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Review

Carrying Capacity of Spatially Distributed Metapopulations

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Carrying capacity is a key concept in ecology. A body of theory, based on the logistic equation, has extended predictions of carrying capacity to spatially distributed, dispersing populations. However, this theory has only recently been tested empirically. The experimental results disagree with some theoretical predictions of when they are extended to a population dispersing randomly in a two-patch system. However, they are consistent with a mechanistic model of consumption on an exploitable resource (consumer–resource model). We argue that carrying capacity, defined as the total equilibrium population, is not a fundamental property of ecological systems, at least in the context of spatial heterogeneity. Instead, it is an emergent property that depends on the population's intrinsic growth and dispersal rates.

A Brief History of Carrying Capacity – a Fundamental but Confusing Concept

Carrying capacity (commonly defined as the upper limit on the size of the population), has been one of the most important concepts in ecology for the last century. As such, it has been broadly used, from cell populations up to that of ecological communities at landscape and ecosystem levels [1,2]. Wildlife biologists introduced the term in the early 20th century as a tool in wildlife management. Aldo Leopold viewed carrying capacity as the population density reached at a particular site, determined by both the resources available and intraspecific competition [3]. Although, in Leopold's view, the realized carrying capacity was usually less than the maximum population density reached under optimum conditions. He called this the saturation point – the maximum density that could be achieved by careful habitat manipulation.

Leopold's definition was by no means the only one held among ecologists. For instance, Paul Errington viewed carrying capacity as the maximum size that a population could reach if there was refuge from predation available. Dhondt [4] documented the use of both Leopold's and Errington's definitions by other wildlife biologists and ecologists, noting, for example, that Dasmann [5] carried distinctions further by introducing four different definitions related to carrying capacity: subsistence density, optimum density, security density, and tolerance density. Dhondt [4] reviewed the multiplicity of views of carrying capacity and called it confusing, concluding that, at least for wildlife biology, the term should be avoided.

However, carrying capacity had already entered the mainstream of ecology. Odum [6] took the first step of giving carrying capacity a formal mathematical meaning. He defined it as the constant K in the Pearl–Verhulst form of the logistic population equation:

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N \qquad [1]$$

where N is population size and r is the intrinsic population growth rate. This equation defines the carrying capacity as the equilibrium point that a population would always approach from lesser or

Highlights

The logistic equation, with carrying capacity, K, and growth rate, r, has traditionally been used to describe dynamics of ecological populations.

Experiments confirmed the prediction that dispersal could increase metapopulation abundance in heterogeneous environments, whereas they rejected the prediction that heterogeneous environments support a larger metapopulation abundance than homogeneous environments with the same sum over K values.

Consumer-resource models, which explicitly consider the resource inputs and time scales of feedbacks between organisms and their resource, agree consistently with experimental results, suggesting they are more appropriate for describing populations in space.

The theoretical results have important management implications on wildlife, such as the important role of dispersal, or habitat connectivity, in influencing population abundance in patchy environments.

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greater values, and hence is regulated around K. Odum [6] assumed that the value of K depends on the limiting resource of the population. It appears in the logistic equation as a constant value, although Odum acknowledged that it could vary as the environment changes.

Although the use of the logistic equation with carrying capacity K to describe ecological populations might seem to have ended the confusion over its meaning, both the logistic and the carrying capacity concept it formalizes have continued to be criticized from the empirical side. While logistic population growth is often observed in laboratory studies of microbial populations, Botkin [7] noted that it has never been observed in nature, and many ecologists have embraced more qualitative concepts of population regulation, such as density-vague regulation [8]. Nevertheless, the Pearl–Verhulst form of the logistic equation, with carrying capacity K being an equilibrium determined by resources, has been standard in ecology textbooks since the 1970s [4], and has a central place in theoretical ecology. For that reason, we focus on carrying capacity based on Equation 1 and show that there are serious complexities related to this model when extended to heterogeneous space.

Scaling up Carrying Capacity from the Local Site to the Landscape or Region

Predicting population dynamics at a landscape or regional level is a paramount problem in ecology, especially under the changing environment and human disturbance [9,10]. It has been said that 'the emerging discipline of landscape ecology must serve as the foundation for effective biodiversity conservation programming' [11]. For example, forest fragmentation is creating barriers that will hinder, or respectively, slow, dispersal capacity [12–14]. As dispersal rates decline with habitat fragmentation, understanding the combined effect of heterogeneity and dispersal on the attainable population size will be essential for fostering population persistence of desired species [15–17] or limiting invasive species in these environments [18]. Additionally, general patterns of species range shifts (to higher elevations and latitudes) are anticipated with warming temperatures [19–21], so projecting shifting population dynamics along environmental gradients is essential.

