or at random. Several previous models have used simulations to evaluate the likely distribution of individuals. We instead derive equations for the equilibrium distribution of the population, which can be solved numerically. This avoids the need to choose an initial distribution for the population, and enables us to obtain the probability with which rare events occur. This may not be possible when simulations are used, since a rare event may not occur at all. We find that when random movements are rare, an increase in the rate of random movements out of a patch can increase the number of individuals on that patch. We consider an approximation to the model with rare random movements, which provides an explanation for this phenomenon.

Keywords: Ideal Free Distribution; Patch feeding; Random movements; Markov chain; Equilibrium

1. Introduction

The Ideal Free Distribution (IFD) of Fretwell and Lucas (1970) describes the distribution of animals among a number of patches of a resource, such as food. Under this distribution, the proportion of individuals on a patch is equal to the proportion of resources on that patch. This model assumes that all animals are equally competitive and can move between the patches at no cost.

In practice, all individuals are rarely equal competitors. Sutherland and Parker (1985) altered the IFD to allow for unequal competitors. Under their model, it is the proportion of competitive units, rather that the proportion of individuals, which equals the proportion of resources on each patch. In this case there are several stable equilibria.

In a review of several empirical studies on the subject Kennedy and Gray (1993) found that under-matching often occurs, meaning that the better patch is under-used. Although several equilibria are possible when competitors are unequal, only a few have been observed in practice; these being close to the equal numbers equilibrium. This is the sole equilibrium when competitors are equal.

Houston and McNamara (1988) have provided an explanation for this. Using statistical mechanics, they obtain the probability of each equilibrium occurring, and find that the most likely are close to the equal numbers equilibrium. They also show that the number of individuals of a given type on the best patch increases with competitive ability, meaning that the proportion of the population on that patch is less than the proportion of resources, thus explaining observations of under-matching.

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It is possible that the animals do not base their decision to move purely on their intake rate. They may also move to avoid predators or to find a mate (Hugie and Grand, 1998). It is also possible that they do not have perfect knowledge of the intake rates in other locations, or they may not be able to distinguish between intake rates when the difference between them is small. Abrahams (1986) proposed the perceptual limit model, in which animals move randomly between patches when the difference between potential intake rates is below a certain fixed level, the perceptual limit. He used Monte Carlo simulation to estimate the distribution of a population of identical animals between locations. More recently, formulae have been developed which give the probability of observing each possible distribution of the population between two patches, along with the expected intake rate on each patch and overall (Collins et al., 2002). Under this model discrete time steps are used, with an individual selected at each time step, which decides whether to move or not. This decision is based on the individual's potential intake rates on each patch if the difference between these is larger than the perceptual limit, otherwise the animal either moves or remains on the same patch with equal probability.

Several models which incorporate movements for non-IFD reasons in populations of unequal competitors have been developed in recent years. Each of these has had its problems. Hugie and Grand's (1998) analytical model, which predicted a unique stable equilibrium distribution close to the equal numbers distribution when both IFD and non-IFD movements occur, received criticism from Ruxton and Humphries (1999). They developed an individual-based model, in which movements occurred during discrete time intervals. During each interval there was an opportunity for one IFD and one non-IFD movement. Their simulations resulted in several of the possible unequal competitors IFDs close to the equal competitors distribution occurring.

The assumptions of this model have in turn been criticized by Hugie and Grand (2003), who argue that alternating between the two types of movement is unrealistic; as is the restriction that only one individual can move per time interval. They reiterate their earlier finding (Hugie and Grand, 1998) that there is a unique population distribution. This is based both upon an infinite population model and an individual-based finite population model.

Jackson et al.'s (2004) model, which includes unequal competitors, avoids most of the problems of previous individual-based models. This model consists of two patches and a population of two phenotypes. Individuals move either to increase their intake rate, or at random. They use a Markov Chain Monte Carlo approach, where the probability of each type of movement occurring is assessed at each time step. This avoids the necessity to alternate between IFD and non-IFD movements, as in Ruxton and Humphries' (1999) model, while providing a realistic mechanism for removing the possibility of mass movements which is present in Hugie and Grand's (2003) model. Hugie and Grand (2003) use a damping constant to do this, which is argued to be biologically unrealistic by Jackson et al. (2004).

Jackson et al.'s (2004) simulations of this process show that when competitors are unequal and the levels of resources on each patch differ, only a few equilibria close to the equal numbers equilibrium can occur.

Our model is similar to that of Jackson et al. (2004). There is one important difference which is described in the next section. In addition, we derive equations for the probability of being in each possible state at equilibrium, which can be solved numerically. This is advantageous, since we are able to obtain probabilities for very rare events, which may never occur in simulations. We also avoid the problem of having to choose a starting state, which may cause bias in simulation results.

We also investigate an approximation to our model which can be used when random movements are rare. This cuts down on the amount of equations which need to be solved, since it is assumed that the process will be at one of the unequal competitor IFD states at equilibrium.

Our model shows up novel features, such as an increase in non-IFD movements from Patches 1 to 2 can increase the number of individuals on Patch 1. Another feature is that equilibria can occur where the proportion of competitive units on a patch does not equal the proportion of resources, when there are no random movements. Fig. 8 shows an example where this is the case.

2. The model

The population is divided between two patches, labelled 1 and 2. A resource is available at these patches at the constant rates Q_1 and Q_2, respectively. There are two phenotypes within the population; types N and M. These have competitive abilities K_N and K_M, respectively, which are positive constants used to weight the number of individuals of a given type on each patch. We assume that type M individuals have a higher competitive ability than those of type N, hence $K_N < K_M$. The number of individuals of type N on Patch i is denoted N_i, while the number of type M individuals on Patch i is denoted M_i.

Under the IFD for unequal competitors, the proportion of resources on Patch 1 is equal to the proportion of competitive units, rather than the proportion of the population (Sutherland and Parker, 1985). That is

$$\frac{Q_1}{Q_1+Q_2}=\frac{K_N N_1+K_M M_1}{K_N N_T+K_M M_T},$$

where N_T and M_T are the total numbers of individuals of types N and M, respectively. This equation may have several solutions, which lie on what is known as the unequal competitors IFD line. This line is defined by the equation

$$M_1=\frac{Q_1(K_N N_T+K_M M_T)}{K_M(Q_1+Q_2)}-\frac{K_N}{K_M}N_1. \tag{1}$$

There are random movements out of each patch at a rate proportional to the number of individuals on that patch, along with movements made to increase an individual's intake rate. Fig. 1 shows the possible transitions and their rates. The constants α_i scale the rates of random movements, while the λs give the rate at which an individual moves in order to increase its intake rate.

