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Léo Girardin. The effect of random dispersal on competitive exclusion – A review. 2019. hal-02153631v2

HAL Id: hal-02153631

<https://hal.science/hal-02153631v2>

Preprint submitted on 11 Sep 2019 (v2), last revised 11 Feb 2020 (v4)

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THE EFFECT OF RANDOM DISPERSAL ON COMPETITIVE EXCLUSION – A REVIEW

LÉO GIRARDIN

ABSTRACT. Does a high dispersal rate provide a competitive advantage when risking competitive exclusion? To this day, the theoretical literature cannot answer this question in full generality. The present paper focuses on the simplest mathematical model with two populations differing only in dispersal abilities and whose one-dimensional territories are spatially segregated. Although the motion of the border between the two territories remains elusive in general, all cases investigated in the literature concur: either the border does not move at all because of some environmental heterogeneity or the fast diffuser chases the slow diffuser. Counterintuitively, it is better to randomly explore the hostile enemy territory, even if it means highly probable death of some individuals, than to “stay united”. This directly contradicts a celebrated result on the intermediate competition case, emphasizing the importance of the competition intensity. Overall, the larger picture remains unclear and the optimal strategy regarding dispersal remains ambiguous. Several open problems worthy of a special attention are raised.

1. INTRODUCTION

The interplay between dispersion and competition is a vast and important problem in theoretical population biology, with applications in ecology but also in evolution (natural selection precisely originates in the interplay between competitive pressure and mutations, namely “dispersion” in the phenotypical space), epidemiology (competition between pathogen strains during spreading epidemics), medicine (populations being in this context cell populations). This interplay leads to qualitative outcomes (displacement, segregation, etc.) that would not appear in the spatially homogeneous, well-mixed counterpart, which makes them difficult to predict. But such predictions are of the utmost importance, especially since these outcomes usually result in some form of spatialized extinction process, which could be a goal or on the contrary something to be avoided, depending on the exact biological problem. An exhaustive overview of the biology and mathematical biology literature on this wide topic is of course impossible; the reader is referred for instance to some recent works and references therein [3, 13, 19, 27, 56, 60, 62, 65].

A common phenomenological mathematical model to study this interplay, inspired by the general population dynamics equation:

$$\text{variation in time of the population size} = \text{dispersion} + \text{births} - \text{deaths},$$

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2010 Mathematics Subject Classification. 35K40, 35K57, 92D25.

Key words and phrases. Lotka–Volterra, competition–diffusion system, bistability, traveling wave.

This work was supported by a public grant as part of the Investissement d’avenir project, reference ANR-11-LABX-0056-LMH, LabEx LMH. This work has been carried out in the framework of the NONLOCAL project (ANR-14-CE25-0013) funded by the French National Research Agency (ANR).

is the deterministic, diffusive and competitive Lotka–Volterra system [32, 51, 76]:

$$\begin{cases} \partial_t N_1 &= \nabla \cdot (d_1 \nabla N_1) + r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - c_1 N_1 N_2, \\ \partial_t N_2 &= \nabla \cdot (d_2 \nabla N_2) + r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - c_2 N_1 N_2, \end{cases}$$

where $N_1(t, x) \geq 0$ and $N_2(t, x) \geq 0$ are two continuous population densities depending on time t (a real variable) and space x (a Euclidean variable $x = (x_1, x_2, \dots)$), $\partial_t = \frac{\partial}{\partial t}$ is the partial derivative with respect to time, $\nabla = (\partial_{x_1}, \partial_{x_2}, \dots)$ is the nabla operator (so that $\nabla \bullet$ is the spatial gradient and $\nabla \cdot \bullet$ is the spatial divergence), $d_1(t, x)$ and $d_2(t, x)$ are the diffusion (dispersal) rates, $r_1(t, x)$ and $r_2(t, x)$ are the intrinsic (per capita) growth rates, $K_1(t, x) \geq 0$ and $K_2(t, x) \geq 0$ are the carrying capacities, $c_1(t, x) \geq 0$ and $c_2(t, x) \geq 0$ are the interpopulation competition rates. The dependencies on time and space of the various coefficients account for instance for seasonality or unfavorable regions of space.

Note that in absence of one population, the other grows logistically (no Allee effect) and its density solves the well-known Fisher–Kolmogorov–Petrovskii–Piskunov partial differential equation (PDE) [29, 50, 72]:

$$\partial_t N_i = \nabla \cdot (d_i \nabla N_i) + r_i N_i \left(1 - \frac{N_i}{K_i}\right).$$

Note also that the paper adopts an ecology vocabulary for the sake of simplicity but, again, the model is abstract and quite general: “individuals” could be cancer cells or infected hosts, etc.

Assuming for a moment that the environment is spatio-temporally homogeneous (heterogeneous environments will come back later on), all the coefficients become positive constants and space, time and the two population densities can be nondimensionalized to obtain the reduced system:

$$(1) \quad \begin{cases} \partial_t u = \Delta u + u(1 - u) - huv, \\ \partial_t v = d\Delta v + rv(1 - v) - kuv, \end{cases}$$

where d, r, h, k are positive constants that can be estimated using field data and where the Fickian diffusion operator reduces to the simpler spatial Laplacian (corresponding to isotropic Brownian motion of individuals). Such a PDE system has indeed been used and discussed extensively for more than fifty years by modelers in biology. A non-exhaustive list illustrating the variety of biological applications includes for instance studies on the competitive displacement of the red squirrel by the invasive grey squirrel in the British Isles [61], optimization of cancer therapy taking into account the competition between cancer cells that are sensitive to the treatment and those that are resistant to it [20, 21], biodiversity conservation in fire-prone savannas accounting for competition for light and nutrients between trees and grass [78], reproduction–dispersion trade-offs in experimental bacterial invasions used to study the evolution of dispersal [23].

