数理解析研究所講究録
第 870 巻 1994 年 43-55

On the relationship between the Kramers-Moyal expansion and the transition matrix model.

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Kramers-Moyal 展開と推移行列モデルの関係について

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Abstaract The relationship between the diffusion equation and the Lefkovitch matrix model is examined. It is shown that the dynamics with the one-step Lefkovitch matrix model corresponds to a difference equation of the diffusion equation and that the dynamics with the two-step and three-step Lefkovitch matrix model correspond to the difference equation of the 4-th order and 6-th order Kramers-Moyal expansion equation, respectively. The type of a Lefkovitch matrix is determined by the distribution function of growth rate and the ratio of the interval of size-classes to that of successive censuses.

Introduction In these ten years, the diffusion equation model has been employed in plant population ecology in order to analyze the dynamics of growth and size structure in annual plants and trees (e. g. Hara1984a, b, 1985, 1986b; Petersen 1988; Kohyama 1987, 1989; Kohyama and Hara 1989; West et al. 1989; Petersen et al. 1990; Hara et al. 1991). The models is continuous in time and size, and can describe the dynamics of size distribution mathematically based on individual growth, mortality, recruitment as continuous functions of time and size. The diffusion equation model (Hara 1984a,b, 1988) contains three parameter functions, mean of growth rates of individuals of size x at time t, variance in growth rate of individuals of size x at time t and mortality rate of individuals of size x at time t, together with a left boundary condition as a recruitment rate.

On the other hand, many authors (Sarukhán and Gadgil (1974), Hartshorn (1975), Bierzychudek (1982), Meagher (1982), Burns and Ogden (1985), Kinoshita (1987), Kawano et al. (1987)) have employed the Lefkovitch matrix model as a useful tool for demographic analysis. This model is discrete in time and size, and can describe mathematically the dynamics of discrete size-class structure of a population with reproduction. Therefore, most of the authors examined the yearly demography of perennial plant populations using the Lefkovitch matrix model. The Lefkovitch matrix model contains s^2 parameters (s is the number of size-classes), each of which represents the transition probability from one size-class to another at the next time-step,

Although both models describe the dynamics of size structure of populations and thus there seems to be some relationships between them, there has been no theoretical studies on the relationship. In the present paper, we first examine the relationship between the diffusion equation and the Lefkovitch matrix model without both mortality and reproduction.

The relationship between the Lefkovitch matrix and the diffusion equation

Let $n_{it}, \mathbf{n}_t = (n_{1t}, n_{2t}, \ldots, n_{st})^T$ be the population density of size-class i at time t and the size-class vector at time t, respectively, where s is the number of size-classes. The sizes of individuals in the size-class i ranges between (i-1/2)h and (i+1/2)h, where h is the interval of size-classes. Let **A** be the Lefkovitch matrix, each of whose elements, a_{ij}, represents the transition probability from the size-class j to i per unit time and depends on the interval h, i.e. $a_{ij} \equiv a_{ij}(h)$. According to the knowledge on Lefkovitch matrix model (Lefkovitch1965), the dynamics of population with size-structure can be written as:

(1) $$\mathbf{n}_{t+\Delta t} = \mathbf{A}\Delta t\, \mathbf{n}_t \quad ,$$

i.e.

(2) $$n_{i,t+\Delta t} = \sum_{j=1}^{s} a_{ij}\Delta t\, n_{j,t} \qquad (i=1,\ldots,s).$$

For simplicity, assuming that the population has no mortality and no recruitment,

(3) $$\sum_{k=1}^{s} a_{ki}\Delta t = 1 \quad (i=1,\ldots,s)$$

since individuals of size-class i at time t move to another size-classes at time t+Δt without loss. From Eq. (3), equation (2) can be rewritten as:

$$(4) \quad \frac{n_{i,t+\Delta t} - n_{i,t}}{\Delta t} = \sum_{j \neq i}^{s} a_{ij} n_{j,t} - (\sum_{k \neq i}^{s} a_{ki}) n_{i,t} \qquad (i=1,....,s).$$

The k-th order moment of growth rate of individuals belonging to the i-th size-class during the time Δt is

$$(5) \quad \frac{1}{\Delta t} \sum_{j} (a_{i+j,i} \Delta t) \ (jh)^k \equiv M_{k,i} \ .$$

