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## Introducing stage-specific spatial distribution into the Levins metapopulation model

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The Levins model is a classical but still widely used metapopulation model that describes temporal changes in the regional abundance of a species by extinction and colonization of subpopulations. A fundamental assumption of the model is that the landscape is homogeneous and the species moves between identical patches at random. However, this assumption clearly contrasts with the common observation that different stages prefer or require different habitat types. Here I studied a minimum extension of the Levins model in which the species has stage-specific (juvenile and adult) spatial distributions and dispersal occurs at the timing of reproduction and maturation (i.e., ontogenetic habitat shifts). I examined how the persistence of the stage-structured metapopulations would be affected by rescue effect and interspecific competition. The models predict that rates of ontogenetic habitat shifts are particularly crucial for the persistence or coexistence of stage-structured metapopulations because the species need to complete biphasic life cycles. The present study opens a new avenue for exploring stage- and space-structured population dynamics and will contribute to better landscape management for the conservation of stage-structured animals.

Space matters in population dynamics. Even if local populations go extinct, species can persist at a regional scale through immigration from other habitats. This idea is known as metapopulation theory<sup>1</sup>, and its basic idea was founded by Levins<sup>2</sup> who developed a simple patch occupancy model:

$$\frac{dP}{dt} = cP(1 - P) - eP \quad (1)$$

where  $P$  is the fraction of patches occupied by the species in the landscape and two parameters  $c$  and  $e$  are the colonization rate of empty patches and the extinction rate of occupied patches, respectively. The Levins model describes temporal changes in the regional abundance of a species by extinction and colonization of subpopulations. The equilibrium fraction of occupied patches is  $P^* = 1 - e/c$ , which means that the metapopulations persist if colonization exceeds extinction.

A fundamental assumption of the Levins model is that the landscape is homogeneous and the species moves between identical patches at random. However, this is a simplified assumption for model development. Many researchers have extended the Levins model by implicating additional factors for more realistic representations of metapopulations. For example, local extinction rate may decrease with increasing fraction of occupied patches as a result of increased immigrants (i.e., rescue effect<sup>3</sup>). Besides, different patches may have different colonization or extinction rates because of landscape heterogeneity<sup>4</sup> or different demographic structures in subpopulations<sup>5</sup>. These assumptions make sense because demographic parameters vary with the local environments and ontogenetic stage. As for colonization, immigrants may have different preferences for different habitat types<sup>6</sup>. Furthermore, the incorporation of interspecific competition was an initial step for extending the Levins model in the metacommunity context<sup>7,8</sup>.

In this study, I propose to introduce stage-specific spatial distributions into the Levins model. The most obvious examples are metapopulations of amphibians<sup>9–13</sup> and aquatic insects<sup>14–16</sup>, as their biphasic life cycles separate juvenile and adult distributions at aquatic-terrestrial interface areas. However, similar situations are widely observed even within aquatic or terrestrial systems. Aquatic examples include metapopulations of lake fish moving offshore after birth and growth in littoral zones<sup>17</sup>, migratory fish moving between marine and freshwater environments for spawning<sup>18,19</sup>, and many coastal organisms dispersing offspring that develop in pelagic



waters<sup>20,21</sup>. Butterfly metapopulations have been best studied in terrestrial systems<sup>22–24</sup>. Recent data showed that many species of Lepidoptera utilize different host plant species at larval and adult stages<sup>25</sup>, which implies that their spatial distributions may be stage-specific depending on the vegetation. Indeed, many taxa (both aquatic and terrestrial) exhibit ontogenetic habitat shifts or breeding migration<sup>26</sup>, and stage-specific spatial distribution is very common in nature. Nevertheless, no previous study, to my knowledge, has considered it in the Levins model.

My primary aim here is to address the important issue of stage-structured metapopulations mediated by ontogenetic habitat shifts. To do this, first I re-interpret the Levins-type model of Vandermeer and Carvajal<sup>4</sup> who considered landscape heterogeneity (suitable and unsuitable habitats) as a minimum extension of the metapopulation model including stage-specific (juvenile and adult) spatial distributions. Then, I extend the model to examine how the persistence of the stage-structured metapopulations would be affected by two additional factors, rescue effect<sup>3</sup> and interspecific competition<sup>7,8</sup>, which were proposed soon after the Levins model and have widely been studied in metapopulation ecology. Finally, I discuss future directions in developing more realistic models.

