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Mathematical Modelling of Metapopulation Dynamics: Revisiting its Meaning

H. Seno *

Research Center for Pure and Applied Mathematics, Department of Computer and Mathematical Sciences, Graduate School of Information Sciences, Tohoku University, Japan

Abstract. In this paper, we revisit the metapopulation dynamics model of typical Levins type, and reconsider its mathematical modeling. For the metapopulation dynamics with three states for the patch of a habitat composed of a number patches available for the reproduction, 'vacant', 'small' (i.e., threatened to the extinction) and 'large' (i.e., far from the extinction risk) in terms of population size in the patch, we reconstruct the mathematical model in a general form, making use of the difference in time scale between the state transition and the dispersal of individuals within the patchy habitat. The typical Levins type of metapopulation dynamics model appears only for a specific case with some additional assumptions for mathematical simplification. Especially we discuss the rationality of mass-action terms for the patch state transition in the Levins model, and find that such mass-action term could be rational for the modeling of metapopulation dynamics only in some ideal condition.

Keywords and phrases: metapopulation dynamics, mathematical modeling, quasi-stationary state approximation

Mathematics Subject Classification: 97M60, 93A30, 92D25, 92D40, 92B99

1. Introduction

Hanski [9] presented the following 3-state metapopulation dynamics model (see also [10] and [11, p. 61]):

$$\begin{aligned}\frac{dE}{dt} &= e_{\mathrm{S}}S - cLE\\ \frac{dS}{dt} &= cLE + e_{\mathrm{L}}L - e_{\mathrm{S}}S - rS - mLS\\ \frac{dL}{dt} &= rS + mLS - e_{\mathrm{L}}L,\end{aligned} \tag{1.1}$$

where in a patchy habitat E, S and L are the frequency of patches which have the state 'vacant', 'small', and 'large'. They satisfy the condition that $E + S + L = 1$ independently of time. They may be mathematically regarded as the probability of the existence of patches with the state 'vacant', 'small' and 'large', respectively. In this model, the patch state is categorized into three types, 'vacant', 'small', and

*Corresponding author. E-mail: `seno math.is.tohoku.ac.jp`

'large': The 'vacant' patch has no resident of the population inhabiting in the habitat after the extinction of previous resident subpopulation or before the settlement of some immigrants. The 'small' patch has a small size of its subpopulation as the resident which is likely to be endangered to its extinction, while the 'large' patch has an established size of its subpopulation so as not to be endangered from any stochastic ecological disturbance.

The mathematical model (1.1) gives the temporal variation of patch frequencies of these three states, E, S and L. It includes the temporal transition of patch state due to the migration of individuals between patches, which is introduced by the terms of production of E and L, and that of L and S, what is frequently called the 'mass-action' term.

Parameter c means the coefficient for the appearance of small population in a patch which was previously vacant and accepted the successful settlement of some immigrants from the 'large' patches. The effect of immigrants from the 'small' patches is ignored. Parameter e_{S} means the coefficient for the occurrence of transition from the state 'small' to 'vacant' which is due to the extinction of small population in the 'small' patch. Parameter r means the coefficient for the occurrence of transition from the state 'small' to 'large' which is owing to the population growth by reproduction in the 'small' patch. In contrast, the parameter e_{L} means the coefficient for the occurrence of transition from the state 'large' to 'small' due to a certain cause, for example, a predation effect. Parameter m the coefficient reflecting the contribution of immigration to the 'small' patch for the transition from the state 'small' to 'large'. In [11], it is mentioned that the term with the parameter m is important for the dynamics of 3-state model (1.1), which is sometimes called "rescue effect" for extinction-endangered small population [2, 5].

In a patchy habitat, there is no direct interaction between patches. In other words, the state of a patch cannot be affected by the state of any other patch itself. However, as seen in the model (1.1), the transition of patch state depends on an indirect interaction of them when different states coexist in the patchy habitat. Such indirect interaction is caused by migration of individuals inhabiting in it [12].

Mathematical model (1.1) introduces the contribution of patch state distribution with different states to the state transition of each patch by the mass-action terms with the production of frequencies L and E, and with that of L and S. Originally in the application of such a mass-action terms for the population dynamics by Lotka and Volterra [20, 21, 27], it was an analogy from the reaction velocity theory for a simple chemical reaction under the complete mixing. So from the viewpoint of the reasonability of mathematical modeling, we should reconsider and understand its application for the metapopulation dynamics model such as (1.1) about the patch state transition without any direct interaction.

The 3-state model (1.1) is originated from the following 2-state model by Levins [17, 18]:

$$\begin{aligned}\frac{dE}{dt} &= e_{\mathrm{P}}P - cPE\\ \frac{dP}{dt} &= cPE - e_{\mathrm{P}}P.\end{aligned} \tag{1.2}$$

In a patchy habitat, E and P mean the frequency (or the probability of existence) of patches with 'vacant' state and that with 'occupied' state, respectively. Since E and P satisfy the condition that $E + P = 1$ independently of time, this model can be described in a mathematically equivalent form by the following single ordinary differential equation as known well:

$$\frac{dP}{dt} = cP(1-P) - e_{\mathrm{P}}P. \tag{1.3}$$

The parameter e_{P} means the coefficient for the occurrence of transition from the state 'occupied' to 'vacant' which is due to the extinction of population in the 'occupied' patch, and c means the coefficient for the transition of vacant patch to the 'occupied' state due to the successful settlement of some immigrants from the 'occupied' patches.

