CONCEPTS & THEORY

The perfect mixing paradox and the logistic equation: Verhulst vs. Lotka

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Abstract. A theoretical analysis of density-dependent population dynamics in two patches sheds novel light on our understanding of basic ecological parameters. Firstly, as already highlighted in the literature, the use of the traditional *r-K* parameterization for the logistic equation (due to Lotka and Gause) can lead to paradoxical situations. We show that these problems do not exist with Verhulst's original formulation, which includes a quadratic "friction" term representing intraspecific competition (parameter α) instead of the so-called carrying capacity *K*. Secondly, we show that the parameter α depends on the number of patches, or more generally on area. This is also the case of all parameters that quantify the interaction strengths between individuals, either of the same species or of different species. The consequence is that estimates of interaction strength will vary when population size is measured in absolute terms. In order to obtain scale-invariant parameter estimates, it is essential to express population abundances as densities. Also, the interaction parameters must be reported with all explicit units, such as ($m^2 \cdot individual^{-1} \cdot d^{-1}$), which is rarely the case.

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INTRODUCTION

All simple population dynamics models make the implicit assumption of "perfect mixing" of individuals. This applies to single-species models as well as to models with several interacting populations, such as the Lotka–Volterra predation and competition models. For the sake of simplicity, we consider in this study the case of a single population only. Perfect mixing is assumed in all "point models," that is, models with no space structure, but is also assumed in spatially structured patch models: Individuals are assumed to be perfectly mixed within each patch.

Here, we only consider the category of spatial models with random, passive, dispersal. We do not consider situations of intentional, directed movement for which a very abundant literature exists in the context of optimal foraging theory (see the seminal papers of Charnov [1976] for patchy space and of Arditi and Dacorogna [1988] for continuous space) or in the context of group formation (e.g., Cosner et al. 1999, Tyutyunov et al. 2004).

Regarding patch models, they must obey an obvious logical property: If two patches are linked by migration, and if the migration rate becomes infinite, the two patches become perfectly mixed among each other, and the system must behave as a one-patch model for the total population (Fig. 1).

In this study, we re-visit in the context of a patchy environment some of the basic properties of
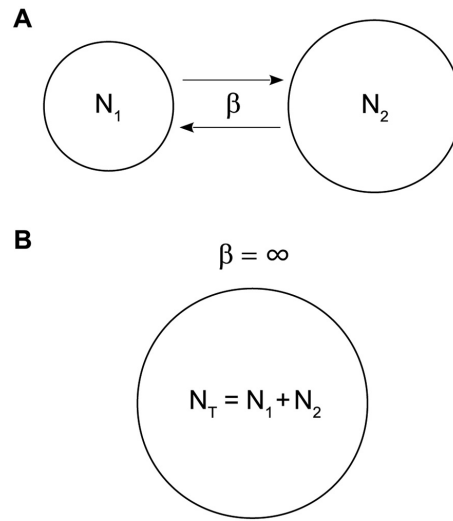
Fig. 1. (A) In this study, we consider a single population split into two patches linked by a migration rate β. (B) When β → ∞, the two patches merge into a single one.

the most fundamental models of single population dynamics: the Malthus law and the logistic model. Originally, these models were not developed with a spatial context in mind. We will first show that when adapted to a patchy environment, both of these models satisfy the above-stated logical criterion. However, we will also show that they present one important difference. With Malthusian growth, the resulting merged patch has intermediate demography between the two constitutive patches, while the situation can be counterintuitive and paradoxical with the logistic model in its usual *r-K* formalization. Furthermore, we will show that the original Verhulst form of the logistic equation is free of this paradox. This original form used an *r-α* parameterization, with α being a direct quantification of intraspecific competition.

Another important general message will be that all interaction coefficients (intraspecific competition in the case of the logistic model; interaction strength in the case of the generalized Lotka–Volterra model) depend on the number of patches when population size is measured in absolute terms. To account for this dependence, population size must be expressed as a density.

MALTHUSIAN GROWTH IN TWO PATCHES

Let us first consider a population with no intraspecific competition. In a perfectly mixed

single patch, the population follows exponential growth:

$$\frac{dN}{dt} = rN.$$

If the same population is split into two patches linked by migration, the system dynamics can be described as:

$$\frac{dN_1}{dt} = r_1 N_1 + \beta(N_2 - N_1),$$
$$\frac{dN_2}{dt} = r_2 N_2 + \beta(N_1 - N_2), \tag{1}$$

where the parameter β quantifies the migration rate between the two patches, assumed (for simplicity) to be the same in both directions (see Fig. 1). Of course, each patch is supposed to be perfectly mixed, with local growth rate r_i.