## Model

Vandermeer and Carvajal<sup>4</sup> studied a two-state metapopulation model including suitable and unsuitable habitats, in which they specifically assumed that the species moved from one suitable patch to another by passing through unsuitable habitat. The situation resembles ontogenetic habitat shifts between juvenile and adult stages. Thinking so, I change the interpretation of their model as follows:

$$\frac{dP_J}{dt} = rP_A(h_J - P_J) - e_J P_J \quad (2)$$

$$\frac{dP_A}{dt} = mP_J(h_A - P_A) - e_A P_A \quad (3)$$

where  $P_i$  ( $i = J$  or  $A$ ) is the fraction of patches occupied by juveniles or adults and  $h_i$  is the fraction of stage-specific suitable patches ( $0 \leq P_i \leq h_i \leq 1$ ). Suitable empty patches  $h_i - P_i$  are colonized by newborns or mature individuals from the other stage. Here I define that  $m$  (or  $r$ ) is the rate of ontogenetic habitat shifts from juvenile (or adult) to adult (or juvenile) patches following maturation (or reproduction).  $e_i$  is the stage-specific local extinction rate. Local extinction may occur not only due to habitat disturbance but also due to ontogenetic habitat shifts, considering that all individuals need to disperse to complete their life cycles. Such a situation can be described by defining  $e_i$  as a constant parameter depending on  $m$  or  $r$ .

At the equilibrium, the model has the two nullclines,  $P_J^* = h_J r P_A^* / (e_J + r P_A^*)$  and  $P_A^* = h_A m P_J^* / (e_A + m P_J^*)$ , which are saturating functions of each other. Their slopes at the origin determine whether the stable interior equilibrium exists (i.e., the metapopulations persist) or not. Calculations show that the metapopulations persist (Fig. 1a) if

$$mr > \frac{e_J e_A}{h_J h_A} \quad (4)$$

and otherwise regional extinction occurs (Fig. 1b) (see Vandermeer and Carvajal<sup>4</sup> for the same result while they set  $h_i = 1$ ). This suggests that sufficiently high rates of reproduction and maturation are crucial for the persistence of the stage-structured metapopulations.

Although I intuitively re-interpreted the Levins-type model of Vandermeer and Carvajal<sup>4</sup> for stage-structured metapopulations, I offer a word of caution before extending it. The Levins model

assumes that within-patch population dynamics occur on a much faster time scale than colonization-extinction dynamics and subpopulations immediately reach carrying capacity, whereas in the present model the population dynamics and spatial processes occur on a similar time scale as ontogenetic habitat shifts accompany reproduction. This difference may imply that the present model likewise assumes that newborns mature immediately after birth and matured individuals produce offspring immediately after maturation. However, this assumption may not be biologically plausible if I follow another common idea in the Levins model that only a small fraction of individuals disperse and their emigration does not affect local population dynamics, because such small subpopulations of newborns or matured individuals are unlikely to persist during the stage without population growth. One way to overcome this concern is to implicitly assume that many individuals disperse and thus juvenile and adult subpopulations can persist during the stage, which would be possible under the assumption that local extinction may occur due to ontogenetic habitat shifts (see above). The present model may not strictly be regarded as Levins-type, however I emphasize the potential utility in that it provides good approximations and biologically reasonable predictions of stage-structured metapopulations by capturing the fundamental feature that spatial distribution of juveniles (or adults) expands depending on the fractions of empty patches of juveniles (or adults) and occupied patches by juveniles (or adults). For more realistic representations of stage-structured metapopulations, future research should incorporate local population dynamics of juveniles and adults, which however is beyond my scope here (see Discussion).