Much previous work has focused on understanding the forces that determine the size of natural populations, using the assumption of a spatially homogeneous (environmentally uniform) system [22–24]. With that assumption, the population dynamics can be described by the logistic Equation 1 in which r and K have constant values across the spatial environment [25]. However, almost all environments are heterogeneous, with habitat quality varying either continuously or occurring as discrete, disjointed patches [26]. Habitat heterogeneity has increased due to fragmentation by human activity and the conversion of natural ecosystems into agricultural or urban areas [27,28], and the effect of environmental change [29,30]. Such heterogeneous environments consist of a variety of local population growth rates and carrying capacities; hence, varying r and K. Importantly, a growing body of research has highlighted that spatial heterogeneity may be as important as the spatial mean for assessing environmental impacts on populations [31]. Including spatial heterogeneity, in combination with population dispersal, can alter and even reverse certain population-level predictions based only on the mean [32–34]. As a result, understanding the role of environmental heterogeneity in affecting natural population dynamics is crucial [35].

Dispersal, as a fundamental ecological process, plays an important role in shaping population dynamics [36,37], community diversity and composition [38], and ecosystem functioning [39]. All organisms, including microbes, disperse within their ranges and dispersal can occur in different ways. Two classic dispersal patterns are the ideal free distribution (IFD) and random dispersal. According to the IFD, if other factors besides carrying capacity of a habitat patch, such as

predator density, can be ignored, and animals are free to move, they will continue to move until further movement cannot improve their fitness. That is the point when the maximum population abundance attained at equilibrium is equal to the sum of the carrying capacities on the individual patches, or is the integral of continuously varying carrying capacity over the whole area. In the alternative to the IFD, random movement, if there is no directional bias, is called symmetric dispersal, of which diffusion is a special case where the dispersal proceeds by local steps. In the absence of knowledge of how individuals of a population actually move, symmetric dispersal is assumed in the preponderance of ecological models with dispersal [40], such as reaction–diffusion models [41]. Therefore, we use this assumption with the logistic model (Equation 1) to show how random movement complicates the total size that a population can reach in a heterogeneous environment. Note, however, that the results here can be extended to asymmetric dispersal (Box 1).

It might seem that determining the total carrying capacity of a randomly dispersing population in heterogeneous environments would be a straightforward summation of each carrying capacity, K_i, over all the local habitats. However, when mathematical ecologists analyzed this seemingly simple extension of the logistic equation beyond its nonspatial form to a population dispersing randomly in heterogeneous space, they found the following surprising mathematical results (Boxes 1 and 2), which we will refer to as predictions to be tested empirically.

Box 1. Mathematical Explanation of Prediction 1

Extending the logistic model to heterogeneous space can be done by including logistic growth as the reaction term in a reaction-diffusion model, or by modeling space as a collection of discrete patches, among which populations can disperse. To demonstrate the effects of population movement, consider the latter approach, simplified to two patches and described by an equation for each patch, in which population dispersal rates are the same in both directions and carrying capacities and intrinsic growth rates differ on the two patches;

$$\frac{dN_1}{dt} = r_1\left(1 - \frac{N_1}{K_1}\right)N_1 - DN_1 + DN_2; \qquad [\text{Ia}]$$

$$\frac{dN_2}{dt} = r_2\left(1 - \frac{N_2}{K_2}\right)N_2 - DN_2 + DN_1. \qquad [\text{Ib}]$$

where D is the symmetric dispersal between the two patches. As found by Freedman and Waltman [87] and Holt [88] and stated in corrected form by Arditi [89], in the limit of large dispersal rate ($D \rightarrow \infty$), which corresponds to diffusion occurring on a much faster time scale than population change, the equilibrium abundance that can be reached by the population in this system is

$$\text{Total population} = K_1 + K_2 + (K_1 - K_2)\frac{r_1K_2 - r_2K_1}{r_1K_2 + r_2K_1}, \qquad [\text{II}]$$

