IS DISPERSAL ALWAYS BENEFICIAL TO CARRYING CAPACITY ?

NEW INSIGHTS FROM THE MULTI-PATCH LOGISTIC EQUATION

C. Lobry

Joint work with R. Arditi and T. Sari

- The SLOSS debate
- The two-patches logistic
- A paradoxical result
- Coupling "reduced models" of resource-consumer models.

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Theoretical Population Biology 106 (2015) 45–59

Contents lists available at ScienceDirect

Theoretical Population Biology

journal homepage: www.elsevier.com/locate/tpb

Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation

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ARTICLE INFO

Article history:
Received 27 May 2015
Available online 16 October 2015

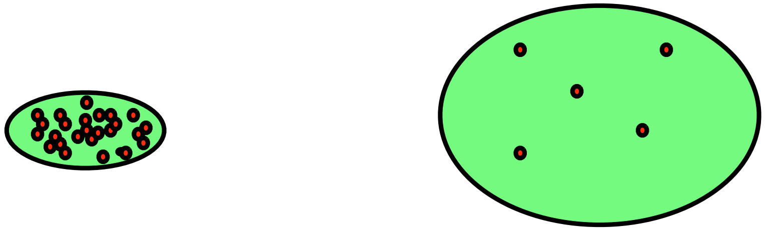
Keywords:
Intraspecific competition
Fragmentation
SLOSS
Slow–fast systems

ABSTRACT

The standard model for the dynamics of a fragmented density-dependent population is built from several local logistic models coupled by migrations. First introduced in the 1970s and used in innumerable articles, this standard model applied to a two-patch situation has never been completely analysed. Here, we complete this analysis and we delineate the conditions under which fragmentation associated to dispersal is either beneficial or detrimental to total population abundance. Therefore, this is a contribution to the SLOSS question. Importantly, we also show that, depending on the underlying mechanism, there is no unique way to generalize the logistic model to a patchy situation. In many cases, the standard model is not the correct generalization. We analyse several alternative models and compare their predictions. Finally, we emphasize the shortcomings of the logistic model when written in the r-K parameterization and we explain why Verhulst's original polynomial expression is to be preferred.

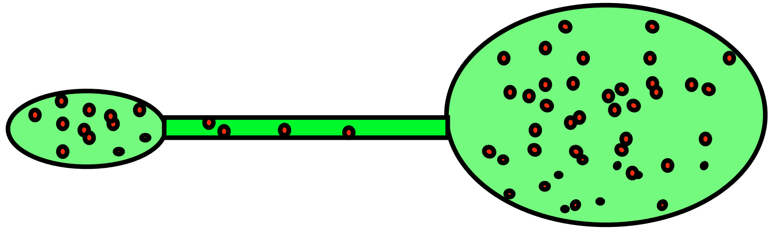
The SLOSS debate

Single Large Or Several Small (SLOSS) patches
is a big issue for biodiversity conservation.



The simplest case :

- Two patches
- One population on each patch (the same)
- Logistic growth + linear dispersal



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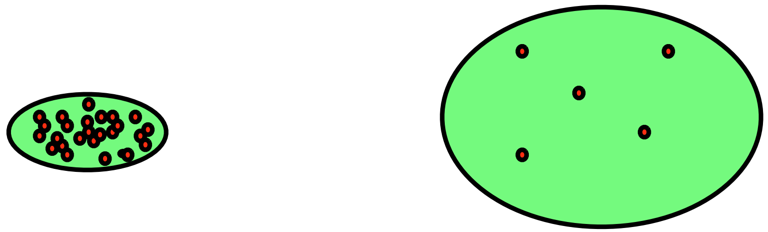

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$$\frac{dN_1}{dt} = r_1 \, N_1 - \lambda_1 N_1^2 \; .$$

$$\frac{dN_2}{dt} = r_2 \, N_2 - \lambda_2 N_2^2 \; .$$

$$K_i = \frac{r_i}{\lambda_i}$$

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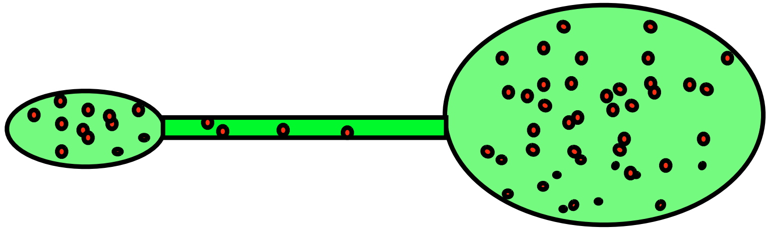

$$\frac{dN_1}{dt} = r_1\, N_1 - \lambda_1 N_1^2 + \beta(N_2 - N_1)$$

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The SLOSS debate

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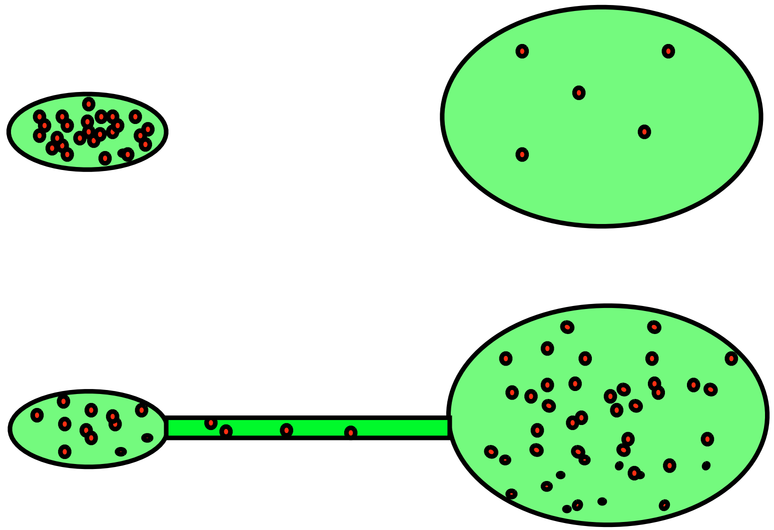

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Let (N_1^*, N_2^*) be the equilibrium

Compare $N_1^* + N_2^*$ with $K_1 + K_2$

The two-patches logistic

- First investigations : Freedman-Waltman 77, DeAngelis et al 79, Holt 85, Hanski 99...
- $\beta \to \infty$: Freedman-Waltman 77
- $\frac{r_1}{K_1} = \frac{r_2}{K_2}$: DeAngelis-Zhang 14
- Surprisingly no general treatment in 2014
- Arditi, Lobry and Sari, T.P.B. 2015

