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**Is a nonlocal diffusion strategy convenient
for biological populations in competition?**

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Abstract: We study the convenience of a nonlocal dispersal strategy in a reaction-diffusion system with a fractional Laplacian operator. We show that there are circumstances - namely, a precise condition on the distribution of the resource - under which a nonlocal dispersal behavior is favored.

In particular, we consider the linearization of a biological system that models the interaction of two biological species, one with local and one with nonlocal dispersal, that are competing for the same resource. We give a simple, concrete example of resources for which the equilibrium with only the local population becomes linearly unstable. In a sense, this example shows that nonlocal strategies can become successful even in an environment in which purely local strategies are dominant at the beginning, provided that the resource is sufficiently sparse.

Indeed, the example considered presents a high variance of the distribution of the dispersal, thus suggesting that the shortage of resources and their unbalanced supply may be some of the basic ingredients that favor nonlocal strategies.

“When the sun comes up, you better be running.”

The Fable of the Lion and the Gazelle,

popular quotation by Undetermined Author,

<http://quoteinvestigator.com/2011/08/05/lion-gazelle/>

1 Introduction

The goal of this paper is to study the possible convenience of a nonlocal diffusion strategy for a biological population in presence of a highly oscillating distribution of resource.

The study of dispersal strategies and the comparison between local and nonlocal diffusive behaviors have recently attracted a great attention and several researches have been developed both in terms of experiments and from the purely mathematical point of view (see for instance [25, 17, 15, 22] and references therein). Remarkably, the phenomenon of possibly nonlocal hunting strategies has attracted also the attention of the mass-media, and related news can be found in popular newspapers and magazines (see e.g. [1]).

In this framework, even the distinction between local and nonlocal strategies is somehow a delicate issue and it is still not exactly clear in all situations what factors favor one behavior with respect to the other. Of course, in general, as we know even from experience in our everyday life, it may be very difficult to deduce from “overall principles” the optimal strategy to follow in each complex situation. Therefore, it should not be surprising that the question of detecting the optimal strategy in a logistic mathematical model cannot have just a simple

answer that is valid in every situation, and, concretely, very different dispersal strategies have been directly observed in nature.

Detecting, analyzing and understanding the differences between diffusive strategies is therefore a difficult, but important, task in biology. One of the possible distinctions among the different strategies lies in rigorously defining the concept of “locality” (when a predator, roughly speaking, diffuses randomly in the neighborhood looking for an available prey) versus “nonlocality” (the short periods of hunting activity are followed by rather long journeys of the predator in the search for food). As expected, hunting strategies of predators are definitely influenced by the distribution of the resources. When the resources are “easily” available, it is conceivable that predators do not need to elaborate a nonlocal hunting strategy and indeed it can be more convenient not to drift too much to take advantage of the rather abundant resource in their neighborhood. Conversely, when the prey is sparse, it may be worth for predators to interchange the local hunting activity with suitable nonlocal travels in different possible regions.

Of course, the more sophisticated the species involved in the hunt, the easier the latter phenomenon is expected to occur: namely, an intelligent species of preys will run away from the danger, thus making the distribution of resources for the predator sparse, and therefore making a nonlocal hunting strategy possibly more favorable. However, in the model considered in this paper the resource σ is independent of the distribution of the populations, so this effect is not taken into consideration by the setting discussed here.

It is also evident that the distinction between local or nonlocal strategy is a mathematical abstraction based on the consideration of different space/time scales: i.e., the ambient space that the population has at its disposal is not infinitely large in the real cases, and species cannot really perform discontinuous, nonlocal jumps. Nevertheless, a good mathematical model in which different scales are taken into account may furnish a justification for the diffusive strategy in a “large enough” environment in which the time scales of travel and hunting activities can be somehow distinguished in practice.

We will try to give a rigorous mathematical framework to these naïves considerations by showing the possible advantages of the long-jump dispersal strategies (i.e. the ones based on nonlocal diffusion) in regimes where the distribution of resources may be considerably different at different points of the ambient space. Not too surprisingly having in mind the concrete applications, we will use for this scope the mathematical framework of linearized systems and scaling properties of the eigenvalues, which take into account the stability property of equilibrium configurations.

Our mathematical framework can be discussed as follows. Reaction-diffusion systems provide an effective continuous model for the biological problem of competition between different species. The typical example of local reaction-diffusion equation is

$$u_t = \Delta u + (\sigma - u)u \quad \text{in } (0, T) \times \Omega \quad (1.1)$$

with either Dirichlet or Neumann boundary condition (and other boundary conditions may be also taken into account to model different situations). In this model, the environment is represented by the open bounded set $\Omega \subset \mathbb{R}^n$, with $n \geq 2$, and a heterogeneous resource $\sigma : \Omega \rightarrow [0, +\infty)$ is given (stationary in time). The growth of the population density u depends on a dispersal differential operator and on the reproductive rate of the population itself, which is proportional to the temporary availability of the resource ($\sigma - u$). Dirichlet boundary conditions model a lethal environment for the population u outside the domain Ω .

A reaction-diffusion system involves at least two species, with distribution u and v , whose behavior is ruled by a reaction-diffusion equation like (1.1). The two competing species differ for some special features: indeed, (1.1) has to be modified in order to describe the foraging and reproductive habits of the species and further data concerning the environment. In [15] one can find a comprehensive survey of the problem; many different features have been studied and compared in [14, 5, 6] (different dispersal rates and genetic mutations), in [19] (time-periodic sources) and in [7, 8, 10] (addition of a chemotactic component depending on the gradient of the resource).

We are interested in the comparison of the dispersal strategies: in particular, we focus on the competition between a population with “standard” diffusion and a second population with nonlocal dispersal. Therefore, our model is

$$\begin{cases} u_t = \Delta u + (\sigma - (u + v)) u \\ v_t = -(-\Delta)^s v + (\sigma - (u + v)) v. \end{cases}$$

At a discrete level, the “standard” assumption is that the motion of the population is governed by a random walk and this obviously leads to a Laplacian operator in the continuous model. Analogously, since our interest is focused on a second population with nonlocal dispersal, we adopt the fractional Laplacian operator as dispersal operator for the second distribution. The choice of such nonlocal diffusion operator is motivated by the fact that the fractional Laplacian has good stability properties in terms of the associated stochastic processes (it is the “continuous version” of the discrete motion governed by Lévy flights, see e.g. [24] for a simple motivation and [3] for more advanced material), it possesses natural scaling features and it seems also to appear in real experiments (see e.g. [25, 17]). The present literature on the subject of nonlocal dispersal mostly considers convolution operators (see [14, 20, 21, 9, 11]). Of course, it is a delicate business to decide, in concrete situations, which models better describe the dispersion of a real biological population, and many nonlocal terms have been taken into account in order to comprise long-range effects. In general, we believe that fractional equations may be an important tool to further understand the complex problems arising in the mathematical modelization of biological species and we hope that the framework given in this paper can lead to a further development of the subject.

In Section 2 we provide details and further explanations about the model considered here and some basic facts about the fractional Laplacian operator.

We study the stability of a stationary solution $(\tilde{u}, 0)$ of the aforementioned system, by means of a formal linearization at $(\tilde{u}, 0)$, that we explain in Subsection 2.3. The complete understanding of the global dynamics of a general system of diffusive and competing populations is beyond the scope of this paper and it seems, at first glance, very challenging from a mathematical point of view, since a variety of possible situations may occur. Nevertheless, let us stress that even the analysis of the stability of a stationary solution is interesting and meaningful from an evolutionary point of view. In fact, a small perturbation around $(\tilde{u}, 0)$ mirrors the occurrence of a genetic mutation in the first population, involving the dispersal strategy. At $(\tilde{u}, 0)$ the first population benefits from an equilibrium state, while the second one does not even exist. Then a small portion of the first population (with density \tilde{u}) undergoes a genetic mutation, which starts a second population (with very small density v) which competes for the resource with the former. Of course, the genetic mutation of this theoretical experiment involves only the hunting/dispersal strategy, passing from a local to a nonlocal one. In this context, the expected outcome of the analysis of the stationary solution is, in most of the cases experienced in practice, stability, that is, the second population does not find the right conditions to evolve and it gets rapidly extinguished. On the contrary, (even partial) instability of these type of equilibria is rather surprising and interesting, since in this case the new dispersal strategy is convenient enough to allow a short term survival of the second species and to provide a situation of coexistence of two different populations.