A type N individual on Patch 1 will have intake rate

$$\frac{K_N Q_1}{K_N N_1+K_M M_1}.$$

The other three intake rates are defined similarly. Were this individual to move to Patch 2, its intake rate would become

$$\frac{K_N Q_2}{K_N(N_2+1)+K_M M_2},$$

meaning that it is only beneficial to move if

$$\frac{K_N Q_2}{K_N(N_2+1)+K_M M_2}>\frac{K_N Q_1}{K_N N_1+K_M M_1}.$$

The rate at which a type N individual on Patch 1 moves to Patch 2 for IFD reasons, λ_{11}, is given by

$$\lambda_{11}=\max\left\{0,\frac{K_N Q_2}{K_N(N_2+1)+K_M M_2}-\frac{K_N Q_1}{K_N N_1+K_M M_1}\right\}.$$

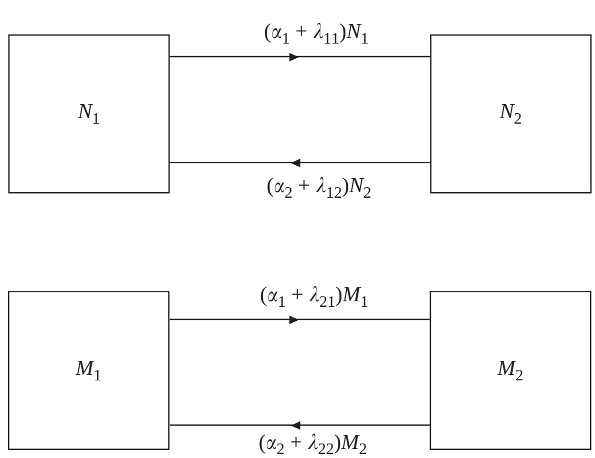

Fig. 1. The transition rates for a population of two phenotypes.

This is only positive if a move from Patches 1 to 2 increases a type N individual's intake rate, and the value of λ_{11} increases with the potential increase in intake rate, making a move more likely.

Since each type N individual on Patch 1 moves independently to Patch 2 at rate λ_{11}, the total rate at which type N individuals leave Patch 1 is $\lambda_{11}N_1$. This differs from Jackson et al.'s (2004) model, where this factor of N_1 is not included. Our inclusion of this factor seems more intuitive, and also means that the proportion of IFD to non-IFD movements remains constant as the population size increases. This is not the case for Jackson et al.'s (2004) model, where this proportion tends asymptotically to zero.

The other individual rates, λ_{12}, λ_{21} and λ_{22}, are defined similarly to λ_{11}. These differ slightly from those in Jackson et al.'s (2004) paper, since each of their IFD movement rates contains a constant factor β, which has been omitted from our model. Jackson et al. (2004) always set $\beta=1$, meaning that comparisons between the two models can be made. If β were not 1 then dividing α_1 and α_2 by β in our model would again result in a comparable model to Jackson et al.'s (2004).

The differential equations for this process are

$$\begin{aligned}\frac{d}{dt}p_{n_1,m_1}(t)
&=(\alpha_2+\lambda_{12}(n_1-1,m_1))(N_T-n_1+1)p_{n_1-1,m_1}(t)\\
&\quad+(\alpha_1+\lambda_{11}(n_1+1,m_1))(n_1+1)p_{n_1+1,m_1}(t)\\
&\quad+(\alpha_2+\lambda_{22}(n_1,m_1-1))(M_T-m_1+1)p_{n_1,m_1-1}(t)\\
&\quad+(\alpha_1+\lambda_{21}(n_1,m_1+1))(m_1+1)p_{n_1,m_1+1}(t)\\
&\quad-[(\alpha_2+\lambda_{12}(n_1,m_1))(N_T-n_1)\\
&\quad+(\alpha_1+\lambda_{11}(n_1,m_1))n_1\\
&\quad+(\alpha_2+\lambda_{22}(n_1,m_1))(M_T-m_1)\\
&\quad+(\alpha_1+\lambda_{21}(n_1,m_1))m_1]p_{n_1,m_1}(t)\end{aligned} \tag{2}$$

for $n_1=0,1,\ldots,N_T$ and $m_1=0,1,\ldots,M_T$. If $n_1<0$, $m_1<0$, $n_1>N_T$ or $m_1>M_T$ then $p_{n_1,m_1}(t)=0$.

At equilibrium $dp_{n_1,m_1}(t)/dt=0$ and equations (2) become a set of linear equations for $p_{n_1,m_1}=P(N_1=n_1,M_1=m_1)$ at equilibrium. These equations can be solved numerically using Matlab. Unlike the simulations used by Jackson et al. (2004), we have a value for the probability of each possible pair of values (N_1,M_1) being reached. When simulations are used, rare events may not occur at all, giving no information about how likely they are.

It is possible to calculate the probability distribution of N_1 from the values for p_{n_1,m_1}, using the formula $P(N_1=n_1)=\sum_{m_1=0}^{M_T}p_{n_1,m_1}$. The distribution for M_1 can be calculated similarly, and from these distributions it is possible to obtain values for the means and variances of N_1 and M_1.

3. Evaluations

Table 1 shows the results of some evaluations. The poorer patch often seems to be over used, except when random movements are rare (α_1 and α_2 are small).

Figs. 2–5 show the equilibrium distributions of N_1 and M_1 in 4 cases. In each of these cases the number of individuals of each type, their competitive abilities and the rate at which resources become available at each patch are unchanged and M_1 has a single modal value in each case. When $\alpha_1 = \alpha_2 = 1$ (Fig. 2), this is also true of N_1. When $\alpha_1 = \alpha_2 = 0.01$ (Fig. 3) the distribution has several peaks, close to points on the IFD line, while when α_1 and α_2 are $O(10^{-6})$ (Figs. 4 and 5), only a few values of N_1 on the IFD line have a noticeable probability of occurring. The value which is most likely is determined by the relative values of α_1 and α_2.