**Rescue Effect.** Immigrants may reduce local extinction risk (rescue effect<sup>3</sup>). Linearly decreasing functions have typically been used to describe negative relationships between extinction rate and occupied patch fraction. First, I assume that the extinction rates decrease linearly with increasing colonizing propagules:

$$\frac{dP_J}{dt} = rP_A(h_J - P_J) - e_J \{1 - \alpha_J r P_A\} P_J \quad (5)$$

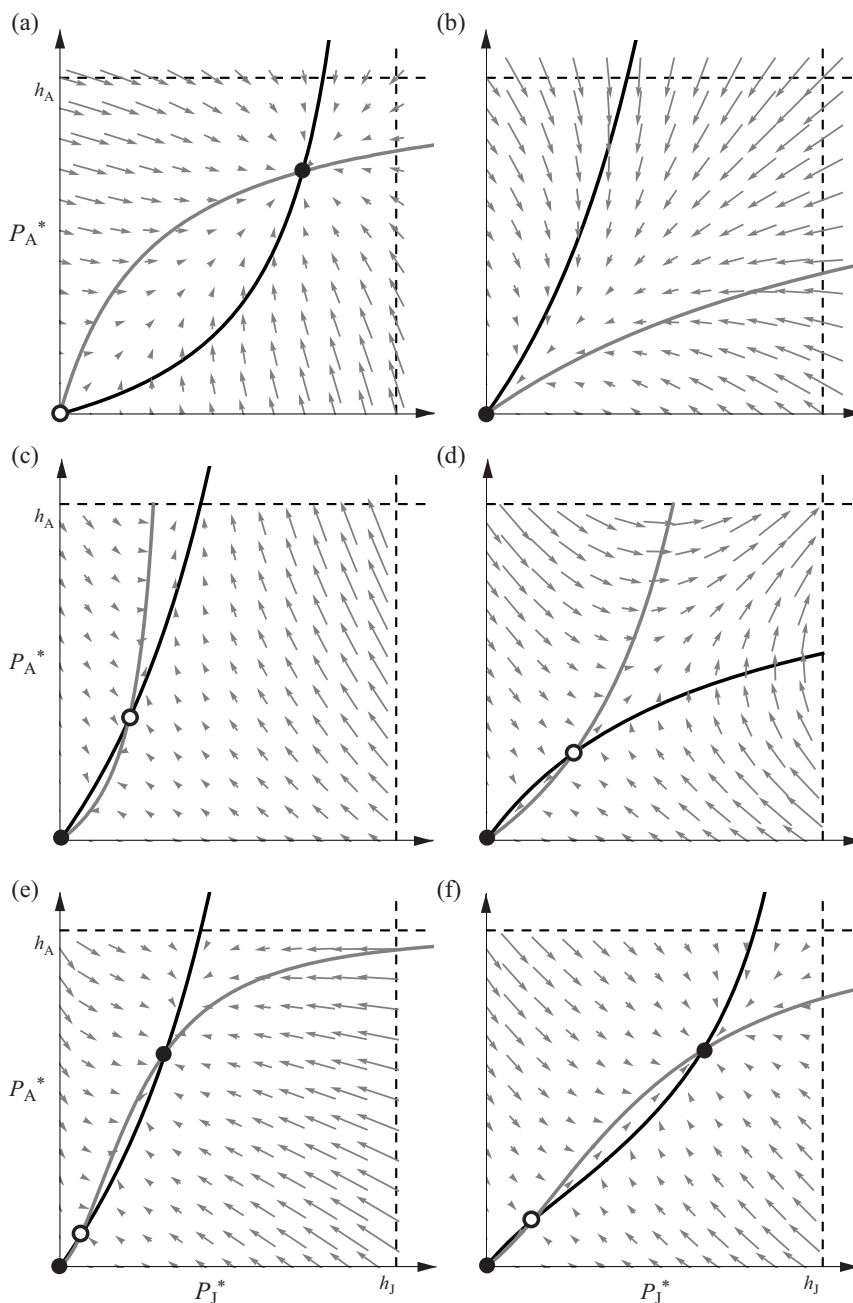
$$\frac{dP_A}{dt} = mP_J(h_A - P_A) - e_A \{1 - \alpha_A m P_J\} P_A \quad (6)$$