The core of this paper is Section 3, where we show how the stability of $(\tilde{u}, 0)$ (namely, the sign of the eigenvalues associated with the linearized system) depends on the distribution of the resource σ . In particular, we will show that if a certain relationship between the variation of σ and the fractional Poincaré-Sobolev constant in Ω is fulfilled (see Definition 3.1), then the linearized system has a positive eigenvalue and $(\tilde{u}, 0)$ is unstable. It is transparent from Definition 3.1 that the distributions leading to instability of $(\tilde{u}, 0)$ (and suggesting convenience of a nonlocal dispersal strategy) are those with a “huge variation”. The last part of Section 3 is devoted to show that such a distribution σ may occur. Summarizing, the result that states that the local dispersive strategy may become unstable in presence of a new population endowed with nonlocal diffusive strategies can be formally stated as follows:

Theorem 1.1. *Let $\Omega \subset \mathbb{R}^n$ be an open subset of \mathbb{R}^n with Lipschitz boundary and let $s \in (0, 1)$. There exist bounded functions $\sigma : \Omega \rightarrow [0, +\infty)$ and $\tilde{u} : \Omega \rightarrow [0, +\infty)$ such that $(u, v) := (\tilde{u}, 0)$ is a linearly unstable equilibrium for the system*

$$\begin{cases} u_t = \Delta u + (\sigma - (u + v))u & \text{in } \Omega \\ v_t = -(-\Delta)^s v + (\sigma - (u + v))v & \text{in } \Omega \\ u = v = 0 & \text{on } \partial\Omega. \end{cases} \quad (1.2)$$

More precisely, the functions \tilde{u} is a solution of

$$\begin{cases} \Delta \tilde{u}(x) + (\sigma(x) - \tilde{u}(x))\tilde{u}(x) = 0 & \text{in } \Omega, \\ \tilde{u} = 0 & \text{on } \partial\Omega, \end{cases} \quad (1.3)$$

and the linearization of system in (1.2) at $(\tilde{u}, 0)$ has a negative and a positive eigenvalue.

We remark that Theorem 1.1 states that \tilde{u} is a linearly stable solution of the autonomous, scalar Fisher-KPP equation in (1.3), but $(\tilde{u}, 0)$ is a linearly unstable equilibrium for the system in (1.2). More explicitly, the positive eigenvalue of the linearized system takes into account the fact that if the density of the first population undergoes a small variation without the appearance of the second species, then the system has the tendency to return to the original position. Conversely, the negative eigenvalue shows that if a second population appears, then the system does not go back to the original situation, and the second species has indeed chances to survive and colonize the environment.

Roughly speaking, the condition (in Definition 3.1) which allows the instability of the system records the fact that the first population, with local diffusion, cannot saturate the given resource and leaves enough “leftovers” for the second species to survive.

In this sense, a natural question is to determine whether a population exhausts the resource. For this, as a second result, we provide an example of a purely nonlocal phenomenon in population modeling. We show that, fixed any arbitrarily small $\varepsilon > 0$ and given any resource $\sigma \in C^k(B_1, [0, +\infty))$, there exists a resource $\sigma_\varepsilon \in C^k(B_1, [0, +\infty))$ that is ε -close to σ in the norm of $C^k(B_1)$, a radius $R_{\varepsilon, \sigma} > 1$ and a function u_ε which vanishes outside $B_{R_{\varepsilon, \sigma}}$, which is s -harmonic in B_1 , which equals to σ_ε in B_1 and which therefore satisfies

$$(-\Delta)^s u_\varepsilon = (\sigma_\varepsilon - u_\varepsilon)u_\varepsilon \quad \text{in } B_1.$$

That is, up to an arbitrarily small error, a nonlocal population can locally adapt to any given resource (provided that the density of the population is artificially and appropriately regulated in a suitable region). The formal statement of this result goes as follows.

Theorem 1.2. *Let $k \in \mathbb{N}$ and $\sigma \in C^k(B_1, [0, +\infty))$. Fix $\varepsilon > 0$. Then there exists $\sigma_\varepsilon \in C^k(B_1)$ with*

$$\|\sigma - \sigma_\varepsilon\|_{C^k(B_1)} \leq \varepsilon \quad (1.4)$$

and there exist $R_{\varepsilon, \sigma} > 1$ and $u_\varepsilon \in C^k(B_1) \cap C^s(\mathbb{R}^n)$ such that

$$u_\varepsilon(x) = \sigma_\varepsilon(x) \quad \text{for any } x \in B_1 \quad (1.5)$$

$$(-\Delta)^s u_\varepsilon(x) = 0 \quad \text{for any } x \in B_1 \quad (1.6)$$

$$u_\varepsilon(x) = 0 \quad \text{for any } x \in \mathbb{R}^n \setminus B_{R_{\varepsilon, \sigma}}. \quad (1.7)$$

In particular

$$(-\Delta)^s u_\varepsilon(x) = (\sigma_\varepsilon(x) - u_\varepsilon(x))u_\varepsilon(x) \quad \text{for any } x \in B_1. \quad (1.8)$$

It is worth to notice that Theorem 1.2 heavily relies on the nonlocal feature of the equation and it does not have any local counterpart (this will be clearly explained in Section 4).

The rest of this paper is organized as follows. In Section 2 we recall the basic notation about the population dynamics model that we study. The linearized dynamics of the system is then analyzed in Section 3, where we will also give two examples that establish Theorem 1.1. Finally, in Section 4 we will prove Theorem 1.2 and show that it is a new phenomenon, which only arises in nonlocal dispersion models.

2 Biological models and mathematical tools

2.1 Population dynamics

Let us denote by $u, v : [0, T] \times \Omega \rightarrow [0, +\infty)$ the densities of two species living together in the same domain Ω and competing for a common resource $\sigma : \Omega \rightarrow \mathbb{R}$. Here and in the rest of the paper we consider as a domain an open, bounded set $\Omega \subset \mathbb{R}^n$ with Lipschitz boundary $\partial\Omega$. The resource σ belongs to the space of measurable, essentially bounded functions $L^\infty(\Omega)$. We study the linear stability of a stationary point of the reaction-diffusion system with Dirichlet boundary conditions

$$\begin{cases} u_t = \Delta u + (\sigma - (u + v))u & \text{in } [0, T] \times \Omega \\ v_t = -(-\Delta)^s v + (\sigma - (u + v))v & \text{in } [0, T] \times \Omega \\ u(t, \cdot) = v(t, \cdot) = 0 & \text{on } \partial\Omega, \forall t \in [0, T]. \end{cases} \quad (2.1)$$

For this, we perform a formal linearization around a stationary point $(\tilde{u}, 0)$ of (2.1) and then we focus only on the corresponding linearized system, that is

$$\begin{cases} -\Delta u = (\sigma - 2\tilde{u})u - \tilde{u}v & \text{in } \Omega \\ (-\Delta)^s v = (\sigma - \tilde{u})v & \text{in } \Omega \\ u = v = 0 & \text{on } \partial\Omega. \end{cases}$$

Before focusing on the aforementioned linearized system, let us recall some useful definitions and facts about the pseudodifferential operator $(-\Delta)^s$ that is involved in (2.1).

2.2 The nonlocal dispersive strategy and the fractional Laplacian

Consider an open set $\Omega \subset \mathbb{R}^n$ and $s \in (0, 1)$, the Gagliardo seminorm of a measurable function u is defined as

$$[u]_{H^s(\mathbb{R}^n)} := \left(\int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \frac{|u(x) - u(y)|^2}{|x - y|^{n+2s}} dx dy \right)^{\frac{1}{2}}.$$

The fractional Sobolev space that we denote here $H_0^s(\Omega)$ is the linear set containing all the measurable functions $u : \mathbb{R}^n \rightarrow \mathbb{R}$ such that:

- $\|u\|_{L^2(\Omega)} < +\infty$,
- $[u]_{H^s(\mathbb{R}^n)} < +\infty$, and
- $u(x) = 0$ for a.e. $x \in \mathbb{R}^n \setminus \Omega$.

The Gagliardo seminorm is naturally related to the fractional Laplacian, since

$$(-\Delta)^s u(x) := \left(\frac{\Gamma(n/2 + s)}{\pi^{2s+n/2}\Gamma(-s)} \right) \lim_{\varepsilon \rightarrow 0} \int_{\mathbb{R}^n \setminus B_\varepsilon(x)} \frac{u(x) - u(y)}{|x - y|^{n+2s}} dy,$$

where Γ is the Euler's function. For an introduction to the fractional Laplacian and the fractional Sobolev spaces see for instance [12]. In our framework, the scalar version of (2.1), that is

$$v_t = -(-\Delta)^s v + (\sigma - v)v,$$

is known as Fisher-KPP equation with fractional diffusion and for the many established results one can see, for instance, [4] and [23].

In this section we summarize the results needed in this paper only.

Theorem 2.1 (Fractional Poincaré-Sobolev embedding theorem). *Fix $s \in (0, 1)$ and an open bounded set $\Omega \subset \mathbb{R}^n$ with Lipschitz boundary. There exists a positive constant $C_{\sharp} = C_{\sharp}(s, \Omega)$ such that*

$$\forall \phi \in H_0^s(\Omega), \quad \|\phi\|_{L^2(\Omega)} \leq C_{\sharp} [\phi]_{H^s(\mathbb{R}^n)}. \quad (2.2)$$

This means that $H_0^s(\Omega)$ is continuously embedded in $L^2(\Omega)$.