We here define the one-step Lefkovitch matrix, which describes the only one-step transition from the starting size-class; i.e.

$$(6) \quad \begin{aligned} a_{ij} &= 0 \quad \text{for } | i-j | > 1 \\ a_{ij} &> 0 \quad \text{otherwise,} \end{aligned}$$

$$A_1 = \begin{bmatrix} \ddots & 0 & \vdots & \vdots & \vdots \\ \ddots & a_{i-2,i-1} & 0 & \vdots & \vdots \\ \ddots & a_{i-1,i-1} & a_{i-1,i} & 0 & \vdots \\ 0 & a_{i,i-1} & a_{ii} & a_{i,i+1} & 0 \\ \vdots & 0 & a_{i+1,i} & a_{i+1,i+1} & \ddots \\ \vdots & \vdots & 0 & a_{i+2,i+1} & \ddots \\ \vdots & \vdots & \vdots & 0 & \ddots \end{bmatrix}.$$

When the Lefkovitch matrix is the one-step matrix, the right-hand side of Eq. (4) can be written as:

$$(7) \quad a_{i,i-1} n_{i-1,t} + a_{i,i+1} n_{i+1,t} - (a_{i-1,i} + a_{i+1,i}) \ n_{i,t} \ .$$

The mean growth rate of individuals belonging to the i-th size-class during the time Δt is

$$(8\text{-}1) \quad h(a_{i+1,i} - a_{i-1,i}) \equiv M_{1,i}.$$

Similarly, the second moment of growth rate during the time Δt is

$$(8\text{-}2) \quad h^2 (a_{i+1,i} + a_{i-1,i}) \equiv M_{2,i}$$

and so on.

Since the variables $n_{k,t}$ are independent of the elements of the matrix, we assume that the coefficients of $n_{k,t}$ (k=1,...,s) in Eq. (7) are the linear combination of the moments of growth of individuals with size-class k ($M_{1,k}$ and $M_{2,k}$), i. e.

(9-1) $a_{i,i-1} = x_{1,i-1}M_{1,i-1} + x_{2,i-1}M_{2,i-1}$

(9-2) $-a_{i-1,i} - a_{i+1,i} = x_{1,i}M_{1,i} + x_{2,i}M_{2,i}$

(9-3) $a_{i,i+1} = x_{1,i+1}M_{1,i+1} + x_{2,i+1}M_{2,i+1}$,

where x_{ij} represents the coefficient of M_{ij}. To satisfy Eq.(9) for arbitrary a_{ij}.

$$(10)\quad \begin{bmatrix} x_{1,i-1} & x_{2,i-1} \\ x_{1,i} & x_{2,i} \\ x_{1,i+1} & x_{2,i+1} \end{bmatrix} \begin{bmatrix} -h & h \\ (-h)^2 & h^2 \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ -1 & -1 \\ 1 & 0 \end{bmatrix}$$

or

$$(11)\quad \begin{bmatrix} x_{1,i-1} & x_{2,i-1} \\ x_{1,i} & x_{2,i} \\ x_{1,i+1} & x_{2,i+1} \end{bmatrix} = \begin{bmatrix} \frac{1}{2h} & \frac{1}{2h^2} \\ 0 & -\frac{1}{h^2} \\ -\frac{1}{2h} & \frac{1}{2h^2} \end{bmatrix} .$$

Thus, by substituting Eq.(11) into Eq.(9), Eq.(4) can be rewritten as:

$$(12)\quad \frac{n_{i,t+\Delta t} - n_{i,t}}{\Delta t} = -\frac{M_{1,i+1}n_{i+1,t} - M_{1,i-1}n_{i-1,t}}{2h} + \frac{1}{2}\frac{M_{2,i+1}n_{i+1,t} - 2M_{2,i}n_{i,t} + M_{2,i-1}n_{i-1,t}}{h^2} \quad (i=1,....,s).$$

Eq. (12) is a discrete form of the diffusion equation, i. e.

$$(13)\quad \frac{\partial n(x,t)}{\partial t} = -\frac{\partial(M_1(x)\, n(x,t))}{\partial x} + \frac{1}{2}\frac{\partial^2(M_2(x)\, n(x,t))}{\partial x^2} .$$

Letting Δt and $h \to 0$, Eq. (12) becomes Eq. (13). This result corresponds to the derivation of diffusion equation by Goel and Richter-Dyn (1974).

