A mathematical model for invasion range of population dispersion through a patchy environment

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Abstract

We focus on the question of how the dispersion of an invading population is affected by the spatial distribution of patches that have resource available for the population's settlement and reproduction. We have developed and analyzed a mathematical model with a simple stochastic process. The patches are grouped into three classes – *free*, *occupied* and *abandoned* – depending on the state of the patch used by the population. We especially consider the range expanded by invaded patches, the *invaded range R*, assuming a certain generalized relation between R and the total number of invaded patches k, making use of an index, a sort of *fractal dimension*, to characterize the spatial distribution of invaded patches. We show that the expected velocity is significantly affected by the nature of spatial distribution of resource patches, and is temporally variable. When the invading population finally becomes extinct at a certain moment, the terminal size of the invaded range at that the moment is closely related to the nature of the spatial distribution of resource patches, which is explicitly demonstrated by our analysis.

Introduction

In nature, a variety of species expand their spatial distribution depending on their ecological characteristics, settling into habitats composed of patchy environments containing, for instance, trees, wetland, or mountains (Anderson and May 1986; O'Neill et al. 1988; Jeger 1989; Andow et al. 1990; Johnson et al. 1992; Levin 1992; Russell et al. 1992; Dwyer et al. 1997; van den Bosch et al. 1997; Neuhauser 2001; Turner et al. 2001; Pascual et al. 2002; With 2002). In general, such a patchy environment corresponds to the spatially patchy distribution of resources required for set-tlement and population reproduction. In the case of humans, we may consider a geographical location suitable for constructing a town or village as such a patch. Since such a spatial distribution of resources could be reflected in the resulting population distribution, the spatial distribution of population would often appear to be patchy. Such patchiness of population distribution can also be discussed from the fractal viewpoint (Mandelbrot 1982; Morse et al. 1985; Palmer 1988; Sugihara and May 1990; Russell et al. 1992; Gautestad and Mysterud 1994; With 1994, 2002; With and King 1999; Keymer et al. 2000; Turner et al. 2001; Haskell et al. 2002).

In this paper we use a mathematical model to consider the effect of spatial distribution of resource patches on the nature of spatial expansion of population distribution. We focus in particular on the velocity of its spatial expansion from the original location where the population invasion begins. The velocity of spatial expansion of the invaded region must be affected by the nature of the spatial distribution of resource patches. The velocity of spatial expansion of population distribution has been theoretically discussed in a variety of contexts, mostly with mathematical models of a reaction-diffusion system (Shigesada and Kawasaki 1997; Metz et al. 1999; Diekmann and Heesterbeek 2000; Brauer and Castillo-Chávez 2001; Fagan et al. 2002; Murray 2002a, b), integro-differential or integro-difference equations (Atkinson and Reuter 1976; Brown and Carr 1977; Mollison 1977; Kot and Schaffer 1986; Metz et al. 1999; Neubert et al. 2000; Medlock and Kot 2003), percolation theory or network theory (Grassberger 1983; Stauffer and Aharony 1991; Keeling 1999; Bailey et al. 2000; Tan et al. 2000; Newman 2002; Sander et al. 2002; Meyers et al. 2003; Otten et al. 2004), and cellular automaton or lattice dynamics (Sato et al. 1994; Levin and Durrett 1997; Filipe and Gibson 1998; Brown and Bolker 2004; Filipe et al. 2004). Mathematical models using percolation theory or network theory have been especially attractive to researchers interested in the invasion threshold, which is the critical condition for determining whether the infection stops in a finite period or keeps on expanding spatially.

In contrast to this, here we discuss the velocity using a mathematical model of a stochastic process, analyzing the expected velocity. To incorporate the effect of heterogeneous spatial distribution of resource patches on the spatial expansion of an invaded region, our model characterizes the spatial distribution of resource patches with an index, a *fractal dimension* (Mandelbrot 1982; Hastings and Sugihara 1993). Our model thus describes the population dynamics in terms of a stochastic process, and the spatial expansion of an invaded region in terms of the fractal nature of the spatial distribution of resource patches. This type of combination of population dynamics and spatial expansion may be regarded as an approximation to the actual interrelationship between them. We show that our modeling method would be useful for gaining theoretical insights or developing a more advanced or practical model of the spatial expansion of an invaded region.

Modeling

Assumptions

In our modeling method we classify the patches into three classes, depending on the state of patch use by the population: *free*, *occupied* and *abandoned*. An occupied patch is a patch where the population is consuming the resource in it and reproducing. An abandoned patch means the patch is exhausted of resource and abandoned by the population. A free patch is a patch that has not yet been invaded. Population dispersion occurs only from occupied patches, and the disperser invades some free patches. Such an invasion of free patches causes the expansion of the invaded region, determined by the population distribution in space.

Another way of looking at the class of abandoned patch is that the population becomes extinct within the patch. If the population considered is a harmful insect that has to be exterminated, such an abandoned patch may be regarded as the artificially exterminated patch aggregating the insect. In our modeling method, it is essential that any patch belonging to the class of abandoned patch has no dispersion from it, not must it attract any disperser into it. In this sense, the abandoned patch may be regarded as an *isolated* patch.

With inclusion of such abandoned patches, our model could be regarded as a spatial dispersion of population which appears as an outbreak at a certain habitat and moves away from the origin, consuming every available resource, such as a grasshopper outbreak.

Our model assumptions are as follows:
- Invasion rate depends only on the total number of occupied patches.
- Only free patches can be invaded.
- An abandoned patch is never invaded or used again.
- Settlement and abandonment of a patch are independent of any other patches.