Proof. We give the proof, which is of classical flavor, for the facility of the reader. We argue by contradiction, supposing that there exists a sequence $\phi_k \in H_0^s(\Omega)$ such that $\|\phi_k\|_{L^2(\Omega)} \geq k[\phi_k]_{H^s(\mathbb{R}^n)}$. We define

$$\psi_k := \frac{\phi_k}{\|\phi_k\|_{L^2(\Omega)}}.$$

Then $\psi_k \in H_0^s(\Omega)$ and

$$\left(\int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \frac{|\psi_k(x) - \psi_k(y)|^2}{|x - y|^{n+2s}} dx dy \right)^{\frac{1}{2}} = [\psi_k]_{H^s(\mathbb{R}^n)} = \frac{[\phi_k]_{H^s(\mathbb{R}^n)}}{\|\phi_k\|_{L^2(\Omega)}} \leq \frac{1}{k}. \quad (2.3)$$

Therefore

$$\left(\int_{\Omega} \int_{\Omega} \frac{|\psi_k(x) - \psi_k(y)|^2}{|x - y|^{n+2s}} dx dy \right)^{\frac{1}{2}} \leq \frac{1}{k}.$$

Also, $\|\psi_k\|_{L^2(\Omega)} = 1$. Therefore, by compactness (see e.g. Theorem 7.1 in [12], used here with $p = q = 2$), we obtain that, up to a subsequence, ψ_k converges to some ψ in $L^2(\Omega)$ and a.e. in Ω . Defining $\psi(x) := 0$ for any $x \in \mathbb{R}^n \setminus \Omega$, we have that $\psi_k = \psi = 0$ a.e. in $\mathbb{R}^n \setminus \Omega$, and consequently ψ_k converges to ψ a.e. in \mathbb{R}^n .

Thus, by taking the limit in (2.3) and using Fatou's Lemma,

$$\begin{aligned} \int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \frac{|\psi(x) - \psi(y)|^2}{|x - y|^{n+2s}} dx dy &\leq \liminf_{k \rightarrow +\infty} \int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \frac{|\psi_k(x) - \psi_k(y)|^2}{|x - y|^{n+2s}} dx dy \\ &\leq \liminf_{k \rightarrow +\infty} \frac{1}{k^2} = 0. \end{aligned}$$

Accordingly ψ must be constant in \mathbb{R}^n and therefore identically equal to zero (up to sets of null measure). This implies that

$$1 = \lim_{k \rightarrow +\infty} \|\psi_k\|_{L^2(\Omega)} = \lim_{k \rightarrow +\infty} \|\psi_k - \psi\|_{L^2(\Omega)} = 0.$$

This is a contradiction and it proves the desired result. \square

In the following, we will always assume $C_{\sharp}(s, \Omega)$ to be the sharp constant such that (2.2) holds, namely

$$C_{\sharp}^{-1}(s, \Omega) = \inf_{\substack{\phi \in H_0^s(\Omega) \\ \phi \neq 0}} \frac{[\phi]_{H^s(\mathbb{R}^n)}}{\|\phi\|_{L^2(\Omega)}} = \inf_{\substack{\phi \in H_0^s(\Omega) \\ \phi \neq 0}} \frac{[\phi]_{H^s(\mathbb{R}^n)}}{\|\phi\|_{L^2(\mathbb{R}^n)}}. \quad (2.4)$$

Remark 2.2. If $r > 0$ and $\phi \in H_0^s(B_1)$, one can consider the rescaled function $\phi_r(x) := r^{-n/2} \phi(x/r)$. Then ϕ_r vanishes a.e. outside B_r . Moreover, $\|\phi_r\|_{L^2(\mathbb{R}^n)} = \|\phi\|_{L^2(\mathbb{R}^n)}$ and $[\phi_r]_{H^s(\mathbb{R}^n)} = r^{-s} [\phi]_{H^s(\mathbb{R}^n)}$. Accordingly,

$$C_{\sharp}(s, B_r) = r^s C_{\sharp}(s, B_1).$$

2.3 Linearization of the system

Let $\Omega \subset \mathbb{R}^n$ and $\sigma \in L^\infty(\Omega)$ be as in Section 2. Our purpose is a qualitative study of an equilibrium state of the following system

$$\begin{cases} u_t = \Delta u + (\sigma - (u + v)) u \\ v_t = -(-\Delta)^s v + (\sigma - (u + v)) v \end{cases} \quad (2.5)$$

More precisely, we look for an equilibrium state of the form $(\tilde{u}, 0)$ with $\tilde{u} \in H_0^1(\Omega)$ and $\tilde{u} \geq 0$.

Definition 2.3. Given a bounded function $\sigma : \Omega \rightarrow [0 + \infty)$, we say that σ satisfies a reverse Poincaré-Sobolev condition if

$$\sup_{u \in H_0^1(\Omega)} \int_{\Omega} \sigma(x) u(x)^2 dx - \int_{\Omega} |\nabla u|^2 dx > 0. \quad (2.6)$$

In order to make computations easier, we give a sufficient condition that ensures (2.6).

Lemma 2.4. Let $\lambda_1(\Omega)$ be the first eigenvalue of the Laplacian in Ω with Dirichlet boundary condition and let $\phi_1 \in H_0^1(\Omega)$ be the corresponding eigenfunction. If

$$\lambda_1(\Omega) \int_{\Omega} \phi_1(x)^2 dx < \int_{\Omega} \sigma(x) \phi_1(x)^2 dx, \quad (2.7)$$

then the reverse Poincaré-Sobolev condition in (2.6) is satisfied.

Proof. By construction

$$\begin{cases} -\Delta \phi_1 = \lambda_1(\Omega) \phi_1 & \text{on } \Omega \\ \phi_1 = 0 & \text{in } \partial\Omega, \end{cases}$$

and so, by (2.7),

$$\int_{\Omega} |\nabla \phi_1(x)|^2 dx = \lambda_1(\Omega) \int_{\Omega} \phi_1(x)^2 dx < \int_{\Omega} \sigma(x) \phi_1(x)^2 dx$$

which proves (2.6). \square

Remark 2.5. It is worth noticing that condition (2.7) is satisfied, for a fixed domain Ω , for any resource σ that is sufficiently large in an open subset of Ω . Hence, fixed Ω , there are many examples of smooth resources satisfying (2.7) and therefore (2.6).

Remark 2.6. We also observe that the converse of Lemma 2.4 does not hold true, i.e. the reverse Poincaré-Sobolev condition in (2.6) does not necessarily imply (2.7): as an example, one may consider $\Omega = (0, \pi)$, $\sigma(x) = \varepsilon^{-29/10} \chi_{(0, \varepsilon)}(x)$ and $u(x) = |x|^{2/3}$, with $\varepsilon > 0$ suitably small. Then $u \in H_0^1(\Omega)$ and (2.6) holds true, since

$$\begin{aligned} \int_{\Omega} \sigma(x) u(x)^2 dx - \int_{\Omega} |\nabla u|^2 dx &= \varepsilon^{-29/10} \int_0^{\varepsilon} x^{4/3} dx - \frac{4}{9} \int_0^{\pi} x^{-2/3} dx \\ &= \frac{3}{7} \varepsilon^{-29/10} \varepsilon^{7/3} - \frac{4\pi^{1/3}}{3} > 0. \end{aligned}$$

On the other hand, in this case $\phi_1(x) = \sin x$, $\lambda_1(\Omega) = 1$, and

$$\begin{aligned} \lambda_1(\Omega) \int_{\Omega} \phi_1(x)^2 dx - \int_{\Omega} \sigma(x) \phi_1(x)^2 dx &= \int_0^{\pi} \sin^2 x dx - \varepsilon^{-29/10} \int_0^{\varepsilon} \sin^2 x dx \\ &= \frac{\pi}{2} - \frac{\varepsilon^{-29/10}}{2} (\varepsilon - \sin \varepsilon \cos \varepsilon). \end{aligned}$$

Thus, since, by a Taylor expansion,

$$\sin \varepsilon \cos \varepsilon = (\varepsilon + O(\varepsilon^3))(1 + O(\varepsilon^2)) = \varepsilon + O(\varepsilon^3)$$

it follows that

$$\varepsilon^{-29/10}(\varepsilon - \sin \varepsilon \cos \varepsilon) = O(\varepsilon^{1/10})$$

and so

$$\lambda_1(\Omega) \int_{\Omega} \phi_1(x)^2 dx - \int_{\Omega} \sigma(x) \phi_1(x)^2 dx = \frac{\pi}{2} - O(\varepsilon^{1/10}) > 0,$$

which shows that ϕ_1 does not satisfy (2.7).

The reverse Poincaré-Sobolev condition in (2.6) is a useful tool to obtain non-trivial solution of the local stationary equation, as stated in the following result.

Theorem 2.7. *Consider a bounded function $\sigma : \Omega \rightarrow [0, +\infty)$ satisfying the reverse Poincaré-Sobolev condition in (2.6). Then there exists a non-trivial, non-negative function $\tilde{u} \in H_0^1(\Omega)$ (i.e. $\tilde{u} \geq 0$ and $\tilde{u} \not\equiv 0$) satisfying*

$$\begin{cases} -\Delta \tilde{u}(x) = (\sigma(x) - \tilde{u}(x))\tilde{u}(x) & \text{on } \Omega \\ \tilde{u} = 0 & \text{in } \partial\Omega. \end{cases} \quad (2.8)$$

Proof. Consider the following energy

$$E(u) := \int_{\Omega} \frac{|\nabla u|^2}{2} - \sigma \frac{u^2}{2} + \frac{|u|^3}{3}$$

defined on $H_0^1(\Omega)$. Notice that the Euler-Lagrange equation for E gives

$$-\Delta u = (\sigma - |u|)u.$$

We show that the energy E is coercive in $H_0^1(\Omega)$, that is

$$E(u) \rightarrow +\infty \text{ as } \|u\|_{H_0^1(\Omega)} \rightarrow +\infty. \quad (2.9)$$

For this, we use the Young inequality with exponents $3/2$ and 3 to see that, for any $a, b \geq 0$,

$$ab \leq \frac{2}{3}a^{3/2} + \frac{1}{3}b^3.$$

In particular, taking $a := 2^{-2/3}u^2$ and $b := 2^{-1/3}\|\sigma\|_{L^\infty(\Omega)}$, we obtain that

$$\sigma \frac{u^2}{2} \leq \|\sigma\|_{L^\infty(\Omega)} \frac{u^2}{2} \leq \frac{|u|^3}{3} + \frac{\|\sigma\|_{L^\infty(\Omega)}^3}{6},$$

hence

$$-\sigma \frac{u^2}{2} + \frac{|u|^3}{3} \geq -c_0,$$

for some $c_0 > 0$ independent of u . Accordingly,

$$E(u) \geq \int_{\Omega} \frac{|\nabla u(x)|^2}{2} dx - c_0|\Omega|,$$

that establishes (2.9).