As β becomes infinite, one can prove (see Appendix S1) that the abundances become equal in both patches and that the ensuing global growth rate is the average of both growth rates. That is, the total population $N_T = N_1 + N_2$ obeys the following equation:

$$\frac{dN_T}{dt} = \bar{r}N_T,$$
$$\text{where } \bar{r} = \frac{r_1 + r_2}{2}. \tag{2}$$

Thus, exponential growth satisfies the above-mentioned logical condition that mixing

perfectly two perfectly mixed patches leads to the same situation as having a single perfectly mixed patch. Moreover, the total population's demography is intermediate between the two constituent subpopulations. The notion of patch *size* is meaningless here because population abundance is unlimited. The only meaningful character of the patch structure is the *number* of patches, which can lead to counterintuitive effects, such as the following.

Starting from a reference situation with a single patch in which a population grows with some growth rate r_1, adding a second patch with a lower growth rate r_2 will have a detrimental effect on the total population growth. Although, on first thought, adding a patch should be beneficial to the total population, this second patch actually acts as a sink to the first patch because its growth rate is lower (even though it is positive).

Because of these difficulties in reconciling exponential growth and patchy population dynamics, it is sensible to use a bounded growth model instead. Indeed, the simplest growth model that is commonly used in patch situations is the logistic model rather than the Malthus law.

Logistic Growth in Two Patches

The natural way to model a two-patch system with logistic growth is

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) + \beta(N_2 - N_1),$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) + \beta(N_1 - N_2). \tag{3}$$

The full mathematical study of this system with intermediate values of β is rather complex (see Arditi et al. 2015), but we will only focus here on the properties of the perfectly mixed system (i.e., $\beta \rightarrow \infty$).

In isolation (i.e., with $\beta = 0$), each patch equilibrates at $N_1^* = K_1, N_2^* = K_2$. Thus, the notion of "patch size" can be equated with the "carrying capacity" K. Actually, this is the way that most textbooks define the parameter K: The very choice of words suggests that it is the environmental capacity to carry a given population. However, as we will show, K must only be considered as the asymptotic population size, not as

an environmental parameter, and we will refrain from calling it "carrying capacity."

When the two patches are perfectly mixed into a single one ($\beta \rightarrow \infty$), one would expect that the resulting total population stabilizes at the sum of the two patch sizes: $N_T^* = K_1 + K_2$. However, this is generally not the case. It can be shown (see Appendix S2) that the entire perfectly mixed population N_T obeys the following logistic equation:

$$\frac{dN_T}{dt} = \bar{r} N_T \left(1 - \frac{N_T}{K_T}\right), \tag{4}$$

where $\bar{r} = \dfrac{r_1 + r_2}{2}$ and $K_T = 2\dfrac{r_1 + r_2}{r_1/K_1 + r_2/K_2}$. (5)

In order to compare the perfectly mixed total asymptotic population K_T with the sum of the separate asymptotic values K_1, K_2, this quantity K_T can also be written as

$$K_T = (K_1 + K_2) + (K_1 - K_2)\frac{r_1/K_1 - r_2/K_2}{r_1/K_1 + r_2/K_2}. \tag{6}$$

This expression was derived long ago by Freedman and Waltman (1977), but it was published with typographical errors that were partly corrected by Holt (1985) and completely corrected by Arditi et al. (2015).

The expression (6) makes it clear that K_T can be either greater or smaller than $K_1 + K_2$. Assuming that patch 1 is the smaller one, that is, $K_1 < K_2$, Eq. (6) says that merging the patches will be beneficial if and only if $r_1/K_1 < r_2/K_2$. Thus, connecting two patches into a single one can be either beneficial or detrimental to the total asymptotic population size. In the case that the patches differ only with respect to K_i (i.e., $K_1 < K_2$) and do not differ with respect to the intrinsic growth rate (i.e., $r_1 = r_2$), the effect is always detrimental.

Obviously, the total patch *size* is (by definition) the sum of the two patch *sizes*. However, because the total asymptotic population size is not equal to the sum of the two separate asymptotic values, this implies that it is an error to identify the asymptotic population size with "patch size." This is a serious problem for the interpretation of the parameter K. For this reason, a more appropriate notation could be N_∞ instead of K, as used by Lotka (1925), or K_∞ as proposed by Gabriel et al. (2005).

Verhulst Growth in Two Patches

The logistic equation is presented in virtually all textbooks in the r-K formalism that we have just used in the previous section. This model is generally credited to Verhulst (1838). However, this is historically somewhat inaccurate: Verhulst coined indeed the term "logistic growth" and was first to suggest a second-degree model, but he used a different parameterization. He proposed the following polynomial expression:

$$\frac{dN}{dt} = rN - \alpha N^2. \tag{7}$$

This equation has the stable equilibrium $N^* = r/\alpha$.