We should note that the invasion rate is determined by the number of patches rather than population size, like Seno and Matsumoto (1996). The population size of a disperser would be closely related to the population size in occupied patches as the source of dispersers. Hence, in our model, we assume that the population size of a disperser is positively related to the number of occupied patches.

We do not consider the population dynamics within each patch, rather classifying the patch, as mentioned above, in terms of its use by the population. In this sense, our model can be regarded as a sort of metapopulation dynamics (for instance, see Johnson et al. 1992; Hanski 1994a, b, 1999; With and King 1999; Keymer et al. 2000; Ovaskainen and Hanski 2001). Furthermore, according to the grouping of patches into three classes and their definitions, our model may be regarded as corresponding to a kind of SIR epidemic dynamics (see, for instance, Shigesada and Kawasaki 1997; Diekmann and Heesterbeek 2000; Brauer and Castillo-Chávez 2001; Murray 2002a).

In this paper, we focus on the number of *occupied* patches, h, and the number, k, of *invaded* patches, comprising both occupied and abandoned patches. An invaded patch is an occupied or abandoned one, that is, a patch which has experienced the invasion. The number of abandoned patches is given by the difference $k-h$.

Model construction

Probability distribution for the state of patch use

We donote by $P(k, h, t)$ the probability of state such that there are k *invaded* patches and h *occupied* patches at time t in the considered system. To determine the probability $P(k, h, t)$, we consider the possible transitions of state in sufficiently small time interval $(t, t+\Delta t]$ with our modeling assumptions, and derive the following system of differential equations that govern the temporal variation of probability $P(k, h, t)$:

$$\frac{dP(k,h,t)}{dt} = -(\beta + \gamma)hP(k,h,t)$$
$$+ \gamma(h+1)P(k,h+1,t)$$
$$+ \beta(h-1)P(k-1,h-1,t), \qquad (1)$$

for $k \geq 2$, $h \geq 1$, $k \geq h+1$, and the following additional two:

$$\frac{dP(k,0,t)}{dt} = \gamma P(k,1,t), \qquad (2)$$

$$\frac{dP(k,k,t)}{dt} = -k(\beta + \gamma)P(k,k,t)$$
$$+ (k-1)\beta P(k-1,k-1,t) \qquad (3)$$

for $k \geq 1$. Parameter β is the settlement rate, and γ the abandonment rate. If the population considered is of a harmful insect to be exterminated, γ may be regarded as the extermination rate for a patch aggregating the insect.

The essence of modeling for the derivation of the above equations is as follows: the probability that a free patch is invaded during a sufficiently small period Δt by the disperser from an occupied patch is assumed to be given by $\beta\Delta t + o(\Delta t)$ independently of the distance between these patches. Since we assume that the settlement into a free patch by the disperser from an occupied patch is independent of any other occupied patch, the probability that a free patch is invaded by any dispersers from h occupied patch becomes $\beta h\, \Delta t + o(\Delta t)$. The probability that an occupied patch is abandoned is assumed to be given by $\gamma \Delta t + o(\Delta t)$. When there are h occupied patches, the probability that only one of them is abandoned is given by the probability of the abandonment of an occupied patch and that of the non-abandonment of the other $h-1$ occupied ones. Therefore, the probability that only one occupied patch is abandoned during a sufficiently small period Δt is given by $\gamma h\, \Delta t + o(\Delta t)$. The probability that more than one occupied patch is abandoned is $o(\Delta t)$. Moreover, from the assumption of independence between settlement and abandonment, the probability that both settlement and abandonment occur during the time period Δt is given by $o(\Delta t)$, because the probability for each of them is of the order Δt.

Initial condition

We assume that the invasion begins with a patch at time 0, so that the initial condition is given by

$$P(k,h,0) = \begin{cases} 1 & \text{if } k = h = 1, \\ 0 & \text{otherwise.} \end{cases} \qquad (4)$$

An invader species is assumed to be introduced into the environment for an artificial or natural reason. The invader species then settles in a patch which is the original place of invasion.

Expansion of invaded range
Next we consider the range expanded by invaded patches, calling it the *invaded range*. We characterize the invaded range by the minimal diameter R which includes all invaded patches.

In the case when the invaded range expands in every direction with the same probability, the shape of the invaded region can be approximated by the disc, and therefore, assuming the spherical nature of the earth is negligible and can be well approximated by a plane, the range R has approximately the following relation with the number of invaded patches k: $k \propto R^2$. However, since the expansion of the invaded range is constrained by the spatial distribution of resources, which could in general be heterogeneous, the shape is possibly inhomogeneous in direction. It is likely that the shape can be characterized by its *fractal* nature (for the concept of "fractal", see for instance, Mandelbrot 1982; Sugihara and May 1990; Hastings and Sugihara 1993). To deal with such a case, we assume the generalized relation between the invaded range and the total number of invaded patches as follows:

$$k \propto R^d \quad (1 \leq d \leq 2), \tag{5}$$

where the exponent d characterizes the spatial pattern of invaded region occupied by invaded patches (Figure 1). Exponent d is called the *cluster dimension* or *mass dimension*, which is a sort of *fractal dimension* (Mandelbrot 1982; Hastings and Sugihara 1993). When $d \approx 2$, the spatial distribution of invaded patches can be approximated well by a disc. When $d \approx 1$, the distribution can be approximately regarded as one dimensional, that is, the invaded patches can be regarded as being arrayed along a curve.