The expected number of individuals on Patch 1 at equilibrium is $E(N_1) + E(M_1)$. When $N_T = M_T = 36$, $\alpha_2 = 10^{-6}$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$, the expected number of individuals on Patch 1 is larger when $\alpha_1 = 2 \times 10^{-6}$ than when $\alpha_1 = 10^{-6}$ (see Table 1). This is unexpected, since an increase in α_1 from 10^{-6} to 2×10^{-6} equates to an increase in the likelihood that a random movement takes an individual from Patch 1 to 2, which suggests that the expected number of individuals in Patch 1 should decrease. The next section provides an explanation as to why this occurs.

Fig. 6 shows a contour plot of the joint distribution of N_1 and M_1 when $\alpha_1 = \alpha_2 = 0.02$ and the remaining parameters are unchanged. The parameters given are as close as possible to the parameters used by Jackson et al. (2004) in their Fig. 6. The competitive abilities, resource availability rates and number of individuals of each type are identical, while the α_is are 20 times larger than those in Jackson et al.'s (2004) model in order to make the rate of random movements comparable. The factor 20 was chosen because this is roughly half the amount of individuals of each phenotype. This contour plot shows that the equilibria at (14, 8) and (19, 7) are the most

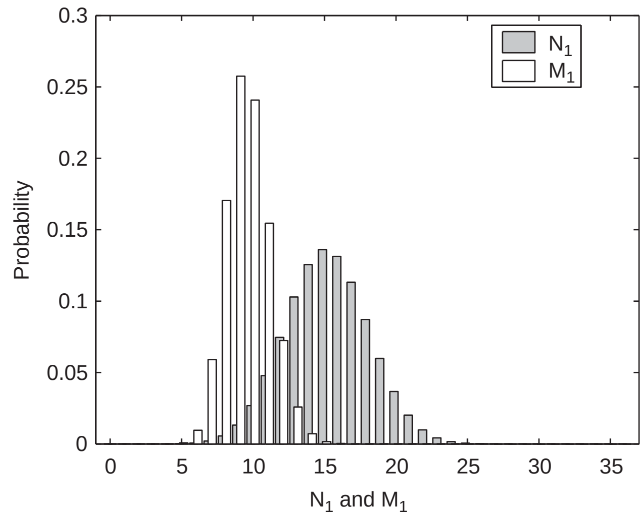

Fig. 2. The equilibrium distributions of N_1 and M_1. The parameter values are: $N_T = M_T = 36$, $\alpha_1 = \alpha_2 = 1$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$.

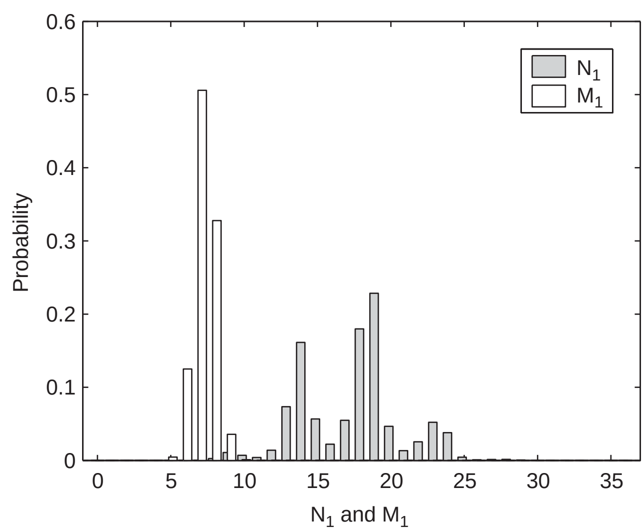

Fig. 3. The equilibrium distributions of N_1 and M_1. The parameter values are: $N_T = M_T = 36$, $\alpha_1 = \alpha_2 = 0.01$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$.

Table 1
Two phenotypes

N_T	M_T	α_1	α_2	Q_1	Q_2	K_N	K_M	$E(N_1)$	$E(M_1)$	$\frac{Q_1}{Q_1+Q_2}$	$\frac{K_N E(N_1)+K_M E(M_1)}{K_N M_T + K_M N_T}$	$Var(N_1)$	$Var(M_1)$
36	36	1	1	100	300	1	5	15.2663	9.5973	0.2500	0.2928	8.4510	2.3254
36	36	1	1	100	300	1	10	16.5477	9.7598	0.2500	0.2882	8.8540	1.9204
36	36	1	1	100	300	1	7.5	16.0956	9.6835	0.2500	0.2899	8.7449	2.0509
36	36	1	1	100	100	1	1	18.0000	18.0000	0.5000	0.5000	5.9653	5.9653
24	24	1	1	100	300	1	5	10.0509	6.1117	0.2500	0.2820	5.6336	1.2953
36	36	0.1	0.1	100	300	1	5	14.8118	8.0670	0.2500	0.2553	8.7958	0.7817
36	36	0.01	0.01	100	300	1	5	17.4467	7.2683	0.2500	0.2490	11.3282	0.5523
36	36	0.001	0.001	100	300	1	5	19.1535	6.9488	0.2500	0.2495	15.5944	0.6471
36	36	0.0001	0.0001	100	300	1	5	19.6179	6.8736	0.2500	0.2499	18.0708	0.7263
36	36	10^{-05}	10^{-05}	100	300	1	5	19.6854	6.8626	0.2500	0.2500	18.5024	0.7405
36	36	2×10^{-06}	10^{-06}	100	300	1	5	22.2825	6.3434	0.2500	0.2500	18.6979	0.7480
36	36	10^{-06}	10^{-06}	100	300	1	5	19.6926	6.8615	0.2500	0.2500	18.5494	0.7420

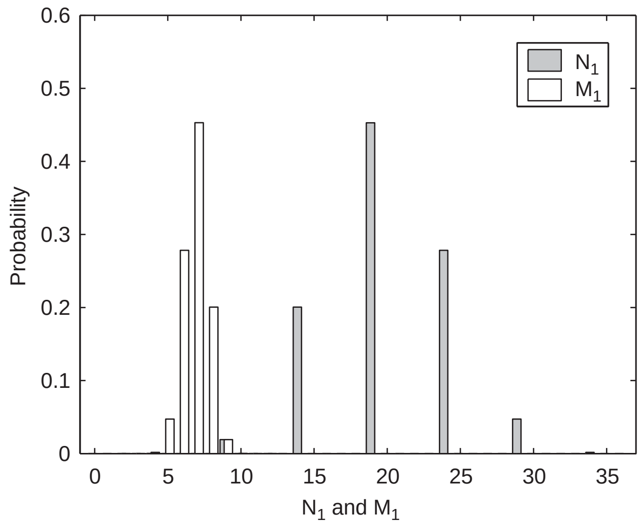

Fig. 4. The equilibrium distributions of N_1 and M_1. The parameter values are: $N_T = M_T = 36$, $\alpha_1 = \alpha_2 = 10^{-6}$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$.