As a consequence of (2.9), we have that E has a global minimum $\bar{u} \in H_0^1(\Omega)$, satisfying

$$-\Delta \bar{u} = (\sigma - |\bar{u}|)\bar{u}.$$

Since \bar{u} is a minimum, then $\tilde{u} := |\bar{u}|$ is a minimum too, because $E(\bar{u}) = E(|\bar{u}|)$. Thus we can consider a non-negative function $\tilde{u} \geq 0$ satisfying

$$-\Delta \tilde{u} = (\sigma - \tilde{u})\tilde{u}.$$

We conclude the proof by showing that condition (2.6) guarantees that $E(\tilde{u}) < 0$ and then $\tilde{u} \not\equiv 0$. By (2.6), there exists a function $u \in H_0^1(\Omega)$ with

$$\int_{\Omega} \sigma(x)u(x)^2 dx - \int_{\Omega} |\nabla u|^2 dx > 0.$$

By density, we can suppose that $u \in C_0^\infty(\Omega)$. For every $\varepsilon > 0$ we can rewrite the energy E evaluated at εu as

$$E(\varepsilon u) = \varepsilon^2 \left(\int_{\Omega} \frac{|\nabla u|^2}{2} - \sigma \frac{u^2}{2} + \varepsilon \frac{u^3}{3} \right),$$

hence $E(\tilde{u}) \leq E(\varepsilon u) < 0$ provided ε is small enough. \square

The result in Theorem 2.7 and several variations of it are rather of classical flavor: with slightly different assumptions on σ (take, for instance, $\sigma > 0$ in Ω) and a branching condition matching (2.6) for the existence of non-trivial solutions, it can be found in [2] and in [3].

Remark 2.8. As a byproduct of the proof of Theorem 2.7, we have that the solution found is an energy minimizer. That is, if \tilde{u} is the solution obtained in Theorem 2.7, then $E(\tilde{u} + \varepsilon u) \geq E(\tilde{u})$, for any $u \in H_0^1(\Omega)$. Accordingly, the map

$$\varepsilon \mapsto \mathcal{E}(\varepsilon) := E(\tilde{u} + \varepsilon u)$$

attains its minimum at $\varepsilon = 0$ and therefore

$$0 \leq \mathcal{E}''(0) = \int_{\Omega} |\nabla u|^2 - \sigma u^2 + 2\tilde{u}u^2 dx. \quad (2.10)$$

Also, it is useful to recall that the population \tilde{u} cannot beat the resource σ , as stated in the following result:

Lemma 2.9. *Consider a bounded function $\sigma : \Omega \rightarrow [0, +\infty)$ and a non-negative solution $\tilde{u} \in H_0^1(\Omega)$ of (2.8). Then $\tilde{u}(x) \leq \|\sigma\|_{L^\infty(\Omega)}$, for any $x \in \Omega$.*

Proof. Let $\Theta := \|\sigma\|_{L^\infty(\Omega)}$. We test equation (2.8) against $v := \max\{\tilde{u} - \Theta, 0\}$ and we see that

$$\int_{\Omega} |\nabla v|^2 = \int_{\Omega} \nabla \tilde{u} \cdot \nabla v = \int_{\Omega} (\sigma - \tilde{u})\tilde{u}v = \int_{\{\tilde{u} \geq \Theta\}} (\sigma - \tilde{u})\tilde{u}(\tilde{u} - \Theta).$$

Now observe that, in $\{\tilde{u} \geq \Theta\}$, we have $\sigma - \tilde{u} \leq \Theta - \tilde{u} \leq 0$, which shows that

$$\int_{\Omega} |\nabla v|^2 \leq 0.$$

Accordingly, v vanishes identically and so $\tilde{u} \leq \Theta$. \square

Corollary 2.10. *Consider a bounded function $\sigma : \Omega \rightarrow [0, +\infty)$ and a non-negative solution $\tilde{u} \in H_0^1(\Omega)$ of (2.8). Then \tilde{u} is continuous inside Ω .*

Proof. By Lemma 2.9, we know that \tilde{u} is bounded. Thus, $g := (\sigma - \tilde{u})\tilde{u}$ is bounded, too. This means that $\tilde{u} \in H_0^1(\Omega)$ is a solution of $-\Delta \tilde{u} = g \in L^\infty(\Omega)$, hence the desired claim follows from Theorem 8.22 of [16]. \square

From now on, we focus on the stability of the system around the stationary point $(\tilde{u}, 0)$, where the distribution of resources σ satisfies (2.6) and $\tilde{u} \in H_0^1(\Omega)$ is a non-trivial, non-negative solution of (2.8).

The linearization of the system (2.5) at $(\tilde{u}, 0)$ gives, as a result, the linear operator

$$\begin{aligned} L_{(\tilde{u}, 0)}(u, v) &= \begin{pmatrix} \Delta + (\sigma - 2\tilde{u}) & -\tilde{u} \\ 0 & -(-\Delta)^s + (\sigma - \tilde{u}) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} \\ &= \begin{pmatrix} \Delta u + (\sigma - 2\tilde{u})u - \tilde{u}v \\ -(-\Delta)^s v + (\sigma - \tilde{u})v \end{pmatrix}, \end{aligned} \quad (2.11)$$

for any $(u, v) \in H_0^1(\Omega) \times H_0^s(\Omega)$. The associated quadratic form, with respect to the duality in $H_0^1(\Omega) \times H_0^s(\Omega)$, is

$$Q_{(\tilde{u}, 0)}(u, v) = -[u]_{H^1(\mathbb{R}^n)}^2 - [v]_{H^s(\mathbb{R}^n)}^2 + \int_{\Omega} (\sigma - 2\tilde{u})u^2 - \tilde{u}uv + (\sigma - \tilde{u})v^2 dx, \quad (2.12)$$

for any $(u, v) \in H_0^1(\Omega) \times H_0^s(\Omega)$. From the triangular form of $L_{(\tilde{u}, 0)}$, the relevant information is concentrated on the signs of the principal eigenvalues of the pseudodifferential operators on the diagonal of (2.11). In this spirit, we first point out that the direction $(\tilde{u}, 0)$ is always linearly stable. This is pretty obvious if we think at the biological model, since $(\tilde{u}, 0)$ is the stationary configuration of just one population, and slightly and proportionally modifying the density of this population without letting any new population come into the environment should not drive the system too far from the previous equilibrium. The formal statement goes as follows:

Lemma 2.11. *If the reverse Poincaré-Sobolev condition in (2.6) is satisfied, then*

$$Q_{(\tilde{u}, 0)}(\tilde{u}, 0) < 0.$$

Proof. By testing (2.8) against \tilde{u} , we obtain that

$$[\tilde{u}]_{H^1(\mathbb{R}^n)}^2 = \int_{\Omega} (\sigma - \tilde{u})^2 \tilde{u}^2 dx.$$

As a consequence,

$$Q_{(\tilde{u},0)}(\tilde{u},0) = -[\tilde{u}]_{H^1(\mathbb{R}^n)}^2 + \int_{\Omega} (\sigma - 2\tilde{u})\tilde{u}^2 dx = - \int_{\Omega} \tilde{u}^3 dx.$$

The latter term is strictly negative, thanks to Theorem 2.7 and so we obtain the desired result. \square

We point out that Lemma 2.11 is a particular case of a more general stability result. Namely, the stationary configuration $(\tilde{u},0)$, which corresponds to the local population colonizing the whole of the environment, is also linearly stable with respect to all the perturbations in which only the density of the local species varies (i.e. the possible source of instability in this setting may only come from the advent of a nonlocal population). The formal result goes as follows:

Lemma 2.12. *If the reverse Poincaré-Sobolev condition in (2.6) is satisfied, then*

$$Q_{(\tilde{u},0)}(u,0) \leq 0$$

for any $u \in H_0^1(\Omega)$.

Proof. From (2.12),

$$Q_{(\tilde{u},0)}(u,0) = - \int_{\Omega} |\nabla u|^2 dx + \int_{\Omega} (\sigma - 2\tilde{u})u^2 dx,$$

hence the claim follows from (2.10). \square

In view of Lemma 2.11, we obtain that a good way to detect the possible linear instability of the point $(\tilde{u},0)$ is to rely upon the perturbations of the form $(0,v)$, i.e. in the possible advent of a new population with different diffusive strategy. The purpose of the next section is therefore to understand when it is possible to obtain that

$$Q_{(\tilde{u},0)}(0,v_{\star}) > 0,$$

for a suitable choice of $v_{\star} \in H_0^1(\Omega)$.

