

## COMPETITION OF FAST AND SLOW MOVERS FOR RENEWABLE AND DIFFUSIVE RESOURCE

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**ABSTRACT.** In many studies of mathematical ecology, researchers have been discussing the competition of fast and slow species in the presence of a renewable and diffusive resource. To explore this competition, most of these studies have used the Lotka-Volterra competition model with diffusion, which includes resources implicitly. A mechanistic model should explicitly incorporate resource dynamics. We construct such a resource-explicit competition model with linear or nonlinear resource uptake functions. Conclusions from our linear model are consistent with Lotka-Volterra type models: i) the fast mover is excluded and the slow mover stays at a positive constant level; ii) both go extinct. Our nonlinear model exhibits two new outcomes: iii) the fast mover is excluded and the slow mover survives at oscillations; iv) oscillatory coexistence. If we further assume the fast mover has a larger resource uptake rate than the slow mover, it is possible that v) the slow mover is excluded by the fast mover.

**1 Introduction** Movement of animals is a characteristic feature for species. The role of moving speed in species competition has been studied recently in many papers. Applying the Lotka-Volterra competition model with diffusion, previous studies showed that the slow mover excludes the fast mover after a long time [1, 2, 4]. However, it is actually possible to have the coexistence case or the case that the fast mover excludes the slow mover [3, 5, 6]. The well-known Lotka-Volterra competition model with diffusion is a phenomenological model which incorporates the effect of a resource implicitly. A better model should incorporate resource dynamics explicitly.

The main goal of this short note is to develop a mechanistic but simple model to examine the competition of fast and slow species in the presence of a renewable and diffusive resource. These two species are

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assumed to be genetically identical except for their moving speeds. The environment is assumed to be continuous but not homogeneous. Using these assumptions, we construct a resource-explicit model with linear or nonlinear resource uptake functions.

Simulations of our linear model show two cases: the fast mover goes extinct but the slow mover survives at a positive constant level, or both species go extinct. These are consistent with the previous results [2]. Simulations of our nonlinear model show two new outcomes: the fast mover goes extinct but the slow mover survives at oscillations, or both species survive at oscillations. The coexistence scenario can definitely appear in nature, thus our resource-explicit competition model with nonlinear resource uptake functions is a more realistic model than the Lotka-Volterra type models or our model with linear resource uptake functions.

**2 Models and simulations** We consider the competition of two species with different moving speeds. These two species compete for a renewal and diffusive resource, and they are genetically identical except for their diffusion coefficients. The PDE model has three variables:  $F$  (density of the fast mover),  $S$  (density of the slow mover), and  $R$  (density of renewable resource):

$$\begin{aligned}\frac{\partial F}{\partial t} &= D_1 \Delta F + [h_1(R) - \delta_1] F, \\ \frac{\partial S}{\partial t} &= D_2 \Delta S + [h_2(R) - \delta_2] S, \\ \frac{\partial R}{\partial t} &= D_3 \Delta R + R(m(x) - R) - \frac{1}{\gamma_1} h_1(R) F - \frac{1}{\gamma_2} h_2(R) S,\end{aligned}$$

where the resource uptake functions  $h_i(R)$  satisfy the conditions  $h_i(0) = 0$ ,  $h_i'(t) > 0$ , and  $h_i''(t) \leq 0$ , for example,  $h_i(R) = \alpha_i R / (k_i + R)$  or  $h_i(R) = \alpha_i R$ . Here,  $\alpha_i$ 's are maximum resource uptake rates,  $k_i$ 's are half-saturation constants for resource uptake (representing resource uptake efficiencies),  $\delta_i$ 's are mortality rates,  $\gamma_i$ 's are yield constants, and  $D_i$ 's are diffusion coefficients. According to the definitions of  $F$  and  $S$ , we should have  $D_1 \gg D_2$ . In our simulations, we apply zero flux boundary conditions. We choose the resource renewal rate (or carrying capacity) function  $m(x) = r(1 + \tanh(x - 0.5)/0.1)$  or  $r \exp((x - 0.5)^2)/0.1$  or  $r \exp(-(x - 0.5)^2)/0.1$ . The first function ( $\tanh(x - 0.5)/0.1$ ) is monotone, the second function ( $\exp((x - 0.5)^2)/0.1$ ) has its minimum in the middle, and the third function  $\exp(-(x - 0.5)^2)/0.1$  has its maximum in the middle. Environments are heterogeneous across space and time.