The relationship between the Lefkovitch matrix model and the Kramers-Moyal expansion.

We secondly define the two-step Lefkovitch matrix, which describes the one- and two-step transitions from the starting size-class, i. e.

$$(14)\qquad \begin{cases} a_{ij} = 0 & \text{for } |i-j| > 2 \\ a_{ij} > 0 & \text{otherwise,} \end{cases}$$

$$A_2 = \begin{bmatrix} \ddots & a_{i-4,i-2} & 0 & \vdots & \vdots & \vdots & \vdots \\ \ddots & a_{i-3,i-2} & a_{i-3,i-1} & 0 & \vdots & \vdots & \vdots \\ \ddots & a_{i-2,i-2} & a_{i-2,i-1} & a_{i-2,i} & 0 & \vdots & \vdots \\ \ddots & a_{i-1,i-2} & a_{i-1,i-1} & a_{i-1,i} & a_{i-1,i+1} & 0 & \vdots \\ 0 & a_{i,i-2} & a_{i,i-1} & a_{ii} & a_{i,i+1} & a_{i,i+2} & 0 \\ \vdots & 0 & a_{i+1,i-1} & a_{i+1,i} & a_{i+1,i+1} & a_{i+1,i+2} & \ddots \\ \vdots & \vdots & 0 & a_{i+2,i} & a_{i+2,i+1} & a_{i+2,i+2} & \ddots \\ \vdots & \vdots & \vdots & 0 & a_{i+3,i+1} & a_{i+3,i+2} & \ddots \\ \vdots & \vdots & \vdots & \vdots & 0 & a_{i+4,i+2} & \ddots \end{bmatrix}.$$

Thus the right-hand side of Eq. (4) can be written as:

$$(15)\qquad a_{i,i-2}n_{i-2,t} + a_{i,i-1}n_{i-1,t} + a_{i,i+1}n_{i+1,t} + a_{i,i+2}n_{i+2,t} - (a_{i-2,i} + a_{i-1,i} + a_{i+1,i} + a_{i+2,i})\, n_{i,t}\ .$$

The first to 4-th moment of growth rate of individuals belonging to the i-th size-class during the time Δt is as: .

$$(16\text{-}1)\qquad h(\,2a_{i+2,i} + a_{i+1,i} - a_{i-1,i} - 2a_{i-2,i}) \equiv M_{1,i}$$

$$(16\text{-}2)\qquad h^2\,(\,4a_{i+2,i} + a_{i+1,i} + a_{i-1,i} + 4a_{i-2,i}) \equiv M_{2,i}$$

$$(16\text{-}3)\qquad h^3\,(\,8a_{i+2,i} + a_{i+1,i} - a_{i-1,i} - 8a_{i-2,i}) \equiv M_{3,i}$$

$$(16\text{-}4)\qquad h^4\,(\,16a_{i+2,i} + a_{i+1,i} + a_{i-1,i} + 16a_{i-2,i}) \equiv M_{4,i}\ .$$

We assume that the coefficients of $n_{k,t}$ $(k=1,...,s)$ in Eq. (15) are the linear combination of the moments of growth of individuals with size-class k ($M_{1,k}$, $M_{2,k}$, $M_{3,k}$ and $M_{4,k}$) similarly as in the previous section. The coefficients x_{ij} can be solved as

$$(17)\quad \begin{bmatrix} x_{1,i-2} & x_{2,i-2} & x_{3,i-2} & x_{4,i-2} \\ x_{1,i-1} & x_{2,i-1} & x_{3,i-1} & x_{4,i-1} \\ x_{1,i} & x_{2,i} & x_{3,i} & x_{4,i} \\ x_{1,i+1} & x_{2,i+1} & x_{3,i+1} & x_{4,i+1} \\ x_{1,i+2} & x_{2,i+2} & x_{3,i+2} & x_{4,i+2} \end{bmatrix} = \begin{bmatrix} \frac{-1}{12h} & \frac{-1}{24h^2} & \frac{1}{12h^3} & \frac{1}{24h^4} \\ \frac{2}{3h} & \frac{2}{3h^2} & \frac{-1}{6h^3} & \frac{-1}{6h^4} \\ 0 & \frac{-5}{4h^2} & 0 & \frac{1}{4h^4} \\ \frac{-2}{3h} & \frac{2}{3h^2} & \frac{1}{6h^3} & \frac{-1}{6h^4} \\ \frac{1}{12h} & \frac{-1}{24h^2} & \frac{-1}{12h^3} & \frac{1}{24h^4} \end{bmatrix}.$$