This idea of introducing a fractal nature into the mathematical model for spatial patch distribution is the same as that described in Seno (1993). This modeling may be regarded as a sort of mean-field approximation for the percolation process on an anisotropic/fractal lattice or the growing network (Grassberger 1983; Stauffer and Aharony 1991; Bailey et al. 2000; Tan et al. 2000; Newman 2002; Sander et al. 2002; Meyers et al. 2003; Otten et al. 2004). In such previous models, the main problem was the invasion threshold, which is the critical condition to determine if the invasion stops in a finite period or keeps on expanding spatially. In contrast, we are now going to focus on the velocity of spatial expansion of the invaded range.

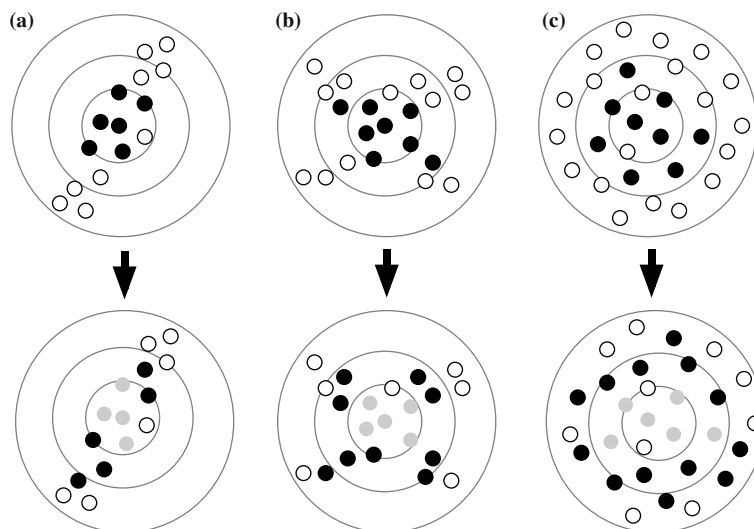For convenience to apply the relation (5) for our modeling, we now define the proportional constant C:

Figure 1. Illustration of the relation of the fractal dimension d to the spatial pattern of patch distribution. Schematic process of settlement and abandonment is also shown. White disc indicates free patch, black occupied, and grey abandoned. (a) $d \approx 1$; (b) $1 < d < 2$; (c) $d \approx 2$.

$$k = CR^d \quad (1 \le d \le 2). \tag{6}$$

Next, conventionally we define the mean distance $\overline{R}_{(2)}$ from one patch to the nearest neighbor (Figure 2). In our modeling, $\overline{R}_{(2)}$ is assumed to correspond to the expected invaded range expanded by two invaded patches, that is, $k = 2$. Therefore, from (6), we assume that

$$2 = C\overline{R}_{(2)}^d. \tag{7}$$

Hence, from (6) and (7), for the *expected* number of invaded patches $\langle k \rangle_t$ at time t, we assume the following relation for the *expected* invaded range $\overline{r}_t$ at time t:

$$\langle k \rangle_t = 2\overline{r}_t^d \quad (1 \le d \le 2), \tag{8}$$

where $\overline{r}_t$ is the expected invaded range measured in terms of the mean distance $\overline{R}_{(2)}$: $\overline{r}_t \equiv \overline{R}_t / \overline{R}_{(2)}$.

Further, we can define the *expected* velocity $\overline{V}_t$ of expansion of the invaded range at time t by

$$\overline{V}_t = \frac{d\,\overline{r}_t}{dt}.$$

So, from (8), we can obtain the following relation between the expected velocity $\overline{V}_t$ and the expected number $\langle k \rangle_t$ of invaded patches at time t:

$$\overline{V}_t = \frac{1}{d}\left(\frac{1}{2}\right)^{1/d} \langle k \rangle_t^{1/d-1} \cdot \frac{d\langle k \rangle_t}{dt}. \tag{9}$$

Analysis

Expected number of occupied patches

We denote by $\langle h \rangle_t$ the *expected* number of occupied patches at time t, defined by
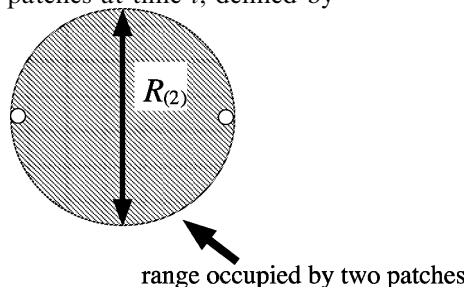

range occupied by two patches

Figure 2. Illustration of range $R_{(2)}$.

$$\langle h \rangle_t = \sum_{k=1}^{\infty} \sum_{h=1}^{k} hP(k, h, t). \tag{10}$$

From (1) and (3), we can obtain the following:

$$\frac{d}{dt}\langle h \rangle_t = (\beta - \gamma)\langle h \rangle_t,$$

and then

$$\langle h \rangle_t = e^{(\beta-\gamma)t}, \tag{11}$$

where we used the initial condition (4) for (10): $\langle h \rangle_0 = 1$.

Expected number of invaded patches

As for invaded patches, we denote by $\langle k \rangle_t$ the *expected* number of invaded patches at time t, defined by

$$\langle k \rangle_t = \sum_{k=1}^{\infty} k\left\{\sum_{h=0}^{k} P(k, h, t)\right\}. \tag{12}$$

From (1), (2) and (3), we can obtain the following:

$$\frac{d}{dt}\langle k \rangle_t = \beta\langle h \rangle_t.$$

With (11), we can solve this differential equation and get

$$\langle k \rangle_t = \frac{\beta}{\beta - \gamma}\{e^{(\beta-\gamma)t} - 1\} + 1, \tag{13}$$

where we used the initial condition (4) for (12): $\langle k \rangle_0 = 1$.