This has the implication that the intrinsic growth rates on the two patches, r_1 and r_2, have an effect on the total equilibrium population when the population disperses symmetrically between the two patches. If $K_1 > K_2$ and $r_1/K_1 > r_2/K_2$, the population in a heterogeneous two-patch system could reach a total equilibrium population size greater than the sum of the carrying capacities of the two patches (equivalent to the population not diffusing) (Prediction 1). Conversely, if $r_1/K_1 < r_2/K_2$, the total equilibrium population is less than $K_1 + K_2$. An analogous result was found in continuous space by Lou [90], using a partial differential reaction diffusion equation. Arditi *et al.* [68] showed that making the dispersal asymmetric does not change the results qualitatively. Although these results are for $D \rightarrow \infty$, simulations show that the total population deviates from $K_1 + K_2$ for smaller values of D as well, though approaching $K_1 + K_2$ as $D \rightarrow \infty$. Therefore, dispersal rate, along with the intrinsic growth rate, influence the equilibrium total population size in a heterogeneous environment.

Thus, the total size of a diffusing population can differ from that of the sum of the local carrying capacities, if the intrinsic growth rates also differ. Prediction 1 was confirmed experimentally [47].

Box 2. Mathematical Explanation of Prediction 2

Prediction 2 follows as a special case of Equation II in Box 1. It states that a diffusing population can reach a greater equilibrium population size in the heterogeneous case than in the homogeneous case when the two carrying capacities differ but sum to the same in the two cases. That is, in the homogeneous case, $K_1 = K_2 = K$, while in the heterogeneous case $K_1 = K + a]$, $K_2 = K - \Delta$, where is a deviation in K. From Equation II in Box 1 it can be found that

$$\text{Total population} = 2K + 2\Delta \left[\frac{K(r_1 - r_2) + \Delta(r_1 + r_2)}{K(r_1 + r_2) + \Delta(r_1 - r_2)} \right], \qquad [\text{I}]$$

which exceeds $2K$ when $r_1 > r_2$. Prediction 2 is mathematically correct, but it does not agree with the experimental results. The reason is that the experiment differed in an important way from the model based on coupled logistic equations. In the experiment, input of a limiting resource/nutrient, was provided to the yeast populations. The input was regulated such that the sum of the inputs to the two patches was same in the homogeneous and heterogeneous cases, although the amounts going to each patch differed in the heterogeneous case. It can be shown that Equation I for $r_1 > r_2$ violates the equality of resource inputs in the heterogeneous and homogeneous cases.

To show this, note that in terms of the coupled logistic equations, the rate of input of resource at equilibrium is $r_1 N_1^* + r_2 N_2^* = r_1 K_1 + r_2 K_2$, which can be seen by adding Equations Ia and Ib in Box 1 at equilibrium. Now, comparing the heterogeneous case, $r_1(K + \Delta) + r_2(K - \Delta)$ with the homogeneous case, $r_1 K + r_2 K$, it can be seen that the total input cannot be the same for the two cases unless $r_1 = r_2$. Therefore, it is impossible for the total population to exceed $K_1 + K_2$ while keeping total input constant. It can further be shown that, if total resource input is kept the same in the heterogeneous and homogeneous cases, the population abundance will always be the same or larger in the homogeneous than the heterogeneous case, as found in the experiment. The opposite can occur if r_1 and r_2 are different. This is a special case of a more general result (Theorem 11 in [91]; see also [53]). If a consumer–resource model is instead of the logistic model, the equality of input in the heterogeneous and homogeneous cases is satisfied in a more straightforward way (Box 3).

Prediction 1: in a heterogeneous system, where both growth rate and carrying capacity vary spatially, total population abundance of a dispersing population may exceed total population abundance of a nondispersing population. Prediction 2: the total population abundance of a dispersing population in a heterogeneous environment can be higher than in the homogeneous environment, even if the sum of all local carrying capacities is the same for both cases. This is a special case of Equation I in Box 1, which is the basis of Prediction 1.

These two predictions were made based on the spatial extension of the logistic model, but Prediction 1 has also been recognized intuitively. Oksanen [42] cited those mathematical results by imagining a situation in which a population distributes itself between productive and nonproductive patches, referring the population in the nonproductive patches as a spillover population. Sutherland [43] described a similar situation where this spill-over population could boost the total population above the combined equilibria of the productive patches. This finding motivated him to cast doubt on the logistic equation interpretation of carrying capacity.