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Arditi, Lobry, Sari 15. Let the system in Lotka notations :

$$\frac{dN_1}{dt} = r_1\, N-1 \left(1 - \frac{N_1}{K_1}\right) + \beta(N_2 - N_1)$$

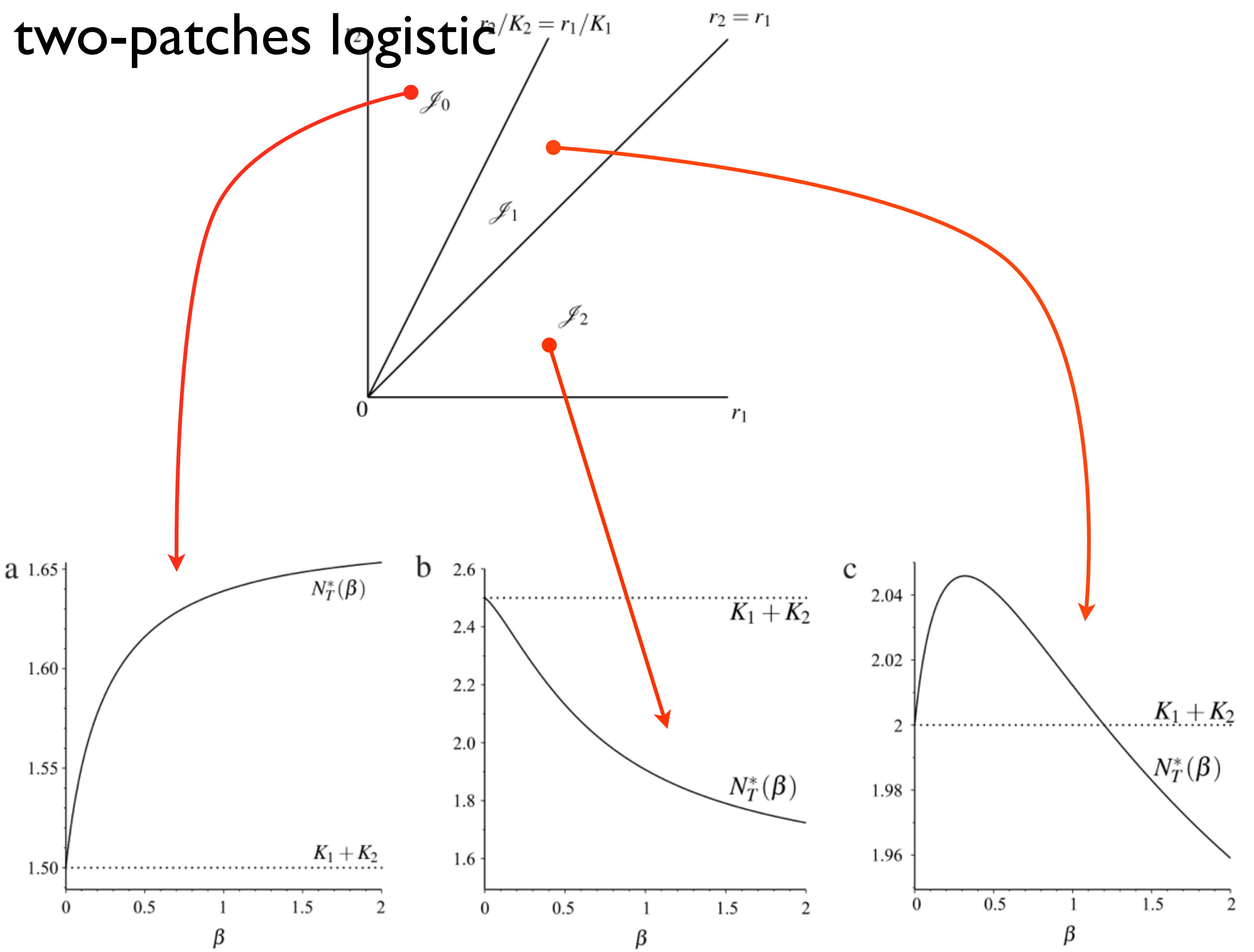
$$\frac{dN_2}{dt} = r_2\, N-2 \left(1 - \frac{N_2}{K_2}\right) + \beta(N_1 - N_2)$$

Assume $K_1 < K_2$ then :

$$K_1 < N_1^* < N_2^* < K_2$$

$$N_T^* = N_1^* + N_2^* = K_1 + K_2 + \beta \frac{N_2^* - N_1^*}{\frac{r_1 r_2}{K_1 K_2} N_1^* N_2^*} \left(\frac{r_2}{K_2} N_2 - \frac{r_1}{K_1} N_1\right)$$

The two-patches logistic



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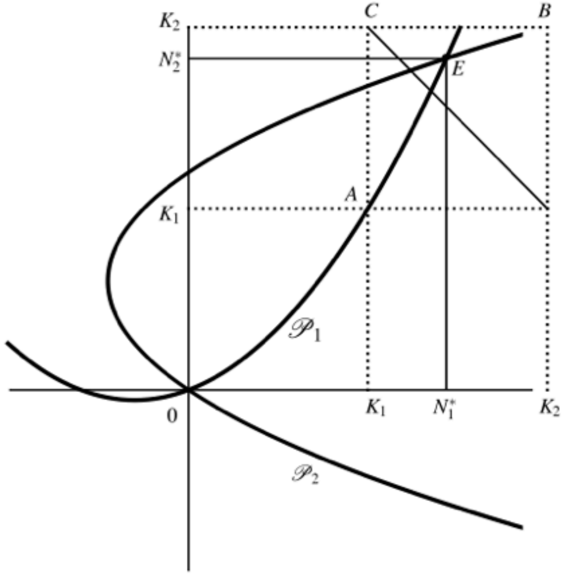
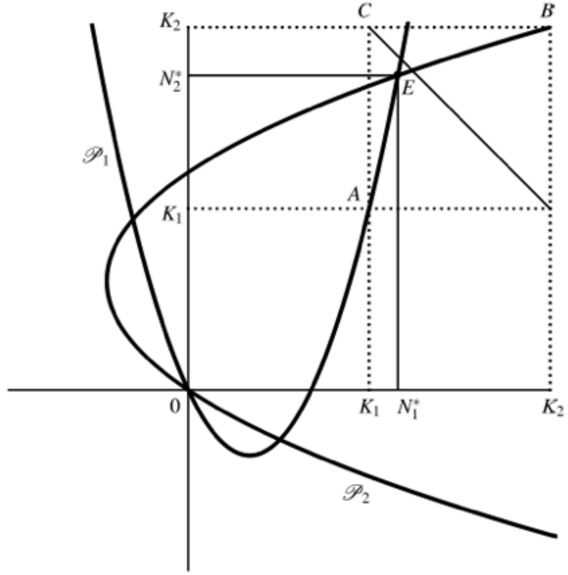