This synthesis is concerned with results investigating whether the population v , in order to outcompete the population u , should have a high or low dispersal rate d , all else being equal. Here, all else being equal means that the two populations only differ in dispersal rate, namely $r = 1$ and $h = k$:

$$(2) \quad \begin{cases} \partial_t u = \Delta u + u(1 - u) - kuv, \\ \partial_t v = d\Delta v + v(1 - v) - kuv. \end{cases}$$

The symmetry assumption ($h = k$ and $r = 1$) prevents pure reaction-driven extinctions that would strongly perturb the analysis (in other words, cases where, for instance, one competitor feels much less pressure than the other and might prevail despite a poorly chosen dispersal strategy are discarded). This assumption will

simplify a lot the forthcoming presentation, although many results actually remain true under specific, yet more general, assumptions on h and r .

In spatially homogeneous, well-mixed cases, the system (2) is strongly determined by the sign of $k - 1$ (e.g., [45, Chapter 7, Section 7.9]). On one hand, in the weak competition case ($k < 1$), the system is systematically driven to coexistence. On the contrary, in the strong competition case ($k > 1$), both populations are able to wipe out the other provided they are numerically sufficiently superior. The intermediate case ($k = 1$), corresponding to a competitive pressure exerted completely blindly, is degenerate (all pairs (u, v) satisfying $u + v = 1$ are steady states) and is usually discarded. Note that “blind” competition means here that one individual competes uniformly with all surrounding individuals, independently of the population to which they belong; the population label of competitors is in some sense not seen, not taken into account.

In spatially structured systems, the picture is more complicated. A very important paper of mathematical biology, due to Dockery, Hutson, Mischaikow and Pernarowski [24], established that the blind competition case $k = 1$ becomes relevant in spatially heterogeneous environments with an intrinsic growth rate $a(x)$:

$$\begin{cases} \partial_t u = \Delta u + u(a - u) - uv, \\ \partial_t v = d\Delta v + v(a - v) - uv. \end{cases}$$

Assuming that the domain where the populations evolve is bounded with no-flux boundary conditions (say, an island or a Petri dish), the authors showed that v wipes out u whenever it is the slower diffuser, $d < 1$. Of course, by symmetry, u wipes out v if $d > 1$. This was interpreted as follows: because of the interplay between heterogeneity and competition, it is a better strategy to claim favorable areas and to defend them collectively by remaining concentrated there than to randomly explore unfavorable areas, where deaths due to the environment are more likely. In other words, v wins if and only if, compared to u , its individuals remain “united” instead of venturing alone in unknown areas. In the present paper, such a result is referred to as a “Unity is strength”-type result. The analysis of Dockery *et al.* relied entirely upon the monostability of the system induced by the combination of spatial heterogeneity and difference in diffusion rates: the only stable steady state is the one where the slow diffuser persists while the fast diffuser vanishes. Initial conditions do not matter: even if, initially, the fast diffuser is vastly superior numerically, the slow diffuser will eventually prevail.

But what if both semi-extinct steady states are stable, so that the stability analysis does not suffice to conclude and initial conditions matter? As explained above, bistability is for instance achieved in spatially homogeneous systems (2) with strong competition ($k > 1$). With such systems, the success of a dispersal strategy is a more delicate notion that can be defined in a few ways.

For instance, the diffusion-induced extinction property could be used to define this success. This criterion uses initial conditions that are exactly calibrated so that neither u nor v takes over in the absence of diffusion or with equal diffusion rates ($d = 1$). Given such initial conditions, what is the outcome when taking the unequal diffusion into account? In homogeneous environments, where this balance condition simply reads $u(0, x) = v(0, x)$ at every x , and provided the habitat is one-dimensional with no-flux boundary conditions and the interpopulation competition rate k is equal to 2, Ninomiya [58] showed that there exist values of d larger than 1 but close to it and carefully chosen initial conditions satisfying the above condition such that v wipes out u . The fast diffuser prevails: in this sense, “Unity is not strength” (one could even say “Disunity is strength”).

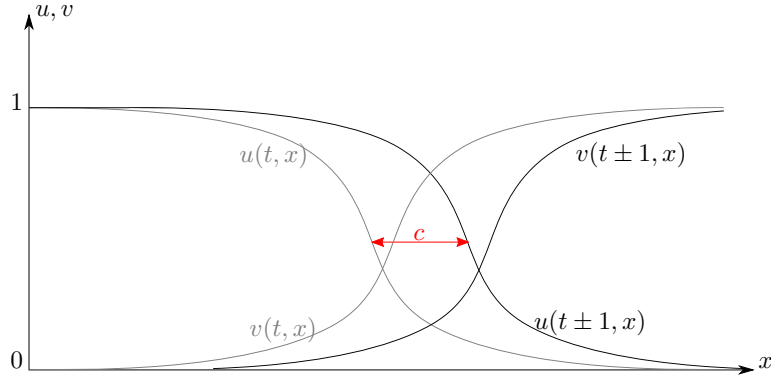


FIGURE 1. Bistable traveling wave solution of the system (2) with speed c . Depending on the sign of c , the black curves correspond to the time $t + 1$ or $t - 1$.

Nevertheless, this definition of success is unsatisfying, as it uses very precise initial conditions that are in some sense artificial and would not appear in the nature. Is there a more robust and natural definition (that might *a priori* disagree with the conclusions of Ninomiya [58] and agree with those of Dockery *et al.* [24])?

The strong competition case $k > 1$ is also known in the mathematical ecology literature as the competitive exclusion case [32]: persistence of both species can occur only if the two niches are differentiated. In the setting of this paper, niches are purely geographical, and their differentiation means that, roughly speaking, u is positive where v is close to 0 and vice-versa (note the sharp contradistinction with Ninomiya's balance condition $u(0, x) = v(0, x)$). If the territories are segregated, then borders between these territories naturally arise. At these interfaces, the two populations meet frequently and individuals compete fiercely to chase competitors and take over. In this context, it seems natural to track the motion of the interface and to define a dispersal strategy as successful if it leads to taking over the territory of the opponent, namely to territorial expansion.

This definition agrees with situations studied in the biological literature (*e.g.*, [13, 15, 16, 57]).