The function  $m(x)$  represents their natural growth rates and it reflects the quality and quantity of resources available at position  $x$ . We vary two key resource parameters  $r$  and  $D_3$  to discuss the competition results of fast and slow movers (see Tables 1–6).

We integrate both variables  $F$  and  $S$  over space to obtain the (total) densities of the two competing species. All possible competition outcomes of the (total) densities are listed below:

- $C_1 \rightarrow$  both go extinct;
- $C_2 \rightarrow$  the fast mover goes extinct but the slow mover survives at a positive constant level;
- $C_3 \rightarrow$  the fast mover goes extinct but the slow mover survives at oscillations;
- $C_4 \rightarrow$  the fast mover survives at a positive constant level but the slow mover goes extinct;
- $C_5 \rightarrow$  the fast mover survives at oscillations but the slow mover goes extinct;
- $C_6 \rightarrow$  both survives at an internal steady state;
- $C_7 \rightarrow$  both survives at oscillations.

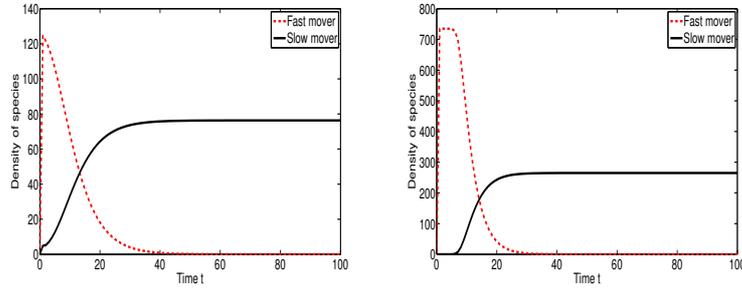
**2.1 Linear model** The model with linear resource uptake functions is mathematically tractable, especially for stability analysis. The linear resource uptake functions apply the well-mixing assumption, which is widely accepted in many biological interactions. The linear model is provided by

$$(1) \quad \begin{aligned} \frac{\partial F}{\partial t} &= D_1 \Delta F + [\alpha_1 R - \delta_1] F, \\ \frac{\partial S}{\partial t} &= D_2 \Delta S + [\alpha_2 R - \delta_2] S, \\ \frac{\partial R}{\partial t} &= D_3 \Delta R + R(m(x) - R) - \frac{1}{\gamma_1} \alpha_1 R F - \frac{1}{\gamma_2} \alpha_2 R S, \end{aligned}$$

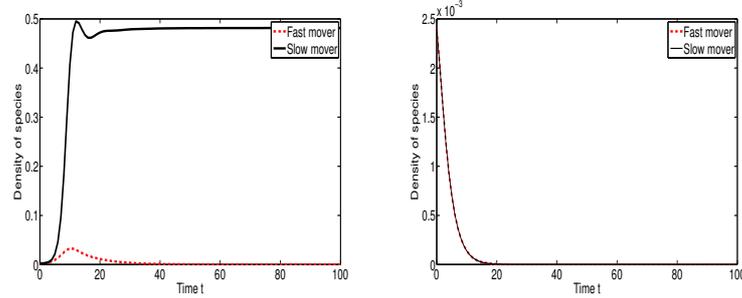
where  $m(x) = r(1 + \tanh(x - 0.5)/0.1)$ ,  $D_1 = 1$ ,  $D_2 = 0.01$ ,  $D_3 = 0.001 - 10$ ,  $\alpha_1 = \alpha_2 = 0.7$ ,  $\delta_1 = \delta_2 = 0.4$ ,  $\gamma_1 = \gamma_2 = 0.49$ , and  $r = 0.01 - 10$ .