The first author to present the logistic model in the r-K parameterization was probably Lotka at a New York meeting of the American Statistical Association, where he used the notation N_∞ for the parameter later known as K (Lotka 1925, see also Kingsland 1985: 85–86). To our knowledge, the first author to use the notation K was Gause in his seminal work with protozoans, where he viewed K as the "maximal population that can exist in the given microcosm with the given level of food resources" (Gause 1934: 34), and the quantity $(K - N)/K$ as the "relative number of still vacant places" (Gause 1934: 35).

Of course, the original r-α formulation can be brought to the r-K formulation with the re-parameterization $K = r/\alpha$. However, there is an important difference in terms of ecological interpretation. In the form (7), the parameter α has the immediate meaning of quantifying intraspecific competition. In a perfectly mixed environment, it can be interpreted as the negative contribution to growth due to interindividual encounters. Thus, in the form (7), both parameters have a demographic meaning and there is no difficulty in assuming that r and α are independent. This assumption implies that $K = r/\alpha$ should be positively correlated to r, and available empirical evidence shows that this is actually the case (Mallet 2012: 641–642, DeAngelis et al. 2016). The correlation between K and r is a problem of the r-K parameterization, which normally assumes that they are independent parameters. For this reason, we strongly advocate the r-α formulation. If the r-K formulation is used nonetheless, this correlation must be acknowledged and taken into account.

Using the Verhulst expression (7), the two-patch model (3) becomes

$$\frac{dN_1}{dt} = r_1 N_1 - \alpha_1 N_1^2 + \beta(N_2 - N_1),$$
$$\frac{dN_2}{dt} = r_2 N_2 - \alpha_2 N_2^2 + \beta(N_1 - N_2). \tag{8}$$

If the perfectly mixed Verhulst equation is written for the total population N_T (see Appendix S3), it becomes:

$$\frac{dN_T}{dt} = \bar{r} N_T - \alpha_T N_T^2, \ \ \text{with } \bar{r} = \frac{r_1 + r_2}{2},$$
$$\alpha_T = \frac{\bar{\alpha}}{2}, \text{ and } \bar{\alpha} = \frac{\alpha_1 + \alpha_2}{2}. \tag{9}$$

As with the r-K logistic model, the total mixed population equilibrium can be either greater or smaller than the sum of the isolated equilibria, depending on the parameter values:

$$N_T^* = \left(\frac{r_1}{\alpha_1} + \frac{r_2}{\alpha_2}\right) + \left(\frac{r_1}{\alpha_1} - \frac{r_2}{\alpha_2}\right)\frac{\alpha_1 - \alpha_2}{\alpha_1 + \alpha_2}. \tag{10}$$

Because of the change of parameterization, Eq. (10) can be interpreted with a different perspective from that of Eq. (6). Assuming again that patch 1 is the poorer one (i.e., $r_1/\alpha_1 < r_2/\alpha_2$), Eq. (10) says that merging the patches is beneficial if and only if intraspecific competition is weaker in patch 1 than in patch 2 ($\alpha_1 < \alpha_2$).

Two issues emerge when considering the total population size N_T. Firstly, as with the r-K formulation, the total mixed population equilibrium can be different from the sum of the equilibria in the isolated patches. Secondly, the Verhulst second-degree term due to intraspecific competition is twice as small as its average value. Mathematically, this is simply due to the fact that $N_T^2 = 4\bar{N}^2$. As we will now show, this apparent spatial dependence of the competition parameter is an artifact due to treating population size in absolute numbers. If population size is measured as a density (as it should) or as the average population in the context of our patch model, the problem disappears.

Considering the dynamics of the average population in the two perfectly mixed patches, $\bar{N} = N_T/2$, Eq. (9) becomes:

$$\frac{d\bar{N}}{dt} = \bar{r}\bar{N} - \bar{\alpha}\bar{N}^2. \tag{11}$$

Here, the average population follows a Verhulst equation with both parameters being simply the averages of the corresponding patch parameters. This equation is scale-invariant, and the apparent scale dependence of the parameter α disappears. It is easy to check that a similar equation holds in the case of n perfectly mixed patches. Consequently, in a patch context, it is reasonable to study the average population $\bar{N}$ or, more generally, to express population size as a density with dimension [individual/area]. In this case, the dimension of the intraspecific competition parameter α is [area·individual^{-1}·time^{-1}] and r has, as usual, dimension [time^{-1}].

Discussion

We have shown that the logistic equation in its usual r-K parameterization presents paradoxical properties when generalized to a multi-patch situation. Eqs. (5, 6) show that the total asymptotic population size K_T is not the simple sum of the local asymptotic population sizes: The calculation of K_T requires the knowledge of the local growth rates r_i. For this reason, we consider it as misleading to designate K with the term "carrying capacity" in the context of the logistic equation. However, the term can be useful in other contexts, as in conservation biology, to express the number of habitable sites in a given environment.