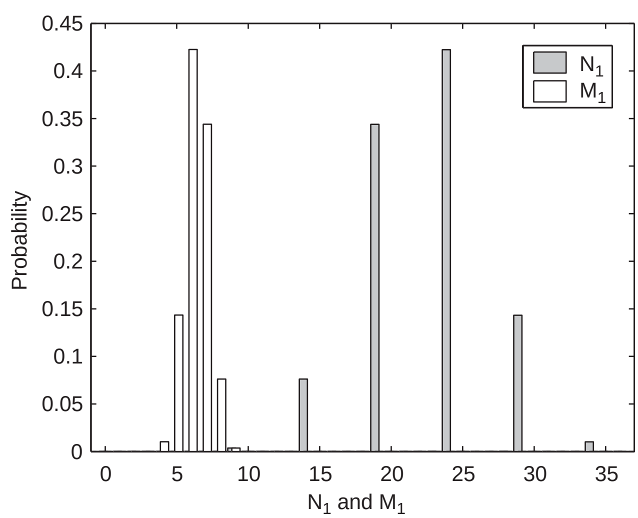

Fig. 5. The equilibrium distributions of N_1 and M_1. The parameter values are: $N_T = M_T = 36$, $\alpha_1 = 2 \times 10^{-6}$, $\alpha_2 = 10^{-6}$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$.

likely to be reached under our model. In contrast, Jackson et al.'s (2004) simulations resulted in $(19, 7)$ and $(24, 6)$ occurring a similar number of times. This may be due to the use of simulation, for which it is necessary to choose initial values for N_1 and M_1. The values chosen can have a large effect on the outcome. Our differing IFD transition rates are another possible cause of the differences observed.

In order to try to explain which equilibrium is most likely to be reached the number of ways in which N_1-type N individuals and M_1 type M individuals can be selected to be on Patch 1 was calculated, for each

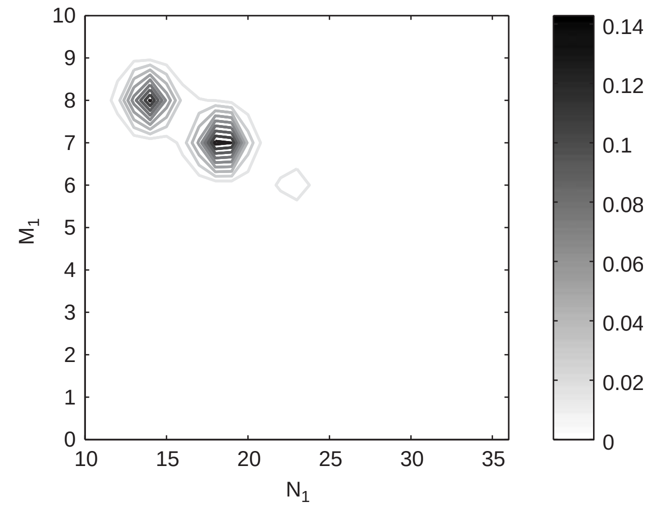

Fig. 6. The joint equilibrium distribution of N_1 and M_1. Note that a continuous state-space is assumed in the production of this contour plot. The parameter values are: $N_T = M_T = 36$, $\alpha_1 = \alpha_2 = 0.02$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$.

Table 2
The number of ways in which N_1 type N individuals and M_1 type M individuals can be placed on Patch 1

N_1	M_1	Permutations	Probability
0	11	6.0081×10^{8}	3.0349×10^{-9}
4	10	1.4973×10^{13}	7.5634×10^{-5}
9	9	8.8630×10^{15}	4.4770×10^{-2}
14	8	1.1488×10^{17}	5.8029×10^{-1}
19	7	7.1769×10^{16}	3.6253×10^{-1}
24	6	2.4380×10^{15}	1.2315×10^{-2}
29	5	3.1470×10^{12}	1.5897×10^{-5}
34	4	3.7110×10^{7}	1.8746×10^{-10}
36	3	7.1400×10^{3}	3.6067×10^{-14}

equilibrium point (N_1, M_1). These are given by

$$\binom{N_T}{N_1}\binom{M_T}{M_1}$$

and are shown in Table 2. This method has been used by Houston and McNamara (1988) to identify the most likely distribution of individuals. Table 2 also shows, for each equilibrium, the proportion of these ways of distributing the population which give that equilibrium.

According to Table 2, the most likely equilibrium is $(N_1, M_1) = (14, 8)$, but this is not the case for either Figs. 4 or 5. However, the modes of N_1 and M_1 in Fig. 2, where random movements play a significant part, are close to these values. This method of calculating the most likely equilibrium assumes that the population is randomly distributed between the patches, subject to the constraint that all IFD transition rates are zero. The fact that the probabilities in Table 2 do not agree with those in Figs. 4 or 5 suggests that this assumption is invalid under our model. This seems particularly likely for the parameter set used in Fig. 5, where the α_is are not equal.

4. An approximation to the model when random movements are rare

This approximation models the population as a discrete time Markov chain, where the states are the equilibria of the model when no random movements occur. The transition probabilities are calculated in two stages.

If (n_1, m_1) is an equilibrium point of the model with no random movements then it is certain that the next movement will be a random one. The probability with which each possible random movement occurs is given by

$$P((N_1, M_1) \to (N_1+1, M_1)) = \frac{\alpha_2 N_2}{\alpha_1(N_1+M_1)+\alpha_2(N_2+M_2)},$$

$$P((N_1, M_1) \to (N_1-1, M_1)) = \frac{\alpha_1 N_1}{\alpha_1(N_1+M_1)+\alpha_2(N_2+M_2)},$$

$$P((N_1, M_1) \to (N_1, M_1+1)) = \frac{\alpha_2 M_2}{\alpha_1(N_1+M_1)+\alpha_2(N_2+M_2)},$$

$$P((N_1, M_1) \to (N_1, M_1-1)) = \frac{\alpha_1 M_1}{\alpha_1(N_1+M_1)+\alpha_2(N_2+M_2)}.$$

As soon as a random movement has occurred, one or more of the IFD movement rates is positive and we assume that α_1 and α_2 are small enough that the possibility of random movements can be ignored.