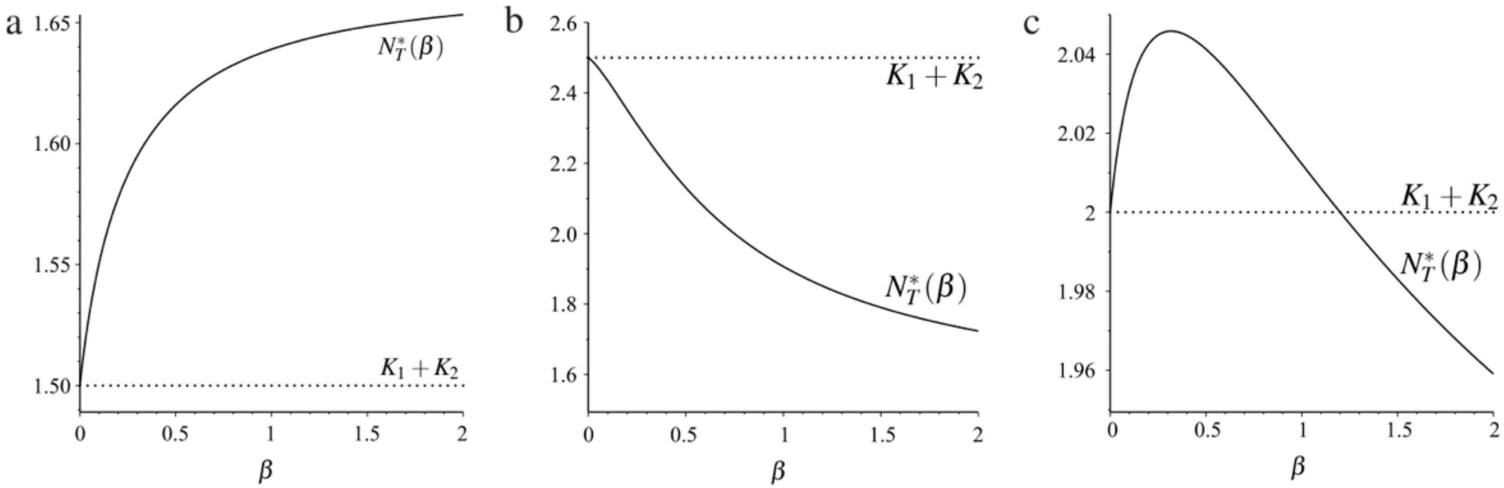
$$K_1 < N_1^* < N_2^* < K_2$$

$$N_T^* = K_1 + K_2 + \beta \frac{N_2^* - N_1^*}{\frac{r_1}{K_1}\frac{r_2}{K_2} N_1^* N_2^*} \left(\frac{r_2}{K_2} N_2^* - \frac{r_1}{K_1} N_1^* \right)$$

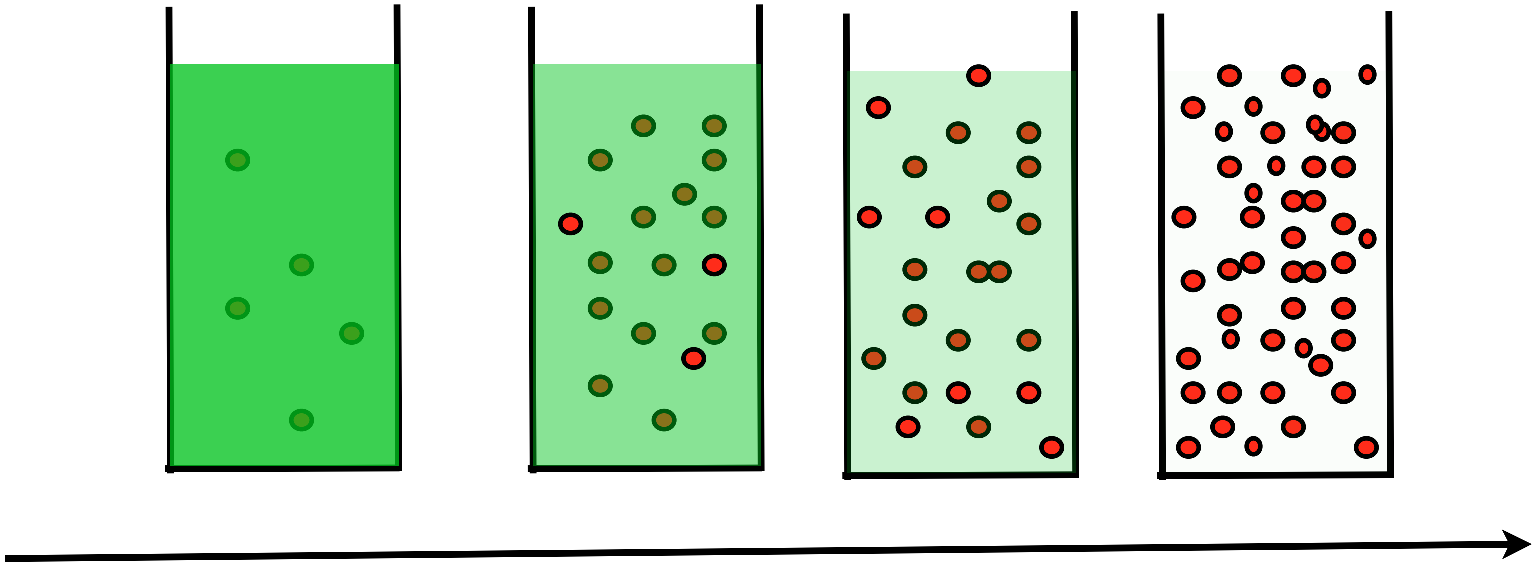
Not just simulations : uses

$$\frac{dN_T^*}{d\beta} = \frac{N_2^* - N_1^*}{B(N_1^*, N_2^*)} \times \left[\beta\left(\frac{N_1^*}{N_2^*} - \frac{N_2^*}{N_1^*}\right) + \frac{r_2}{K_2}N_2^* - \frac{r_1}{K_1}N_1^*\right]$$

$$\text{where } B(N_1, N_2) = \frac{r_1}{K_1}\frac{r_2}{K_2}N_1N_2 + \beta\left[\frac{r_1}{K_1}\frac{N_1^2}{N_2} + \frac{r_2}{K_2}\frac{N_2^2}{N_1}\right].$$