We run a group of simulations for three different forms of the function  $m(x)$ . Comparing Figure 1(b) with Figure 1(a) for different forms of  $m(x)$ , we find that the density of the slow mover quickly increases from very beginning in panel (a), but the density of the slow mover starts to increase after a while in panel (b). The asymptotic behaviors are about the same in these two panels: the fast mover goes extinct and the slow mover survives at a positive constant level. Comparing panel (c) with

panel (a), the fast mover dominates the community in the beginning in panel (a), but when we choose smaller value for the parameter  $r$  in panel (c), the slow mover seems dominant all the time. When we choose the parameter  $r$  extremely small in the panel (d), then both species go extinct due to the shortage of resource. We vary the resource related parameters  $r$  and  $D_3$  in Tables 1–3, which provide more thorough results. From these tables, we observe that both species go extinct when  $r$  is small, while the fast mover goes extinct and slow mover survives at a positive constant level when  $r$  is large. These two outcomes are consistent to Lotka-Volterra type models [2].



(a)  $m(x) = r(1 + \tanh(x - 0.5)/0.1)$ ,  $r = 10$   
 (b)  $m(x) = r \exp((x - 0.5)^2/0.1)$ ,  $r = 10$



(c)  $m(x) = r(1 + \tanh(x - 0.5)/0.1)$ ,  $r = 1$   
 (d)  $m(x) = r(1 + \tanh(x - 0.5)/0.1)$ ,  $r = 0.1$

FIGURE 1: Plots of total density as a function of time for linear case with different values of the parameter  $r$  and different forms of the function  $m(x)$ . Chosen values of parameters are:  $D_1 = 1$ ,  $D_2 = 0.01$ ,  $D_3 = 0.001 - 10$ ,  $\alpha_1 = \alpha_2 = 0.7$ ,  $\delta_1 = \delta_2 = 0.4$ ,  $\gamma_1 = \gamma_2 = 0.49$ .

$D_3 \backslash r$	0.01	0.1	1	10
0.001	$C_1$	$C_1$	$C_2$	$C_2$
0.01	$C_1$	$C_1$	$C_2$	$C_2$
0.1	$C_1$	$C_1$	$C_2$	$C_2$
1	$C_1$	$C_1$	$C_2$	$C_2$
10	$C_1$	$C_1$	$C_2$	$C_2$

TABLE 1: Linear case with  $m(x) = r(1 + \tanh \frac{x-0.5}{0.1})$ .

$D_3 \backslash r$	0.01	0.1	1	10
0.001	$C_1$	$C_1$	$C_2$	$C_2$
0.01	$C_1$	$C_1$	$C_2$	$C_2$
0.1	$C_1$	$C_1$	$C_2$	$C_2$
1	$C_1$	$C_1$	$C_2$	$C_2$
10	$C_1$	$C_1$	$C_2$	$C_2$

TABLE 2: Linear case with  $m(x) = r \exp[\frac{(x-0.5)^2}{0.1}]$ .

$D_3 \backslash r$	0.01	0.1	1	10
0.001	$C_1$	$C_1$	$C_2$	$C_2$
0.01	$C_1$	$C_1$	$C_2$	$C_2$
0.1	$C_1$	$C_1$	$C_1$	$C_2$
1	$C_1$	$C_1$	$C_1$	$C_2$
10	$C_1$	$C_1$	$C_1$	$C_2$

TABLE 3: Linear case with  $m(x) = r \exp[-\frac{(x-0.5)^2}{0.1}]$ .