Mathematically, this definition translates in homogeneous environments into the study of a particular solution of the system (2), referred to as a traveling wave, that has a constant profile and a constant speed and evolves in the infinite real line (approximating a very large one-dimensional domain where propagation phenomena matter). This solution is illustrated in Figure 1. Its existence and its uniqueness were confirmed in the '80s and '90s [30, 46, 75]. In this context, the success of the dispersal strategy is simply given by the sign of the speed of the wave. However, in contrast with the existence and uniqueness of the wave, this sign is in general a very difficult mathematical problem, that cannot be solved by any standard tool of the analysis of PDEs. Only partial results are known and these are the main topic of this synthesis paper. It turns out that they are all in agreement with Ninomiya [58]: in situations of competitive exclusion due to strong interpopulation competition, "Unity is not strength".

The paper is organized as follows. Section 2 gives an exhaustive survey of these partial results, the last subsection being devoted to a delicate extension in spatially periodic media. Section 3 lists some open problems that should, in my opinion, attract the attention of the community.

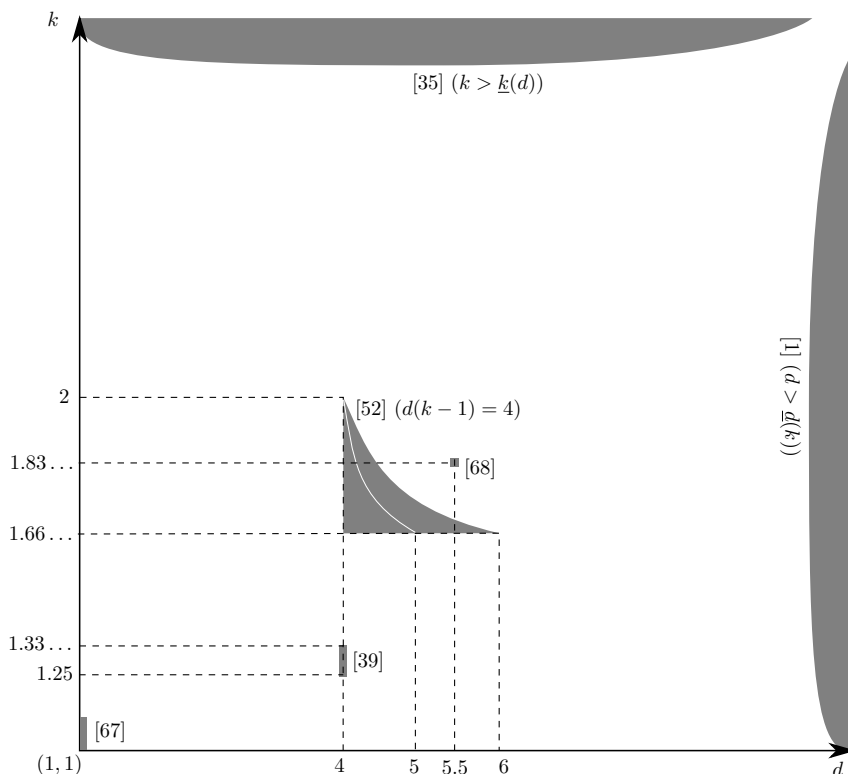


FIGURE 2. Localization in the (d, k) plane of the known results for the sign of the traveling wave speed. Shaded areas: $c_{k,d} < 0$; white areas: unknown sign; on the k axis: $c_{k,1} = 0$. The (in)equations describe the non-straight lines.

2. KNOWN RESULTS

In this section the known results are presented.

2.1. Homogeneous environment. In this subsection the focus is on homogeneous environments (constant coefficients), so that the system is (2) and the interesting solution is indeed the traveling wave solution of Figure 1. Its speed is denoted $c_{k,d}$. By symmetry and without loss of generality, the assumption $d > 1$ stands, so that “Unity is strength” holds true if and only if $c_{k,d} > 0$.

Note that the opposite invasion (u on the right, v on the left, with speed $\tilde{c}_{k,d} = -c_{k,d}$) could be considered and is in fact the one considered in some of the forthcoming references. Without loss of generality, the only case considered hereafter is that of Figure 1.

All these results are summarized in Figure 2.

2.1.1. Very special choices of parameters. In 2001, Rodrigo and Mimura [68] computed nine exact families of traveling wave solutions of the system (1) by looking for closed-form solutions (a hyperbolic tangent ansatz) and compatibility conditions on the parameters d, r, h, k . A comparison of their results with the symmetry assumption ($r = 1, h = k$) yields

$$c_{11/6,11/2} = -\frac{\sqrt{6}}{12} < 0.$$

In 2013, using the strict monotonicity of the wave speed of the system (1) with respect to h and k , established in 1995 by Kan-on [46], and an analysis of the special case where the wave speed is zero, Guo and Lin [39] stated a few algebraic conditions on the parameters d, r, h, k sufficient to characterize the sign of the speed. A comparison of their results with the symmetry assumption yields

$$c_{k,4} < 0 \quad \text{if } \frac{5}{4} \leq k \leq \frac{4}{3}.$$

In 2019, using comparison arguments and super- and sub-solutions, Ma, Huang and Ou [52] obtained five new algebraic conditions on the parameters d, r, h, k sufficient to characterize the sign of the speed. With the symmetry assumption, their conditions read

$$c_{k,d} < 0 \quad \text{if } k > \frac{5}{3} \text{ and } d \in \left(4, \frac{2k}{k-1}\right) \cup \left(\frac{2k}{k-1}, \frac{4}{k-1}\right).$$

Note that the case $d = \frac{2k}{k-1}$ is not solved (see Figure 2).