Thus, using Eq.(17), Eq.(4) can be rewritten as:

$$(18)\quad \frac{n_{i,t+\Delta t} - n_{i,t}}{\Delta t} = -\left\{\frac{4}{3}\frac{M_{1,i+1}n_{i+1,t} - M_{1,i-1}n_{i-1,t}}{2h} - \frac{1}{3}\frac{M_{1,i+2}n_{i+2,t} - M_{1,i-2}n_{i-2,t}}{4h}\right\}$$

$$+\frac{1}{2!}\left\{\frac{4}{3}\frac{M_{2,i+1}n_{i+1,t} - 2M_{2,i}n_{i,t} + M_{2,i-1}n_{i-1,t}}{h^2} - \frac{1}{3}\frac{M_{2,i+2}n_{i+2,t} - 2M_{2,i}n_{i,t} + M_{2,i-2}n_{i-2,t}}{(2h)^2}\right\}$$

$$-\frac{1}{3!}\left\{\begin{array}{l} \frac{1}{2}\frac{M_{3,i+2}n_{i+2,t} - 3M_{3,i+1}n_{i+1,t} + 3M_{3i}n_{it} - M_{3,i-1}n_{i-1,t}}{h^3} \\ +\frac{1}{2}\frac{M_{3,i+1}n_{i+1,t} - 3M_{3i}n_{it} + 3M_{3,i-1}n_{i-1,t} - M_{3,i-2}n_{i-2,t}}{h^3} \end{array}\right\}$$

$$+\frac{1}{4!}\left\{\frac{M_{4,i+2}n_{i+2,t} - 4M_{4,i+1}n_{i+1,t} + 6M_{4,i}n_{i,t} - 4M_{4,i-1}n_{i-1,t} + M_{4,i-2}n_{i-2,t}}{h^4}\right\}.$$

Eq. (18) is a discrete form of 4-th order Kramers-Moyal expansion of the diffusion equation (Kramers 1940, Moyal 1949, Gardiner 1990), i. e.

$$(19)\quad \frac{\partial n(x,t)}{\partial t} = -\frac{\partial(M_1(x)\,n(x,t))}{\partial x} + \frac{1}{2!}\frac{\partial^2(M_2(x)\,n(x,t))}{\partial x^2} - \frac{1}{3!}\frac{\partial^3(M_3(x)\,n(x,t))}{\partial x^3} + \frac{1}{4!}\frac{\partial^4(M_4(x)\,n(x,t))}{\partial x^4}$$

Letting Δt and $h \to 0$, Eq. (18) becomes Eq. (19). Thus the dynamics of the two-step Lefkovitch matrix model can be rewritten to the discrete form 4-th order Kramers-Moyal expansion in terms of the linear combination of the 1st to the 4-th moment.

Similarly, we can define the three-step Lefkovitch matrix, obtain the coefficient matrix of linear combination, $\mathbf{X} = \{x_{ij}\}$, and then derive a discrete form of the 6-th order Kramers-Moyal expansion (See Appendix). Thus, generally speaking, the dynamics of the n-step Lefkovitch matrix model is expected to correspond to the discrete form of 2n-th order expansion.

Discussion

(I) The Lefkovitch matrix obtained from field data and the diffusion equation model.