where  $\alpha_i$  controls the strength of the rescue effect. At the equilibrium, the following nullclines are obtained:

$$P_J^* = \frac{h_J r P_A^*}{e_J + r(1 - \alpha_J) P_A^*} \quad (7)$$

$$P_A^* = \frac{h_A m P_J^*}{e_A + m(1 - \alpha_A) P_J^*} \quad (8)$$

Suppose that the metapopulations go extinct in the absence of the rescue effects ( $\alpha_i = 0$ ), where the graph of nullcline (8) is saturating (gray line in Fig. 1b). Note that the coefficient of  $P_A^*$  in the denominator of nullcline (8) becomes negative for  $\alpha_A > 1/e_A$ . Under this condition, the graph becomes accelerating and, as a result, the interior equilibrium emerges although locally unstable (Fig. 1c). The nullcline analysis indicates that the fraction of occupied patches goes to zero or the maximum, depending on the initial conditions. The interior equilibrium remains repelling even when the rescue effects are present at both juvenile and adult stages (Fig. 1d).



**Figure 1** | The nullclines for juvenile (black) and adult (gray) patch occupancy dynamics in the  $P_J^*$ - $P_A^*$  plane. The dotted lines represent the asymptotes  $P_i^* = h_i$ . The arrows denote vectors of patch occupancy dynamics. The solid and open circles are stable and unstable equilibria, respectively. The stable interior equilibrium exists in (a) but not in (b). Linear and nonlinear rescue effects are assumed in (c), (d) and (e), (f), respectively. The default parameter values are  $h_i = 0.9$  and  $m = r = 0.05$ . (a)  $e_i = 0.05$ , (b)  $e_i = 0.25$ , (c)  $\alpha_j = 0$  and  $\alpha_A = 20$ , (d)  $\alpha_i = 10$ , (e)  $\beta_j = 0$  and  $\beta_A = 120$ , and (f)  $\beta_i = 25$ .

Different biological processes give rise to different functional forms for rescue effects. For example, if immigrants prevent inbreeding<sup>27</sup>, the rescue effect would be most pronounced at low levels of immigration. Next, I consider nonlinear rescue effects:

$$\frac{dP_J}{dt} = rP_A(h_J - P_J) - \frac{e_J P_J}{1 + \beta_J r P_A} \tag{9}$$

$$\frac{dP_A}{dt} = mP_J(h_A - P_A) - \frac{e_A P_A}{1 + \beta_A m P_J} \tag{10}$$

where  $\beta_i$  controls the strength of the rescue effect. This model has the following nullclines:

$$P_J^* = \frac{h_J r P_A^* (1 + r \beta_J P_A^*)}{e_J + r P_A^* (1 + r \beta_J P_A^*)} \tag{11}$$

$$P_A^* = \frac{h_A m P_J^* (1 + m \beta_A P_J^*)}{e_A + m P_J^* (1 + m \beta_A P_J^*)} \tag{12}$$



The saturating graph of nullcline (12) in the absence of the rescue effect (gray line in Fig. 1b) becomes sigmoid when  $\beta_A$  is large (gray line in Fig. 1e). In contrast to the linear case, therefore, two interior equilibria can emerge, one of which is locally stable and the other unstable. The stable interior equilibrium exists also when weak rescue effects are present at both juvenile and adult stages (Fig. 1f). Numerical simulations provide qualitatively similar patterns when the nonlinear rescue effects are described by exponentially decreasing functions (not shown). In sum, a stable interior equilibrium can emerge when rescue effects are nonlinear in this stage-structured metapopulation model (see Harding and McNamara<sup>28</sup> for similar results in non-structured cases).

**Interspecific competition.** The incorporation of interspecific competition is an initial step for extending the present model in the metacommunity context. There are many ways of doing this, depending on the competition relationship (reviewed by Taneyhill<sup>8</sup>). Four-state patch occupancy models have been developed in which each patch is occupied by either, both, or neither of the two species<sup>29</sup>. However, this approach is not attractive because of the structural complexity. A simpler alternative is to assume that the species do not coexist locally. In this case, competing metapopulations are described by three-state patch occupancy models in which each patch is empty or occupied by either of the two species.