Empirical Testing of Mathematical Results

As populations exist on landscapes with heterogeneous resources within which they disperse (e.g., Iijima and Ueno [44], Sirén [45]), these mathematical predictions are important to determine which distribution of resource could support a larger metapopulation abundance. Despite these implications, these results were not tested empirically until recently. A greenhouse experiment using floating plant [duckweed (*Lemna minor* Linn.)], considered the difference in plant total biomass when the total nutrient resources were distributed heterogeneously or homogeneously among a discrete series of water-filled containers [46]. This showed, for the first time, that total biomass in heterogeneous environments peaked at an intermediate, relatively low, dispersal rate, and was higher than the total carrying capacity of the system without dispersal. To provide a more rigorously controlled environment and include exploitable resources, a subsequent study was conducted using spatially dispersing laboratory populations of yeast (*Saccharomyces cerevisiae*) [47]. This study created heterogeneous and homogeneous

environments by distributing the same amount of resource inputs in different patterns among discrete cells [47]. Consistent with Prediction 1, spatial dispersal increased total equilibrium population abundance in heterogeneous environments only when r and K were positively correlated. Surprisingly, however, the results contradicted Prediction 2; that is, the homogeneously distributed resources supported a higher total consumer population than heterogeneously distributed resources, even with population dispersal [47]. The mathematical explanation as to why Prediction 1 was supported by the experiment is shown in Box 1, while the explanation as to why Prediction 2 was not supported is in Box 2.

A more recent study, which was also used yeast (*S. cerevisiae*), examined how a stressor's spatial distribution interacted with dispersal to influence metapopulation dynamics [48]. In agreement with previous work that showed dispersal increased metapopulation abundance in heterogeneous environments with resources [47], this study also demonstrated that dispersal increased the metapopulation abundance when a stressor was heterogeneously distributed [48]. In contrast to the previous finding that a homogeneously distributed resource led to a higher metapopulation abundance [47], this study found that a homogeneous spatial distribution of stressor minimized metapopulation abundance due to the opposite impact of the stressor on populations than resources [48]. Together, these studies consistently supported Prediction 1 but highlighted that confirmation of Prediction 2 was contingent on the specific variable that was distributed either heterogeneously or homogeneously in the region.

Ecological Implications of Mathematical Results

The logistic equation, particularly in the Pearl–Verhulst form, has been called 'probably the most well-known and influential population model in ecology, serving as the basis for many other models and theories' [49]. We point out that carrying capacity, K, does not scale up in a simple way to give total population in heterogeneous space, but is affected by both the population's intrinsic growth rate and its dispersal rate. Despite the increasing mathematical work motivated by the new experimental and theoretical results [48,50–56], more attention is still needed from ecologists. The concept of carrying capacity has long been central in the fields of wildlife management and conservation biology [57]. The emerging results on the scaling up of predictions of carrying capacity from local scale to the landscape and regional scales have broad ecological implications.

For example, Prediction 1, which was confirmed experimentally [46–48], demonstrated that dispersal could increase total population abundance in heterogeneous environments. This prediction highlights the important role of dispersal, or habitat connectivity, in patchy environments. For instance, massive management efforts have been made to facilitate wildlife movement across different patches of habitat, such as building road-crossing bridges [58] and such efforts could play an essential role on increasing and conserving wildlife populations. On the contrary, since dispersal increases population abundance in a heterogeneous environment, limiting the rate of invasive species from dispersal by creating dispersal barriers could help limit size of undesirable populations [59].

Experimental finding partially disagreed with Prediction 2, a special case of Equation I in Box 1 disagreed with experimental findings. The more appropriate consumer–resource model (Box 3) agreed with the experimental results that a homogeneous distribution of resource can support a higher total population size at equilibrium than can the same total resource input distributed heterogeneously [47]. Conversely, a homogeneous pattern of stressor can reduce total population abundance to a lower level than if the stressor was heterogeneously distributed [48]. Indeed, while Prediction 2 is a theoretical result based on very restrictive assumptions that are made by