3 Linear instability

Our aim in this section is to enlighten the connection between the distribution of resources σ and the possible instability of the system, which would suggest some convenience in a nonlocal dispersal strategy of the second species v . For this, we introduce the following notation:

Definition 3.1. Let $\sigma : \Omega \rightarrow [0, +\infty)$ satisfy the reverse Poincaré-Sobolev condition of Definition 2.3. Let $\tilde{u} \geq 0$ be a non-trivial solution of the non-linear equation (2.8), provided by Theorem 2.7. We say that the pair (σ, \tilde{u}) is mismatched in Ω if there exists $x_0 \in \Omega$ and $r > 0$ with $B_r(x_0) \subset \Omega$ and

$$\inf_{x \in B_r(x_0)} (\sigma(x) - \tilde{u}(x)) > \frac{1}{C_{\sharp}^2(s, B_r(x_0))}. \quad (3.1)$$

In this formula, the constant $C_{\sharp}(s, B_r(x_0))$ is the sharp fractional Poincaré-Sobolev constant with respect to the ball $B_r(x_0)$ provided by Theorem 2.1.

Roughly speaking, condition (3.1) says that the solution \tilde{u} is not capable to exhaust the whole of the resource σ in the whole of the domain: that is, at least, in the region $B_r(x_0)$, the population does not manage to take advantage of all the resource at its disposal and there is at least a quantity $C_{\sharp}(s, \Omega)^{-1}r^{-2s}$ as a leftover.

In Subsection 3.2 we will see an example of mismatching (σ, \tilde{u}) and it will be clear in that case that the mismatch condition depends basically on σ only.

In our setting, condition (3.1) is sufficient to ensure linear instability, as given by the following result.

Proposition 3.2. *If the mismatch condition in (3.1) is satisfied, then there exists $v_{\star} \in H_0^s(\Omega)$ such that $Q_{(\tilde{u}, 0)}(0, v_{\star}) > 0$.*

Proof. By (2.4) and (3.1), we know that there exists $x_0 \in \Omega$ and $r > 0$ such that

$$B_r(x_0) \subset \Omega \quad (3.2)$$

and

$$\inf_{x \in B_r(x_0)} (\sigma(x) - \tilde{u}(x)) > \frac{1}{C_{\sharp}^2(s, B_r(x_0))} = \inf_{\substack{\phi \in H_0^s(B_r(x_0)) \\ \phi \neq 0}} \frac{[\phi]_{H^s(\mathbb{R}^n)}^2}{\|\phi\|_{L^2(B_r(x_0))}^2}.$$

As a consequence, there exists $v_{\star} \in H_0^s(B_r(x_0))$ such that $v_{\star} \not\equiv 0$ and

$$\inf_{x \in B_r(x_0)} (\sigma(x) - \tilde{u}(x)) > \frac{[v_{\star}]_{H^s(\mathbb{R}^n)}^2}{\|v_{\star}\|_{L^2(B_r(x_0))}^2}. \quad (3.3)$$

Now notice that $\|v_{\star}\|_{L^2(B_r(x_0))} = \|v_{\star}\|_{L^2(\Omega)}$ and v_{\star} vanishes a.e. outside Ω , thanks to (3.2). This gives that $v_{\star} \in H_0^s(\Omega)$. Moreover, by (2.12) and (3.3),

$$\begin{aligned} Q_{(\tilde{u}, 0)}(0, v_{\star}) &= -[v_{\star}]_{H^s(\mathbb{R}^n)}^2 + \int_{B_r(x_0)} (\sigma - \tilde{u})v_{\star}^2 dx \\ &> -[v_{\star}]_{H^s(\mathbb{R}^n)}^2 + \frac{[v_{\star}]_{H^s(\mathbb{R}^n)}^2}{\|v_{\star}\|_{L^2(B_r(x_0))}^2} \int_{B_r(x_0)} v_{\star}^2 dx = 0, \end{aligned}$$

which gives the desired result. \square

Remark 3.3. Proposition 3.2 proves the linear instability of the point $(\tilde{u}, 0)$ with respect to perturbation of the type $(0, v_{\star})$. Heuristically, this can be understood as follows: by formally plugging $(u, v) = (\tilde{u}, 0) + \varepsilon(0, v_{\star}) + o(\varepsilon)$ into (1.2) we obtain

$$v_t = -(-\Delta)^s v + (\sigma - (u + v))v = -\varepsilon(-\Delta)^s v_{\star} + \varepsilon(\sigma - \tilde{u} - \varepsilon v_{\star})v_{\star} + o(\varepsilon).$$

Thus, since $v_t = \varepsilon \partial_t v_\star + o(\varepsilon)$, we formally obtain

$$\partial_t v_\star = -(-\Delta)^s v_\star + (\sigma - \tilde{u})v_\star + o(1).$$

Hence

$$\partial_t \|v_\star\|_{L^2(\mathbb{R}^n)}^2 = 2 \int_{\mathbb{R}^n} v_\star \partial_t v_\star dx = Q_{(\tilde{u}, 0)}(0, v_\star) + o(1),$$

which is positive by Proposition 3.2.

Therefore, at least at a formal level, Proposition 3.2 states that the size of the new population (measured in the L^2 -norm) has chances to increase (at least for short times).

These type of linearization arguments in the neighborhood of equilibria that correspond to only one biological species are widely used in mathematical biology, see for instance [18] and the references therein.

The rest of this section is devoted to show that the assumptions of Proposition 3.2 hold for some $\sigma : \Omega \rightarrow \mathbb{R}$.

3.1 Rescaling arguments

We propose here a rather simple rescaling argument which gives the existence of a domain Ω_λ and a distribution of resources σ_λ satisfying the assumptions in Proposition 3.2. The main drawback of this argument is the fact that the domain Ω_λ changes with the parameter. On the other side, it is immediately evident that the resource σ_λ leads to instability at $(\tilde{u}_\lambda, 0)$ when it starts being sparse and far from being homogeneous.

We consider here a smooth function $\sigma : \Omega \rightarrow [0, +\infty)$ satisfying the reverse Poincaré-Sobolev condition in (2.6) (recall Remark 2.5) and the corresponding stationary solution \tilde{u} given by Theorem 2.7. We see that, in this case, the population \tilde{u} does not exhaust the resource σ in the whole of Ω . More precisely, we have:

Lemma 3.4. *Let $\sigma : \Omega \rightarrow [0, +\infty)$ be a smooth function satisfying the reverse Poincaré-Sobolev condition in (2.6) and let \tilde{u} be the corresponding stationary solution given by Theorem 2.7.*

Then there exist $x_0 \in \Omega$, $r > 0$ and $c_0 > 0$ such that $B_r(x_0) \subset \Omega$ and

$$\sigma(x) - u(x) \geq c_0$$

for any $x \in B_r(x_0)$.

Proof. By testing (2.8) against \tilde{u} , we obtain that

$$0 < \int_{\Omega} |\nabla \tilde{u}(x)|^2 dx = \int_{\Omega} (\sigma(x) - \tilde{u}(x)) \tilde{u}^2(x) dx.$$

This implies that there exists $x_0 \in \Omega$ such that $\sigma(x_0) - \tilde{u}(x_0) > 0$. The desired result follows from the continuity of \tilde{u} given by Corollary 2.10. \square

In the notation of Lemma 3.4, by possibly translating the domain, we can assume that $x_0 = 0$, and so

$$\sigma - \tilde{u} \geq c_0 > 0 \text{ in } B_r. \quad (3.4)$$

Then we consider the family of rescaled domains

$$\Omega_\lambda := \{\lambda^{-\frac{1}{2}}y : y \in \Omega\}$$

and rescaled functions

$$\sigma_\lambda(x) := \lambda\sigma(\sqrt{\lambda}x), \quad \forall x \in \Omega_\lambda$$

with $\lambda \geq 1$. Then

$$\tilde{u}_\lambda(x) := \lambda\tilde{u}(\sqrt{\lambda}x), \quad \forall x \in \Omega_\lambda$$

is a positive stationary solution for the equation (2.8) with resource σ_λ , since

$$(\Delta\tilde{u}_\lambda + (\sigma_\lambda - \tilde{u}_\lambda)\tilde{u}_\lambda)(x) = (\lambda^2\Delta\tilde{u} + \lambda^2(\sigma - \tilde{u})\tilde{u})(\sqrt{\lambda}x) = 0, \quad \forall x \in \Omega_\lambda.$$

Proposition 3.5. *There exists $\Lambda \geq 1$ such that, for every $\lambda \geq \Lambda$, the pair $(\sigma_\lambda, \tilde{u}_\lambda)$ is mismatched in the corresponding domain Ω_λ , according to Definition 3.1.*

Proof. We take $r_\lambda := \lambda^{-\frac{1}{2}}r$. By (3.4),

$$\begin{aligned} \inf_{|x| < r_\lambda} (\sigma_\lambda(x) - \tilde{u}_\lambda(x)) &= \inf_{|x| < \lambda^{-\frac{1}{2}}r} \lambda (\sigma(\sqrt{\lambda}x) - \tilde{u}_\lambda(\sqrt{\lambda}x)) \\ &= \inf_{|y| < r} \lambda (\sigma(y) - \tilde{u}_\lambda(y)) \geq c_0\lambda. \end{aligned} \quad (3.5)$$

On the other hand, by Remark 2.2,

$$C_{\sharp}^s(s, B_{r_\lambda}) = r_\lambda^s C_{\sharp}^s(s, B_1) = \lambda^{-\frac{s}{2}} r^s C_{\sharp}^s(s, B_1).$$

By comparing this with (3.5), we conclude that

$$\inf_{x \in B_{r_\lambda}} (\sigma_\lambda(x) - \tilde{u}_\lambda(x)) \geq c_0\lambda > \frac{\lambda^s}{r^{2s} C_{\sharp}^2(s, B_1)} = \frac{1}{C_{\sharp}^2(s, B_{r_\lambda}(x_0))},$$

provided that

$$\lambda > (c_0 r^{2s} C_{\sharp}^2(s, B_1))^{-\frac{1}{1-s}}. \quad \square$$

From Propositions 3.5 and 3.2, we obtain that there exists $v_{\star, \lambda} \in H_0^s(\Omega_\lambda)$ such that $Q_{(\tilde{u}_\lambda, 0)}(0, v_{\star, \lambda}) > 0$, as long as λ is large enough, hence $(\tilde{u}_\lambda, 0)$ is linearly unstable.