Interspecific competition is often classified as either symmetric or asymmetric. The former refers to the situation that occupied patches by one species are resistant to colonization of the other species (prior residence), while under asymmetric competition outcomes of local competition are deterministic and the superior can exclude immigrants or even residents of the inferior. A well-known prediction in the latter case is that the inferior metapopulations can persist if its colonization rate into empty patches is higher and offsets the competitive disadvantage (competition-colonization trade-off). Here, I focus on two scenarios of asymmetric competition between stage-structured metapopulations: (i) one species is superior at both juvenile and adult stages, and (ii) one species is superior at the juvenile stage and the other at the adult stage. I do not explore symmetric scenarios because the interior equilibrium does not exist (also see Taneyhill<sup>8</sup> for similar results in non-structured cases).

First, I consider that the competitor (i.e., second species) is superior at both juvenile and adult stages:

$$\frac{dP_J}{dt} = rP_A(h_J - P_J - Q_J) - e_J P_J - r'Q_A P_J \quad (13)$$

$$\frac{dP_A}{dt} = mP_J(h_A - P_A - Q_A) - e_A P_A - m'Q_J P_A \quad (14)$$

$$\frac{dQ_J}{dt} = r'Q_A(h_J - P_J - Q_J) - e'_J Q_J + r'Q_A P_J \quad (15)$$

$$\frac{dQ_A}{dt} = m'Q_J(h_A - P_A - Q_A) - e'_A Q_A + m'Q_J P_A \quad (16)$$

where  $Q_i$  is the fraction of occupied patches by the juvenile or adult competitor and the parameter  $r'$  ( $m'$ ,  $e'_J$ , or  $e'_A$ ) is the parameter corresponding to  $r$  ( $m$ ,  $e_J$ , or  $e_A$ ) of the first species. In each equation, the first and last terms represent colonization into empty patches and competitive replacement of the inferior by the superior, respectively.

The interior equilibrium cannot be solved explicitly, so I adopt invasion analysis. The coexistence is achieved when both species can invade the equilibria in which either is absent (mutual invasion). At the boundary equilibrium  $P_1^* = 0$ , the fractions of patches occupied by the second species are solved as follows:

$$Q_J^* = \frac{h_J h_A m' r' - e'_J e'_A}{m'(e'_J + h_A r')} \quad \text{and} \quad Q_A^* = \frac{h_J h_A m' r' - e'_J e'_A}{r'(e'_A + h_J m')} \quad (17)$$

The first species can invade the competitor's metapopulations if its basic reproductive number is greater than one:

$$R_0 = \frac{m(h_A - Q_A^*)}{e_J + r'Q_A^*} \times \frac{r(h_J - Q_J^*)}{e_A + m'Q_J^*} > 1 \quad (18)$$

The former (or latter) term means the expected fraction of adult (or juvenile) patches colonized by immigrants from one juvenile (or adult) patch during its duration period. Note that in the former term both available adult patches and the duration period of a juvenile patch are discounted because of the competitive inferiority ( $h_A - Q_A^*$ ) and replacement ( $e_J + r'Q_A^*$ ), respectively. The same is true for the latter term. Likewise, the basic reproductive number for the invasion by the second species is formulated as follows:

$$R'_0 = \frac{h_A m'}{e'_J} \times \frac{h_J r'}{e'_A} > 1 \quad (19)$$

Note that here  $R'_0$  is not affected by the first species because the second species is competitively superior at both juvenile and adult stages. The two species coexist when both  $R_0 > 1$  and  $R'_0 > 1$  hold.