Interesting and valued point of mathematical modeling by Levins [17, 18] is its treatment of dynamics in terms of 'state' transition of each patch without considering the temporal variation of population size itself in each patch [12]. However, the frequency of migration, that is, the strength of migration effect on the state transition is significant in the modeling since it takes the effect of immigrants into account for the cause of state transition, The strength of migration effect necessarily depends on the size of migrating population. Therefore it requires a rational combination of patch states and population size for the modeling by the idea of Levins [17, 18] to aggregate the population dynamics in a patchy habitat into a dynamics of patch state transition.

Etienne [5] particularly considered this problem about the mathematical modeling, and tried to understand the meaning of 2-state metapopulation model (1.2) by Levins [17, 18], making use of modelings with the mean value dynamics from a stochastic process, and with a singular perturbation owing to the difference in time scales of involved biological processes as we will use in this paper. However, he put the mass-action terms as the precondition for modeling, and gave no discussion about its rationality from the viewpoint of modeling. As for the 3-state model (1.1), we are not aware of any discussion about the rationality of mathematical structure from the viewpoint of modeling.

In this paper, we will discuss a mathematical modeling, focusing on how the strength of migration could be involved in it to construct a metapopulation dynamics model, with the same idea with Levins'. The similar problem has been discussed in previous papers other than [5], for instance, by [6–8, 13]. We will independently consider the mathematical modeling of Levins' idea, focusing at first on the 3-state model (1.1), and try to discuss the problem about the rationality of its modeling typical with the mass-action terms. To consider the modeling of 3-state model (1.1) before the original 2-state model (1.1) is useful to make clear the issues important to discuss the rationality of modeling.

2. Reconsideration of mathematical modeling for metapopulation dynamics

2.1. State transition of patch

In model (1.1), the intermediate state 'small' (S) between 'vacant' (E) and 'large' (L) indicates the patch endangered to the extinction of its population. In a sense, we may regard it as corresponding to the introduction of Allee effect into the model. Indeed, as for the patch of state 'large', such possibility of the extinction is not assumed, so that the patch of state 'large' can be regarded as a patch with sufficiently established population.

Next let us consider the cause for the transition from 'large' to 'small' state, involved by the term with $e_{\mathrm{L}}L$ in the model (1.1). It is easy to consider the stochastic environmental disturbance for it. Stochastic variation in climate and/or uncertain effect by some human activity for the ecosystem are examples to cause it. So we could regard the parameter e_{L} in (1.1) as to be increasing in terms of the magnitude or the frequency (strength) of such stochastic factor.

In the similar way, we could consider that the transition from 'small' to 'vacant' state in (1.1) depends on the stochastic environmental variation by some natural/human factors. Besides, as for the transition from 'small' to 'vacant' state, the demographic stochasticity in the reproduction rate is an important factor. Parameter e_{S} could be regarded as to be incresing in terms of the magnitude or the frequency (strength) of such stochastic factor.

In contrast, as for the transition from 'small' to 'large' state, it is essentially due to the growth of population size, that is, by the reproduction. Immigrants from 'large' patches to 'small' patch cannot be the cause of state transition by themselves, but may contribute to the reproduction in the population of 'small' patch, which is introduced by the term mLS in the model (1.1). It is hard to regard the migration itself as the variation of population size enough to cause the state transition. Thus, as for the term mLS of (1.1) to introduce the effect of immigrants, we should reconsider the meaning with a certain rationality in the mathematical modeling.

In the same reason, the term cLE for the state transition from 'vacant' to 'small' state needs the reconsideration about its mathematical modeling. As for the transition from 'vacant' to 'small' state, it is only due to the immigrants' settlement and growth. So we should reconsider the mathematical modeling about how the effect of such factors contributes to the state transition.

2.2. Assumptions for dispersal in the patchy habitat

First we consider the mathematical modeling for the emigration from 'large' and 'small' patches. Assume that the emigrating population size per unit time (i.e., emigration velocity) is increasing in terms of the size of population from which the emigrant comes out. Hence, the emigration velocity is assumed greater from the 'large' patch than from the 'small' one. This assumption does not necessarily that of Fick's law frequently referred in the theory of diffusion process, because we do not assume the flux proportional to the difference between the densities of different patches. The diffusion with Fick's law is included as a specific case.

Next as for the success of immigration and settlement, we assume that it is less likely for the 'large' patch than for the 'small' or the 'vacant' patch. This is because the larger population would have a stronger pressure of emigration to individuals within it so that the immigration is less acceptable by such larger population. The model (1.1) does not include the effect of immigration to the 'large' patch on the state transition, as it could be reasonable to be negligible. However, when the state transition from 'small' to 'large' is assumed to depend on the immigration and the settlement of disperser population, it would be natural to have also the assumption that the immigration and the settlement of disperser population to the 'large' patch makes the transition probability from the 'large' to the 'small' state smaller.