Box 3. Consumer–Resource Model

The analysis in Box 2 shows that the limiting resource input rate to a population must be considered when calculating total population size in a heterogeneous region. This means that the values of K cannot be manipulated arbitrarily if total production summed over patches is to be conserved. With this constraint, total size of a population dispersing in a heterogeneous environment cannot exceed that in the homogeneous environment. This condition is automatically satisfied by modeling a population as a consumer in a consumer–resource equation, in which a spatially varying limiting resource input rate, R_{Input}, is specified locally. For a multipatch system, the equations for the consumer N_i and its resource, R_i, on a single patch might be

$$\frac{dN_i}{dt} = f_i(R_i) - m_i N_i - g_i N_i^2 \tag{Ia}$$

$$\frac{dR_I}{dt} = R_{Input,j} - \eta_i R_i - \frac{1}{\mu_i} f_i(R_i), \tag{Ib}$$

where the consumers on different patches are linked by dispersal. This model still produces the result that a dispersing population in a heterogeneous region can reach a higher total population abundance than the sum of the local carrying capacities but as long as $\sum_{i=1}^{n} R_{Input,j}$ is held constant, the maximum total population is reached for the homogeneous system. The sketch of the consumer-resource model can be presented (Figure I). The sum of the resource inputs, R_{input1} and $R_{input,2}$, can be set to be equal in the homogeneous and heterogeneous cases.
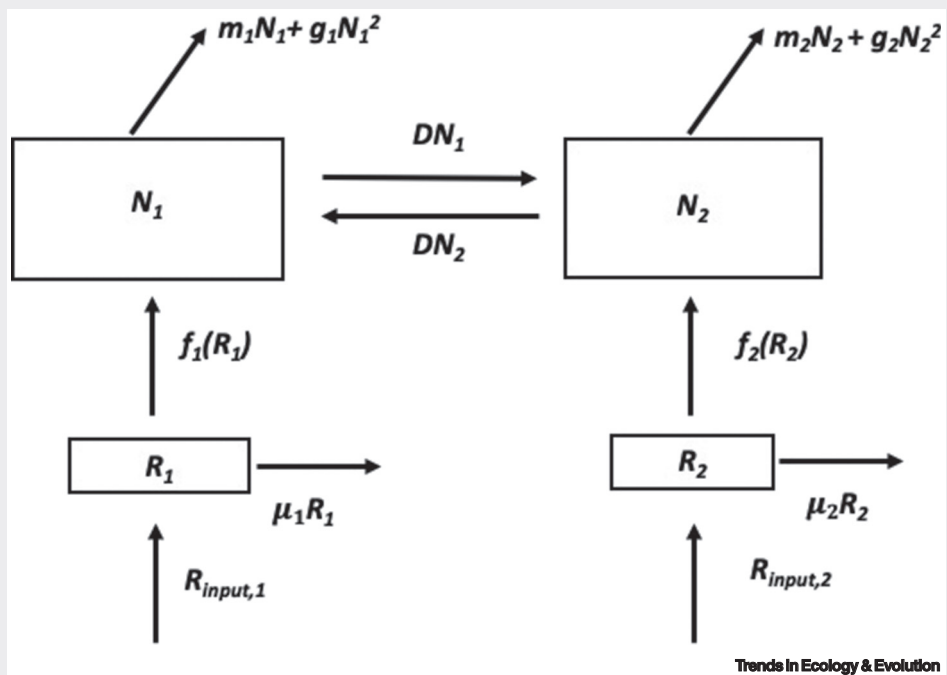

Figure I. The Sketch of the Consumer-resource Model. Here N is the consumer population abundance, R is the nutrient concentration, D is the dispersal rate, m is the mortality rate, g is the density-dependent loss rate, μ is the loss rate of nutrient from the system and f is the consumption rate of nutrient. Flows of limiting resource in consumer-resource model. The sum of the resource inputs, R_{input1} and $R_{input,2}$, can be set to be equal in the homogeneous and heterogeneous cases.

the models, but it still has potential implications for population management. In particular, the first result, regarding to the distribution of resources, is associated with a classic applied ecological question: how to allocate a certain amount of resource or nutrient to increase population abundance. For example, this theory could help to provide guidance on how to increase wood production under different fertilization treatments in natural resource management [60]; how to support larger wildlife populations by altering food distribution and dispersal patterns [61]; how

to maintain population abundance in response to enhanced environmental stochasticity via changing foraging behavior [62]; and perhaps how occupancy choice might change after rapid environmental change [63].

Another implication of our review is that we add a new dimension to earlier critiques of carrying capacity formalized in the Pearl–Verhulst equation. Criticisms were in fact raised from its inception in response to Raymond Pearl's view of the equation as a law of growth [64]. Among more recent criticisms, Wilkinson [65] pointed out that logistic models do not explicitly consider feedbacks between the organisms and their abiotic environment. Mallet [66] noted, based on a meta-analysis of 128 laboratory toxicological studies that r and K are not independent. Instead, they tend to be positively correlated, so that they should not be varied independently in models [67]. Another mathematical study highlighted that the failure of total population in a heterogeneous environment to be the sum of local carrying capacities calls into question carrying capacity being an intrinsic property of an ecosystem [68].