$$\frac{e'_J e'_A m r (e'_J + h_A r') (e'_A + h_J m')}{m' r' \{e'_A (e_J - e'_J) + h_J m' (e_J + h_A r')\} \{e'_J (e_A - e'_A) + h_A r' (e_A + h_J m')\}} > 1 \quad (20)$$

$$\frac{h_J h_A m' r'}{e'_J e'_A} > 1 \quad (21)$$

If stage-specific local extinction rates of the two species are equivalent (i.e.,  $e'_J = e_J$  and  $e'_A = e_A$ ), then the basic reproductive numbers  $R_0$  and  $R'_0$  are simplified as

$$R_0 = \frac{e_J e_A m r}{h_J h_A (m' r')^2} > 1 \quad (22)$$

and

$$R'_0 = \frac{h_J h_A m' r'}{e_J e_A} > 1 \quad (23)$$

respectively. Combining them leads to the following coexistence condition:

$$m r > m' r' > \frac{e_J e_A}{h_J h_A} \quad (24)$$

The left-hand inequality indicates that the inferior can persist if the product of maturation and reproduction rates is greater than that



of the superior. This is analogous to the competition-colonization trade-off in non-structured competition<sup>7</sup>. The right-hand inequality determines the persistence of the superior irrespective of the inferior.

Next, I consider competitive reversals between juvenile and adult stages. Suppose that the second species is superior at the juvenile stage but inferior at the adult stage:

$$\frac{dP_J}{dt} = rP_A(h_J - P_J - Q_J) - e_J P_J - r'Q_A P_J \quad (25)$$

$$\frac{dP_A}{dt} = mP_J(h_A - P_A - Q_A) - e_A P_A + mP_J Q_A \quad (26)$$

$$\frac{dQ_J}{dt} = r'Q_A(h_J - P_J - Q_J) - e'_J Q_J + r'Q_A P_J \quad (27)$$

$$\frac{dQ_A}{dt} = m'Q_J(h_A - P_A - Q_A) - e'_A Q_A - mP_J Q_A \quad (28)$$

The last terms of equations (25) and (27) explain that the adult competitor produces offspring that replace patches occupied by the inferior juveniles of the first species, while the last terms of equations (26) and (28) explain that the inferior juveniles mature and replace patches occupied by the adult competitor.

At the boundary equilibrium  $P_i^* = 0$ , the fractions of patches occupied by the second species are solved as follows:

$$Q_J^* = \frac{h_J h_A m r' - e'_J e'_A}{m'(e'_J + h_A r')} \quad \text{and} \quad Q_A^* = \frac{h_J h_A m r' - e'_J e'_A}{r'(e'_A + h_J m')} \quad (29)$$

The first species can invade the competitor's metapopulations if its basic reproductive number is greater than one:

$$R_0 = \frac{h_A m}{e_J + r'Q_A^*} \times \frac{r(h_J - Q_J^*)}{e_A} > 1 \quad (30)$$

Note that in the former term suitable adult patches are all regarded as empty because of the competitive superiority at the adult stage ( $h_A$ ) while the duration period of a juvenile patch is discounted due to competitive replacement ( $e_J + r'Q_A^*$ ). In contrast, available juvenile patches are discounted due to the competitive inferiority at the juvenile stage ( $h_J - Q_J^*$ ). The basic reproductive number for the invasion by the second species is formulated as follows:

$$R'_0 = \frac{m'(h_A - P_A^*)}{e'_J} \times \frac{h_J r'}{e'_A + mP_J^*} > 1 \quad (31)$$

where

$$P_J^* = \frac{h_J h_A m r - e_J e_A}{m(e_J + h_A r')} \quad \text{and} \quad P_A^* = \frac{h_J h_A m r - e_J e_A}{r(e_A + h_J m)} \quad (32)$$

The two species coexist when both  $R_0 > 1$  and  $R'_0 > 1$  hold.

$$\frac{e'_J h_A m r (e'_A + h_J m')^2}{e_A m' (e'_J + h_A r') \{e'_A (e_J - e'_J) + h_J m' (e_J + h_A r')\}} > 1 \quad (33)$$

$$\frac{e_A h_J m' r' (e_J + h_A r')^2}{e'_J r (e_A + h_J m) \{e_J (e_A - e'_A) + h_A r (e'_A + h_J m)\}} > 1 \quad (34)$$

If stage-specific local extinction rates are identical between the species ( $e'_J = e_J$  and  $e'_A = e_A$ ), inequalities (33) and (34) are summarized as follows:

$$\frac{m r}{(r')^2} \left( \frac{Q_J^*}{Q_A^*} \right)^2 > \frac{e_A h_J}{e_J h_A} > \frac{m^2}{m' r'} \left( \frac{P_J^*}{P_A^*} \right)^2 \quad (35)$$