2.1.2. Almost equal dispersal rates and almost blind competition. In 2017, Risler [67] investigated approximations of $c_{1+(\delta k)^2, 1+\delta d}$. It turns out that there is a singularity at $k = 1$. When $k > 1$, the wave speed is a regular function of (k, d) and, using the identity $c_{k,1} = 0$, the following third-order (in δd and δk) approximation holds true (all partial derivatives being implicitly evaluated at $(k, 1)$ for clarity):

$$c_{k+(\delta k)^2, 1+\delta d} \sim \left[\frac{\partial c}{\partial d} + \frac{1}{2} \frac{\partial^2 c}{\partial d^2} \delta d + \frac{1}{6} \frac{\partial^3 c}{\partial d^3} (\delta d)^2 + \frac{\partial^2 c}{\partial k \partial d} (\delta k)^2 \right] \delta d.$$

By a singular perturbation approach, Risler managed to prove that the quantity $\frac{1}{\delta k} \left(\frac{\partial c}{\partial d} + \frac{\partial^2 c}{\partial k \partial d} (\delta k)^2 \right)$ converges, as $k \rightarrow 1^+$, to some negative constant $A < 0$. As a consequence, in the parameter regime $0 < \delta d \ll \delta k \ll 1$ where the second and third order terms in δd can be safely ignored,

$$c_{1+(\delta k)^2, 1+\delta d} \sim -|A| \delta k \delta d < 0.$$

This result is especially interesting since, compared with the result of Dockery *et al.* [24], it shows a trade-off at $d = 1 + \delta d$, $k = 1$ between the intensity of the interpopulation competition and the heterogeneity of spatial resources. On one hand, changing the homogeneous resources into spatially heterogeneous resources $a(x) = 1 + \delta a(x)$ favors the slow diffuser u ; but on the other hand, adding a small bump in interpopulation competition $(\delta k)^2$ favors the fast diffuser v .

2.1.3. Large gap between the dispersal rates. In 2004 and 2005, Heinze *et al.* [40, 41] studied the degenerate system (1) where one of the two populations does not diffuse at all ($d = 0$). Inspired by this work, Alzahrani, Davidson and Dodds [1] studied in 2010 the strong dispersal limit $d \rightarrow +\infty$ of the system (1) (which is equivalent, up to a change of variable, to the limit $d \rightarrow 0$). In this regime and taking into account the symmetry assumption, they proved by energy methods that $c_{k,d}/\sqrt{d}$ converges to a finite limit $l_{k,\infty} \in [-2, 0)$. Consequently, for any $k > 1$, there exists $\underline{d}(k) \geq 1$ such that

$$c_{k,d} < 0 \quad \text{if } d > \underline{d}(k).$$

The variations (monotonicity, convexity) and limits as $k \rightarrow 1$ or $k \rightarrow +\infty$ of the optimal function \underline{d} are unknown. The graph of the function \underline{d} in Figure 2 is an arbitrary choice.

In 2012, the same authors published a sequel [2] where they numerically completed the picture for intermediate values of d and stated a global ‘‘Disunity is strength’’-type conjecture. This conjecture is summarized in Figure 3, which is basically an adaptation of [2, Figure 6] to the present setting and notations.

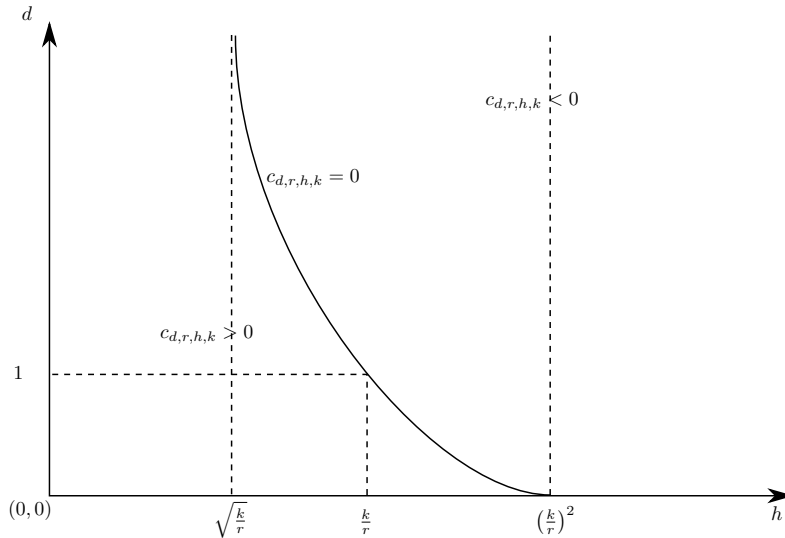


FIGURE 3. Illustration of a global “Disunity is strength”-type conjecture by Alzahrani, Davidson and Dodds [2]. Here, the parameters r and k of the system (1) are arbitrarily fixed and the traveling wave speed is studied as a function of (h, d) . The fact that it is zero at the point $(\frac{k}{r}, 1)$ is obvious; the fact that it is asymptotically zero at $(\sqrt{k/r}, +\infty)$ and $((k/r)^2, 0)$ is proved in [1]. The rest, and in particular the fact that the 0-level set is a monotone graph, is only supported by numerical experiments.

2.1.4. *Very strong interpopulation competition.* In 2015, Girardin and Nadin [35] studied the very strong competition limit $k \rightarrow +\infty$. In this regime, the two territories are completely segregated ($uv = 0$ everywhere). Using this property, the authors managed to prove that $c_{k,d}$ converges to a limit $c_{\infty,d} \in (-2\sqrt{d}, 0)$. Therefore, for any $d > 1$, there exists $\underline{k}(d) \geq 1$ such that

$$c_{k,d} < 0 \quad \text{if } k > \underline{k}(d).$$

Note that the identity $c_{k,1} = 0$ leads to $\lim_{d \rightarrow 1} \underline{k}(d) = +\infty$. Apart from this limit, the graph of the optimal function \underline{k} is unknown and the choice in Figure 2 is arbitrary.