The regions where each of the IFD transition rates are positive are given by

$$\lambda_{11} > 0 \iff M_1 > \frac{Q_1(K_N(N_T+1)+K_M M_T)}{K_M(Q_1+Q_2)} - \frac{K_N}{K_M} N_1, \quad (3)$$

$$\lambda_{21} > 0 \iff M_1 > \frac{Q_1(K_N N_T+K_M(M_T+1))}{K_M(Q_1+Q_2)} - \frac{K_N}{K_M} N_1, \quad (4)$$

$$\lambda_{12} > 0 \iff M_1 < \frac{Q_1(K_N N_T+K_M M_T)-Q_2K_N}{K_M(Q_1+Q_2)} - \frac{K_N}{K_M} N_1, \quad (5)$$

$$\lambda_{22} > 0 \iff M_1 < \frac{Q_1(K_N N_T+K_M M_T)-Q_2K_M}{K_M(Q_1+Q_2)} - \frac{K_N}{K_M} N_1. \quad (6)$$

The boundaries of the each of these regions are straight lines with negative gradient $-K_N/K_M$. These are also parallel to the unequal competitors IFD line, which has intercept

$$\frac{Q_1(K_N N_T+K_M M_T)}{K_M(Q_1+Q_2)}.$$

Since $K_N < K_M$,

$$\begin{aligned}\frac{Q_1(K_N N_T+K_M M_T)-Q_2K_M}{K_M(Q_1+Q_2)} &< \frac{Q_1(K_N N_T+K_M M_T)-Q_2K_N}{K_M(Q_1+Q_2)} \\ &< \frac{Q_1(K_N N_T+K_M M_T)}{K_M(Q_1+Q_2)} \\ &< \frac{Q_1(K_N(N_T+1)+K_M M_T)}{K_M(Q_1+Q_2)} \\ &< \frac{Q_1(K_N N_T+K_M(M_T+1))}{K_M(Q_1+Q_2)}\end{aligned}$$

meaning that $\lambda_{21} > 0 \Rightarrow \lambda_{11} > 0 \Rightarrow \lambda_{12} = 0 \Rightarrow \lambda_{22} = 0$ and $\lambda_{22} > 0 \Rightarrow \lambda_{12} > 0 \Rightarrow \lambda_{11} = 0 \Rightarrow \lambda_{21} = 0$. Also it is impossible for λ_{12} or λ_{22} to be positive at any states above the unequal competitors IFD line, and it is impossible for λ_{11} or λ_{21} to be positive at any states below this line.

Fig. 7 shows these regions when $N_T = M_T = 36$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$. The IFD equilibria are also shown. There are two of these which are not on the unequal competitors IFD line. At $(0, 11)$ only λ_{11} is positive, but it is impossible for a type N individual to move from Patch 1 to 2, because they are all on Patch 2 already. Similarly, at $(36, 3)$ only λ_{12} is positive but all of the type N individuals are already on Patch 1. These two equilibria are not mentioned in Jackson et al.'s (2004) paper, although it appears they occur when no random movements are included in their model, since their Fig. 5 gives the frequency with which the simulation finished in 9 different states, while there are only 7 equilibria on the unequal competitors IFD line. If their process reached one of these states, one of the IFD transition rates for type N individuals would be positive (λ_{11} at (0,11), λ_{12} at (36,3)), since they do not include a factor of N_1 or N_2 as our rates do. It is not stated explicitly what they do in this situation.

Fig. 7 shows that at most 2 of the IFD transition rates are positive at any point (N_1, M_1). These move the values of N_1 and M_1 back towards one of the equilibria. This means that having left an equilibrium due to a random movement, it is possible to calculate the probability that the population distribution will return

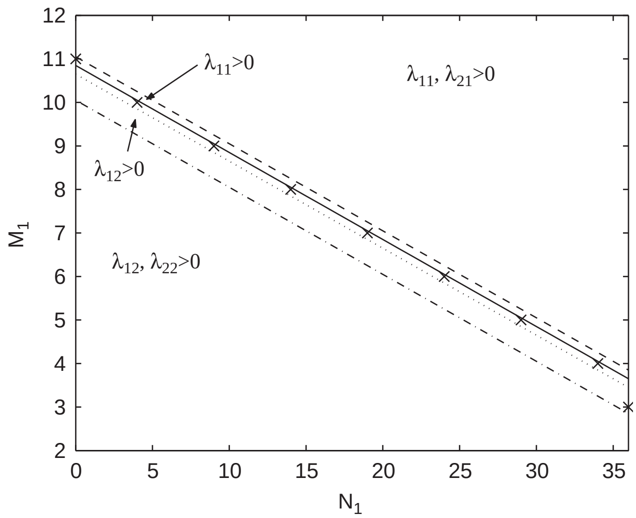

Fig. 7. Regions where the IFD transition rates are positive. Only those listed in each region are positive. The IFD equilibrium points are also shown (X). The parameter values are: $N_T = M_T = 36$, $Q_1 = 100$, $Q_2 = 300$, $K_N = 1$ and $K_M = 5$.

to each of the equilibria. If the state (N_1, M_1) is above the unequal competitors IFD line

$$\left(M_1 > \frac{Q_1(K_N N_T + K_M M_T)}{K_M(Q_1 + Q_2)} - \frac{K_N}{K_M} N_1\right)$$

then

$$P((N_1, M_1) \to (N_1, M_1 - 1)) = \frac{\lambda_{21} M_1}{\lambda_{11} N_1 + \lambda_{21} M_1}$$

and

$$P((N_1, M_1) \to (N_1 - 1, M_1)) = \frac{\lambda_{11} N_1}{\lambda_{11} N_1 + \lambda_{21} M_1},$$

while if (N_1, M_1) is below the unequal competitors IFD line then

$$P((N_1, M_1) \to (N_1, M_1 + 1)) = \frac{\lambda_{22} M_2}{\lambda_{12} N_2 + \lambda_{22} M_2}$$

and

$$P((N_1, M_1) \to (N_1 + 1, M_1)) = \frac{\lambda_{12} N_2}{\lambda_{12} N_2 + \lambda_{22} M_2}.$$

These probabilities can calculated at each step until an equilibrium is reached. Multiplying these together gives the probability of this sequence of events occurring. Adding together the probabilities for all of the sequences of movements which start from the same point and lead to the same equilibrium gives the probability of that equilibrium being reached from a particular state. The probability of arriving at each equilibrium having started from a point close to one of the equilibria is shown in Table 3.