Now we consider the saturated value of $\langle k \rangle_t$ as $t \to \infty$. From (13), for $\beta \ge \gamma$ when the settlement rate is not less than the abandonment rate, $\langle k \rangle_t$ becomes positively infinite as $t \to \infty$. On the other hand, for $\beta < \gamma$ when the abandonment rate is greater than the settlement rate, the saturated value is as follows:

$$\langle k \rangle_{t \to \infty} = \frac{\gamma}{\gamma - \beta}. \tag{14}$$

Expected invaded range

Since, from (8),

$$\overline{r}_t = \left(\frac{\langle k \rangle_t}{2}\right)^{1/d}, \tag{15}$$

we can consider how the expected invaded range $\overline{r}_t$ depends on the fractal dimension d of the spatial distribution of patches, making use of (13). For $0 < \beta/\gamma < 1/2$, when the abandonment rate is sufficiently greater than the settlement rate, the expected invaded range $\overline{r}_t$ becomes larger as d is larger (Figure 3(a)). This means that the invaded range is expected to become wider as patches are more uniformly distributed. In contrast, for $\beta/\gamma \geq 1/2$, the expected invaded range becomes smaller as d is larger (Figures 3b–d). In this case, the invaded range is expected to be narrower as the patches are more uniformly distributed. Therefore, in our model, only if the settlement rate is smaller than half of the abandonment rate does the more uniform distribution of free patches cause a wider expected invaded range.

We now consider the saturated value of expected invaded range as $t \to \infty$ (Figure 4). From (13) and (15), for $\beta \geq \gamma$, $\overline{r}_t$ becomes positively infinite as $t \to \infty$ (Figures 3c, d). For $\beta < \gamma$, it saturates to the following value as $t \to \infty$ (Figures 3a, b):

$$\overline{r}_{t \to \infty} = \left(\frac{\langle k \rangle_{t \to \infty}}{2}\right)^{1/d} = \left(\frac{1}{2}\frac{\gamma}{\gamma - \beta}\right)^{1/d}. \tag{16}$$

Expected expansion velocity of invaded range

From (13), we can get the following expected expansion velocity of invaded range, $\overline{V}_t$ defined by (9):

$$\overline{V}_t = \frac{1}{d}\left(\frac{1}{2}\right)^{1/d} \beta e^{(\beta - \gamma)t} \left[\frac{\beta}{\beta - \gamma}\{e^{(\beta - \gamma)t} - 1\} + 1\right]^{1/d - 1}$$

$$= \frac{1}{d}\left(\frac{1}{2}\right)^{1/d} \langle k \rangle_t^{1/d - 1}\{(\beta - \gamma)(\langle k \rangle_t - 1) + \beta\}. \tag{17}$$

When $\beta/\gamma \leq 1$, that is, when the abandonment rate is not less than the settlement rate, the expected velocity $\overline{V}_t$ decreases monotonically in time (Figure 5a).
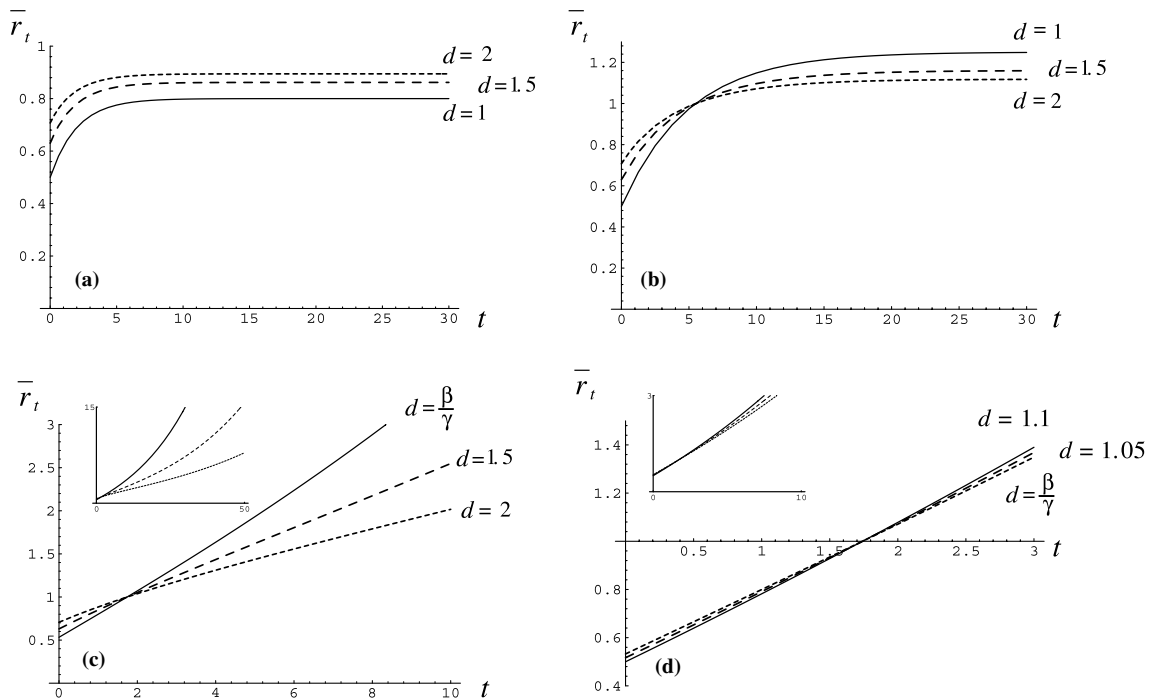