To obtain a Lefkovitch matrix from field data, we first determine the intervals between successive censuses (Δt) and size classes (h) (Caswell 1989). Therefore, values of the elements of the Lefkovitch matrix depend on both intervals. Moreover, the type of the Lefkovitch matrix (one-step or multi-step) depends on both the ratio of h to Δt and the distribution function of growth rate of plants (g(v), where v represents growth rate). For example (Fig. 1-a), if we choose a larger $\frac{h}{\Delta t}$ than the maximum of the absolute value of growth rate, the Lefkovitch matrix becomes a one-step type. Therefore, even if Δt is large, it also becomes a one-step type for sufficiently large h since the size increment during Δt does not exceed h. According to our analysis, the dynamics of the one-step matrix model can be perfectly described by the first ($M_1(x)$) and the second moments ($M_2(x)$) of growth rate, and corresponds to a discrete form of the diffusion equation. Even if the third moment of growth rate ($M_3(x)$) is non-zero, it does not affect the dynamics of the Lefkovitch matrix model.

If $\frac{h}{\Delta t}$ is relatively small compared to the maximum of the absolute value of growth rate (Fig. 1-b, c), the Lefkovitch matrix becomes a multi-step type. Therefore, the ratio of max $|v|$ to $\frac{h}{\Delta t}$ determines the number of steps of the Lefkovitch matrix. Then the matrix model includes the higher-order moments ($M_3(x)$, $M_4(x)$, ...) and is a discrete form of the higher-order Kramers-Moyal expansion. Therefore, the indeterminacy in plant growth is likely to lead to a multi-step matrix. However, the indeterminacy does not always lead to a multi-step one. If $\frac{h}{\Delta t}$ is relatively large, the Lefkovitch matrix is a one-step matrix (Fig. 1-a).

In most of growth analyses of annual plants, Δt is small because measurements of plants' size are usually conducted several times during a growing season, and h is also relatively small compared to the fast growth of annual plants. Therefore, $\frac{h}{\Delta t}$ is not so small and their Lefkovitch matrix is usually a one- or two-step type. In woody plants, censuses are usually conducted every several years, and hence Δt is comparatively large. However, their sizes are also large and are usually divided into several size classes with wide intervals. Therefore, their Lefkovitch matrix is likely to be a one- or two-step types (Hartshorn 1975; Harcombe 1986, 1987; Nakashizuka 1991). That is the reason why the diffusion equation model has often been employed for the analysis of growth in annual plants and trees, and why the model has fitted field data of them well (e. g. Hara1984a, b, 1985, 1986b; Petersen 1988; Kohyama 1987, 1989; Kohyama and Hara 1989; West et al. 1989; Petersen et al. 1990; Hara et al. 1991).

On the contrary, perennial herbs differ from these two types of plants. While the interval between censuses is usually one year in perennial herbs, the change in their size is unexpectedly large, compared to their small size (Kawano et al. 1987), because in many cases the above-ground organs wither every winter and new above-ground organs emerge every spring. For example, a drastic decrease in size may be found next year after they have produced many seeds ('storage/reproduction trade-off'). Therefore, their Lefkovitch matrix is often a multi-step type and the higher-order moments of growth rate are needed to describe the growth and size-structure dynamics of perennial herbs when we employ the diffusion equation model.

(II) Mortality rate, recruitment rate and time-dependent moments of growth rate

For simplicity, we have dealt with the populations without mortality and assumed that the elements of the Lefkovitch matrix are constant irrespective of time. However, the mortality rate at each size-class is usually not zero and changes temporally, and elements of the Lefkovitch matrix also change during a growing season or year by year. Even if the mortality rate at each size-class is not equal to zero and the matrix elements depend on time t, the same conclusion can be obtained as before. Assuming the mortality rate per unit time at size-class i at time t and the time-dependent matrix elements, $D_{i,t}$ and $a_{ij,t}$, respectively, we obtain

$$(20) \qquad D_{i,t}\Delta t = 1 - \sum_{k=1}^{s} a_{ki,t}\Delta t \quad (i=1,\ldots.,s)$$

instead of Eq. (3). Thus, Eq. (4) can be rewritten as

$$(21) \qquad \frac{n_{i,t+\Delta t} - n_{i,t}}{\Delta t} = \sum_{j\neq i}^{s} a_{ij,t}n_{j,t} - (\sum_{k\neq i}^{s} a_{ki,t})n_{i,t} - D_{i,t}n_{i,t} \qquad (i=1,\ldots.,s).$$

If we assume that the first two terms of the right-hand side of Eq. (21) can be given as the linear combination of the moments of growth rate, we can obtain the same result. Therefore, Eq. (21) can be rewritten to a discrete form of

$$(22) \qquad \frac{\partial f(t,x)}{\partial t} = \sum_k \frac{(-1)^k}{k!} \frac{\partial^k (M_k(t,x) f(t,x))}{\partial x^k} - D(t,x) \ .$$

with the time-dependent mortality rate (D(t,x)) and the time-dependent moments of growth rate ($M_k(t,x)$; k=1, 2, ...).