Because the resource equation has faster dynamics than the equations of the competing species, we apply the quasi-steady state approximation to obtain

$$R = k(x) - \frac{r}{\gamma}(F + S)$$

which implies

$$\begin{aligned}\frac{\partial F}{\partial t} &= D_1 F_{xx} + \left( rk(x) - d - \frac{r^2}{\gamma} F - \frac{r^2}{\gamma} S \right) F, \\ \frac{\partial S}{\partial t} &= D_2 S_{xx} + \left( rk(x) - d - \frac{r^2}{\gamma} F - \frac{r^2}{\gamma} S \right) S.\end{aligned}$$

This is the same model as the Lotka-Volterra competition model with diffusion [2]. Hence, the results of our linear model are qualitatively same as Lotka-Volterra type models.

**2.2 Nonlinear model** The linear resource uptake function tends to infinity as the resource availability tends to infinity. This is obviously unrealistic. The Monod function gives a saturation level of the resource uptake function when the resource availability is sufficiently high. This nonlinear nutrient uptake function can lead to more realistic predictions. The nonlinear model is provided by

$$\begin{aligned}(2) \quad \frac{\partial F}{\partial t} &= D_1 \Delta F + \left[ \frac{\alpha_1 R}{k_1 + R} - \delta_1 \right] F, \\ \frac{\partial S}{\partial t} &= D_2 \Delta S + \left[ \frac{\alpha_2 R}{k_2 + R} - \delta_2 \right] S, \\ \frac{\partial R}{\partial t} &= D_3 \Delta R + R(m(x) - R) - \frac{1}{\gamma_1} \frac{\alpha_1 R}{k_1 + R} F - \frac{1}{\gamma_2} \frac{\alpha_2 R}{k_2 + R} S,\end{aligned}$$

where  $m(x) = r(1 + \tanh(x - 0.5)/0.1)$ ,  $D_1 = 1$ ,  $D_2 = 0.01$ ,  $D_3 = 0.001 - 10$ ,  $\alpha_1 = \alpha_2 = 0.7$ ,  $\delta_1 = \delta_2 = 0.4$ ,  $\gamma_1 = \gamma_2 = 0.49$  and  $r = 0.01 - 10$ .

We simulate the ODE Case in (Figure 3) with high and low resource renewal rates. The movers (without moving in this case) always go extinct.

We plot representative simulation results for the nonlinear model in Figure 2. If we fix  $r$  and increase  $D_3$  from the panel (a) to panel (b), we have the transition from the case when the fast mover goes extinct and the slow mover survives at oscillations, to the oscillatory coexistence case. If we fix  $D_3$  and increase  $r$  from panel (c) to panel (d), we have a transition from the extinction case to the case when the fast mover goes extinct and the slow mover survives at a positive constant level.

We vary  $r$  and  $D_3$  for different forms of the function  $m(x)$  in Tables 4–6, which provide more thorough results. When we choose the monotone