This is a first example that shows the validity of Theorem 1.1 (a different one will be constructed in the remaining part of this paper). It is worth to point out that the condition that λ is large translates into the fact that the domain Ω_λ is small and the resource σ_λ is very unevenly distributed. In some sense, the nonlocal diffusion may allow the population to take advantage of the small region in which the resource is abundant, while a less diffusive population may starve in the portion of the environment with limited resource.

3.2 Branching arguments

In this subsection we focus on a particular family of distributions, indeed we assume $B_r(x_0) \subset \Omega$ and

$$\sigma_\tau(x) := \tau \chi_{B_r(x_0)}(x) = \begin{cases} \tau & x \in B_r(x_0) \\ 0 & x \notin B_r(x_0) \end{cases}$$

We show that there exist $\tau, r > 0$ such that the assumptions of Proposition 3.2 hold. First of all we have to deal with with Definition 2.3, which located a branching point for solutions of (2.8). For this, for any $\tau \in \mathbb{R}$, $x_0 \in \mathbb{R}^n$, $r > 0$, such that $B_r(x_0) \subset \Omega$, we introduce the quantity

$$e(\tau, x_0, r) := \sup_{\substack{u \in H_0^1(\Omega) \\ \|u\|_{L^2(\Omega)}=1}} \tau \int_{B_r(x_0)} u^2 - \int_{\Omega} |\nabla u|^2. \quad (3.6)$$

We observe that if $\tau \leq 0$ then obviously $e(\tau, x_0, r) \leq 0$. Thus we use the following notation.

Definition 3.6. We denote

$$\underline{\tau}(x_0, r) := \sup \{ \tau \in \mathbb{R} : e(\tau, x_0, r) \leq 0 \}.$$

Now we discuss some basic properties of the quantities that we have just defined.

Lemma 3.7. *The quantity introduced in Definition 3.6 is finite, namely*

$$\underline{\tau}(x_0, r) \in [0, +\infty).$$

Proof. Let $\phi \in C_0^\infty(B_r)$ with $\|\phi\|_{L^2(B_r)} = 1$, and let $u(x) := \phi(x - x_0)$. Then $\|u\|_{L^2(\Omega)} = \|u\|_{L^2(B_r(x_0))} = \|\phi\|_{L^2(B_r)} = 1$, and

$$e(\tau, x_0, r) \geq \tau \int_{B_r(x_0)} u^2 - \int_{\Omega} |\nabla u|^2 = \tau - \int_{B_r} |\nabla \phi|^2 > 0$$

provided that $\tau > \int_{B_r} |\nabla \phi|^2$. \square

Lemma 3.8. *For any $\tau_1 \leq \tau_2$ we have that*

$$e(\tau_2, x_0, r) - e(\tau_1, x_0, r) \in [0, \tau_2 - \tau_1].$$

Proof. Fix $\varepsilon > 0$. For any $i \in \{1, 2\}$, there exists $u_{(i,\varepsilon)} \in H_0^1(\Omega)$, with $\|u_{(i,\varepsilon)}\|_{L^2(\Omega)} = 1$ such that

$$e(\tau_i, x_0, r) \leq \varepsilon + \tau_i \int_{B_r(x_0)} u_{(i,\varepsilon)}^2 - \int_{\Omega} |\nabla u_{(i,\varepsilon)}|^2.$$

Therefore

$$\begin{aligned}
e(\tau_2, x_0, r) - e(\tau_1, x_0, r) &\geq \tau_2 \int_{B_r(x_0)} u_{(1,\varepsilon)}^2 - \int_{\Omega} |\nabla u_{(1,\varepsilon)}|^2 - e(\tau_1, x_0, r) \\
&\geq \tau_1 \int_{B_r(x_0)} u_{(1,\varepsilon)}^2 - \int_{\Omega} |\nabla u_{(1,\varepsilon)}|^2 - e(\tau_1, x_0, r) \\
&\geq -\varepsilon,
\end{aligned}$$

and

$$\begin{aligned}
e(\tau_1, x_0, r) - e(\tau_2, x_0, r) &\geq \tau_1 \int_{B_r(x_0)} u_{(2,\varepsilon)}^2 - \int_{\Omega} |\nabla u_{(2,\varepsilon)}|^2 - e(\tau_2, x_0, r) \\
&\geq (\tau_1 - \tau_2) \int_{B_r(x_0)} u_{(2,\varepsilon)}^2 - \varepsilon \\
&\geq -(\tau_2 - \tau_1) \int_{\Omega} u_{(2,\varepsilon)}^2 - \varepsilon \\
&= -(\tau_2 - \tau_1) - \varepsilon.
\end{aligned}$$

The desired result now follows by taking ε as small as we wish. \square

Corollary 3.9. *If $\tau \downarrow \underline{\tau}(x_0, r)$, then $e(\tau, x_0, r) \rightarrow 0$.*

Proof. Suppose not, i.e. there exists a sequence

$$\tau_j \geq \underline{\tau}(x_0, r) \tag{3.7}$$

with $\tau_j \rightarrow \underline{\tau}(x_0, r)$ as $j \rightarrow +\infty$, such that

$$|e(\tau_j, x_0, r)| \geq a, \tag{3.8}$$

for some $a > 0$. We claim that

$$e(\tau_j, x_0, r) \geq a. \tag{3.9}$$

We prove it by contradiction: if not, by (3.8), we would have that $e(\tau_j, x_0, r) \leq -a$. Thus, we set

$$\tau_a := \underline{\tau}(x_0, r) + \frac{a}{2}.$$

We notice that $\tau_a > \underline{\tau}(x_0, r)$, therefore, by Definition 3.6, we have that

$$e(\tau_a, x_0, r) > 0.$$

In addition, we have that $\tau_a > \tau_j$ if j is large enough, thus we make use of Lemma 3.8 and we obtain that, for large j ,

$$0 + a \leq e(\tau_a, x_0, r) - e(\tau_j, x_0, r) \leq \tau_a - \tau_j.$$

Taking the limit in j , we conclude that

$$a \leq \tau_a - \underline{\tau}(x_0, r) = \frac{a}{2}.$$

This is a contradiction and (3.9) is established.

Also, by Definition 3.6, we know that there exists a sequence $\tilde{\tau}_j \leq \underline{\tau}(x_0, r)$ with $\tilde{\tau}_j \rightarrow \underline{\tau}(x_0, r)$, such that $e(\tilde{\tau}_j, x_0, r) \leq 0$. Accordingly, by (3.9),

$$e(\tau_j, x_0, r) - e(\tilde{\tau}_j, x_0, r) \geq a. \quad (3.10)$$

Notice that $\tau_j \geq \underline{\tau}(x_0, r) \geq \tilde{\tau}_j$ and

$$\lim_{t \rightarrow +\infty} \tau_j - \tilde{\tau}_j = \underline{\tau}(x_0, r) - \underline{\tau}(x_0, r) = 0.$$

Thus, by Lemma 3.8

$$\lim_{t \rightarrow +\infty} e(\tau_j, x_0, r) - e(\tilde{\tau}_j, x_0, r) \leq \lim_{t \rightarrow +\infty} \tau_j - \tilde{\tau}_j = 0.$$

This is in contradiction with (3.10) and so the desired result is proved. \square

Before stating and proving the main theorem of this subsection, we investigate the behavior of $\underline{\tau}(x_0, r)$ under scaling.

Proposition 3.10. *Fix $s' \in (0, 1)$. There exists a constant $\tau_* := \tau_*(s', \Omega)$ such that*

$$\underline{\tau}(x_0, r) \geq r^{-2s'} \tau_*(s', \Omega)$$

for every $x_0 \in \Omega$ and $r > 0$ such that $B_r(x_0) \subset \Omega$.