A paradoxical result



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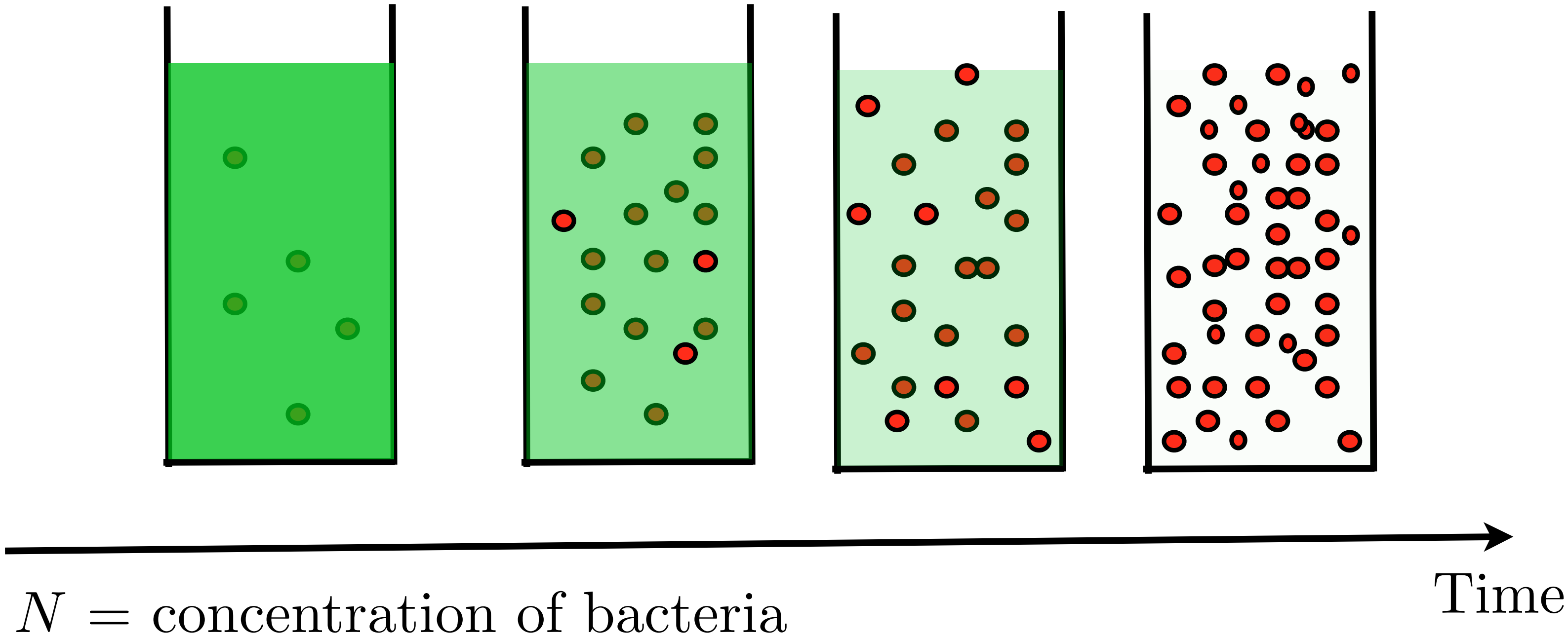