This is difficult to interpret biologically, but by comparing the first and last quantities it is possible to derive a necessary condition that has a clear biological meaning:

$$P_A^* Q_J^* \sqrt{m' r'} > P_J^* Q_A^* \sqrt{m r'} \quad (36)$$

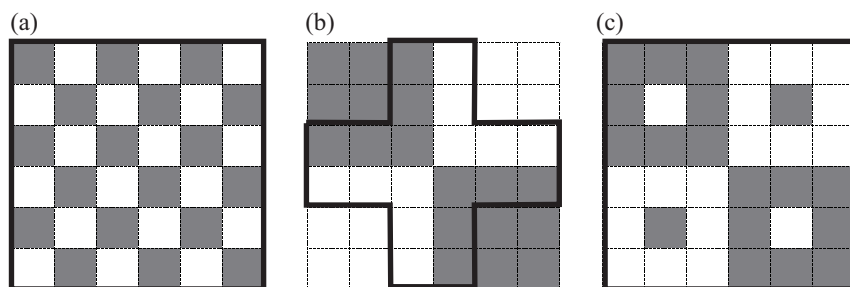
Recall that juvenile patches of the first species are replaced by the second species. To compensate for the habitat loss, the first species needs to occupy adult patches more efficiently ( $P_A^* > Q_A^*$ ) and disperse more offspring ( $r > r'$ ). In contrast, the juvenile of the second species needs to occupy more patches ( $Q_J^* > P_J^*$ ) and mature faster ( $m' > m$ ) to compensate for the competitive replacement at the adult stage. It is worthwhile to note that they cannot coexist when they have the same rates of ontogenetic habitat shifts ( $r' = r$  and  $m' = m$ ) because both sides of inequality (36) become identical, which means that the juvenile-adult competitive reversals cannot be a trade-off to realize the coexistence of competing stage-structured metapopulations.

There are many variants of Levins-type competition models<sup>8</sup>. More systematic investigations are needed for various scenarios including stage-specific competition symmetry (either juveniles or adults may exhibit symmetric competition), competition with non-structured (resident) species, and local coexistence (double occupancy).

## Discussion

This study explored the persistence and coexistence of the stage-structured metapopulations mediated by ontogenetic habitat shifts. First, I emphasize that the present modeling framework is relevant to many taxa exhibiting ontogenetic habitat shifts. While spatial distributions of those animals have been discussed in the metapopulation context (see Introduction), there has been even a debate over whether amphibian populations which seem to be the most obvious example of metapopulations are actually metapopulations or not<sup>9,10,13</sup>. The reason for such a fundamental problem may partly be that previous theoretical studies have overlooked multiphasic life cycles of those animals in metapopulation models and not provided testable predictions for empirical observations. The present framework helps bridge the gap by providing new theoretical insights.

The applicability of the present modeling framework would actually be much wider because spatial distributions of species are to some degree stage-specific. Almost all organisms on Earth are multicellular, and ontogenetic growth is one of the most fundamental aspects of an organism, largely determining its physiology and



**Figure 2 | Schematic pictures of landscape configuration effects on the metapopulation persistence.** Juvenile (white) and adult (gray) patches are distributed in the heterogeneous landscape. Juvenile and adult patches are (a) evenly distributed and well mixed, (b) clustered separately, and (c) newly created at the center of the patch cluster of the other stage. The patch composition is identical in all three cases. The bold lines enclose the habitat which the species can colonize by short distance of ontogenetic habitat shifts.

behavior. Because demographic parameters and their environmental responses are stage-dependent, it is highly possible that different subpopulations have different demographic structures in heterogeneous landscapes as a result of environmental filtering. For example, young (small) individuals may be dominant in productive or refuge-rich environments due to high fecundity or low mortality, whereas old (large) individuals may be dominant in severe or dangerous environments due to high ability of starvation tolerance or predation avoidance<sup>30,31</sup>. If dispersal ability or habitat preference is also stage-dependent, the pattern could be much stronger. These situations may be described by the present framework.