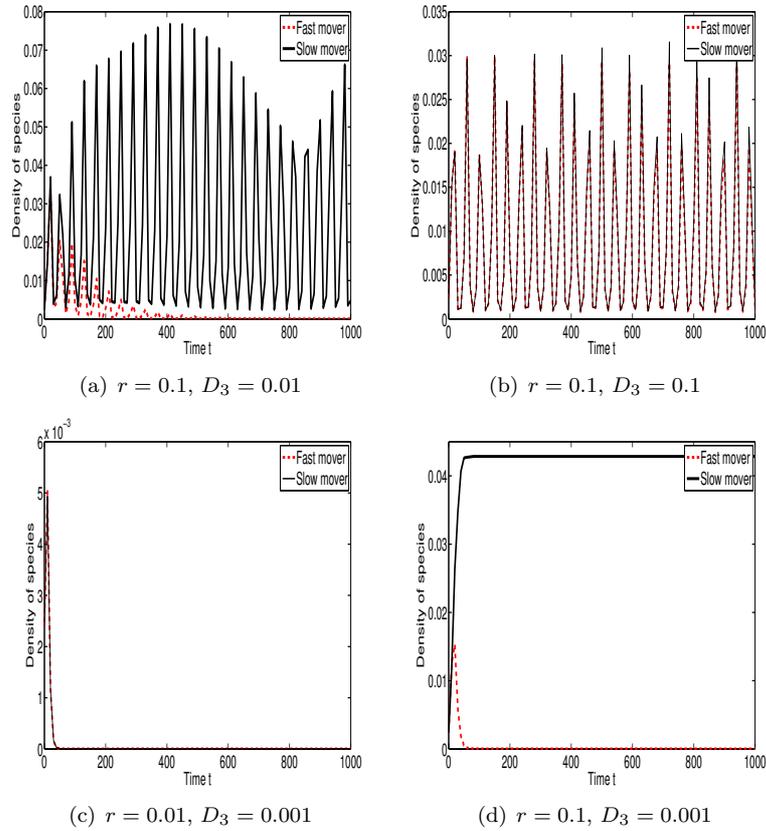


FIGURE 2: Plots of total density as a function of time for nonlinear case with different values of  $r$  and  $D_3$ . Chosen values are  $D_1 = 1, D_2 = 0.01, D_3 = 0.001 - 10, \alpha_1 = \alpha_2 = 0.7, \delta_1 = \delta_2 = 0.4, k_1 = k_2 = 0.06, \gamma_1 = \gamma_2 = 0.49$ .

$m(x)$ , the possible outcomes are same as the linear model or Lotka-Volterra type models. When we choose the other two types of  $m(x)$  (min or max in the middle), the nonlinear model leads to two new outcomes: the fast mover goes extinct and the slow mover survives at oscillations, or both survive at oscillations. These new observations seem to occur in the intermediate values of  $r$  (between 0.1 and 1). These possibilities can never be obtained from the linear model or Lotka-Volterra type models.

$D_3 \backslash r$	0.01	0.1	1	10
0.001	$C_1$	$C_2$	$C_1$	$C_1$
0.01	$C_1$	$C_2$	$C_1$	$C_1$
0.1	$C_1$	$C_2$	$C_1$	$C_1$
1	$C_1$	$C_2$	$C_1$	$C_1$
10	$C_1$	$C_2$	$C_1$	$C_1$

TABLE 4: Nonlinear case with  $m(x) = r(1 + \tanh \frac{x-0.5}{0.1})$ .

$D_3 \backslash r$	0.01	0.1	1	10
0.001	$C_1$	$C_2$	$C_2$	$C_2$
0.01	$C_1$	$C_3$	$C_2$	$C_2$
0.1	$C_1$	$C_7$	$C_1$	$C_2$
1	$C_1$	$C_7$	$C_1$	$C_1$
10	$C_1$	$C_7$	$C_1$	$C_1$

TABLE 5: Nonlinear case with  $m(x) = r \exp[\frac{(x-0.5)^2}{0.1}]$ .

$D_3 \backslash r$	0.01	0.1	1	10
0.001	$C_1$	$C_1$	$C_3$	$C_2$
0.01	$C_1$	$C_1$	$C_3$	$C_1$
0.1	$C_1$	$C_1$	$C_7$	$C_1$
1	$C_1$	$C_1$	$C_7$	$C_1$
10	$C_1$	$C_1$	$C_7$	$C_1$

TABLE 6: Nonlinear case with  $m(x) = r \exp[-\frac{(x-0.5)^2}{0.1}]$ .