In view of the limitations of the logistic model, consumer–resource modeling (Box 3) of heterogeneous systems may be the appropriate approach to other areas of theory (e.g., Tilman [69]). In line with this, McLeod [70] has advocated the use of consumer–resource models to describe population of herbivores that can be supported in a variable environment. Loreau [71] criticized the closure of the logistic model to explicit external inputs, which led to their recommending the consumer-resource modeling approach. The consumer–resource approach may then be a more realistic framework for personality-dependent spatial ecology by offering specific predictions on the interactions between movement and environmental factors, such as resource distribution or landscape structure [72,73]. Further, it could provide a foundation of merging individual behavior to population and community levels [74]. Lastly, it can contribute to disease research via incorporating movement analyses [75]. Therefore, we are in agreement with Mallet [66], Arditi [68], and other critics of the logistic model, that the consumer–resource model is a better alternative to the logistic model in many cases, although it adds to model complexity.

Concluding Remarks and Future Perspectives

A large body of theory has been produced to predict dispersal evolution in temporal heterogenous environments [76–78], and to investigate evolution of dispersal in spatially structured landscapes based on individual-based models [79–82]. Temporal variability in environmental conditions also affects what is understood be carrying capacity [83]. How estimates of carrying capacities under different conditions scale to an average carrying capacity over a long time period has the same complexity as for spatial heterogeneity. It appears that, analogous to the spatially heterogeneous situation, temporal variation in the intrinsic growth rate is important in determining time average population size, although more detailed analysis is needed. Empirical testing is needed to validate all these directions, and beyond, as suggested in Figure 1.

Other interesting ideas remain to be explored, some examples of which are listed in Figure 1. Despite the fact that mathematical theories have not been developed in most cases in Figure 1, possible predictions and suitable testing systems are presented in Figure 1. For instance, extending understanding from 'stepping-stone dispersal' (local dispersal or diffusion in mathematical terms) to global dispersal (nonlocal dispersals in mathematical terms) could advance our prediction on disease spread [84].

Future work will be needed to incorporate other dimensions of dispersal to provide a more comprehensive understanding (see Outstanding Questions). For example, it appears that stage structure or body size may change the dispersal behavior. Large birds travel farther in homogeneous

Outstanding Questions

What is the impact of global dispersal on altering population dynamics in heterogeneous environments? How can we incorporate other dimensions of dispersal (e.g., distance and direction) to provide a more comprehensive understanding?

How do age-structured dispersal processes regulate population dynamics in heterogeneous environments? Which age classes contribute most to maintain a higher population abundance?

How can we capture the role of a temporal change of heterogeneous environment or an environment with multiple layers of heterogeneity?