Acknowledgement We would like to express our sincere thanks to Dr. Shin-ichi Yamamoto, Dr. Takashi Kohyama and Dr. Tohru Nakashizuka for valuable discussion and helpful advice. This study was partly supported by grants from the Ministry of Education, Science and Culture, Japan (No. 03304003 and No. 04640613).

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Appendix

We define the three-step Lefkovitch matrix as

$$\text{(A1)}\qquad \begin{cases} a_{ij} = 0 & \text{for } | i-j | > 3 \\ a_{ij} > 0 & \text{otherwise.} \end{cases}$$

Similarly as in Appendix A and B, the coefficients of linear combination of the first to 6th moments (x_{ij}) satisfy the following equation:

$$\text{(A2)}\quad \begin{bmatrix} x_{1,i-3} & x_{2,i-3} & x_{3,i-3} & x_{4,i-3} & x_{5,i-3} & x_{6,i-3} \\ x_{1,i-2} & x_{2,i-2} & x_{3,i-2} & x_{4,i-2} & x_{5,i-2} & x_{6,i-2} \\ x_{1,i-1} & x_{2,i-1} & x_{3,i-1} & x_{4,i-1} & x_{5,i-1} & x_{6,i-1} \\ x_{1,i} & x_{2,i} & x_{3,i} & x_{4,i} & x_{5,i} & x_{6,i} \\ x_{1,i+1} & x_{2,i+1} & x_{3,i+1} & x_{4,i+1} & x_{5,i+1} & x_{6,i+1} \\ x_{1,i+2} & x_{2,i+2} & x_{3,i+2} & x_{4,i+2} & x_{5,i+2} & x_{6,i+2} \\ x_{1,i+3} & x_{2,i+3} & x_{3,i+3} & x_{4,i+3} & x_{5,i+3} & x_{6,i+3} \end{bmatrix} \begin{bmatrix} -3h & -2h & -h & h & 2h & 3h \\ (-3h)^2 & (-2h)^2 & (-h)^2 & h^2 & (2h)^2 & (3h)^2 \\ (-3h)^3 & (-2h)^3 & (-h)^3 & h^3 & (2h)^3 & (3h)^3 \\ (-3h)^4 & (-2h)^4 & (-h)^4 & h^4 & (2h)^4 & (3h)^4 \\ (-3h)^5 & (-2h)^5 & (-h)^5 & h^5 & (2h)^5 & (3h)^5 \\ (-3h)^6 & (-2h)^6 & (-h)^6 & h^6 & (2h)^6 & (3h)^6 \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ -1 & -1 & -1 & -1 & -1 & -1 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