2.3. Dynamics of dispersal depending on patch states

Let D be the mean density of disperser population over the patchy habitat. Here we shall give the dynamics of temporal variation of D with the following one of the simplest mathematical models:

$$\frac{dD}{dt} = m_{\mathrm{L}}LN + m_{\mathrm{S}}SN - \kappa_{\mathrm{L}}LND - \kappa_{\mathrm{S}}SND - \kappa_{\mathrm{E}}END - qND, \tag{2.1}$$

where m_{L}, m_{S}, κ_{L}, κ_{S}, κ_{E}, N, and q are positive constants. Now some parameters are introduced. N means a representative number of patches with respect to the dispersal, as [5] did, for example. κ_{L}, κ_{S}, and κ_{E} are the state-dependent coefficients of successful immigration and settlement in 'large', 'small', and 'vacant' patches, respectively. We give the detail of their meanings later in this section.

Terms LN, SN and EN correspond to the representative number of 'large' patches, that of 'small' ones, and that of 'vacant' ones, respectively. Parameters m_{L} and m_{S} are the emigration velocity per patch from 'large' patch, and that from 'small' patch. Parameters κ_{L}, κ_{S}, and κ_{E} are the per capita rate of successful immigration and settlement of the dispersing individual into the 'large' patch, the 'small' one, and the 'vacant' one, respectively. Parameter qN means the per capita death rate for the dispersing individual, which depends on the representative number of patches N (its meaning is given later).

Dispersal and the parameter N

It has been frequently mentioned for the metapopulation dynamics model of Levins type including (1.1) and (1.2) that the number of patches in the whole habitat is mathematically assumed to be infinite [4, 5, 7, 14, 15]. This is a translation for the mathematical treatment of the model: The infinite number of patches could be regarded as an *approximation* in order to make the model mathematically simpler and more tractable. Our introduction of the parameter N may be controversial from such a mathematical point of modeling. We could give the meaning about the introduction of the parameter N as follows from a rationality of mathematical modeling: Parameter N corresponds to the expected number of patches in the representative range of dispersal (to be defined as the home range in a certain case), which could be regarded as the metapopulation scale in space, being mentioned in [12]. It is now assumed to be sufficiently large. So applying the mean field approximation for the spatial distribution of patch states within the whole habitat (the geographical scale in [12]), we could regard the distribution of patch states within the representative range as approximately equivalent to that in the whole habitat.

From this meaning of mathematical modeling, the parameter N has a significant relation to the dispersibility/mobility of individual in the considered population. As the dispersibility/mobility of individual is stronger, the representative range of dispersal tends to get wider, so that the number of involved patches N subsequently gets larger.

Next, along this modeling, we consider the probability that the dispersing individual encounters a patch in sufficiently short period Δt. We assume that the probability can be approximated to be proportional to $N\Delta t$: As the dispersibility/mobility of dispersing individual is stronger, that is, as the representative number of patches is larger, the dispersing individual is more likely to encounter a patch. When the dispersing individual encounters a patch, the probability that the encountered patch is vacant is assumed to be given by E, making use of the mean field approximation. Similarly, the probability that it is a 'small' patch is S, and that it is a 'large' patch is L. The success of the immigration and the settlement of migrants in the encountered patch would significantly depend on its state. So we let in general κ_{L}, κ_{S}, and κ_{E} be the state-dependent coefficients of successful immigration and settlement in 'large', 'small', and 'vacant' patches, respectively.

Per capita death rate qN for dispersing individual

Following the meaning of parameter N described in the previous section, the variable D could be regarded as the population size per representative range of dispersal. The wider range of dispersal is regarded as to correspond to the longer mean period of dispersal or the wider area of dispersal per unit time. Hence it could be supposed that the per capita death rate for the dispersing individual could simultaneously get larger for the wider range of dispersal. From this correlation between the death rate and the dispersal range, we put the per capita death probability $qN\Delta t$ for the dispersing individual in a sufficiently short period Δt for the disperser in the patchy habitat with the representative number of patches N. This modeling follows out the supposition that the per capita death probability per unit time is supposed to be increasing in terms of the dispersibility which is assumed to be increasing in terms of the number of patches N in the range of dispersal.

Parameters m_{L} and m_{S}

We set the mean number of emigrants per 'small' patch $m_{\mathrm{S}}\Delta t$ in a sufficiently short period Δt. Thus the total number of emigrants from 'small' patches within the representative range of dispersal in Δt is given by $NS \cdot m_{\mathrm{S}}\Delta t$. In the same way, the total number of emigrants from 'large' patches within the representative range of dispersal in Δt is given by $NS \cdot m_{\mathrm{L}}\Delta t$. As mentioned before, the emigration is assumed to be likely to occur from the 'large' patch than from the 'small' one. In this reason, we may assume that $m_{\mathrm{S}} \leq m_{\mathrm{L}}$ in general. It would be hard to consider the case that $m_{\mathrm{S}} > m_{\mathrm{L}}$ as the rationality of modeling described above.

We remark that the migration is now assumed not to affect the state of patch from which it occurs. No state transition from 'small' to 'vacant' occurs due to the emigration from the 'small' patch. No state transition from 'small' to 'large' occurs due to the immigration to the 'large' patch. As described in the next section, the time scale of the state transition is assumed to be sufficiently larger than that of the dispersal.