How can we apply the mathematical theory on wildlife management to support a larger population abundance, especially under anthropogenic actions and climate change?
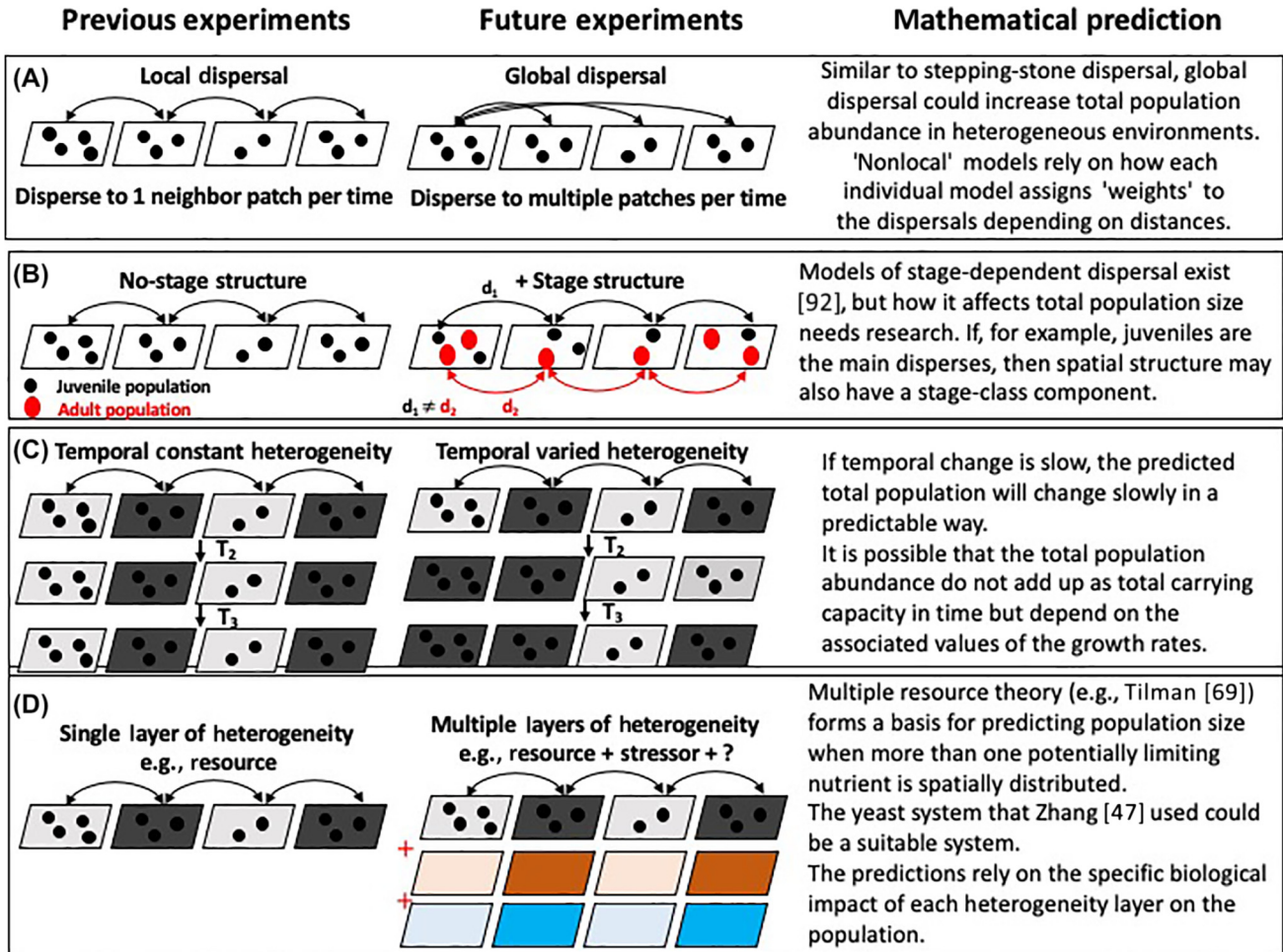
Figure 1. Future Work That Can Be Explored Extending from Previous Work. (A) Previous work only performed 'stepping-stone dispersal' (or local dispersal), to which population only disperse to the two neighbor patches (left and right) each time. Future work could consider the effects of diverse dispersal patterns on metapopulation abundance, for instance, the so-called nonlocal dispersal (in mathematical terms) – population could disperse to nonadjacent patches. (B) Models of stage-dependent dispersal exist [92], but how it affects total population size needs research. Hence, it would be very interesting to test if juvenile (black dots) and adult populations (red dots) having different dispersal rates would alter metapopulation dynamics. (C) Previous work focused on a temporally constant heterogeneous environment. It is possible to look at the impact of a temporally heterogeneous environment on population dynamics. (D) Only the way in which dispersal alters metapopulation in a single layer of heterogeneous environment has been studied, so it is unclear but important to consider how multiple layers of heterogeneity with dispersal play a role on changing the metapopulation dynamics.

environments due to the need for different habitat types associated with foraging and reproduction [85]. Therefore, in these systems, incorporating stage-structured dispersal processes will be necessary. Additionally, as there are multiple layers of heterogeneity in a natural system [86], and heterogeneity changes temporally due to disturbance and climate change, investigating the role of both multiple layers of spatial heterogeneity and temporal heterogeneity change is essential.

Lastly, we noted earlier that the IFD and random symmetric dispersal are two idealizations of dispersal that have been examined mathematically. Arditi [68] has shown that dispersal asymmetry can have a strong quantitative influence, depending on its magnitude and on its direction, but little qualitative difference from the symmetric case. This work will help towards a synthesis of the

combined effects of spatial heterogeneity and movement. Hopefully this can be pushed further into other factors that influence total population size.

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