Proof. We claim that

$$\int_{B_r(x_0)} u^2 \leq c(s', \Omega) r^{2s'} \|\nabla u\|_{L^2(\Omega)}^2, \quad (3.11)$$

for some constant $c(s', \Omega) > 0$. Once (3.11) is proved, one can finish the proof of the desired result by arguing as follows. One sets $\tau_*(s', \Omega) := 1/c(s', \Omega)$. Then, for every $\tau \leq r^{-2s'} \tau_*(s', \Omega)$ (i.e. for every $\tau \leq 1/(c(s', \Omega) r^{2s'})$), one has that

$$\int_{\Omega} |\nabla u|^2 - \tau \int_{B_r(x_0)} u^2 \geq \int_{\Omega} |\nabla u|^2 - \frac{1}{c(s', \Omega) r^{2s'}} \int_{B_r(x_0)} u^2 \geq 0,$$

where the latter inequality is a consequence of the claim (3.11). This gives that $e(\tau, x_0, r) \geq 0$ for any $\tau \leq r^{-2s'} \tau_*(s', \Omega)$, and so, by Definition 3.6, we have that $\underline{\tau}(x_0, r) \geq r^{-2s'} \tau_*(s', \Omega)$, thus proving the desired result.

Due to these observations, it only remains to prove (3.11). To this scope, we observe that, given $p > 2$, by the Hölder inequality with exponents $\frac{p}{2}$ and $\frac{p}{p-2}$, we have

$$\int_{B_r(x_0)} u^2 \leq (\omega_n r^n)^{\frac{p-2}{p}} \|u\|_{L^p(\Omega)}^2.$$

Therefore, the claim in (3.11) is established if we show that there exists $p > 2$ such that

$$r^{\frac{(p-2)n}{p}} \|u\|_{L^p(\Omega)}^2 \leq C(s', \Omega, p) r^{2s'} \|\nabla u\|_{L^2(\Omega)}^2, \quad (3.12)$$

for some $C(s', \Omega, p) > 0$. So, now it only remains to prove (3.12). To this goal, we deal separately¹ with the cases $n = 2$ and $n \geq 3$.

We start with $n \geq 3$. In this case, we denote by $p := \frac{2n}{n-2} > 2$ the Sobolev conjugate exponent of 2. Notice that $\frac{(p-2)n}{p} = 2$ and the Sobolev inequality (see e.g. formula (7.26) in [16]) bounds $\|u\|_{L^p(\Omega)}^2$ with $C(\Omega) \|\nabla u\|_{L^2(\Omega)}^2$, for some $C(\Omega) > 0$. Hence, if we denote by $D_0 > 0$ the diameter of Ω , we have that

$$r^{\frac{(p-2)n}{p}} \|u\|_{L^p(\Omega)}^2 = r^2 \|u\|_{L^p(\Omega)}^2 \leq C_0 r^{2s'} D_0^{2-2s'} \|\nabla u\|_{L^2(\Omega)}^2,$$

and estimate (3.12) follows in this case.

For the case $n = 2$, we observe that

$$\lim_{p \rightarrow +\infty} \frac{p-2}{p} = 1 > s',$$

so we can choose an even integer $p = p(s') \in (2, +\infty)$ large enough such that

$$\frac{p-2}{p} > s'. \quad (3.13)$$

Also, the critical Sobolev embedding (see e.g. formula (7.38) in [16]) yields that

$$\int_{\Omega} \exp\left(\frac{|u(x)|}{c_1 \|\nabla u\|_{L^2(\Omega)}}\right)^2 dx \leq c_2 |\Omega|, \quad (3.14)$$

for suitable $c_1, c_2 > 0$. Then, since

$$e^t = \sum_{k=0}^{+\infty} \frac{t^k}{k!} \geq \frac{t^{p/2}}{(p/2)!},$$

we deduce from (3.14) that

$$\int_{\Omega} \left(\frac{|u(x)|}{\|\nabla u\|_{L^2(\Omega)}}\right)^p dx \leq C(\Omega, p),$$

for some $C(\Omega, p) > 0$. Therefore

$$\|u\|_{L^p(\Omega)}^2 \leq C'(\Omega, p) \|\nabla u\|_{L^2(\Omega)}^2,$$

for some $C'(\Omega, p) > 0$. As a consequence, if $D_0 > 0$ is the diameter of Ω ,

$$\begin{aligned} r^{\frac{(p-2)n}{p}} \|u\|_{L^p(\Omega)}^2 &= r^{2\left(\frac{(p-2)}{p} - s'\right)} r^{2s'} \|u\|_{L^p(\Omega)}^2 \\ &\leq C'(\Omega, p) D_0^{2\left(\frac{(p-2)}{p} - s'\right)} r^{2s'} \|\nabla u\|_{L^2(\Omega)}^2. \end{aligned}$$

This completes the proof of (3.12) when $n = 2$. \square

¹The case $n \geq 3$ is simpler because the Sobolev conjugated exponent $2^* = 2n/(n-2)$ is not critical. Indeed, in this case the parameter s' does not play much role.

Theorem 3.11. *Let $r, \tau > 0$. Consider the family of distributions $\sigma_\tau = \tau \chi_{B_r(x_0)}$ and a corresponding family of stationary solutions $\tilde{u}_\tau \in H_0^1(\Omega)$, that is*

$$-\Delta \tilde{u}_\tau = (\sigma_\tau - \tilde{u}_\tau) \tilde{u}_\tau.$$

If $\tau \downarrow \underline{\tau}(x_0, r)$, then $\tilde{u}_\tau \rightarrow 0$ uniformly.

Proof. First of all, we notice that

$$\tilde{u}_\tau \leq \tau, \tag{3.15}$$

thanks to Lemma 2.9. Now we fix $\varepsilon \in (0, 1)$ and we claim that

$$\|\tilde{u}_\tau\|_{L^3(\Omega)} \leq \varepsilon, \tag{3.16}$$

provided that τ is close enough to $\underline{\tau}(x_0, r)$. To establish this, we test the equation against \tilde{u}_τ itself, and we obtain that

$$\int_{\Omega} |\nabla \tilde{u}_\tau|^2 = \int_{\Omega} (\sigma_\tau - \tilde{u}_\tau) \tilde{u}_\tau^2 = \tau \int_{B_r(x_0)} \tilde{u}_\tau^2 - \int_{\Omega} \tilde{u}_\tau^3,$$

which in turn gives

$$\|\tilde{u}_\tau\|_{L^3(\Omega)}^3 = \int_{\Omega} \tilde{u}_\tau^3 = \tau \int_{B_r(x_0)} \tilde{u}_\tau^2 - \int_{\Omega} |\nabla \tilde{u}_\tau|^2 \leq \varepsilon(\tau, x_0, r),$$

thanks to (3.6). This and Corollary 3.9 imply (3.16).

Now we set $g(x) := (\sigma_\tau - \tilde{u}_\tau) \tilde{u}_\tau$. Notice that $-\Delta u_\tau = g$ in Ω and, by (3.15) and Lemma 3.7,

$$|g| \leq (\sigma_\tau + \tilde{u}_\tau) \tilde{u}_\tau \leq 2\tau \tilde{u}_\tau \leq 2(\underline{\tau}(x_0, r) + 1) \tilde{u}_\tau \leq C_0 \tilde{u}_\tau,$$

for some $C_0 > 0$ independent of τ , as long as τ is sufficiently close to $\underline{\tau}(x_0, r)$. In particular, by (3.15) and (3.16),

$$\|g\|_{L^{n+3}(\Omega)} \leq C_0 \left(\int_{\Omega} \tilde{u}_\tau^{n+3} \right)^{\frac{1}{n+3}} \leq C_1 \left(\int_{\Omega} \tilde{u}_\tau^3 \right)^{\frac{1}{n+3}} \leq C_1 \varepsilon^{\frac{3}{n+3}}, \tag{3.17}$$

for some $C_1 > 0$. Moreover, using the Hölder inequality with exponents 3 and 3/2,

$$\|\tilde{u}_\tau\|_{L^2(\Omega)}^2 = \int_{\Omega} \tilde{u}_\tau^2 \leq |\Omega|^{\frac{1}{3}} \left(\int_{\Omega} \tilde{u}_\tau^3 \right)^{\frac{2}{3}} = |\Omega|^{\frac{1}{3}} \|\tilde{u}_\tau\|_{L^3(\Omega)}^2,$$

therefore, recalling (3.16) and (3.17),

$$\|\tilde{u}_\tau\|_{L^2(\Omega)} + \|g\|_{L^{n+3}(\Omega)} \leq |\Omega|^{\frac{1}{6}} \varepsilon + C_1 \varepsilon^{\frac{3}{n+3}} \leq C_2 \varepsilon^{\frac{3}{n+3}},$$

for some $C_2 > 0$. We combine this information with Theorem 8.15 of [16] (used here with $f := 0$ and $q := 2(n+3) > n$), thus we obtain that

$$\|\tilde{u}_\tau\|_{L^\infty(\Omega)} \leq C (\|\tilde{u}_\tau\|_{L^2(\Omega)} + \|g\|_{L^3(\Omega)}) \leq C C_2 \varepsilon^{\frac{3}{n+3}},$$

for some $C > 0$, as long as τ is sufficiently close to $\underline{\tau}(x_0, r)$, which is the desired claim. \square

Corollary 3.12. Fix $s' \in (s, 1)$. Let $r, \tau > 0$. Assume that

$$r < \left(\frac{C_{\sharp}^2(s, B_1) \tau_*(s', \Omega)}{2} \right)^{\frac{1}{2(s'-s)}}, \quad (3.18)$$

where $C_{\sharp}(s, B_1)$ is the Poincaré-Sobolev constant in (2.4) and $\tau_*(s', \Omega)$ is given by Proposition 3.10.