N = concentration of bacteria

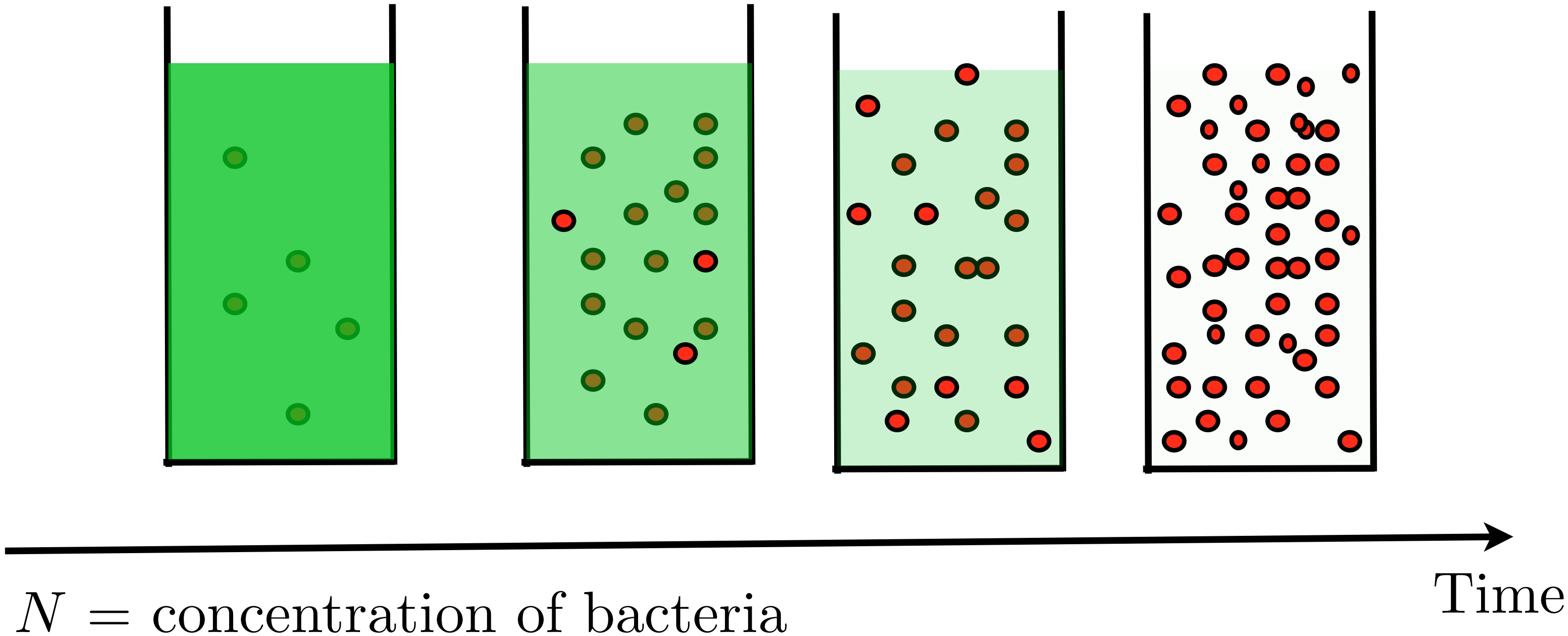
s = concentration of substrate

$$\frac{dN}{dt} = \mu N s$$

$$\frac{ds}{dt} = -\mu N s$$

$$N(t) + s(t) = cst = s(0) + N(0) = M$$

A paradoxical result

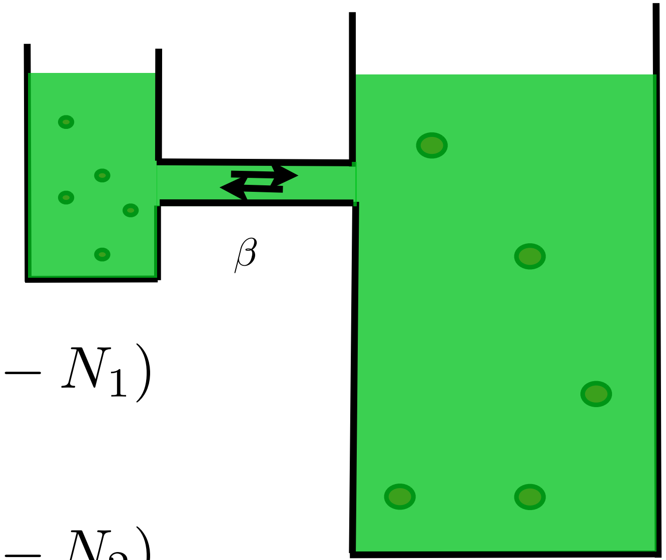


N = concentration of bacteria
s = concentration of substrate

$$\frac{dN}{dt} = \mu N\, s$$

$$\frac{ds}{dt} = -\mu N\, s \qquad \Longrightarrow \frac{dN}{dt} = \mu N(M - N) = \mu M\, N \left(1 - \frac{N}{M}\right)$$

A paradoxical result



$$\frac{dN_1}{dt} = \mu M_1 N_1 \left(1 - \frac{N_1}{M_1}\right) + \beta(N_2 - N_1)$$

$$\frac{dN_2}{dt} = \mu M_2 N_2 \left(1 - \frac{N_2}{M_2}\right) + \beta(N_1 - N_2)$$

$$N_T^* = K_1 + K_2 + \beta \frac{N_2^* - N_1^*}{\frac{r_1}{K_1}\frac{r_2}{K_2} N_1^* N_2^*} \left(\frac{r_2}{K_2} N_2^* - \frac{r_1}{K_1} N_1^*\right)$$

$$N_T^* = M_1 + M_2 + \beta \frac{N_2^* - N_1^*}{\frac{\mu M_1}{M_1}\frac{\mu M_2}{M_2} N_1^* N_2^*} \left(\frac{\mu M_2}{M_2} N_2^* - \frac{\mu M_1}{M_1} N_1^*\right)$$

$$N_T^* = M_1 + M_2 + \beta \frac{N_2^* - N_1^*}{\mu N_1^* N_2^*} (N_2^* - N_1^*) \quad > O$$

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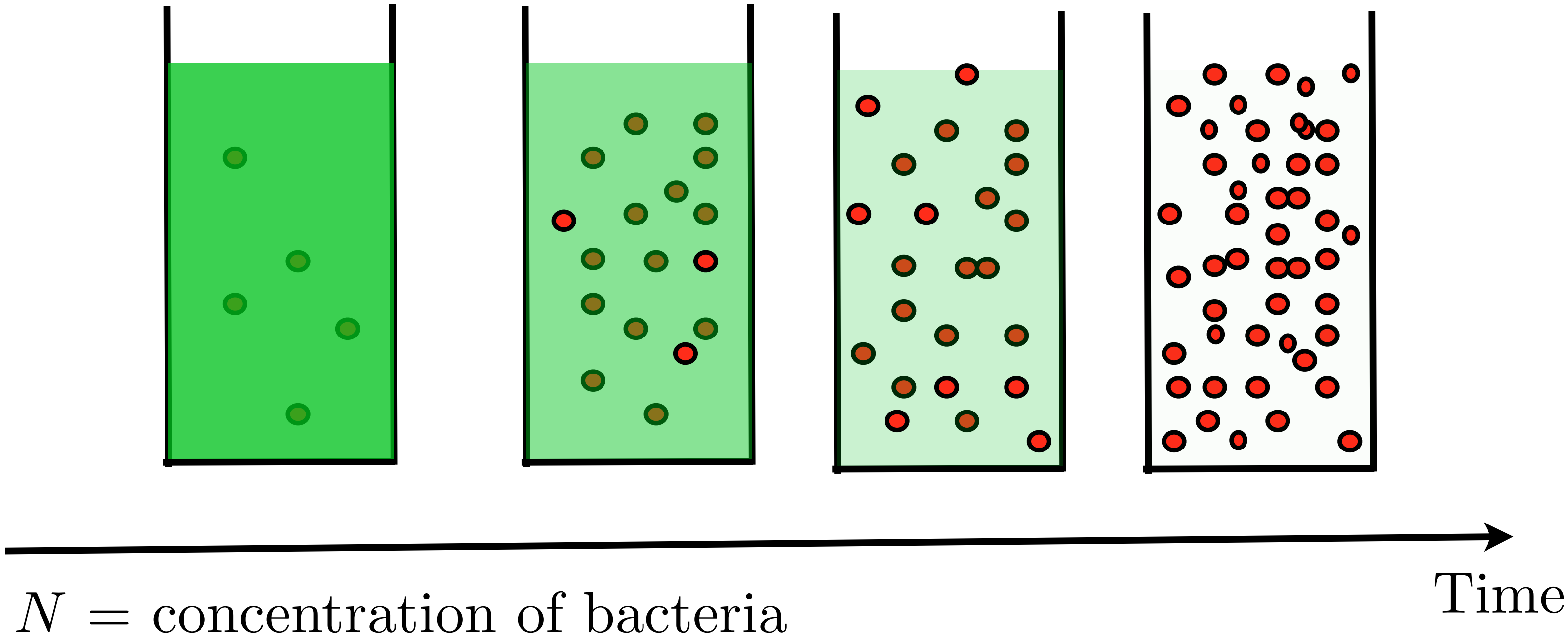
A paradoxical result