2.4. Time scales for dispersal and state transition

In our modeling, we make use of the difference in the representative time scale of the individual's dispersal and the transition of patch state. In models (1.1) and (1.2), the representative time scale is such that the transition of patch state could be identifiable in it. Further it should be such a time scale that the transition from one state to the other (e.g., 'small' state to 'vacant' state) could be approximated to be observed as a continuous temporal variation. So it must be large enough to make the temporal variation of population size within a patch recognizable as the state transition of the patch.

In contrast, the time scale for the population dispersal is in general much shorter than that for the significant variation of population size. This means that the dynamics of disperser population (2.1) follows a sufficiently small time scale in comparison to the time scale for the state transition of patch. Therefore, the dynamics of disperser population (2.1) can be regarded as the "fast process" by contrast to the dynamics of state transition as the "slow process". We shall now take account of the difference in time scale into our modeling. Some similar assumption about the difference in time scale has been applied for the modeling on the metapopulation dynamics in previous works [5–8, 13].

2.5. Dependence of patch state transition on the dispersal of individuals

From 'vacant' to 'small' state

The individuals' dispersal plays essential role for the patch state transition from 'vacant' to 'small'. Such a state transition requires the immigration of some individuals and their successful settlement with the population growth. We assume that the probability of successful immigration and settlement is increasing in terms of the net immigration rate of dispersing individual: More frequent immigration could make the transition rate from 'vacant' to 'small' larger.

According to the modeling for the dynamics of disperser population (2.1), the mean immigration rate of dispersing individual per 'vacant' patch is given by $\kappa_{\mathrm{E}}END/(EN) = \kappa_{\mathrm{E}}D$. Thus the probability that the patch state transition from 'vacant' to 'small' is now assumed to be increasing in terms of $\kappa_{\mathrm{E}}D$.

From 'small' to 'vacant' state

Immigration of dispersing individuals to a 'small' patch contributes to a small increase of its inhabiting population size, so that it could make the possibility of transition to the 'vacant' state smaller. This can be related to the concept of "rescue effect" mentioned in [2, 5]. We take the rescue effect into accout for our modeling about the patch state transition from 'small' to 'vacant'. Probability of the state transition from 'small' to 'vacant' is now assumed to be decreased by the immigration of dispersing individuals into the 'small' patch. That is, the probability is assumed to be decreasing in terms of the mean immigration rate to the 'small' patch $\kappa_{\mathrm{S}}SND/(SN) = \kappa_{\mathrm{S}}D$.

From 'small' to 'large' state

As for the patch state transition from 'small' to 'large', the contribution of immigration of dispersing individuals could be regarded to be less significant with comparison to the above mentioned transition from 'vacant' to 'small'. The growth of inhabiting population size with the reproduction is essential for the transition from 'small' to 'large'.

Since the immigrating population size is assumed to be subtle, we may ignore the contribution of immigrating population size itself to the transition from 'small' to 'large'. However, the immigration and the settlement of dispersing individuals could certainly promote the reproduction even if it would be subtle. Hence in general we assume here that the immigration and the settlement of dispersing individuals would increase the transition rate from 'small' to 'large': The growth rate of population inhabiting in the 'small' patch is assumed to be increasing in terms of the mean immigration rate per 'small' patch $\kappa_{\mathrm{S}}SND/(SN) = \kappa_{\mathrm{S}}D$.

From 'large' to 'small' state

As mentioned in the previous section, we assume that the immigrating population size in the 'large' patch is subtle, and that the settlement of immigrants is hard because of the large population size of residents. From this argument, it may be assumed that the parameter κ_{L} has a sufficiently small value. On the other hand, it may be reasonable that the immigration and the settlement of dispersing individuals in the 'large' patch is assume to have an effect to reduce the state transition probability from 'large' to 'small'. Even though the effect would be weak, let us assume here that the patch state transition rate from 'large' to 'small' is decreasing in terms of the mean immigration rate per 'large' patch $\kappa_{\mathrm{L}}LND/(LN) = \kappa_{\mathrm{L}}D$.

2.6. Patch state transition under the effect of dispersal as fast process

According to the discussion in the previous sections, we consider the following model for the metapopulation dynamics about the patch state transition:

$$\begin{aligned}
\frac{dE}{dt} &= f_{\mathrm{S}}(\kappa_{\mathrm{S}}D)S - \rho(\kappa_{\mathrm{E}}D)E \\
\frac{dS}{dt} &= \rho(\kappa_{\mathrm{E}}D)E + f_{\mathrm{L}}(\kappa_{\mathrm{L}}D)L - f_{\mathrm{S}}(\kappa_{\mathrm{S}}D)S - g(\kappa_{\mathrm{S}}D)S \\
\frac{dL}{dt} &= g(\kappa_{\mathrm{S}}D)S - f_{\mathrm{L}}(\kappa_{\mathrm{L}}D)L \\
\epsilon\frac{dD}{dt} &= m_{\mathrm{L}}NL + m_{\mathrm{S}}NS - \kappa_{\mathrm{L}}LND - \kappa_{\mathrm{S}}SND - \kappa_{\mathrm{E}}END - qND,
\end{aligned} \tag{2.2}$$

where a positive parameter ϵ has such meaning that the representative time scale for the dispersal is ϵ when that for the patch state transition is unity. Since the dispersal is now assumed to be the "fast" process, we put $\epsilon \ll 1$.