Having calculated the probability of each possible random movement from an equilibrium (N_1, M_1), and the probability of arriving at each equilibrium given that a particular random movement has occurred, it is possible to obtain the transition matrix for movements between the equilibria. The stationary distribution for this process can then be found.

These stationary distributions are shown for two cases in Tables 4 and 5. In both cases $\alpha_2 = 10^{-6}$. In the first case $\alpha_1 = 10^{-6}$ also, while in the second $\alpha_1 = 2 \times 10^{-6}$. The distributions agree closely in each case. Note that when $\alpha_1 \neq \alpha_2$ each probability is weighted by the expected time before a movement out of the given state. This is given by $\exp\{-(\alpha_1(n_1 + m_1) + \alpha_2(n_2 + m_2))\}$. If $\alpha_1 = \alpha_2$ then this is equal to $\exp\{-\alpha_1(N_T + M_T)\}$ for all n_1, m_1, which explains why this weighting is not needed when $\alpha_1 = \alpha_2 = 10^{-6}$.

This approximation suggests a reason why an increase in the value of α_1 can be associated with an increase in

Table 3
Probability of arriving at each equilibrium having started at the given starting state

Starting state	Equilibria reached
(0,12)	(0,11)
(1,11)	(0,11) (0.0417), (4,10) (0.9583)
(0,10)	(0,11) (0.2048), (4,10) (0.7952)
(4,11)	(4,10) (1.0000), (0,11) (1.41×10^{-5})
(5,10)	(4,10)
(4,9)	(4,10) (0.6449), (9,9) (0.3551)
(3,10)	(4,10)
(9,10)	(9,9) (0.9986), (4,10) (0.0014)
(10,9)	(9,9)
(9,8)	(9,9) (0.7005), (14,8) (0.2995)
(8,9)	(9,9)
(14,9)	(14,8) (0.9908), (9,9) (0.0092)
(15,8)	(14,8)
(14,7)	(14,8) (0.7603), (19,7) (0.2397)
(13,8)	(14,8)
(19,8)	(19,7) (0.9707), (14,8) (0.0293)
(20,7)	(19,7)
(19,6)	(19,7) (0.8239), (24,6) (0.1761)
(18,7)	(19,7)
(24,7)	(24,6) (0.9331), (19,7) (0.0669)
(25,6)	(24,6)
(24,5)	(24,6) (0.8896), (29,5) (0.1104)
(23,6)	(24,6)
(29,6)	(29,5) (0.8742), (24,6) (0.1258)
(30,5)	(29,5)
(29,4)	(29,5) (0.9523), (34,4) (0.0477)
(28,5)	(29,5)
(34,5)	(34,4) (0.7915), (29,5) (0.2085)
(35,4)	(34,4)
(34,3)	(34,4) (0.9967), (36,3) (0.0033)
(33,4)	(34,4)
(36,4)	(36,3) (0.1885), (34,4) (0.8115)
(36,2)	(36,3)
(35,3)	(36,3) (0.0783), (34,4) (0.9217)

Each of these starting states is one move away from an equilibrium. In the cases where only one equilibrium is listed this is certain to be reached.

Table 4
Comparison of the discrete and continuous time Markov chain models

n_1	m_1	$P(N_1 = n_1, M_1 = m_1)$ under continuous time model	$P(N_1 = n_1, M_1 = m_1)$ under discrete time model	Error	Percentage error
0	11	1.746×10^{-9}	1.746×10^{-9}	3.266×10^{-12}	0.1870
4	10	2.060×10^{-4}	2.060×10^{-4}	4.357×10^{-7}	0.2115
9	9	1.910×10^{-2}	1.910×10^{-2}	8.765×10^{-6}	0.0459
14	8	2.005×10^{-1}	2.005×10^{-1}	6.125×10^{-6}	0.0031
19	7	4.529×10^{-1}	4.529×10^{-1}	2.626×10^{-5}	0.0058
24	6	2.782×10^{-1}	2.782×10^{-1}	1.177×10^{-4}	0.0423
29	5	4.722×10^{-2}	4.722×10^{-2}	6.024×10^{-5}	0.1276
34	4	1.683×10^{-3}	1.683×10^{-3}	6.575×10^{-6}	0.3906
36	3	3.748×10^{-7}	3.748×10^{-7}	1.424×10^{-9}	0.3799

Table 5
Comparison of the discrete and continuous time Markov chain models

n_1	m_1	$P(N_1 = n_1, M_1 = m_1)$ under continuous time model	$P(N_1 = n_1, M_1 = m_1)$ under discrete time model	Error	Percentage error
0	11	1.381×10^{-10}	1.381×10^{-10}	-1.048×10^{-14}	−0.0076
4	10	1.958×10^{-5}	1.959×10^{-5}	6.153×10^{-9}	0.0314
9	9	3.628×10^{-3}	3.626×10^{-3}	-2.137×10^{-6}	−0.0589
14	8	7.614×10^{-2}	7.609×10^{-2}	-4.594×10^{-5}	−0.0603
19	7	3.439×10^{-1}	3.438×10^{-1}	-7.612×10^{-5}	−0.0221
24	6	4.224×10^{-1}	4.226×10^{-1}	2.313×10^{-4}	0.0548
29	5	1.433×10^{-1}	1.436×10^{-1}	2.882×10^{-4}	0.2011
34	4	1.020×10^{-2}	1.026×10^{-2}	6.387×10^{-5}	0.6263
36	3	2.924×10^{-6}	2.941×10^{-6}	1.795×10^{-8}	0.6141

the expected number of individuals on Patch 1, since it enables us to find conditions under which increasing α_1 increases the probability that once the system has returned to equilibrium after a non-IFD movement from an equilibrium on the unequal competitors IFD line, the value of $N_1 + M_1$ has increased. Under such conditions it is reasonable to expect $E(N_1 + M_1)$ to increase also.