Following the same logic as in the linear model, we apply the quasi-steady state approximation to obtain

$$m(x) - R = \frac{1}{\gamma} \left( \frac{\alpha F}{k + R} + \frac{\alpha S}{k + R} \right)$$

which implies

$$R^2 + (k - m(x))R + \left( \frac{\alpha}{\gamma} (F + S) - m(x)k \right) = 0$$

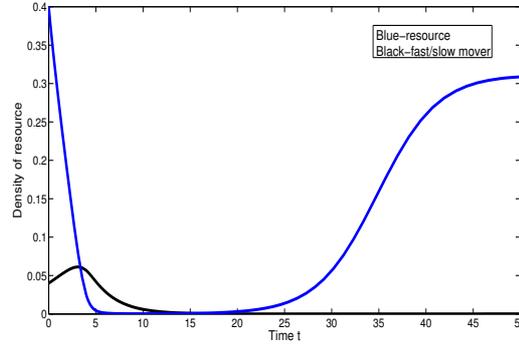
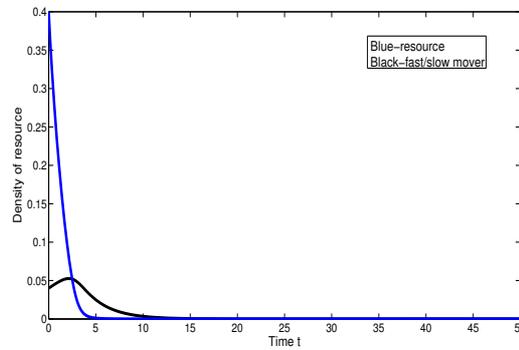
(a)  $r = 0.1, D_1 = D_2 = 0$ (b)  $r = 0.01, D_1 = D_2 = 0$ 

FIGURE 3: ODE case. Chosen values are  $D_1 = 0, D_2 = 0, D_3 = 0,$   
 $\alpha_1 = \alpha_2 = 0.7, \delta_1 = \delta_2 = 0.4, k_1 = k_2 = 0.06, m=3.12228 r.$

whose roots are

$$R = \frac{m(x) - k \pm \sqrt{(k - m(x))^2 - 4\left(\frac{\alpha}{\gamma}(F + S) - m(x)k\right)}}{2}.$$

If we replace  $R$  with one of these roots in the first two equations of the model (2), we will obtain a very complicated model that is quite different from the Lotka-Volterra competition model with diffusion [2]. This is kind of one way to explain the appearance of the two new outcomes from the nonlinear model.

In addition, we consider a special case for the effect of the consumption function  $h_i$  in the nonlinear model. First we plot the solution for resource without being eaten (consumption function  $h_1 = h_2 = 0$ ) (Figure 4), then we plot the solution with resource being eaten by only the fast mover or only the slow mover or both to see the outcomes (Figure 5).