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$$\frac{ds}{dt} = -\mu N s \qquad \Longrightarrow \frac{dN}{dt} = \mu N(M-N) = \mu M N\left(1 - \frac{N}{M}\right)$$

This is a "reduced model"

A paradoxical result

The coupling of the two "reduced models"
is not a "reduced model"
of the coupling of the two models.

$$\frac{dN_1}{dt} = \mu N_1 s_1 + \beta(N_2 - N_1)$$

$$\frac{dN_2}{dt} = \mu N_2 s_2 + \beta(N_1 - N_2)$$

$$\frac{ds_1}{dt} = -\mu N_1 s_1 + \alpha(s_2 - s_1)$$

$$\frac{ds_2}{dt} = -\mu N_2 s_2 + \alpha(s_1 - s_2)$$

$$N_1 + N_2 + s_1 + s_2 = M_1 + M_2$$

$$N_1^* + N_2^* = M_1 + M_2 - (s_1^* + s_2^*)$$

$$\frac{dN_1}{dt} = \mu M_1 N_1 \left(1 - \frac{N_1}{M_1}\right) + \beta(N_2 - N_1)$$

$$\frac{dN_2}{dt} = \mu M_2 N_2 \left(1 - \frac{N_2}{M_2}\right) + \beta(N_1 - N_2)$$

A paradoxical result

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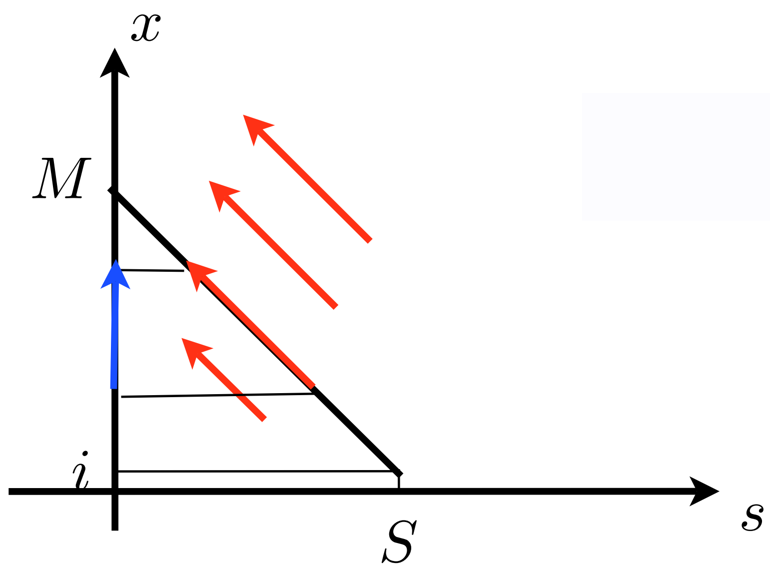

$$\frac{dN}{dt} = \mu N(M-N)$$

$$i \le N \le M$$

The true model

A paradoxical result

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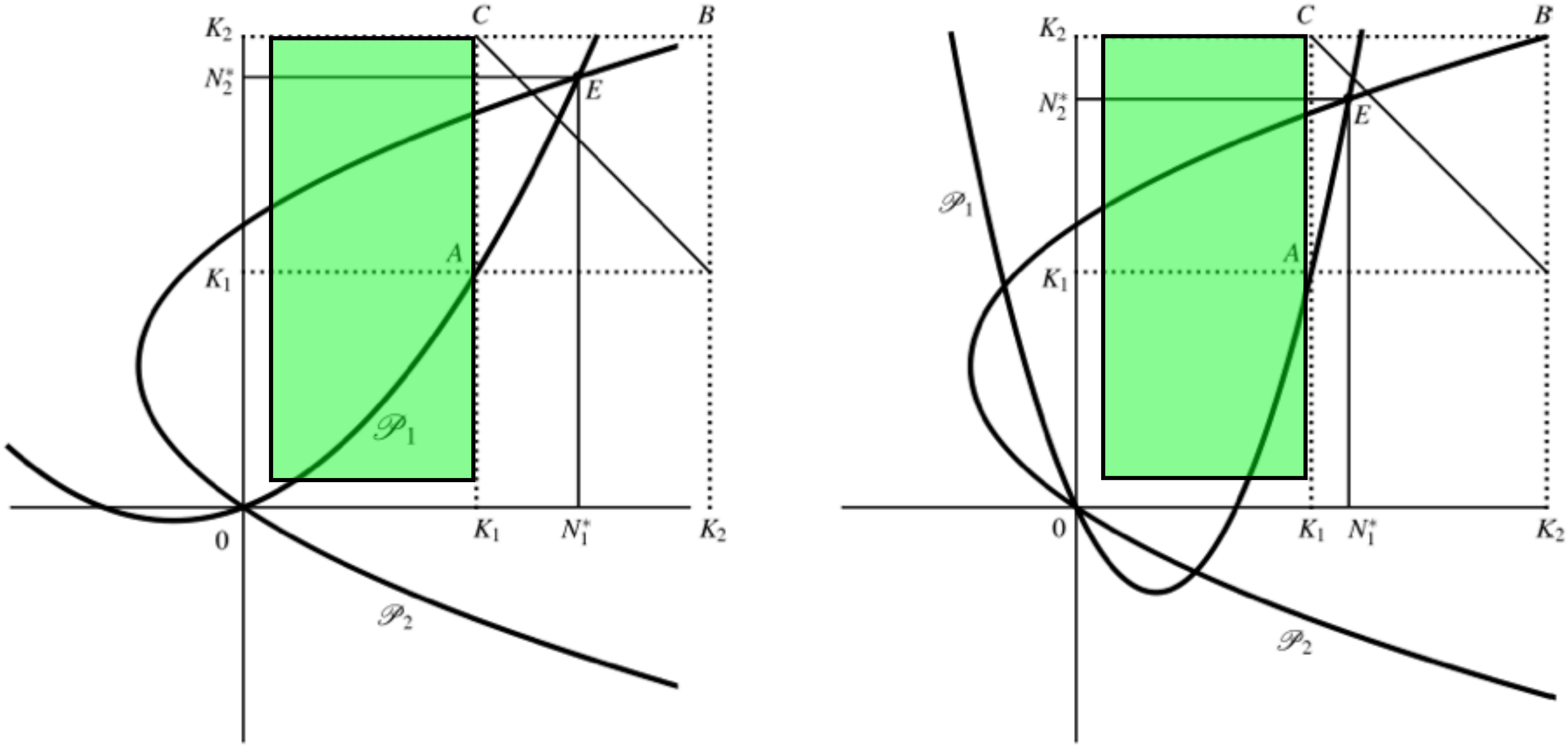