Figure 3. Temporal development of the expected invaded range. (a) $0 < \beta/\gamma < 1/2$, numerically drawn for $\beta = 0.3$ and $\gamma = 0.8$; (b) $1/2 \leq \beta/\gamma \leq 1$, for $\beta = 0.3$ and $\gamma = 0.5$; (c) $1 < \beta/\gamma < d$, for $\beta = 0.55$ and $\gamma = 0.5$; (d) $\beta/\gamma \geq d$, for $\beta = 0.55$ and $\gamma = 0.5$.
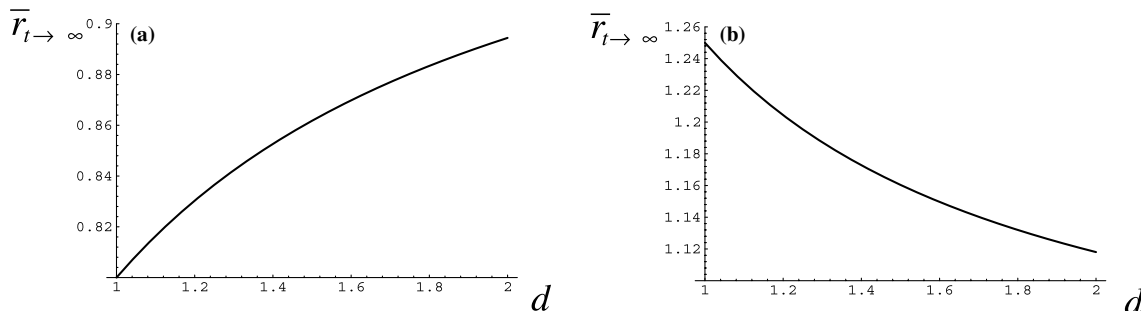
Figure 4. *d*-Dependence of the saturated value of expected invaded range. (a) $0 < \beta/\gamma < 1/2$, numerically drawn for $\beta = 0.3$ and $\gamma = 0.8$; (b) $\beta/\gamma \geq 1/2$, for $\beta = 0.3$ and $\gamma = 0.5$.

When $1 < \beta/\gamma < d$, that is, when the settlement rate is greater than the abandonment rate and small enough so β/γ is less than d, the expected velocity $\overline{V}_t$ decreases in the earlier period and then starts to increase monotonically (Figure 5b). We denote by t_c the time at the moment when the expected velocity turns from decreasing to increasing. From (9), we can get

$$t_c = \frac{1}{\beta - \gamma} \ln \frac{\gamma}{\beta} d. \tag{18}$$

When $\beta/\gamma \geq d$, that is, when the settlement rate is sufficiently greater than the abandonment rate, the expected velocity $\overline{V}_t$ increases monotonically in time (Figure 5c).

In case of $\beta/\gamma > 1$, from (17) for sufficiently large t,

$$\overline{V}_t \approx \frac{1}{d} \left(\frac{1}{2}\right)^{1/d} \beta \left[\frac{\beta}{\beta - \gamma}\right]^{1/d-1} e^{\{(\beta - \gamma)/d\}t}$$

$$= \frac{1}{d} \left(\frac{1}{2}\right)^{1/d} (\beta - \gamma) \langle k \rangle_t^{1/d}. \tag{19}$$

Therefore, if $\beta/\gamma > 1$, the expected velocity $\overline{V}_t$ increases exponentially for sufficiently large t, with the exponent inversely proportional to the fractal dimension d.

Consequently we can see how the expected velocity $\overline{V}_t$ depends on the fractal dimension d of the spatial distribution of patches. The expected velocity becomes smaller as d increases, (Figures 5a–c) for any value of β/γ. Therefore, in our model, a more uniform distribution of patches causes a slower expansion of invaded range.

Probability of termination of invasion

We denote by $P_{h=0}$ the probability of the termination of invasion. Once all the occupied patches disappear in space because of abandonment, the invasion can no longer continue and restart, which means the invasion is terminated. If the invasion terminates at time t, the state of patch use at time $t - \Delta t$ should be only one occupied patch for sufficiently small Δt, and it should be abandoned during Δt without causing any new settlement. When
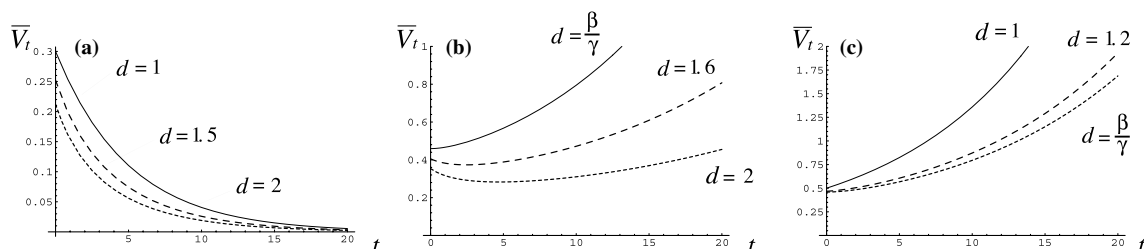

Figure 5. Temporal variation of the expected expansion velocity of invaded range. (a) $0 < \beta/\gamma \leq 1$, numerically drawn for $\beta = 0.3$ and $\gamma = 0.5$; (b) $1 < \beta/\gamma < d$, for $\beta = 0.5$ and $\gamma = 0.4$; (c) $\beta/\gamma \geq d$, for $\beta = 0.5$ and $\gamma = 0.4$.

the number of invaded patches is k at time t, the probability of this event is given by

$$P(k, 1, t)[1 - \beta\Delta t - o(\Delta t)] \cdot [\gamma\Delta t + o(\Delta t)]$$
$$= \gamma P(k, 1, t)\Delta t + o(\Delta t). \tag{20}$$

Therefore, the probability of the termination of invasion between $t-\Delta t$ and t is given by the sum of (20) over any possible k.