2.2. Spatially periodic environment. Recalling the seminal paper of Dockery *et al.* [24], it is quite natural to investigate a possible extension of the preceding “Disunity is strength”-type results to spatially heterogeneous environments. In heterogeneous media, traveling waves as defined above (eternal solutions with constant speed and constant profile) are not solutions anymore, yet generalizations of the concept exist (for instance, the generalized transition fronts [9, 10]). Even so, the aforementioned extension turns out to be an impossible task in full generality: heterogeneities can block bistable invasions (a phenomenon referred to as pinning, quenching or blocking, where the interface between the territories stops moving and both niches persist) [5, 7, 54, 55] and even repel them [80]. Therefore assumptions have to be made prior to any meaningful extension.

To the best of my knowledge, the only special form of heterogeneity whose effect on the motion of the strongly competitive interface has been investigated is the spatially periodic one. It is natural to consider such a form of heterogeneity for mainly

two reasons. First, it has convenient mathematical properties, thanks to which it is reasonable to expect a clear result. Second, it is heterogeneous everywhere – contrarily, say, to an homogeneous domain with one obstacle where individuals cannot go or survive – and therefore the effect of the heterogeneity on the motion of the interface is never attenuated due to an increasing distance. In this sense, the analysis of the periodic framework is an important step forward. Accordingly, researchers have been interested in the invasion of a single population in a periodic environment for several decades (*e.g.*, [31, 70, 77] and more recently [8, 11, 12]), however studies on competitive displacements started much more recently. Again, the stability analysis is the starting point; since the identification of the invader remains quite direct in monostable cases (on which the reader is referred for instance to [53, 79] and references therein), it is again natural to focus on cases with two – or more, see below – stable steady states.

In the periodic framework, traveling waves are replaced by solutions known as traveling pulsating (or periodic) waves (or fronts) [8, 70] (pulsating waves hereafter). Such a solution still has a constant speed $c_{k,d}$ but its profile in the moving frame with speed $c_{k,d}$ varies slightly as time goes on (illustrations can be found for instance in [70]). In contradistinction with the homogeneous case, the existence of pulsating waves is not systematic: stable periodic coexistence steady states might now exist and induce repelling phenomena preventing the formation of wave patterns. A very recent general result by Du, Li and Wu [26] provides conditions on some eigenvalues ensuring the existence of bistable pulsating waves in one-dimensional spatially periodic media, however it remains difficult to convert these abstract conditions into practically verifiable conditions.

2.2.1. Oscillating diffusion rate. In a recent paper, Hutridurga and Venkatamaran [42] considered a system where the reaction term is homogeneous but where the diffusion rate $d(x)$ is spatially periodic in a one- or two-dimensional environment:

$$\begin{cases} \partial_t u = \Delta u + u(1-u) - kuv, \\ \partial_t v = \nabla \cdot (d\nabla v) + v(1-v) - \alpha kuv. \end{cases}$$

They fixed $\alpha < 1$, so that if d is identically equal to 1 then v has a competitive advantage and chases u . Fixing then d of the form

$$d_k(x) = 1 + \frac{3}{4} \sin(2k\pi x)$$

and considering the regime $k \gg 1$ (thus both the interpopulation competition rate and the frequency of the oscillations are very large), they numerically observed invasion reversals: a uniform diffusion rate seems to confer a competitive advantage over an oscillating one with the same mean value. Provided this remains true if the mean value of d is slightly increased (say, by continuity of $c_{k,d}$), then it yields a noticeable case of “Unity is strength”-type result in the strongly competing regime.

2.2.2. Oscillating reaction terms. Girardin [34], together with Nadin [36] and Zilio [37], published from 2017 to 2019 a series of three articles investigating analytically the very strong competition limit $k \rightarrow +\infty$ of a system with spatially homogeneous diffusion rates but with quite general spatially periodic reaction terms in one-dimensional environments. In particular, the form of spatially heterogeneous reaction terms used by Dockery and his collaborators [24] is included in the setting of the first and second parts of the series [34, 36] but, for technical reasons, not in the setting of the third part [37]. The presentation below is simplified by assuming that the system is now, for some uniformly positive periodic distribution

of resources $\mu(x)$,

$$(3) \quad \begin{cases} \partial_t u = \partial_x^2 u + \mu [u(1-u) - kuv], \\ \partial_t v = d\partial_x^2 v + \mu [v(1-v) - kuv]. \end{cases}$$

Nevertheless, keep in mind that many results of the series remain true with more general systems.

In the first part of the series [34], it was proved that a bistable pulsating wave exists provided the interpopulation competition rate k and the frequency of the environment μ are both sufficiently large. This existence result, consistent with the aforementioned abstract one [26], confirms the general principle according to which higher dispersal distances destabilize coexistence [14, 27].

In the second part [36], it was proved that, provided a pulsating wave exists, then in the very strong competition limit $k \rightarrow +\infty$, a ‘‘Disunity is strength’’-type result holds true: there exists a threshold $d^* \geq 1$ such that, if $d > d^*$, $c_{\infty, d} < 0$, whence in particular $c_{k, d} < 0$ if k is large enough. Whatever the exact shape of μ is, the fast diffuser v still has a competitive advantage.

But where does this threshold d^* come from? What is its biological meaning? When $1 < d \leq d^*$, the limit $c_{\infty, d}$ is nonpositive and can actually be zero. This does not mean that $c_{k, d}$ is zero for large values of k , but it remains unclear whether the convergence is from below ($c_{k, d} < 0$ if $k \gg 1$), from above ($c_{k, d} > 0$ if $k \gg 1$), stationary ($c_{k, d} = 0$ if $k \gg 1$) or oscillating (changing signs). Assuming for a moment that $c_{k, d} = 0$ is realized in some cases, then these are cases of coexistence by segregation in a wave-like pattern (pinning phenomenon) with a large but finite (thus more realistic) interpopulation competition rate.