The MacArthur reduction

$$\begin{cases} \dfrac{dR}{dt} = \left[s\left(1 - \dfrac{R}{L}\right) - a\,N \right] R, \\ \dfrac{dN}{dt} = \varepsilon(a\,w\,R - q)N, \end{cases}$$

$$\varepsilon << 1$$

The MacArthur reduction

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$$\varepsilon << 1$$

$$\frac{dN}{dt} = \varepsilon\left(bL - q - \frac{ab}{s}LN\right)N$$

Logistic with : $r = \varepsilon(bL - q)$, $\quad K = \dfrac{s}{a}\,\dfrac{bL - q}{bL}$

Coupling of “reduced models”

$$\begin{cases} \dfrac{dN_1}{dt} = \varepsilon_1 \left(b_1 L_1 - q_1 - \dfrac{a_1 b_1}{s_1} L_1 N_1 \right) N_1 + \beta (N_2 - N_1), \\ \dfrac{dN_2}{dt} = \varepsilon_2 \left(b_2 L_2 - q_2 - \dfrac{a_2 b_2}{s_2} L_2 N_2 \right) N_2 + \beta (N_1 - N_2). \end{cases}$$

Coupling of “full models”

$$\begin{cases} \dfrac{dR_1}{dt} = \left[s_1 \left(1 - \dfrac{R_1}{L_1} \right) - a_1 N_1 \right] R_1 + \alpha (R_2 - R_1), \\ \dfrac{dR_2}{dt} = \left[s_2 \left(1 - \dfrac{R_2}{L_2} \right) - a_2 N_2 \right] R_2 + \alpha (R_1 - R_2), \\ \dfrac{dN_1}{dt} = \varepsilon_1 (b_1 R_1 - q_1) N_1 + \beta (N_2 - N_1), \\ \dfrac{dN_2}{dt} = \varepsilon_2 (b_2 R_2 - q_2) N_2 + \beta (N_1 - N_2). \end{cases}$$

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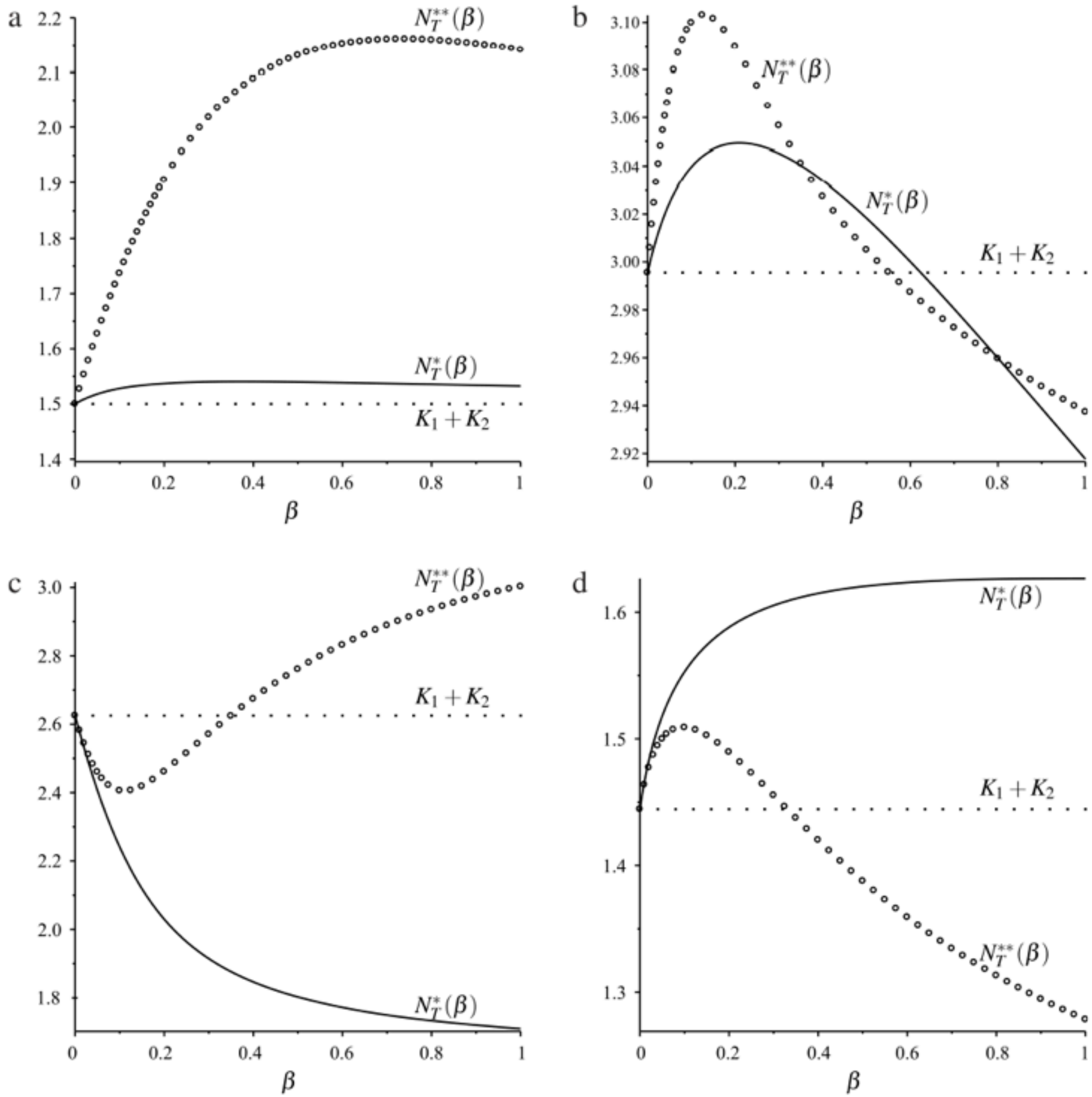
$$N_T^* = N_1^* + N_2^*, \qquad N_T^{**} = N_1^{**} + N_2^{**}.$$

$$\begin{cases} \dfrac{dR_1}{dt} = \left[s_1 \left(1 - \dfrac{R_1}{L_1} \right) - a_1 N_1 \right] R_1 + \alpha (R_2 - R_1), \\ \dfrac{dR_2}{dt} = \left[s_2 \left(1 - \dfrac{R_2}{L_2} \right) - a_2 N_2 \right] R_2 + \alpha (R_1 - R_2), \\ \dfrac{dN_1}{dt} = \varepsilon_1 (b_1 R_1 - q_1) N_1 + \beta (N_2 - N_1), \\ \dfrac{dN_2}{dt} = \varepsilon_2 (b_2 R_2 - q_2) N_2 + \beta (N_1 - N_2). \end{cases}$$