Making use of the probability generating function (p.g.f.) defined by

$$f(x, y, t) = \sum_{k=1}^{\infty} \sum_{h=0}^{k} P(k, h, t)x^k y^h, \tag{21}$$

we can derive the probability $P_{h=0}$ for the termination of infection (for the detail of p.g.f., see the Appendix A):

$$P_{h=0} = \int_0^\infty \gamma \sum_{k=1}^\infty P(k, 1, t)dt$$
$$= \int_0^\infty \gamma \cdot \left.\frac{\partial f}{\partial y}\right|_{x=1, y=0} dt$$
$$= \int_0^\infty \gamma \cdot \frac{e^{-(\beta-\gamma)t}\{(\beta-\gamma)/\beta\}^2}{1 - e^{-(\beta-\gamma)t}\gamma/\beta}dt \tag{22}$$
$$= \min\left\{\frac{\gamma}{\beta}, 1\right\}.$$

When the probability $P_{h=0}$ is 1, that is the case when the abandonment rate is greater than the settlement rate, the invasion certainly terminates in a finite time (Figure 6).

Expected time for termination of invasion

We denote by $\langle t \rangle_{h=0}$ the expected time at which the invasion is terminated. From the arguments in the previous section, we can obtain it as follows:

$$\langle t \rangle_{h=0} = \int_0^\infty t\gamma \sum_{k=1}^\infty P(k, 1, t)dt$$
$$= \begin{cases} +\infty & \text{if } \beta \geq \gamma; \\ \frac{1}{\beta}\ln\frac{\gamma}{\gamma-\beta} & \text{if } \beta < \gamma. \end{cases} \tag{23}$$

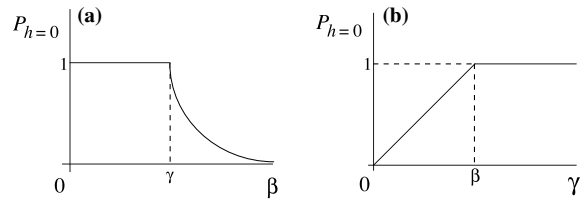For $\beta < \gamma$ when the abandonment rate is greater than the settlement rate, we can expect for the

Figure 6. Parameter dependence of the probability of the termination of invasion, $P_{h=0}$. (a) β-dependence; (b) γ-dependence.

invasion to terminate at a finite time $\langle t \rangle_{h=0}$ (Figure 7).

Expected number of invaded patches at termination of invasion

We denote by $\langle k \rangle_{h=0}$ the expected number of invaded patches at the termination of invasion. Integral $\int_0^\infty \gamma P(k, 1, t)dt$ gives the probability that the number of invaded patches is k at the termination of invasion. Therefore, making use of the p.g.f. (A.4), we can get the following:

$$\langle k \rangle_{h=0} = \sum_{k=1}^\infty k \int_0^\infty \gamma P(k, 1, t)dt$$
$$= \gamma \int_0^\infty \sum_{k=1}^\infty kP(k, 1, t)dt$$
$$= \gamma \int_0^\infty \left.\frac{\partial}{\partial y}\left(\frac{\partial f}{\partial x}\right)\right|_{x=1, y=0} dt \tag{24}$$
$$= \frac{\gamma}{\gamma - \beta}.$$

From (14) and (24), we see that the expected number of invaded patches at the termination of invasion, $\langle k \rangle_{h=0}$, is identical to the saturated value of $\langle k \rangle_t$, $\langle k \rangle_{t\to\infty}$:

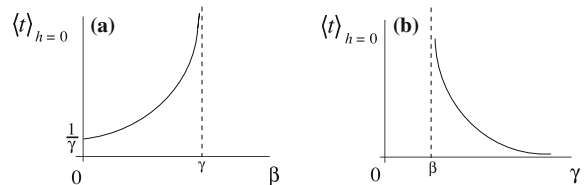*Figure 7.* Parameter dependence of the expected time for the termination of invasion $\langle t \rangle_{h=0}$. (a) β-dependence; (b) γ-dependence.

$$\langle k \rangle_{h=0} = \langle k \rangle_{t \to \infty}.$$

Therefore, $\langle k \rangle_{h=0}$ has the same nature as $\langle k \rangle_{t \to \infty}$. Hence, the expected range at the termination of invasion is also equal to the saturated range of $\bar{r}_t$, $\bar{r}_{t \to \infty}$.

Discussion

In this work we focus on the question of how the dispersion of an invading population is affected by the spatial distribution of patches that have resource available for its settlement and reproduction, by developing and analyzing a mathematical model with a simple stochastic process.