We first consider the conditions under which each IFD transition rate is positive after a non-IFD movement away from an equilibrium on the unequal competitors IFD line. For example, the equation of the unequal competitors IFD line (1) can be rearranged to give

$$N_1 = \frac{Q_1(K_N N_T + K_M M_T)}{K_N(Q_1 + Q_2)} - \frac{K_M}{K_N} M_1,$$

while the equation of the line bounding the region where λ_{21} is positive is

$$N_1 = \frac{Q_1(K_N N_T + K_M(M_T + 1))}{K_N(Q_1 + Q_2)} - \frac{K_M}{K_N} M_1.$$

This means that λ_{21} is positive after a type N individual makes a non-IFD movement from Patch 2 to 1 if

$$\frac{Q_1(K_N N_T + K_M(M_T + 1))}{K_N(Q_1 + Q_2)} - \frac{Q_1(K_N N_T + K_M M_T)}{K_N(Q_1 + Q_2)} < 1.$$

This simplifies to

$$\frac{K_M Q_1}{K_N(Q_1 + Q_2)} < 1 \equiv \frac{K_M}{K_N} < 1 + \frac{Q_2}{Q_1}.$$

The conditions under which each of the other transition rates are positive are shown in Table 6.

By rearranging Inequalities (3) and (5), for the regions where λ_{11} and λ_{12} are positive, it can be seen that the state (n_1, m_1) is an equilibrium if and only if

$$\frac{Q_1(K_N N_T + K_M M_T) - Q_2 K_N}{K_N(Q_1 + Q_2)} - \frac{K_M}{K_N} m_1 \leqslant n_1 \leqslant \frac{Q_1(K_N(N_T + 1) + K_M M_T)}{K_N(Q_1 + Q_2)} - \frac{K_M}{K_N} m_1.$$

Table 6
Conditions under which each transition rate is positive after a movement from (n_1, m_1), which is an equilibrium on the unequal competitors IFD line

Movement	λ_{11}	λ_{21}	λ_{12}	λ_{22}
$(n_1, m_1) \to (n_1+1, m_1)$	Always	$\frac{K_M}{K_N} < 1 + \frac{Q_2}{Q_1}$	Never	Never
$(n_1, m_1) \to (n_1, m_1+1)$	$\frac{K_N}{K_M} < 1 + \frac{Q_2}{Q_1}$	Always	Never	Never
$(n_1, m_1) \to (n_1-1, m_1)$	Never	Never	Always	$\frac{K_M}{K_N} < 1 + \frac{Q_1}{Q_2}$
$(n_1, m_1) \to (n_1, m_1-1)$	Never	Never	$\frac{K_N}{K_M} < 1 + \frac{Q_1}{Q_2}$	Always

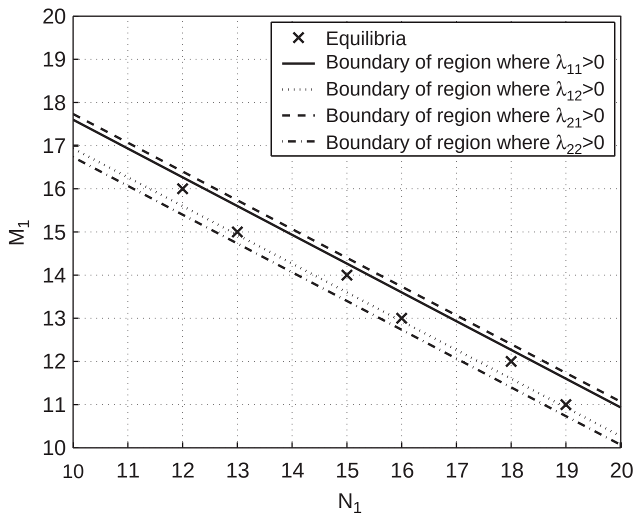

Fig. 8. There are two lines of equilibria. The upper line is the unequal competitors IFD line. Only part of these lines are shown for clarity. The parameter values are: $N_T = M_T = 36$, $Q_1 = 200$, $Q_2 = 300$, $K_N = 1$ and $K_M = 1.5$.

The length of this interval is 1, meaning that it must contain an integer value n_1 for each m_1 (or two values if the end points of this interval are integers). We assume that the end points are not integers, in which case we can denote the nearest equilibria to (n_1, m_1) by $(n_1 - k_1, m_1 + 1)$ and $(n_1 + k_2, m_1 - 1)$, where k_1 and k_2 are positive integers. If the unequal competitors IFD line is the only line of equilibria then $k_1 = k_2$ and $k_1 > 1$, but this is not the case in general. It is possible for there to be more than one line of equilibria. This is the case if $K_N = 1$, $K_M = 1.5$, $Q_1 = 200$ and $Q_2 = 300$, as Fig. 8 shows. In this case there is a further line below the unequal competitors IFD line. There may also be no equilibria on the unequal competitors IFD line, since it is possible that this line does not pass through any integer valued points in the required region. However, here we concentrate on cases where the unequal competitors IFD line is the only line of equilibria. From Table 6, it can be seen that after a single individual moves from the equilibrium (n_1, m_1) on the unequal competitors IFD line, it is possible to return to that equilibrium, since $\lambda_{11}(n_1+1, m_1)$, $\lambda_{12}(n_1-1, m_1)$, $\lambda_{21}(n_1, m_1+1)$ and $\lambda_{22}(n_1, m_1-1)$ are all positive.

We define the probabilities $P_1(n_1, m_1), P_2(n_1, m_1), P_3(n_1, m_1)$ and $P_4(n_1, m_1)$ to be the probabilities that (n_1, m_1) is the first equilibrium reached from the states (n_1+1, m_1), (n_1-1, m_1), (n_1, m_1+1) and (n_1, m_1-1), respectively. As stated above, it is always possible to return to (n_1, m_1) after a non-IFD movement, meaning that $P_1, P_2, P_3, P_4 > 0$.

Under our approximation, after a movement from (n_1, m_1) to (n_1, m_1+1) it is possible to reach the equilibrium at $(n_1 - k_1, m_1 + 1)$, since $\lambda_{11}(n_1, m_1+1) > 0$, meaning that $P_3 < 1$. If $\lambda_{22}(n_1 - 1, m_1) > 0$ it is also possible to reach $(n_1 - k_1, m_1 + 1)$ from $(n_1 - 1, m_1)$. The equilibrium at $(n_1 + k_2, m_1 - 1)$ can be reached from $(n_1, m_1 - 1)$, meaning $P_4 < 1$, and may be reached from $(n_1 + 1, m_1)$ if $\lambda_{21}(n_1 + 1, m_1) > 0$. It is not possible to reach $(n_1 - k_1, m_1 + 1)$ from $(n_1 + 1, m_1)$ or $(n_1, m_1 - 1)$ or to reach $(n_1 + k_2, m_1 - 1)$ from $(n_1 - 1, m_1)$ or $(n_1, m_1 + 1)$.