In the above model (2.2), we give the probability of patch state transition from 'vacant' to 'small' with the immigration and the settlement of dispersing individuals by $\rho(\kappa_{\mathrm{E}}D)\Delta t$ for sufficiently short time interval $[t, t+\Delta t]$ in the time scale of patch state transition. Similarly, the probability of patch state transition from 'small' to 'vacant' due to a certain stochastic disturbance in the 'small' patch is given by $f_{\mathrm{S}}(\kappa_{\mathrm{S}}D)\Delta t$, the probability from 'small' to 'large' with the growth of inhabiting population size in the 'small' patch by $g(\kappa_{\mathrm{S}}D)\Delta t$, and the probability from 'large' to 'small' with the decline of inhabiting population size in the 'large' patch by $f_{\mathrm{L}}(\kappa_{\mathrm{L}}D)\Delta t$, respectively for sufficiently short time interval $[t, t+\Delta t]$ in the time scale of patch state transition.

For those coefficients given by $f_{\mathrm{S}}(\,\cdot\,)$, $\rho(\,\cdot\,)$, $f_{\mathrm{L}}(\,\cdot\,)$, and $g(\,\cdot\,)$ in (2.2), according to their positiveness/non-negativeness and the modeling assumptions given in the previous section, the following conditions are assumed to be satisfied as functions of D with constant parameters κ_{E}, κ_{S}, and κ_{L}:

- f_{S} is non-increasing in terms of D, satisfying that $f_{\mathrm{S}}(0) > 0$ and $f_{\mathrm{S}}(x) \geq 0$ for any $x > 0$;
- ρ is monotonically increasing in terms of D with $\rho(0) = 0$;
- f_{L} is non-increasing in terms of D, satisfying that $f_{\mathrm{L}}(0) > 0$ and $f_{\mathrm{L}}(x) \geq 0$ for any $x > 0$;
- g is non-decreasing in terms of D with $g(x) > 0$ for any $x \geq 0$.

2.7. Application of quasi-stationary state approximation

For the "fast" process, the dynamics of disperser population size, we apply here the quasi-stationary state approximation (QSSA), so as to use $\epsilon\, dD/dt \approx 0$, and get from (2.2)

$$D \approx \frac{m_{\mathrm{L}}L + m_{\mathrm{S}}S}{\kappa_{\mathrm{L}}L + \kappa_{\mathrm{S}}S + \kappa_{\mathrm{E}}E + q}. \tag{2.3}$$

It is clear that this QSSA cannot bring any simple mass-action terms for the patch state transition in (2.2) with substituting (2.3) for it, whatever the concrete formulas of f_{S}, ρ, f_{L}, and g are.

About the application of QSSA for the mathematical modeling on biological population dynamics, for example, see [1, 3, 16] (as for further application, we can refer also [22–26]).

3. Models simplified with additional assumptions

3.1. Case with the migration only from the 'large' to the 'vacant' patch

Let us consider the case that the emigration is only from the 'large' patch while the immigration is only to the 'vacant' patch. This corresponds to the case when $m_{\mathrm{S}} = 0$ and $\kappa_{\mathrm{L}} = \kappa_{\mathrm{S}} = 0$ in (2.2). Then the

QSSA (2.3) becomes

$$D \approx \frac{m_{\mathrm{L}} L}{\kappa_{\mathrm{E}} E + q}, \tag{3.1}$$

and the model (2.2) appears as

$$\begin{aligned}
\frac{dE}{dt} &= f_{\mathrm{S}}(0)S - \rho(\kappa_{\mathrm{E}} D)E \\
\frac{dS}{dt} &= \rho(\kappa_{\mathrm{E}} D)E + f_{\mathrm{L}}(0)L - f_{\mathrm{S}}(0)S - g(0)S \\
\frac{dL}{dt} &= g(0)S - f_{\mathrm{L}}(0)L.
\end{aligned} \tag{3.2}$$

This model has only one nonlinear term given by the function ρ while the other terms are linear with non-negative constant coefficients.

Now let us assume a linear function of $\kappa_{\mathrm{E}} D$ for ρ, which satisfies the condition mention before, that is $\rho(x) = a_{\mathrm{ES}} x$ with a positive constant a_{ES}. Then the model (3.2) with the QSSA (3.1) becomes

$$\begin{aligned}
\frac{dE}{dt} &= f_{\mathrm{S}}(0)S - \frac{a_{\mathrm{ES}} m_{\mathrm{L}} L E}{E + q/\kappa_{\mathrm{E}}} \\
\frac{dS}{dt} &= \frac{a_{\mathrm{ES}} m_{\mathrm{L}} L E}{E + q/\kappa_{\mathrm{E}}} + f_{\mathrm{L}}(0)L - f_{\mathrm{S}}(0)S - g(0)S \\
\frac{dL}{dt} &= g(0)S - f_{\mathrm{L}}(0)L
\end{aligned} \tag{3.3}$$

with a Michaelis–Menten type of reaction term for the effect of dispersal. If we ignore the death rate of dispersing individual as a more simplified case, the model (3.3) is of a system of *linear* ordinary differential equations. For this model (3.3), only when $q/\kappa_E \gg 1$, we can find that it approximately corresponds to (1.1) with $m = 0$.