Another advantage of the present framework is that it can ameliorate a major challenge in spatial modeling. While previous attempts to extend the Levins model have shed new light on metapopulation dynamics (see Introduction), a new challenge has emerged that spatial modeling becomes increasingly complex as additional factors are added. Complex models could describe systems with higher accuracy but are unsuitable for establishing general principles concerning dynamics. Factors implicated in the Levins model so far are already manifold. Obviously, it is hard to deal with a full model containing all factors that have been studied independently, and simplified modeling frameworks have been needed<sup>28,32</sup>. I expect that, given the assumption of stage-specific spatial distribution, it can integrate at least three factors; landscape heterogeneity, local demographic structure, and habitat preference<sup>4–6</sup>. It is easy to recognize that all these factors are involved in metapopulations of amphibians or aquatic insects, wherein juveniles grow in aquatic habitats and land following maturation while adults mate at terrestrial habitats and lay eggs into water. As such, the present framework is to facilitate the development of more manageable spatial models.

Future options for extending the present model are wide ranging. One is to incorporate local population dynamics and density-dependency of parameters<sup>33–35</sup>. Abundance-explicit community dynamics models have predicted that density-dependent (or food-dependent) ontogenetic niche shifts may cause alternative stable states and thus mediate regime shifts in changing environments<sup>36,37</sup>. Intriguingly, even multiple (more than two) stable states can occur in a two-patch model<sup>38</sup>. The explicit consideration of within-patch population dynamics is expected as a promising direction for improving the prediction power of the model.

Stage-structured metapopulations interact not only with competitors but also with predators or prey. Unlike competition, trophic interactions are likely to be stage-specific because predators and prey may have distinct ecological niches (e.g., fish and snakes for amphibians<sup>39</sup>; fish and birds for aquatic insects<sup>40</sup>). In general, the persistence of predator metapopulations will increase with increasing prey patches<sup>41</sup>. It is therefore predicted that stage-specific predators will be more likely to persist as the juveniles or adults are more efficient (higher colonization rate and lower extinction rate). A further step

in this direction is to build patch occupancy food-web models with stage structure, in which the prediction can be more complex<sup>42</sup>.

The original Levins model does not explicitly assume landscape configuration (patch area and connectivity) which critically affects colonization and extinction dynamics. I kept this assumption following the majority of previous studies and because spatially implicit and explicit models may produce qualitatively similar patterns<sup>43</sup>. However, the explicit consideration of landscape configuration is undoubtedly important for application purposes<sup>44</sup>. Suppose that ontogenetic habitat shifts occur at short distances and stage-specific suitable patches are regularly distributed over the landscape. In this case, the species can colonize all available patches (Fig. 2a). When stage-specific patches are clustered separately, the species cannot colonize the interior of the patch clusters and, as a result, the metapopulation persistence will become lower despite the identical patch composition (Fig. 2b). In this situation, the creation of new habitats within the patch clusters allows effective use of available habitats and recovers the persistence (Fig. 2c). Mechanistically, the newly created habitats are similar to stopover sites for long-distance migratory animals<sup>45</sup> rather than conservation corridors in metapopulation theory. Detailed numerical simulations are required to fully explore those situations in spatially explicit landscapes.

In conclusion, although we are still at the early stage of our understanding of how space mediates stage-structured population dynamics, the present study opens a new avenue for exploring stage- and space-structured population dynamics. Unfortunately, relevant animals (amphibians and migratory birds) have been threatened seriously worldwide, and habitat loss and degradation is one of the major causes<sup>9,10,46</sup>. This is certainly related to the ecological characteristics of stage-structured animals that they have different environmental requirements at different ontogenetic stages and loss of environmental diversity readily prevents successful completion of their multiphasic life cycles. It is only recently that researchers have recognized the general importance of ontogenetic growth in ecological dynamics and biodiversity conservation<sup>47–50</sup>. I hope that this study will stimulate further research efforts in exploring stage- and space-structured population dynamics, which could contribute to the establishment of better landscape management for the conservation of stage-structured species.

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