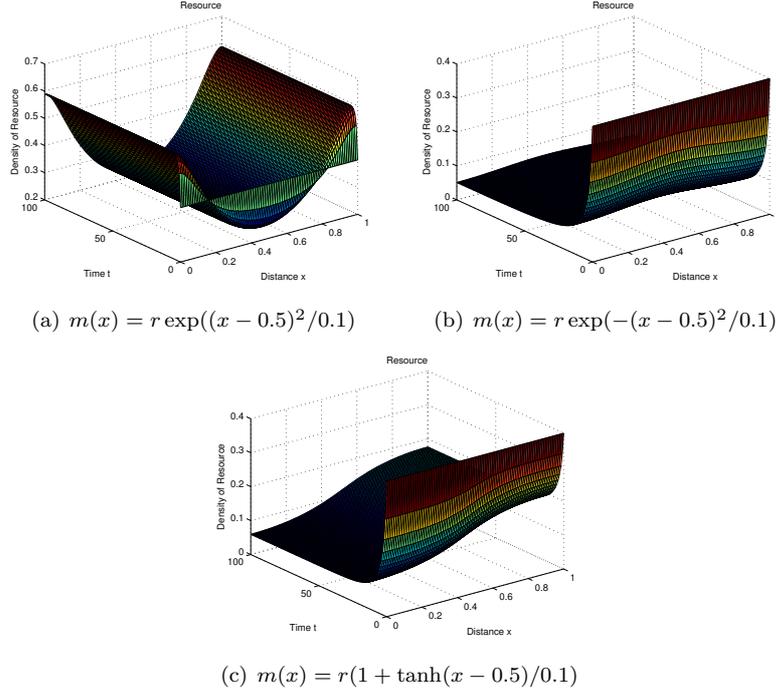
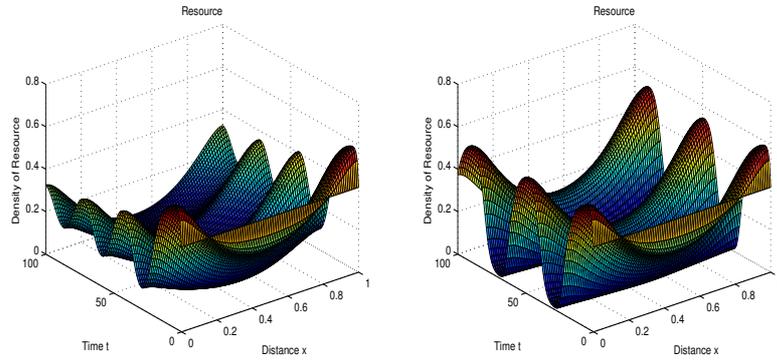
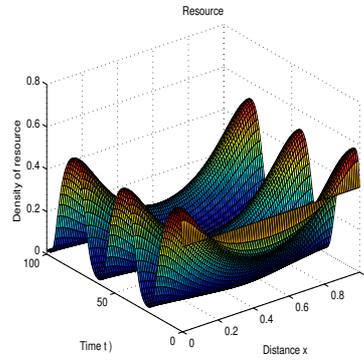


FIGURE 4: Resource without being eaten by fast and slow movers ( $h_1 = h_2 = 0$ ) along space and time for different  $m(x)$ . Chosen values are  $D_1 = 1$ ,  $D_2 = 0.01$ ,  $D_3 = 0.01$ ,  $\alpha_1 = \alpha_2 = 0.7$ ,  $\delta_1 = \delta_2 = 0.4$ ,  $k_1 = k_2 = 0.06$ .

**2.3 Nonsymmetric resource uptake rates** The fast mover has higher energy cost, which leads to higher resource uptake rate than the slow mover, that is,  $\alpha_1 > \alpha_2$ . We apply this nonsymmetric nutrient uptake rates for the linear model in Figures 6 and 7. Figure 6 shows the new outcome that the fast mover survives at a positive constant level



(a) Resource and fast mover ( $h_2 = 0$ )    (b) Resource and slow mover ( $h_1 = 0$ )



(c) Resource, fast mover and slow mover

FIGURE 5: Resource being eaten by (a) only fast mover, (b) only slow mover, (c) both. Chosen values are  $D_1 = 1$ ,  $D_2 = 0.01$ ,  $D_3 = 0.01$ ,  $\alpha_1 = \alpha_2 = 0.7$ ,  $\delta_1 = \delta_2 = 0.4$ ,  $k_1 = k_2 = 0.06$ ,  $\gamma_1 = \gamma_2 = 0.49$ ,  $r = 0.1$   $m(x) = r \exp((x - 0.5)^2/0.1)$ .

and the slow mover goes extinct. In Figure 7, we vary  $\alpha_1$  from  $\alpha_2 (= 0.7)$  to 1.8. The switch occurs at  $\alpha_1 = 1.1$  from the case the slow mover wins to the case the fast mover wins. For the nonlinear model, we can see the similar switch as the linear model, although the fast mover can survive not only at a positive constant level but also at oscillations.