3.2. Case with the immigration-settlement rate independent of patch state

Let us consider the case that no difference in the immigration-settlement rate in terms of the state of destination patch, which is now introduced by putting $\kappa_{\mathrm{L}} = \kappa_{\mathrm{S}} = \kappa_{\mathrm{E}} = \kappa$ for our model (2.2) with the QSSA (2.3). Making use of $E + S + L = 1$, the QSSA (2.3) now appears as a linear combination of L and S:

$$D \approx \frac{m_{\mathrm{L}} L + m_{\mathrm{S}} S}{\kappa + q}. \tag{3.4}$$

Moreover, we apply here an additional assumption that the immigration and the settlement of dispersing individuals in the 'large' and the 'small' patches have negligible effect on their state transition. That is, we assume that $f_{\mathrm{S}}(\kappa_{\mathrm{S}} D) \approx f_{\mathrm{S}}(0)$ and $f_{\mathrm{L}}(\kappa_{\mathrm{L}} D) \approx f_{\mathrm{L}}(0)$. Further, let us assume also that the effect of emigration from the 'small' patch is negligible: $m_{\mathrm{S}} \approx 0$. Then, the QSSA (3.4) becomes a proportional relation between L and D: $D \approx \mu_{\mathrm{L}} L$ with the parameter $\mu_{\mathrm{L}} := m_{\mathrm{L}}/(\kappa + q)$. Thus (2.2) with the QSSA becomes

$$\begin{aligned}
\frac{dE}{dt} &= f_{\mathrm{S}}(0)S - \rho(\kappa \mu_{\mathrm{L}} L)E \\
\frac{dS}{dt} &= \rho(\kappa \mu_{\mathrm{L}} L)E + f_{\mathrm{L}}(0)L - f_{\mathrm{S}}(0)S - g(\kappa \mu_{\mathrm{L}} L)S \\
\frac{dL}{dt} &= g(\kappa \mu_{\mathrm{L}} L)S - f_{\mathrm{L}}(0)L.
\end{aligned} \tag{3.5}$$

Again let us assume a linear function for ρ as the previous case: $\rho(x) = a_{\mathrm{ES}}x$ with a positive constant a_{ES}. If we assume a linear function also for g, that is, $g(x) = r_{\mathrm{S}} + a_{\mathrm{SL}}x$ with positive constants r_{S} and a_{SL}, the model (3.5) becomes

$$\begin{aligned}\frac{dE}{dt} &= f_{\mathrm{S}}(0)S - a_{\mathrm{ES}}\kappa\mu_{\mathrm{L}}LE\\ \frac{dS}{dt} &= a_{\mathrm{ES}}\kappa\mu_{\mathrm{L}}LE + f_{\mathrm{L}}(0)L - f_{\mathrm{S}}(0)S - (r_{\mathrm{S}} + a_{\mathrm{SL}}\kappa\mu_{\mathrm{L}}L)S\\ \frac{dL}{dt} &= (r_{\mathrm{S}} + a_{\mathrm{SL}}\kappa\mu_{\mathrm{L}}L)S - f_{\mathrm{L}}(0)L.\end{aligned} \tag{3.6}$$

As a result, this model (3.6) is mathematically equivalent to (1.1).

4. 2-state model

4.1. Reconsideration of the mathematical modeling

In this section, for the 2-state model (1.2), we apply the modeling of the 3-state model (1.1) reconsidered in the previous section. At first we give the model for the temporal variation of disperser population size as before.

Similarly to (2.1) for the 3-state model, we consider the following simple model for the dynamics of temporal variation of disperser population density D:

$$\frac{dD}{dt} = mNP - \kappa_{\mathrm{P}}PND - \kappa_{\mathrm{E}}END - qND, \tag{4.1}$$

where m, κ_{P}, κ_{E}, N and q are positive constants with their meanings corresponding to those for the 3-state model. Parameter m is the emigration velocity per patch from the 'occupied' patch. Parameter N corresponds to the expected number of patches in the representative range of dispersal, same as before. Parameters $\kappa_{\mathrm{P}}N$ and $\kappa_{\mathrm{E}}N$ are the coefficients of successful immigration and settlement of dispersing individual in the 'occupied' patch and the 'vacant' one, respectively. The per capita death rate for the dispersing individual is given by qN as before.

Next we consider the following model of metapopulation dynamics about the patch state transition with the dynamics of disperser population density (4.1):

$$\begin{aligned}\frac{dE}{dt} &= f_{\mathrm{P}}(\kappa_{\mathrm{P}}D)P - \rho(\kappa_{\mathrm{E}}D)E\\ \frac{dP}{dt} &= \rho(\kappa_{\mathrm{E}}D)E - f_{\mathrm{P}}(\kappa_{\mathrm{P}}D)P\\ \epsilon\frac{dD}{dt} &= mNP - \kappa_{\mathrm{P}}PND - \kappa_{\mathrm{E}}END - qND,\end{aligned} \tag{4.2}$$

where a positive parameter ϵ is the representative time scale for the dispersal when that for the patch state transition is unity. We put $\epsilon \ll 1$ since the dispersal is now assumed to be the "fast" process. For those coefficients given by $f_{\mathrm{P}}(\,\cdot\,)$ and $\rho(\,\cdot\,)$, the following conditions are assumed to be satisfied as functions of D with constant parameters κ_{E} and κ_{P}:

- f_{P} is non-increasing in terms of D, satisfying that $f_{\mathrm{P}}(0) > 0$ and $f_{\mathrm{P}}(x) \geq 0$ for any $x > 0$;
- ρ is monotonically increasing in terms of D with $\rho(0) = 0$.