In the third part [37], the possibility of wave repelling was explored further. The authors considered the specific case of a patchy environment, in which favorable patches where resources are abundant and homogeneous ($\mu \simeq 1$) are separated by neutral patches where only dispersion occurs ($\mu \simeq 0$). Assuming a very large (but finite) competition rate k and a small enough frequency of the environment (*i.e.* large patches or small dispersal distances), they proved the existence of a stable periodic segregated stationary state describing a situation where the population u settles in the oddly numbered favorable patches while the population v settles in the evenly numbered favorable patches (see Figure 4). Although such a steady state solution of the system (3) is unable to induce a repelling phenomenon (*i.e.* a pulsating wave still exists, at least in the limit $k \rightarrow +\infty$ [59]), the exact same result applies if resources are *a priori* specialized (the oddly numbered, respectively evenly numbered, favorable patches are favorable only for u , respectively v) and for such resources, the existence of pulsating waves remains an open problem.

Put together, the second and third part of the series show how spatially periodic reaction terms influence competitive displacements when the interpopulation competition is very strong: the invasion of the fast diffuser v into the territory of u might be blocked or repelled by a coexistence state but it will not be reversed (up to the likely uncommon cases where $1 < d \leq d^*$ and $0 < c_{k, d} \ll 1$, mentioned earlier).

3. OPEN PROBLEMS

In this section, directions of research worthy of a special attention from the community are raised. Although the focus remains on theoretical questions and viewpoints, comparisons with *in vitro* models and field data are also obviously interesting and important.

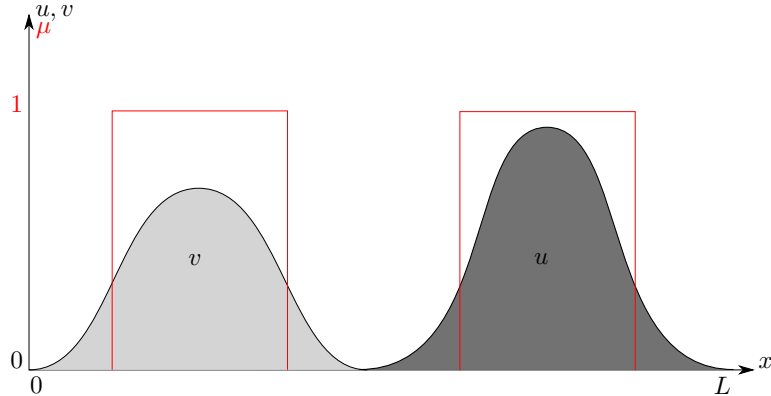


FIGURE 4. A stable periodic segregated stationary state as constructed by Girardin and Zilio [37]. Here the periodic functions μ, u, v are only presented in one spatial period $[0, L]$.

3.1. Complete picture in homogeneous environments. Of course, in view of Figure 2 and Figure 3, it is tempting to conjecture that $c_{k,d} < 0$ is globally true as soon as $d > 1$. As such a result would be in sharp contradistinction with the widely accepted “Unity is strength”-type conclusions of Dockery *et al.* [24] and would therefore confirm the trade-off between interpopulation competition and spatial heterogeneity first hinted by Risler [67], this is definitely the most important open problem raised by the present paper.

In order to support further this conjecture, a series of numerical experiments was conducted during the writing of the present paper ¹. These are presented in Figure 5. In view of these experiments, the conjecture seems to be correct. In addition, a form of monotonicity with respect to both k and d appears in Figure 5. The monotonicity with respect to d was already conjectured and discussed at length in 2012 by Alzahrani, Davidson and Dodds [2]. The monotonicity with respect to k is, to my knowledge, a new conjecture.

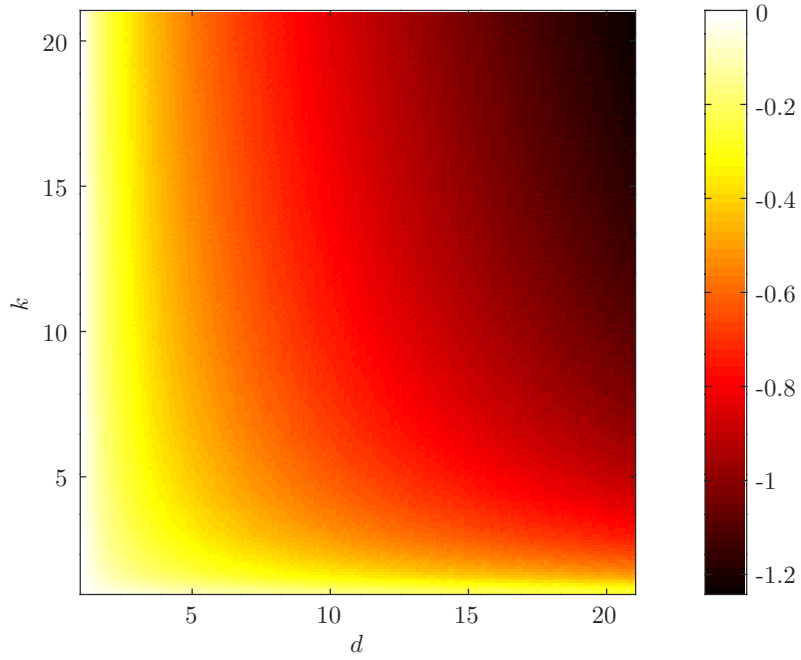
A rigorous analytical proof of the global “Disunity is strength” theorem remains to this day a completely open and challenging mathematical problem.

3.2. Better understanding of the coexistence by segregation in spatially periodic environments. As explained above, the cases where $d > 1$ and $c_{\infty,d} = 0$ in spatially periodic media should definitely be investigated further. How does the convergence as $k \rightarrow +\infty$ occur? In particular, is it possible to observe a pinning phenomenon, namely a wave-like coexistence steady state, with biologically relevant finite values of k ? Of course, this leads to the very natural question of whether, in spatially periodic media, “Unity is strength” can be achieved away from the strong competition regime, say close to $k = 1$. To the best of my knowledge, this is a completely open problem.