or

$$\text{(A3)}\quad \begin{bmatrix} x_{1,i-3} & x_{2,i-3} & x_{3,i-3} & x_{4,i-3} & x_{5,i-3} & x_{6,i-3} \\ x_{1,i-2} & x_{2,i-2} & x_{3,i-2} & x_{4,i-2} & x_{5,i-2} & x_{6,i-2} \\ x_{1,i-1} & x_{2,i-1} & x_{3,i-1} & x_{4,i-1} & x_{5,i-1} & x_{6,i-1} \\ x_{1,i} & x_{2,i} & x_{3,i} & x_{4,i} & x_{5,i} & x_{6,i} \\ x_{1,i+1} & x_{2,i+1} & x_{3,i+1} & x_{4,i+1} & x_{5,i+1} & x_{6,i+1} \\ x_{1,i+2} & x_{2,i+2} & x_{3,i+2} & x_{4,i+2} & x_{5,i+2} & x_{6,i+2} \\ x_{1,i+3} & x_{2,i+3} & x_{3,i+3} & x_{4,i+3} & x_{5,i+3} & x_{6,i+3} \end{bmatrix} = \begin{bmatrix} \frac{1}{60h} & \frac{1}{180h^2} & \frac{-1}{48h^3} & \frac{-1}{144h^4} & \frac{1}{240h^5} & \frac{1}{720h^6} \\ \frac{-3}{20h} & \frac{-3}{40h^2} & \frac{1}{6h^3} & \frac{1}{12h^4} & \frac{-1}{60h^5} & \frac{-1}{120h^6} \\ \frac{3}{4h} & \frac{3}{4h^2} & \frac{-13}{48h^3} & \frac{-13}{48h^4} & \frac{1}{48h^5} & \frac{1}{48h^6} \\ 0 & \frac{-49}{36h^2} & 0 & \frac{7}{18h^4} & 0 & \frac{-1}{36h^6} \\ \frac{-3}{4h} & \frac{3}{4h^2} & \frac{13}{48h^3} & \frac{-13}{48h^4} & \frac{-1}{48h^5} & \frac{1}{48h^6} \\ \frac{3}{20h} & \frac{-3}{40h^2} & \frac{-1}{6h^3} & \frac{1}{12h^4} & \frac{1}{60h^5} & \frac{-1}{120h^6} \\ \frac{-1}{60h} & \frac{1}{180h^2} & \frac{1}{48h^3} & \frac{-1}{144h^4} & \frac{-1}{240h^5} & \frac{1}{720h^6} \end{bmatrix}$$

Thus, using Eq.(A3), Eq.(4) can be rewritten as:

$$\text{(A4)}\quad \frac{n_{i,t+\Delta t} - n_{i,t}}{\Delta t} = -\left\{ \frac{3}{2}\frac{M_{1,i+1}n_{i+1,t} - M_{1,i-1}n_{i-1,t}}{2h} - \frac{3}{5}\frac{M_{1,i+2}n_{i+2,t} - M_{1,i-2}n_{i-2,t}}{4h} + \frac{1}{10}\frac{M_{1,i+3}n_{i+3,t} - M_{1,i-3}n_{i-3,t}}{6h} \right\}$$

$$+ \frac{1}{2!}\left\{ \frac{3}{2}\frac{M_{2,i+1}n_{i+1,t} - 2M_{2,i}n_{i,t} + M_{2,i-1}n_{i-1,t}}{h^2} - \frac{3}{5}\frac{M_{2,i+2}n_{i+2,t} - 2M_{2,i}n_{i,t} + M_{2,i-2}n_{i-2,t}}{(2h)^2} + \frac{1}{10}\frac{M_{2,i+3}n_{i+3,t} - 2M_{2,i}n_{i,t} + M_{2,i-3}n_{i-3,t}}{(3h)^2} \right\}$$

$$-\frac{1}{3!}\left\{\frac{M_{3,i+2}n_{i+2,t}-3M_{3,i+1}n_{i+1,t}+3M_{3,i}n_{i,t}-M_{3,i-1}n_{i-1,t}}{h^3}+\frac{M_{3,i+1}n_{i+1,t}-3M_{3,i}n_{i,t}+3M_{3,i-1}n_{i-1,t}-M_{3,i-2}n_{i-2,t}}{h^3}\right.$$
$$\left.-\frac{M_{3,i+3}n_{i+3,t}-3M_{3,i+1}n_{i+1,t}+3M_{3,i-1}n_{i-1,t}-M_{3,i-3}n_{i-3,t}}{(2h)^3}\right\}$$

$$+\frac{1}{4!}\left\{-\frac{1}{6}\frac{M_{4,i+3}n_{i+3,t}-4M_{4,i+2}n_{i+2,t}+6M_{4,i+1}n_{i+1,t}-4M_{4,i}n_{i,t}+M_{4,i-1}n_{i-1,t}}{h^4}\right.$$
$$+\frac{4}{3}\frac{M_{4,i+2}n_{i+2,t}-4M_{4,i+1}n_{i+1,t}+6M_{4,i}n_{i,t}-4M_{4,i-1}n_{i-1,t}+M_{4,i-2}n_{i-2,t}}{h^4}$$
$$\left.-\frac{1}{6}\frac{M_{4,i+1}n_{i+1,t}-4M_{4,i}n_{i,t}+6M_{4,i-1}n_{i-1,t}-4M_{4,i-2}n_{i-2,t}+M_{4,i-3}n_{i-3,t}}{h^4}\right\}.$$