Using the probabilities of the possible non-IFD movements given above, the probability that $(n_1 - k_1, m_1 + 1)$ is the first equilibrium reached after a non-IFD movement from (n_1, m_1) is

$$\frac{\alpha_2(M_T - m_1)(1 - P_3) + \alpha_1 n_1 (1 - P_2)}{\alpha_1(n_1 + m_1) + \alpha_2(N_T + M_T - n_1 - m_1)}.$$

Since P_2 and P_3 do not depend on α_1, differentiating this expression with respect to α_1 gives

$$\frac{\alpha_2[(M_T + N_T - n_1 - m_1)(1 - P_2)n_1 - (M_T - m_1)(1 - P_3)(n_1 + m_1)]}{[\alpha_1(n_1 + m_1) + \alpha_2(N_T + M_T - n_1 - m_1)]^2}.$$

This is negative if $P_2 = 1$.

Similarly, the probability that $(n_1 + k_2, m_1 - 1)$ is the first equilibrium reached after a non-IFD movement from (n_1, m_1) is

$$\frac{\alpha_2(N_T - N_1)(1 - P_1) + \alpha_1 m_1 (1 - P_4)}{\alpha_1(n_1 + m_1) + \alpha_2(N_T + M_T - n_1 - m_1)}.$$

The probabilities P_1 and P_4 do not depend on α_1, hence the derivative of this expression with respect to α_1 is

$$\frac{\alpha_2[(M_T + N_T - n_1 - m_1)(1 - P_4)m_1 - (N_T - n_1)(1 - P_1)(n_1 + m_1)]}{[\alpha_1(n_1 + m_1) + \alpha_2(N_T + M_T - n_1 - m_1)]^2},$$

which is positive if $P_1 = 1$.

If the unequal competitors IFD line is the only line of equilibria, then $k_1 = k_2 > 1$ for all equilibria. This means that the probability that the value of $N_1 + M_1$ has increased once the system returns to equilibrium after a non-IFD movement from (n_1, m_1) increases with α_1 if either $P_1 = 1$ or $P_2 = 1$, which is equivalent to $\max\{P_1, P_2\} = 1$. $P_1 = 1$ if and only if $\lambda_{21}(n_1 + 1, m_1) = 0$, while $P_2 = 1$ if and only if $\lambda_{22}(n_1 - 1, m_1) = 0$. Therefore, $\max\{P_1, P_2\} = 1$ if and only if

$$\frac{K_M}{K_N} > 1 + \min\left\{\frac{Q_1}{Q_2}, \frac{Q_2}{Q_1}\right\}.$$

In the case considered here, with $K_N = 1$, $K_M = 5$, $Q_1 = 100$ and $Q_2 = 300$, the condition

$$\frac{K_M}{K_N} > 1 + \min\left\{\frac{Q_1}{Q_2}, \frac{Q_2}{Q_1}\right\},$$

is satisfied and $k_1, k_2 > 1$ at all equilibria. Hence, the expected value of $N_1 + M_1$ increases with an increase in α_1. This suggests that when $\alpha_1 = 10^{-6}$, $\alpha_2 = 0$, and K_N, K_M, Q_1 and Q_2 are unchanged, the population should be almost certain to be in the state $(34, 4)$ at equilibrium. This is indeed the case, with $E(N_1) = 33.9998$ and $E(M_1) = 3.9996$ in this case.

5. Discussion

We have derived a model describing the distribution of a population between patches of resources, which is developed from that of Jackson et al. (2004). The major differences between our model and theirs are the rate at which IFD movements occur and the fact that we derive equilibrium probabilities for being in each state, rather than using simulations. Our rates for IFD movement are more realistic than those of Jackson et al. (2004), since they depend both on the possible gain in intake rate and the number of individuals present who can make the move. This seems plausible; for example, each type N individual on Patch 1 moves at rate λ_{11}, meaning that the total rate of IFD movements of type N individuals from Patch 1 is $\lambda_{11} N_1$.

The inclusion of this factor also means that there are up to two equilibria for which one of the λ_{ij}s is positive. For example, if $K_N = 1$, $K_M = 5$, $Q_1 = 100$ and $Q_2 = 300$, then $\lambda_{11}(0, 11) > 0$, meaning that it is beneficial for type N individuals on Patch 1 to move to Patch 2, but there are no such individuals to make the move. Our inclusion of the factor N_1 in the IFD movement rate means that this rate will be 0, while it is not stated explicitly what happens under Jackson et al.'s (2004) model when the state $(0, 11)$ is reached. They do not mention the equilibria at $(0, 11)$ or $(36, 3)$, but it seems they are observed when no random movements occur, since 9 frequencies are given on their Fig. 5, while there are only 7 IFD equilibria for the set of parameters used.

Our evaluations produce similar results to the simulations of Jackson et al. (2004). Under-matching is often observed, and the joint equilibrium distributions of N_1 and M_1 are similar to those observed by Jackson et al. (2004), in that they have one modal value when random movements are common, and several when these movements are rare. In these cases the modal values are close to IFD equilibria.

We have found that it is possible for there to be more than one line of IFD equilibria. There may be points that are not on the unequal competitors IFD line for which all of the IFD transition rates are zero. Such a case is shown in Fig. 8, where there is a further line below the unequal competitors IFD line. It is also possible that there are no equilibria on the IFD line, since it may not pass through any integer valued points such that $0 \leqslant N_1 \leqslant N_T$ and $0 \leqslant M_1 \leqslant M_T$.

Our calculation of equilibrium probabilities rather than the use of simulations enables us to ascertain the likelihood of rare events, which may not occur during simulations, and avoids the need to choose an initial distribution.

The use of our approximate model may assist in the computation of the joint equilibrium distribution of N_1 and M_1, since there is a much smaller number of states under this approximation. For the parameter set considered, it is only necessary to find the stationary distribution of a model with 9 states, as opposed to solving a set of 37^2 equations. It should be noted that the calculation of the probability of moving to each equilibrium after a random movement was not trivial. Nevertheless, significant savings could be made, particularly for very large groups.

An increase in the rate of random movements out of Patch 1 can lead to an increase in the number of individuals on this patch when random movements are rare. Our approximation of the model provides a possible explanation for this, since we are able to find circumstances under which the probability with which the number of individuals on Patch 1 has increased once the system returns to equilibrium after a random movement from an equilibrium on the unequal competitors IFD line increases with α_1. It is reasonable that $E(N_1 + M_1)$ should increase with an increase in α_1 under these conditions.

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