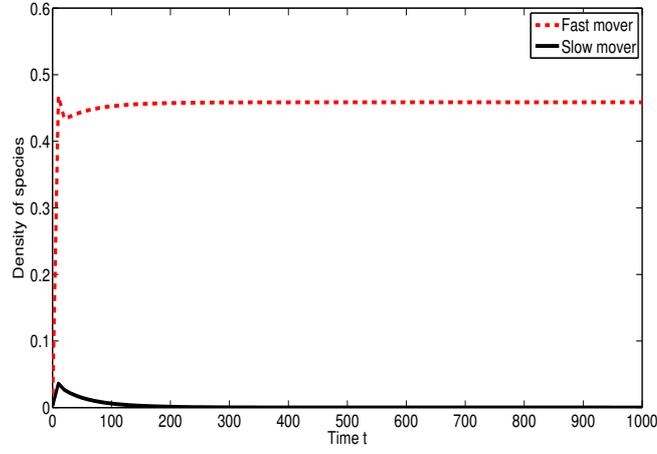


FIGURE 6: Nonsymmetric resource uptake rates  $\alpha_1 > \alpha_2$  with  $r = 1$ ,  $D_3 = 0.01$ .

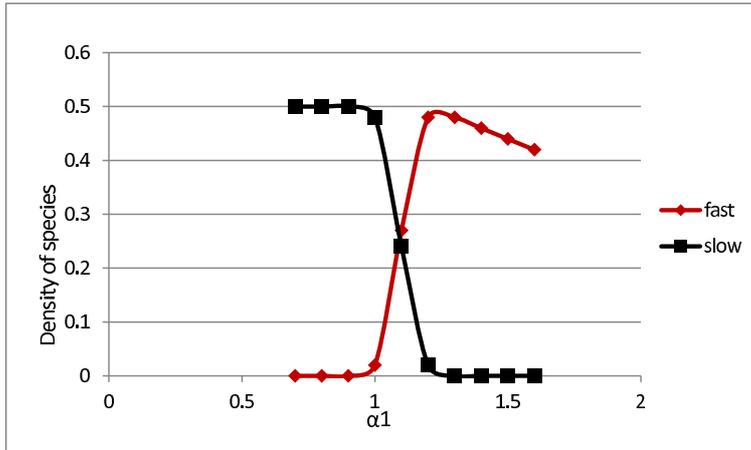


FIGURE 7: Bifurcation diagram with  $m(x) = r(1 + \tanh(x - 0.5)/0.1)$ ,  $r = 1$ ,  $D_3 = 0.01$ .

**3 Discussion** For the competition of fast and slow movers for renewable and diffusive resource, Lotka-Volterra type models only suggest two possibilities: the slow mover excludes the fast mover or both species go extinct. Our linear mechanistic model shows similar results. Our nonlinear mechanistic model, a more realistic framework, suggests two new possibilities: the slow mover excludes the fast mover in oscillatory way or both species coexist in oscillatory way. If the nutrient uptake rate of the fast mover is larger than that of the slow mover, it is possible for the fast mover to exclude the slow mover. The possibility that the fast mover wins can also be caused by stochasticity (extinction of the slower mover in the early stage) or predation (the slow mover is easier to be caught by predators). In our model, results are obtained by the differences in the diffusion rates ( $D_i$ ) because the per-capita rates ( $h_i$ ) of increase are same for both species. In reality the winner should be those who eat and grow fast but not run fast since  $R$  is diffusive.

Our results are independent of the form of the scalar function  $m(x)$ , as long as it is not constant. Therefore, the function  $m(x)$  is not important since  $R$  is diffusive. When the function  $m(x)$  is a constant function (degenerate case), we can observe that both species survive at steady state. This result is a new possibility. We do not provide any simulation of this in the paper because we assume a nonhomogeneous environment. When the parameter  $r$  is large, we have accuracy problems to run the simulation program.

In future, we plan to run simulations for mechanistic models on higher dimensional space. Mathematical results of the proposed models need to be done. Specific species should be discussed later for data fitting. In addition, we will expand our models to incorporate species' resting stage, which may provide more possibilities for the competition results.

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