For the dynamics of disperser population as the "fast" process, we apply the QSSA $\epsilon\, dD/dt \approx 0$, and get from (4.2)

$$D \approx \frac{mP}{\kappa_{\mathrm{P}}P + \kappa_{\mathrm{E}}E + q} = \frac{mP}{\kappa_{\mathrm{P}}P + \kappa_{\mathrm{E}}(1-P) + q}, \tag{4.3}$$

where we make use of $E+P=1$. Substituting (4.3) for (4.2), we can get the following aggregated model of single differential equation:

$$\frac{dP}{dt}=\rho(\frac{\kappa_{\mathrm{E}}mP}{\kappa_{\mathrm{P}}P+\kappa_{\mathrm{E}}(1-P)+q})(1-P)-f_{\mathrm{P}}(\frac{\kappa_{\mathrm{P}}mP}{\kappa_{\mathrm{P}}P+\kappa_{\mathrm{E}}(1-P)+q})P. \tag{4.4}$$

4.2. Case with the immigration only to the 'vacant' patch

We consider here the model (4.4) in the case of $\kappa_{\mathrm{P}}=0$, using a linear function $\rho(x)=a_{\mathrm{EP}}x$ with a positive constant a_{EP}:

$$\frac{dP}{dt}=a_{\mathrm{EP}}m\frac{P(1-P)}{(1-P)+q/\kappa_{\mathrm{E}}}-e_{\mathrm{P}}P. \tag{4.5}$$

It is easily found that the model (4.5) has the similar nature as a dynamical system to that of Levins model (1.3): For Levins model (1.3), if $c\leq e_{\mathrm{P}}$, the population goes extinct since $P\to 0$ as $t\to\infty$ for any positive initial value $P(0)$. If $c>e_{\mathrm{P}}$, it asymptotically approaches the equilibrium with $P=1-e_{\mathrm{P}}/c$ from any positive initial value $P(0)$. On comparison, for the model (4.5), if $a_{\mathrm{EP}}m/(1+q/\kappa_{\mathrm{E}})\leq e_{\mathrm{P}}$, the population goes extinct from any positive initial value $P(0)$. If $a_{\mathrm{EP}}m/(1+q/\kappa_{\mathrm{E}})>e_{\mathrm{P}}$, it asymptotically approaches the equilibrium with

$$P=1-\frac{e_{\mathrm{P}}q/\kappa_{\mathrm{E}}}{a_{\mathrm{EP}}m-e_{\mathrm{P}}}$$

from any positive initial value $P(0)$. We find the threshold m_c for the emigration velocity per patch m with respect to the population persistence:

$$m_c=\frac{e_{\mathrm{P}}}{a_{\mathrm{EP}}}\left(1+\frac{q}{\kappa_{\mathrm{E}}}\right). \tag{4.6}$$

Population can persist if and only if $m>m_c$. The value of threshold m_c is larger as the per capita death rate of dispersing individual gets larger with the greater value of q, or as the immigration-settlement coefficient κ_{E} gets smaller. It is indicated that the satisfactory nature of dispersal is essential for the population persistence in the patchy habitat.

4.3. Case with the immigration-settlement rate independent of patch state

When $\kappa_{\mathrm{P}}=\kappa_{\mathrm{E}}=\kappa$, the QSSA (4.3) becomes

$$D\approx\frac{mP}{\kappa+q}, \tag{4.7}$$

where we used $E+P=1$. Thus D is approximately proportional to P. Then from (4.4), we get the following model:

$$\frac{dP}{dt}=\rho(\mu P)(1-P)-f_{\mathrm{P}}(\mu P)P, \tag{4.8}$$

where $\mu:=m/(\kappa+q)$.

If we assume that ρ is a linear function $\rho(x)=a_{\mathrm{EP}}x$ with a positive constant a_{EP}, and that f_{P} is a positive constant, this model (4.8) becomes mathematically equivalent to Levins model (1.3). The assumption of a positive constant f_{P} means that the immigration and the settlement of dispersing individual in the 'occupied' patch has negligible effect on the patch state transition from 'occupied' to 'vacant'. When the effect is not negligible and is introduced in the model, it is clear that this model (4.8) cannot be mathematically equivalent to Levins model (1.3), since f_{P} must be fundamentally a nonlinear function of D according to the mathematical condition required about it.