With the original Verhulst form (i.e., with the r-α parameterization), Eq. (11) shows that both parameters can simply be averaged independently from one another in order to describe the dynamics of the average population in the two-patch environment. Importantly, this is valid only when population size is expressed as a density, not as absolute abundance. Then, the Verhulst form is invariant, which gives to it a clear advantage over the r-K form in terms of mathematical elegance. Philosophy of science teaches that elegance is often a relevant criterion for selecting among alternative theories (Farmelo 2002, see also Arditi and Ginzburg 2012: chap. 6).

The above considerations add to the long-standing debate about the logistic equation and to the criticisms of the widespread r-K expression when compared to the r-α Verhulst form (Kuno 1991, Ginzburg 1992, Gabriel et al. 2005,

Mallet 2012). We have shown that returning to the original expression resolves the paradox presented by the r-K model when merging two perfectly mixed patches. Mallet (2012) has shown that the r-α form solves other paradoxes as well. Regrettably, most, if not all, textbooks make uncritical and exclusive use of the r-K form of the logistic model.

We have insisted on the fact that population abundance must be treated as a density. This also applies to the interspecific interaction strengths α_{ij} of the generalized Lotka–Volterra equations commonly used in food web theory:

$$\frac{dN_i}{dt} = r_i N_i + \sum_{j=1}^{s} \alpha_{ij} N_i N_j, i = 1\ldots s. \qquad (12)$$

When measuring interaction coefficients in a particular environment or experiment (e.g., Paine 1992, Laska and Wootton 1998, Berlow et al. 2004), the estimates cannot be applied at face value to different conditions if the populations are not measured as densities. Of course, all measured quantities must be reported with their full units, which is unfortunately far from being always the case.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1599/full

Appendix S1: Malthusian growth in two patches

The equation system (1) can be rewritten as:

$$\frac{d(N_1 + N_2)}{dt} = r_1 N_1 + r_2 N_2 ,$$ (A1a)

$$\frac{d(N_1 - N_2)}{dt} = (r_1 N_1 - r_2 N_2) - 2\beta(N_1 - N_2) .$$ (A1b)

As $\beta \to \infty$, the mixing time scale becomes much faster than the demographic time scale. In the RHS of the second equation (A1b), the first term becomes negligible in front of the second one. Using $x = N_1 - N_2$, this equation (A1b) becomes approximately

$$\frac{dx}{dt} = -2\beta x ,$$

whose solution $x = x_0 e^{-2\beta t}$ tends to $x = 0$, i.e., $N_1 = N_2$. Replacing this solution $N_1 = N_2 = N_T / 2$ into eq. (A1a) gives immediately eq. (2).

Appendix S2: Logistic growth in two patches

As in Appendix S1, the equation system (3) can be rewritten as:

$$\frac{d(N_1 + N_2)}{dt} = r_1 N_1 + r_2 N_2 - \frac{r_1}{K_1} N_1^2 - \frac{r_2}{K_2} N_2^2, \qquad\qquad\text{(A2a)}$$

$$\frac{d(N_1 - N_2)}{dt} = \left(r_1 N_1 - r_2 N_2 - \frac{r_1}{K_1} N_1^2 - \frac{r_2}{K_2} N_2^2 \right) - 2\beta(N_1 - N_2). \qquad\qquad\text{(A2b)}$$

As explained in Appendix S1, the system can be simplified to a single equation when $\beta \to \infty$.

With $N_1 = N_2 = N_T / 2$, eq. (A2a) becomes:

$$\frac{dN_T}{dt} = \frac{r_1 + r_2}{2} N_T - \frac{r_1}{K_1} \frac{N_T^2}{4} - \frac{r_2}{K_2} \frac{N_T^2}{4}, \qquad\qquad\text{(A3)}$$

which can be brought to the standard logistic form (4–5).

Appendix S3: Verhulst growth in two patches

As in Appendices S1 and S2, the equation system (8) can be rewritten as:

$$\frac{d(N_1 + N_2)}{dt} = r_1 N_1 + r_2 N_2 - \alpha_1 N_1^2 - \alpha_2 N_2^2, \tag{A4a}$$

$$\frac{d(N_1 - N_2)}{dt} = \left(r_1 N_1 - r_2 N_2 - \alpha_1 N_1^2 - \alpha_2 N_2^2 \right) - 2\beta(N_1 - N_2). \tag{A4b}$$

As explained in Appendices S1 and S2, time scale arguments lead to a single equation when $\beta \to \infty$. With $N_1 = N_2 = N_T / 2$, eq. (A4a) becomes:

$$\frac{dN_T}{dt} = \frac{r_1 + r_2}{2} N_T - \frac{1}{2} \cdot \frac{\alpha_1 + \alpha_2}{2} N_T^2, \tag{A5}$$

which can be written in the standard Verhulst form (9).