In reality, a variety of species expand their spatial distribution depending on their ecological characteristics, settling habitats composed of fragmentated/patchy environments, such as trees, wetland, or mountains (O'Neill et al. 1988; Johnson et al. 1992; Russell et al. 1992; van den Bosch et al. 1997; Caraco et al. 2001; Neuhauser 2001; Turner et al. 2001; Pascual et al. 2002; With 2002; Brown and Bolker 2004; Drenth 2004; Otten et al. 2004). So we can regard each such spatially fragmented habitat as a patch that is available to an invader population. In the human case, we may consider such a patch as a geographical location that is favorable to the construction of a town or village.

We assumed that these available patches can be grouped into three classes: *free*, *occupied* and *abandoned*, depending on the state of the patch used by the population. An occupied patch is one where the population is consuming the resource in it, allowing reproduction. An abandoned patch is where the resource is exhausted and the population has left. It may be regarded as a patch within which the population goes extinct. A free patch is a patch that has not yet been invaded. Dispersers/migrators appear only from occupied patches, and the dispersers/migrators invade some free patches. Such invasion of free patches causes the expansion of the population distribution in space.

In our modeling, we do not consider the population dynamics within each patch, but classify the patch as mentioned above in terms of its use by the population. In this sense, our modeling can be regarded as a sort of *metapopulation dynamics* (Johnson et al. 1992; Hanski 1999; With and King 1999; Keymer et al. 2000), or more specifically a sort of *stochastic patch occupancy modeling* (Hanski 1994a, b; Ovaskainen and Hanski 2001). Moreover, according to the classification of patches into three types and their definitions, our modeling may be regarded as corresponding to a kind of SIR epidemic dynamics (for instance, see Shigesada and Kawasaki 1997; Diekmann and Heesterbeek 2000; Brauer and Castillo-Chávez 2001; Murray 2002a).

We considered the probability of the state such that k *invaded* and h *occupied* patches existing at time t. Invaded patches consist of occupied and abandoned ones, that is, those which have experienced the invasion. We constructed and analyzed a system of differential equations to describe the temporal variation of the probability distribution. We then developed the mathematical model for the expanding range of invaded patches in space, the *invaded range*, which can be characterized by the *expected* minimal diameter R which includes all invaded patches. We assumed a certain generalized relation between R and the total number of invaded patches k, making use of an index called the *cluster dimension* or *mass dimension*, which is a sort of *fractal dimension* (Mandelbrot 1982; Sugihara and May 1990; Hastings and Sugihara 1993), to characterize the spatial distribution of patches. Using this relation, we derived the temporal variation of expected invaded range and its expected expansion velocity. Although we applied the fractal dimension to incorporate some notion of space or heterogeneity in space into our model, the location or the configuration of patches in space is not explicitly introduced. In this sense, our model could be regarded as intermediate between a non-spatial population dynamics model and a numerical spatial dynamic model, and may be a kind of *semi-spatial model* (cf. Filipe et al. 2004).

In our modeling, a free patch is invaded with probability proportional to the *total number* of occupied patches, that is, the total number of habitats with inhabiting population. Our modeling assumption may be translated as follows: the invasion of a free patch would be proportional to the total population size of all occupied pat-

ches, as in Seno and Matsumoto (1996), who analyze a mathematical model for population dynamics to expand its spatial distribution with patch creation by the existing population. This is not exactly comparable to our model, because ours is a sort of metapopulation dynamics with a given spatial distribution of resource patches, with no consideration of the population dynamics within each patch or the patch size.

From the results of our analysis of the mathematical model, we found that the expected velocity is significantly affected by the nature of spatial distribution of resource patches, and is temporally variable, in contrast to the results frequently derived for the mathematical model with the reaction-diffusion system in continuous and homogeneous space (for instance, see Shigesada and Kawasaki 1997; Okubo and Levin 2001; Murray 2002a, b). Consequently we found three types of temporal variation of expected velocity of invaded range expansion, depending on the fractal dimension of the spatial distribution of resource patches: monotonically decreasing, monotonically increasing, and increasing after initially decreasing.

The last case implies that we have to pay attention to the expansion of the invaded region, even if its velocity is observed to decrease, especially in the early period of invasion. An invader population might decrease its velocity of spatial expansion in the early period and then turn to increase the velocity to expand its spatial distribution with increasing rapidity.

It may be more realistic that a free patch would be invaded by dispersers from some *spatially neighboring* occupied patches. For instance, this may be incorporated by introducing a fractal-dimension-dependence of settlement rate. Such an assumption about the location or the configuration of patches in space makes the model less amenable to mathematical analysis, although it must be interesting from the viewpoint of mathematical biology. This will be surely the next step of this type of mathematical model to be considered.

Some cellular automaton models or lattice models have been considered to describe such population invasion in heterogeneous space (Grassberger 1983; Stauffer and Aharony 1991; Sato et al. 1994; Levin and Durrett 1997; Filipe

and Gibson 1998; Keeling 1999; Bailey et al. 2000; Tan et al. 2000; Newman 2002; Sander et al. 2002; Meyers et al. 2003; Brown and Bolker 2004; Filipe et al. 2004; Otten et al. 2004). Computer-aided numerical analysis has always been useful in the analysis of such models, whereas numerical calculations could not necessarily derive the general result about the nature of population invasion in heterogeneous space. Only a few mathematical methods are capable of deriving some general features of such a model, such as, the mean field approximation and the pair approximation etc. (see Sato et al. 1994; Caraco et al. 2001; Filipe and Gibson 2001; Ovaskainen and Hanski 2001; Ovaskainen et al. 2002; Pascual et al. 2002; Filipe et al. 2004) Even though such a model could be easily constructed, for instance, by a type of cellular automaton, we do not argue here in support of such types of numerical models.