The MacArthur reduction

Analysis of the coupling of the "full model" is more complex :

- Take advantage of $\varepsilon << 1$ with a carefull use of Tychonov theorem (mathematics of quasi-steady state analysis).
- Asymptotic analysis for $\alpha,\ \beta \to \infty$
- Asymptotic analysis for $\alpha,\ \beta \to 0$
- Complete with computer simulations.



$\alpha = \beta$

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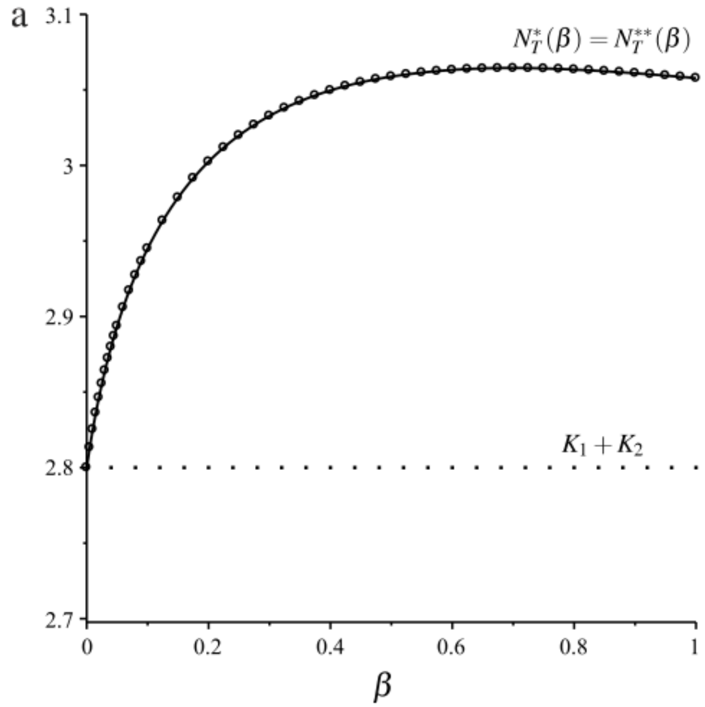
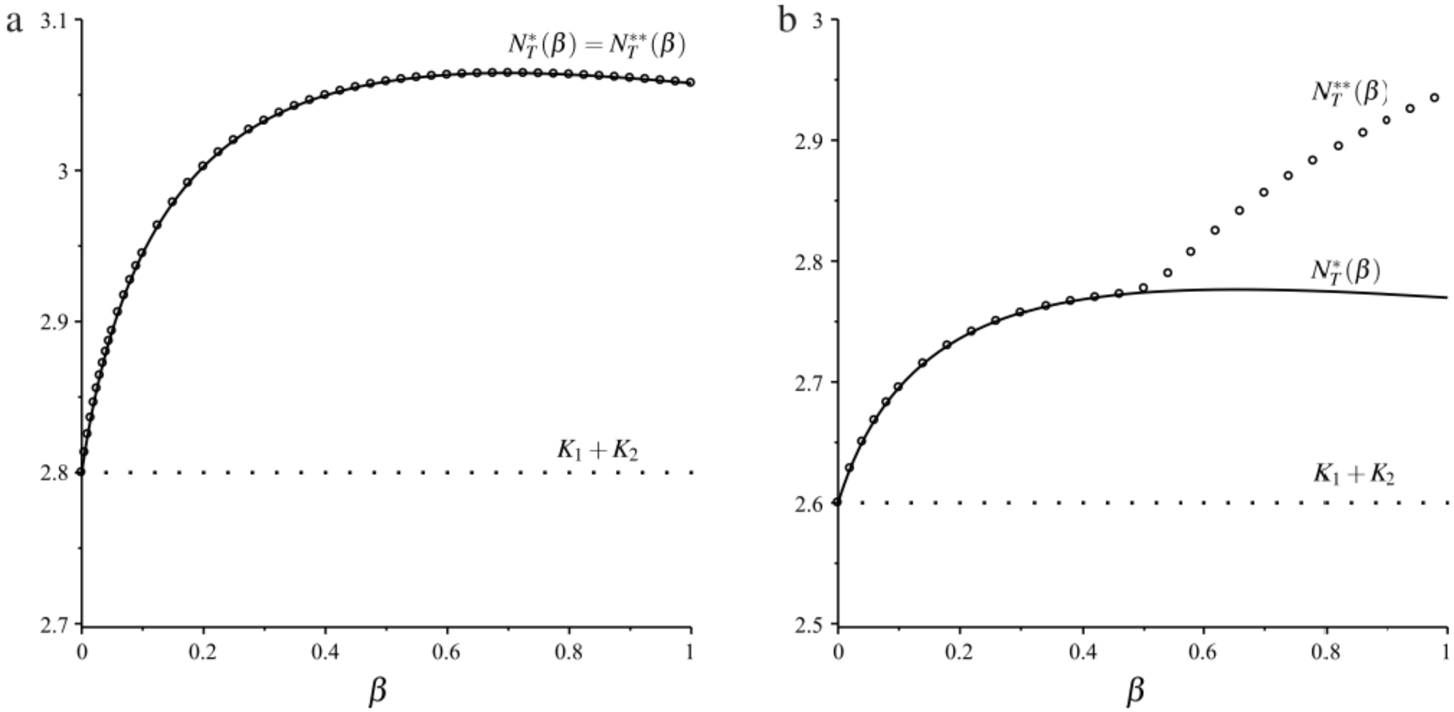


No migration of the resource

$\alpha = 0$ β Increasing



$$\alpha = 0 \qquad \beta$$

Conclusion

- Coupling "reduced models" is meaningless.
- Coupling "full models" is meaningfull.
- Reduce the coupled "full models" and analyse it.