As an other example for (4.8), let us make here a simple choice of functions ρ and $f_{\rm P}$ satisfying the mathematical condition required about them: $\rho(x) = a_{\rm EP}x$ with a positive constant $a_{\rm EP}$, and $f_{\rm P}(x) = f_0 \exp[-a_{\rm PE}x]$ with positive constants f_0 and $a_{\rm PE}$. Then we have

$$\frac{dP}{dt} = a_{\rm EP}\mu P(1-P) - f_0 e^{-a_{\rm PE}\mu P} P. \tag{4.9}$$

In model (4.9), we find that it can have a nature different from Levins model (1.3): Bistable case can appear for a certain region of parameters. We can find the following two threshold values for the emigration velocity per patch m:

$$\overline{m}_c = \frac{(\kappa+q)f_0}{a_{\rm EP}}; \quad \underline{m}_c = \frac{(\kappa+q)f_0}{a_{\rm EP}} \cdot \frac{a_{\rm EP}}{a_{\rm PE}f_0}\left(1 - \ln\frac{a_{\rm EP}}{a_{\rm PE}f_0}\right).$$

It is always satisfied that $\overline{m}_c \geq \underline{m}_c$. The lower threshold value $\underline{m}_c$ becomes negative when $a_{\rm EP}/(a_{\rm PE}f_0) > e$. If $m < \underline{m}_c$ or if $\underline{m}_c \leq m \leq \overline{m}_c$ with $a_{\rm EP}/(a_{\rm PE}f_0) \geq 1$, the population goes extinct from any positive initial value $P(0)$. If $m > \overline{m}_c$, from any positive initial value $P(0)$, the population asymptotically approaches the equilibrium with a uniquely determined value of P such that $0 < P < 1$. If $\underline{m}_c < m < \overline{m}_c$ with $a_{\rm EP}/(a_{\rm PE}f_0) < 1$, the bistable situation occurs, which can be regarded as the case that what is called Allee effect is embedded. The population goes extinct if the initial value $P(0)$ is less than a certain positive threshold determined uniquely for each set of parameter values, while from the initial value $P(0)$ beyond the threshold value the population asymptotically approaches the equilibrium with a uniquely determined value of P such that $0 < P < 1$. In this example for (4.8), the occurrence of bistable situation requires a strong nonlinearity of the function $f_{\rm P}$: It is impossible for sufficiently small $a_{\rm PE}$ which is the case to approximate (4.9) to Levins model (1.3).

5. Concluding Remark

In this paper, we reconsidered the mathematical modeling for the metapopulation dynamics, focusing on the rationality of mathematical structure embedded in the constructed model. In Levins model (1.2) [17,18], the mathematically essential structure appears as the mass-action terms which are the same as in Lotka–Volterra type of interacting population dynamics models. Especially we discussed the modeling of 3-state metapopulation dynamics on which Hanski [9] presented a model (1.1) after Levins model (1.2).

In the metapopulation dynamics model, it is important to consider only the patch state transition in a patchy habitat, and try to discuss the persistence and the extinction of population with it. Temporal variation of population size itself is out of focus. Such a sort of mathematical viewpoint in the metapopulation dynamics model is worth while and is an interesting theoretical approach for population dynamics [12]. On the other hand, the modeling of patch state transition in Levins model is in a black box. Especially the mass-action terms between patch frequencies of different states in Levins model require a reconsideration from the viewpoint of rationality for the mathematical modeling about the indirect interaction through the dispersal of individuals between patches of different states. We should not easily accept the mass-action terms for the indirect interaction because there never exists any direct interaction between patches.

In our modeling, Levins type of models (1.1) and (1.2) with the mass-action terms as the essential mathematical structure can appear only under some specific condition. To make the Levins type of model appear, it is required that the success of the immigration and settlement of dispersing individual must be independent of the state of its destination patch. It is clear that this situation is far from the reality, in other words, is much ideal. Besides, it is required that the decline rate of population size in the patch is not affected by the settlement of immigrants. Especially in the 2-state model (1.2), every 'occupied' patch is exposed to the possibility to become the 'vacant' state, that is, the inhabiting population is likely to go extinct in any patch. In this reason, it would be reasonable to consider that, in the 2-state model (1.2), the population in each patch of 'occupied' state has a size small enough to be endangered to its extinction. For such a small population, the emigration from it must have a much small size, and so do must the immigration to any other patch. This may be regarded as the reason to assume no relation of the settlement of immigrants to the extinction rate for the population inhabiting in the patch (i.e., its state transition from 'occupied' to 'vacant'). On the other hand, even if much small population, the acceptance of immigrants could cause the "rescue effect" on the extinction-endangered population. It is hard to find any general reasonability to ignore the effect of the settlement of immigrants on the decline rate of inhabiting population size. Hence, Levins type of models (1.1) and (1.2) with the mass-action terms would not be regarded as a general basic model for the metapopulation dynamics.

Our mathematical modeling discussed in this paper is not unique or best for the metapopulation dynamics (for the other example, see [5]). However, our modeling is not so specific, and the result indicates that Levins model with the mass-action type of interaction terms could appear only with some ideal/specific assumptions. This means that Levins type of model could not be standard as the metapopulation dynamics model. It could play an instructive role for introducing the mathematical model about the metapopulation dynamics, but could not be regarded even as a rational simplest model about it. If we extend the metapopulation dynamics model to the interacting population dynamics, for example, the competitive system or the prey-predator one over a patchy habitat, we should pay attention to apply the Levins type of model structure straightforward for it. It is easily seen in our discussion of the modeling for the metapopulation dynamics that such interspecific reaction can be very likely to be embedded in the metapopulation dynamics model not with the mass-action terms but with another nonlinear ones. According to the metapopulation dynamics model, we should remark that it could have in general a variety of mathematical structure resulted from a rational modeling, apart from the typical mass-action terms as in Levins model.

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