In this paper, we consider our mathematical model in the general context of spatial expansion of invaded range of population dispersing through a spatially patchy distribution of resource. With some necessary modifications, our model could be easily applied to the more specified case of the spatial expansion of population distributed through patchy/fragmentated habitats in space.

If we consider a population dynamics of sexual reproduction, we may regard the patch as the female individual or a sort of female group, which is searched by dispersing males (for a mathematical model of the same stand point, see, for instance, Hirata and Seno 1997). The abandonment of a patch is regarded as the mated female (group) which ceases to be a mating target.

For the case of prey–predator population dynamics, the patch in our model could correspond to the prey individual or group (for the same stand point, see for instance, Russell et al. 1992). In this case, the prey is regarded as the resource for predator, and the abandonment of a patch is the consumption of prey by predation, or the extinction of both prey and predator in it.

In case of host–parasite population dynamics, the patch corresponds to the host individual or group under parasitism by dispersing parasites.

The abandonment of a patch is regarded as the parasitized host, so that this is the case when the parasitized host cannot be parasitized again without multi-parasitism.

As another context for the application of our model, we could consider the epidemic dynamics of disease transmission through immobile units of infection, as town, plant, etc. and classify these units into three classes: *susceptible*, *infective* and *recovered* (Koshiba and Seno 2005). In this context of epidemic dynamics, the parameter β can be regarded as the infection rate from an infective unit to a susceptible one, while γ can be seen as the recovery rate with immunity or the death rate. In this case, the invaded range considered in this paper corresponds to the range expanded by infected units, so that it means the spatial range damaged by the epidemic disease. Our modeling assumption that the settlement rate depends only on the total number of occupied patches corresponds to, for instance, the case that the epidemic vector has a high mobility to transmit the disease, or the case that the disease transmission is through the matrix environment (e.g. wind, water or soil) surrounding susceptible units (Bailey et al. 2000; Drenth 2004; Otten et al. 2004). An environment-dependent mode of disease transmission and the sanitary/health condition determine the nature of infected area expansion (van den Bosch et al. 1997; Keeling et al. 2001; Gilligan 2002). In case of plants or crops under attack from pests and diseases, the spatial distribution of susceptible hosts is considered as important for the spread of infection (van den Bosch et al. 1997; Caraco et al. 2001; Jules et al. 2002; Brown and Bolker 2004; Drenth 2004; Otten et al. 2004). However, little is known about the effect of environmental heterogeneity on the spatial expansion of epidemics.

For the spatial expansion of population distribution, some well-known mathematical models are constructed with a reaction-diffusion system in spatially continuous space (Shigesada and Kawasaki 1997; Okubo and Levin 2001; Murray 2002a, b). However, in general, it is not easy, or there is sometimes a great tactical advantage to introduce the nature of spatial heterogeneity of habitat distribution into such a reaction-diffusion system model. By contrast, in case of spatially discrete models, frequently constructed by cellular automata or on a lattice space (Sato et al. 1994; Levin and Durrett 1997; Rhodes et al. 1997; Filipe and Gibson 1998; Bailey et al. 2000; Brown and Bolker 2004; Filipe et al. 2004; Otten et al. 2004), the introduction of spatial heterogeneity is relatively easy, whereas mathematical analysis is rarely easy and becomes harder as the number of factors governing the population dynamics increases, so that a number of numerical calculations are required. A stochastic model like ours is another mode of the theoretical study that could give some new insights, as some researches in landscape ecology indicate (Dunning et al. 1995; Wiegand et al. 1999; Turner et al. 2001; Fortin et al. 2003). Since only few models consider the velocity of spatial expansion of invaded region over such a spatially distributed patchy environment, we hope that our modeling methodology offers a pioneering approach to the problem.

Acknowledgements

Appendix A

Applying (1), (2) and (3), and after cumbersome and careful calculation, we can derive the following partial differential equation for the probability generating function (p.g.f.) $f(x, y, t)$ defined by (21):

$$\frac{\partial f(x,y,t)}{\partial t} = \{-(\beta+\gamma)y+\gamma+\beta xy^2\}\frac{\partial f(x,y,t)}{\partial y}. \tag{A.1}$$

From (4), the initial condition is given by

$$\begin{aligned} f(x,y,0) &= \sum_{k=1}^{\infty}\sum_{h=0}^{k} P(k,h,0)x^k y^h \\ &= P(1,1,0)xy \\ &= xy. \end{aligned} \tag{A.2}$$

In addition, the following condition can be derived:

$$f(1, 1, t) = \sum_{k=1}^{\infty} \sum_{h=0}^{k} P(k, h, t) = 1, \qquad (A.3)$$

because the sum of probability for any possible k and h corresponds to the occurrence of any event.

With condition (A.2) and (A.3), we can solve (A.1) as follows (for instance, see pp. 62–63 in Bailey (1957)):

$$f(x, y, t) = x \left[v_+(x) - \frac{\hat{v}(x)\{v_+(x) - y\}}{\Phi(x)} \right], \quad (A.4)$$

where

$$\Phi(x) = \{v_+(x) - y\} + \{y - v_-(x)\}e^{-\beta x \hat{v}(x)t};$$
$$\hat{v}(x) = v_+(x) - v_-(x),$$

and $v_+(x)$ and $v_-(x)$ are functions of x, given by two distinct roots of the following equation in terms of ξ:

$$\beta x \xi^2 - (\beta + \gamma)\xi + \gamma = 0.$$

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