Eq. (A4) is a discrete form of 6-th order Kramers-Moyal expansion of the diffusion equation, i. e.

$$\text{(A5)}\qquad \frac{\partial n(x,t)}{\partial t}=\sum_{k=1}^{6}\frac{(-1)^k}{k!}\frac{\partial^k(M_k(x)\,n(x,t))}{\partial x^k}\;.$$

Thus the dynamics of the three-step Lefkovitch matrix model can be rewritten to the discrete form 6-th order Kramers-Moyal expansion in terms of the linear combination of the 1st to the 6-th moment.

Fig. 1

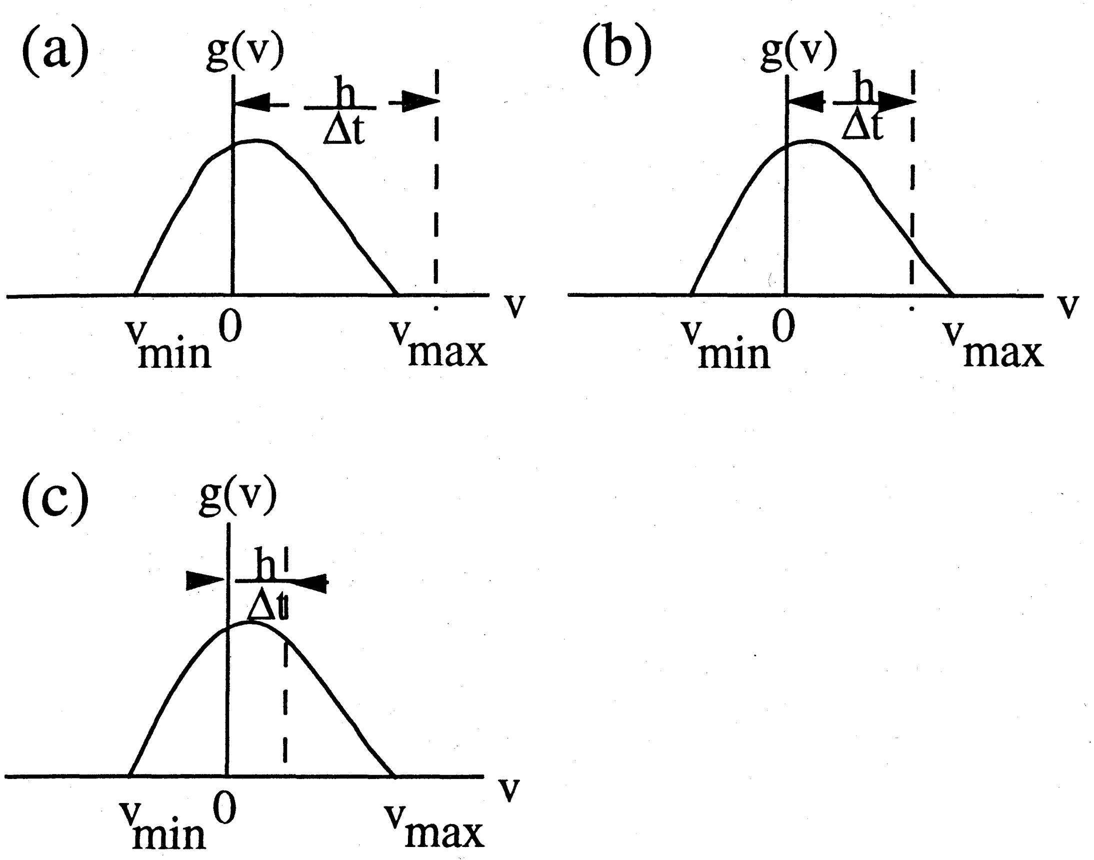

Fig. 1 The relationship between the Lefkovitch matrix and the intervals of time (Δt) and size (h). v, g(v) and n represent the growth rate, the distribution function of v and the number of steps during Δt, respectively. (a) for one-step Lefkovitch matrix; (b) for two-step matrix; (c) for three-step matrix See text for detailed discussion.