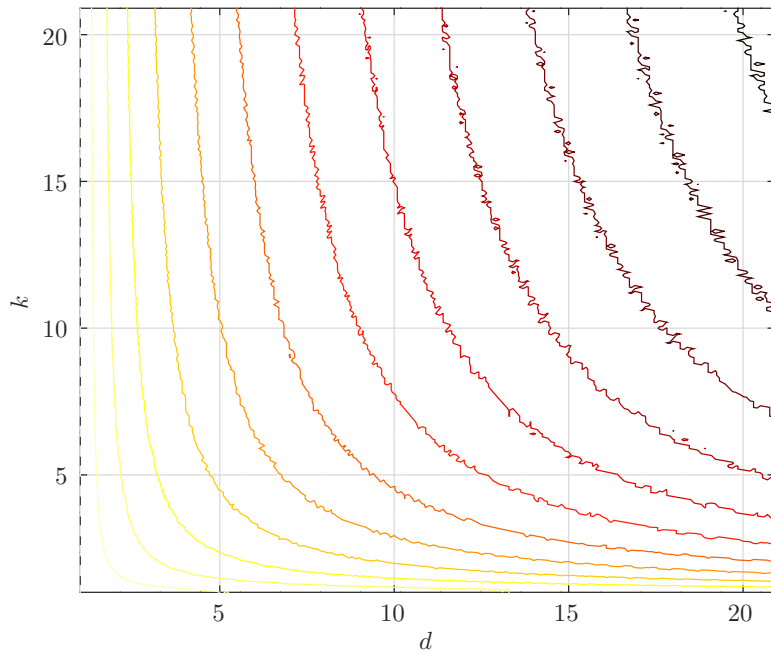
Note that the literature on scalar bistable reaction–diffusion equations tends to indicate that direct constuctions might directly yield the following results in the very strongly competing regime:

- a pinning phenomenon for a system with two oscillating diffusion rates and two uniform reaction terms [77];
- a repelling phenomenon for a system with two uniform diffusion rates and two oscillating reaction terms [80].

¹Simulations were run in *GNU Octave* [28]. Details are given in the appendix.



(A) Heat map

(B) $0, -0.1, -0.2, \dots, -1.2$ -level sets (the 0-level set, in white, is a dashed line for clarity; the lack of smoothness is a numerical artifact)FIGURE 5. Numerical approximations of the traveling wave speed $c_{k,d}$, presented in the (d, k) plane and color-coded according to the bar on the right-hand side of panel (A)

3.3. Extension to more general heterogeneous environments. Extending the spatially periodic “Unity is not strength”-type results of Girardin *et al.* [34, 36, 37] in two- or three-dimensional environments (periodic tilings) should be possible, to a certain degree at least, but difficult mathematical obstacles will arise.

The system (3) still makes sense if the amount of resources μ is sign-changing, namely if some areas are so unfavorable that they are actually deadly even in absence of competition. Periodic environments with deadly areas are more subtle and form a very interesting problem. Indeed, at least intuitively, the more lethal the unfavorable areas are, the more likely “Unity is strength” seems. Applying formally the formulas of the uniformly favorable case [36], a condition for $c_{\infty,d} > 0$ arises: the negativity of the mean value of μ . Although such an environment is obviously unfavorable and even harmful, it does not automatically mean that neither u nor v can settle in it. In fact, it is known from earlier studies that if μ has a specific form, then both u and v will be able to settle in absence of the competitor despite the negativity of the mean value of μ [11, Theorem 2.12]. Hence the negativity of the mean value of μ is not a contradictory condition in itself: a pulsating wave describing the competition between u and v might still exist. In other words, it seems that a “Unity is strength”-type result is within reach: such a problem needs to be investigated more thoroughly (first, existence of the wave; second, sign of the wave speed; the pre-existing methods [34, 36] will not be sufficient as they require the positivity of the minimum of μ but with care it might be possible to build from them).

In temporally periodic environments, the existence of a unique bistable pulsating wave was proved in 2013 by Bao and Wang [4] under some conditions on eigenvalues (reminiscent of those for spatially periodic environments [26]). However the sign of the wave speed is completely unknown and, in particular, it is unclear whether the approach developed by Girardin and Nadin to study the very strong competition limit $k \rightarrow +\infty$ [35, 36] can be used again (in particular, the sign of the wave speed cannot be obtained anymore by integration by parts of the limiting equation [36, Proposition 3.7]). *A fortiori*, spatio-temporally periodic environments are even more elusive. Note that it is known that the introduction of temporal periodicity in the spatially heterogeneous model of Dockery *et al.* [24] provides in some specific cases a competitive advantage to the fast diffuser (“Unity is not strength”-type result) and thus compensates the effect of the spatial heterogeneity [44].

Apart from the periodic regime, the effect of environmental heterogeneities on the motion of the interface is an entirely open problem. In view of the reaction–diffusion literature, other special regimes (almost periodic, ergodic, finite number of obstacles, cylindrical domains, etc.) can reasonably be considered. However this requires a much more involved mathematical analysis, with very specified techniques depending strongly on the choice of special regime. In particular, regarding spatial domains with boundaries, the existence of a stable steady state of the system with segregated niches strongly depends on the exact shape of the domain (*e.g.*, [47, 49, 55]).

3.4. Comparison between the Brownian motion and other motion strategies. Finally, it is important to assert the dependency of the aforementioned results on the exact dispersal strategy of the populations. The use of diffusion to model animal movement in ecology, for instance, is debated by a wide literature and alternative models exist (*e.g.* [6, 19, 38, 63] and references therein).

More specifically, in what follows we briefly discuss three possibilities: density-dependent dispersal, resources-dependent dispersal and long-range dispersal. Note that density-dependent dispersal operators can be coupled (when the dispersal strategy depends on the density of the competitor) or not.

Potts and Petrovskii [66] recently studied numerically the influence of a density-dependent coupled operator with an aggressive taxis term pushing the slow diffuser u towards the fast diffuser v . Interestingly, they found a special range of parameters in which u chases v , thus reversing the conclusion without taxis. The authors refer to their result as a “Fortune favors the bold”-type result: boldness (aggressive advection) can compensate unity (low diffusion rate). An analytical proof of such a result would be interesting. Similarly, the effect of cross-diffusion and self-diffusion (*e.g.*, [25, 55, 71]) could be investigated, although mathematically it is a very challenging problem (to my knowledge, even the existence of traveling waves is unclear) and at the moment it seems that only perturbative results or numerical experiments are within reach. Intuitively, following the “Disunity is strength” logic, it could be conjectured that, opposed to standard diffusion, self-diffusion is a losing strategy whereas cross-diffusion is a winning one.

Regarding resources-dependent dispersal, many models could be considered; let me suggest for instance conditional dispersal and ideal free dispersal [19, Chapter 11].

Finally, in ecological or evolutionary contexts, it is very natural to replace the Laplacian diffusion operator by a nonlocal operator accounting for rare long-range dispersal events (*e.g.*, [6, 43, 48]). Intuitively, such dispersion operators might be roughly understood as diffusion operators with huge diffusion rates [43]. Testing such an intuition against the competitive model is therefore very tempting, and in particular it would be natural to study the case where v still diffuses locally with a rate d but u diffuses nonlocally with a normalized rate: in such a case, does v always lose, whatever the value of d ?

3.5. An evolutionary trap? The “Disunity is strength”-type results presented above and the “Unity is strength”-type evolutionary result can be confronted in an interesting way: what if a population subjected to evolution of dispersal encountered a strong competitor? One possible mathematical model for this problem is the following system:

$$\begin{cases} \partial_t u = \Delta u + u(a - u) - hu(v_1 + v_2), \\ \partial_t v_1 = d_1 \Delta v_1 + v_1(a - v_1 - v_2) - kuv_1 + \alpha(v_2 - v_1), \\ \partial_t v_2 = d_2 \Delta v_2 + v_2(a - v_2 - v_1) - kuv_2 + \alpha(v_1 - v_2), \end{cases}$$

where u is the competitor, v_1 and v_2 are two phenotypes of the species $v = v_1 + v_2$ with $d_1 < d_2$, $\alpha > 0$ is the mutation rate between phenotypes and the intrinsic growth rate $a(x)$ is heterogeneous. Strong competition means that $h > 1$ and $k > 1$.

A similar system but with blind competition between u and v ($h = k = 1$) is studied in a very recent work by Cantrell, Cosner and Yu [18]. In such a case, the long-time outcome still respects “Unity is strength”, as can be expected. But what about the strong competition case? The answer is likely quite complex and specific regimes should be considered instead of the general case; numerical experiments could also be enlightening. Note that even the existence of a pulsating traveling wave describing the confrontation between u and v in a spatially periodic environment $a(x)$ is a difficult problem – it might be solvable when α is so large that the interaction between v_1 and v_2 is essentially cooperative [17], but small values of α are elusive.

3.6. Comparison between the Lotka–Volterra competition and other competition models. Depending on the exact biological problem, there might be a more suitable competition model than the Lotka–Volterra one, namely quadratic competition with a constant rate. As mentioned for instance by Perthame [64,

Chapter 4, Section 4.10, Exercise p. 83], a very straightforward calculation shows that, for the system with cubic competition

$$\begin{cases} \partial_t u = \Delta u + u(1-u) - huv^2, \\ \partial_t v = d\Delta v + rv(1-v) - ku^2v, \end{cases}$$

the speed of the traveling wave connecting $(1, 0)$ and $(0, 1)$ has the sign of $rh - k$. Surprisingly, the value of the diffusion rate d does not matter at all. This definitely shows that the conclusions drawn from the Lotka–Volterra case cannot be generalized without care. Specific competition models require specific studies.

Note that the cubic competition model above is known in the physics literature as the Gross–Pitaevskii model (*e.g.*, [22, 73] and references therein) and in the mathematical biology literature as the Gilpin–Ayala model [33]. For other alternatives, refer for instance to Schoener [69] and Van Vuuren and Norbury [74] and references therein.

4. CONCLUSION

All existing results on strongly competing systems in spatially homogeneous environments concur: “Disunity is strength”. In other words, the fast dispersers win and chase the slow dispersers. Although the map of rigorous results (Figure 2) is far from being complete, numerical investigations (Figure 3 and Figure 5) tend to confirm that this is always the case: whatever the values of the interpopulation competition rate and the gap between the dispersal rates are, fast dispersers prevail.

In heterogeneous environments, the picture is less clear, in particular due to the possibilities of blocking or repelling phenomena. Existing results concern the case of very strongly competing populations in one-dimensional spatially periodic, temporally homogeneous environments. On one hand, numerical investigations indicate that uniform dispersal rates are preferred over highly oscillating ones. On the other hand, analytical works on uniform dispersal rates with periodic growth and competition rates prove that a very large dispersal rate remains a definitive competitive advantage. This last conclusion is surprisingly different from the “Unity is strength”-type one obtained in 1998 [24] for spatially heterogeneous environments where the competitive pressure is exerted blindly by individuals instead of being mainly targeted at individuals of the other population.

More general heterogeneities, different dispersal strategies and different competition models form very interesting but completely open problems that need more attention from the community.

ACKNOWLEDGMENTS

The author thanks Florence Débarre for the attention she paid to this work and two anonymous referees for very valuable suggestions.

APPENDIX A. ON THE NUMERICAL SIMULATION FOR THE WAVE SPEED IN HOMOGENEOUS ENVIRONMENTS

First, for numerical convenience, change the spatial variable x into $x\sqrt{d}$, so that the diffusion rate of u becomes $1/d < 1$, that of v becomes 1 and the wave speed $c_{k,d}$ becomes $c_{k,d}/\sqrt{d}$.

Then, for any couple $(k, d) \in [1, 21]^2$ (with steps of size .1), run a standard semi-implicit finite difference scheme in a bounded 1D domain of size $40 \gg \max(1, 1/d)$ (steps of size .02) and during a time equal to 40 (steps of size .02).

Departing from piecewise-constant wave-like initial data, the numerical solution rapidly converges to the traveling wave. The speed $c_{k,d}/\sqrt{d}$ is evaluated by tracking the motion of the .5-level set of v between $t = 32$ and $t = 40$.

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