Consider the family of distributions $\sigma_\tau = \tau \chi_{B_r(x_0)}$. Then there exists $\tau > \underline{\tau}(x_0, r)$ such that both the reverse Poincaré-Sobolev condition in (2.6) and the mismatch condition in (3.1) are satisfied.

Proof. By taking τ large enough, one can easily fulfill (2.7). This and Lemma 2.4 guarantee the reverse Poincaré-Sobolev condition in (2.6).

In particular, by Theorem 2.7, we can consider the solution \tilde{u}_τ corresponding to the resource σ_τ .

Now we fix

$$\varepsilon \in \left(0, \frac{\tau_*(s', \Omega)}{2 r^{2(s'-s)}} \right). \quad (3.19)$$

Thanks to Theorem 3.11, we can choose τ sufficiently close to $\underline{\tau}(x_0, r)$ such that $\|\tilde{u}_\tau\|_{L^\infty(\Omega)} \leq r^{-2s}\varepsilon$. Therefore, for every $x \in B_r(x_0)$, we have that

$$\sigma_\tau(x) - \tilde{u}_\tau(x) \geq \sigma_\tau(x) - r^{-2s}\varepsilon > \underline{\tau}(x_0, r) - r^{-2s}\varepsilon.$$

From this and Proposition 3.10, we have that, for every $x \in B_r(x_0)$,

$$\sigma_\tau(x) - \tilde{u}_\tau(x) \geq r^{-2s'} \tau_*(s', \Omega) - r^{-2s}\varepsilon.$$

So, recalling (3.19),

$$\inf_{x \in B_r(x_0)} (\sigma_\tau(x) - \tilde{u}_\tau(x)) > \frac{r^{-2s'} \tau_*(s', \Omega)}{2}.$$

Thus, from Remark 2.2 and (3.18), we obtain

$$\begin{aligned} \frac{1}{C_{\sharp}^2(s, B_r(x_0))} &= \frac{1}{r^{2s} C_{\sharp}^2(s, B_1)} = \frac{r^{-2s'} r^{2(s'-s)}}{C_{\sharp}^2(s, B_1)} \\ &< \frac{r^{-2s'} C_{\sharp}^2(s, B_1) \tau_*(s', \Omega)}{2 C_{\sharp}^2(s, B_1)} \\ &= \frac{r^{-2s'} \tau_*(s', \Omega)}{2} < \inf_{x \in B_r(x_0)} (\sigma_\tau(x) - \tilde{u}_\tau(x)). \end{aligned}$$

This establishes the mismatch condition in (3.1). \square

From Proposition 3.2 and Corollary 3.12, it follows that we have constructed another example for which the equilibrium $(\tilde{u}_\tau, 0)$ is linearly unstable, confirming again Theorem 1.1. Once again, this example corresponds to a resource

that is unevenly spread in the environment, and the nonlocal diffusion may compensate such unbalanced distribution of resource.

As a final observation, we would like to stress that most of the techniques discussed in this paper are of quite general nature and can be efficiently exploited in similar problems with different species and different dispersive properties.

4 A purely nonlocal phenomenon

Goal of this section is to prove Theorem 1.2 and to clarify that it is a purely nonlocal feature, with no classical analogue.

Proof of Theorem 1.2. By Theorem 1.1 in [13], we know that we can approximate σ by a s -harmonic function in B_1 : namely, we have that there exist $R_{\varepsilon, \sigma} > 1$ and $u_\varepsilon \in C^k(B_1) \cap C^s(\mathbb{R}^n)$ satisfying (1.6), (1.7) and

$$\|\sigma - u_\varepsilon\|_{C^k(B_1)} \leq \varepsilon. \quad (4.1)$$

Now we define

$$\sigma_\varepsilon := u_\varepsilon. \quad (4.2)$$

In this framework, formula (1.4) follows from (4.1) and (4.2). Moreover, by (1.6) and (4.2),

$$(\sigma_\varepsilon(x) - u_\varepsilon(x)) u_\varepsilon(x) = 0 = (-\Delta)^s u_\varepsilon(x),$$

for any $x \in B_1$, which proves (1.8). \square

Of course, formula (1.5) states that the population locally fits with any given resource, up to an arbitrarily small error estimated by (1.4).

We stress that Theorem 1.2 is only due to the nonlocal feature of the equation and it does not have any local counterpart, as pointed out by the next result.

Proposition 4.1. *Let $M > 0$. Let $\sigma \in C^2(B_1)$ with*

$$\begin{aligned} \sigma(x) &\geq M \quad \text{for any } x \in B_{1/16} \\ \text{and } \sigma(x) &\leq 1 \quad \text{for any } x \in B_1 \setminus B_{1/10}. \end{aligned}$$

Then, there exists $M_0 > 0$ and $\varepsilon > 0$ such that, for any $M \geq M_0$, if $\sigma_\varepsilon \in C^2(B_1)$ satisfies

$$\|\sigma - \sigma_\varepsilon\|_{C^2(B_1)} \leq \varepsilon \quad (4.3)$$

and $u_\varepsilon \in C^2(B_1)$ satisfies

$$-\Delta u_\varepsilon(x) = (\sigma_\varepsilon(x) - u_\varepsilon(x)) u_\varepsilon(x) \quad \text{for any } x \in B_1, \quad (4.4)$$

then

$$\|u_\varepsilon - \sigma_\varepsilon\|_{C^2(B_1)} > \varepsilon \quad (4.5)$$

In particular, the local counterpart of Theorem 1.2 is false.

Proof. Suppose by contradiction that for every $\varepsilon > 0$ there exist σ_ε and u_ε satisfying not only (4.3) and (4.4), but also

$$\|u_\varepsilon - \sigma_\varepsilon\|_{C^2(B_1)} \leq \varepsilon.$$

From (4.3) and (4.5), we know that

$$\|u_\varepsilon - \sigma\|_{L^\infty(B_1)} \leq \|u_\varepsilon - \sigma\|_{C^2(B_1)} \leq 2\varepsilon. \quad (4.6)$$

As a consequence,

$$\|u_\varepsilon\|_{L^\infty(B_1)} \leq 2 + \|\sigma\|_{C^2(B_1)} \leq C_\sigma,$$

for some $C_\sigma > 0$, possibly depending on the fixed resource σ . This, (4.5) and (4.4) give that, in B_1 ,

$$|\Delta u_\varepsilon| \leq |\sigma_\varepsilon - u_\varepsilon| |u_\varepsilon| \leq C_\sigma \varepsilon.$$

Thus, the weak Harnack inequality (see e.g. Theorem 8.18 in [16]) gives that

$$\|u_\varepsilon\|_{L^1(B_{1/4})} \leq C_1 \left(\inf_{B_{1/8}} u_\varepsilon + C_\sigma \varepsilon \right), \quad (4.7)$$

for some constant $C_1 > 0$. Now, by (4.6) and (4.3), we see that $u_\varepsilon(x) \geq M - 2\varepsilon$ in $B_{1/16}$ and therefore

$$\|u_\varepsilon\|_{L^1(B_{1/4})} \geq \int_{B_{1/16}} u_\varepsilon(x) dx \geq C_2 (M - 2\varepsilon), \quad (4.8)$$

for some constant $C_2 > 0$. Similarly, from (4.6) and (4.3), we have that $u_\varepsilon \leq 1 + 2\varepsilon$ in $B_1 \setminus B_{1/10}$ and therefore

$$\inf_{B_{1/8}} u_\varepsilon \leq 1 + 2\varepsilon \leq 2. \quad (4.9)$$

By inserting (4.8) and (4.9) into (4.7) we obtain that

$$M - 2\varepsilon \leq C_3 (2 + C_\sigma \varepsilon),$$

for some $C_3 > 0$. Thus, we take $M \geq M_0 := 3C_3$. This fixes σ and gives that

$$C_3 \leq M - 2C_3 \leq 2\varepsilon + C_3 (2 + C_\sigma \varepsilon) - 2C_3 = (2 + C_3 C_\sigma) \varepsilon.$$

By taking ε small, we obtain a contradiction and we complete the proof of Proposition 4.1. \square

References

- [1] Giuliano Aluffi. Per andare a caccia la medusa si muove come un computer. *Il Venerdì di Repubblica*, August 2014.
- [2] A. Ambrosetti and G. Prodi. On the inversion of some differentiable mappings with singularities between Banach spaces. *Ann. Mat. Pura Appl. (4)*, 93:231–246, 1972.
- [3] H. Berestycki, P.-L. Lions, and L. A. Peletier. An ODE approach to the existence of positive solutions for semilinear problems in \mathbf{R}^N . *Indiana Univ. Math. J.*, 30(1):141–157, 1981.
- [4] Xavier Cabré and Jean-Michel Roquejoffre. Propagation de fronts dans les équations de Fisher-KPP avec diffusion fractionnaire. *C. R. Math. Acad. Sci. Paris*, 347(23-24):1361–1366, 2009.
- [5] Robert Stephen Cantrell, Chris Cosner, and Vivian Hutson. Permanence in ecological systems with spatial heterogeneity. *Proc. Roy. Soc. Edinburgh Sect. A*, 123(3):533–559, 1993.
- [6] Robert Stephen Cantrell, Chris Cosner, and Vivian Hutson. Ecological models, permanence and spatial heterogeneity. *Rocky Mountain J. Math.*, 26(1):1–35, 1996.
- [7] Robert Stephen Cantrell, Chris Cosner, and Yuan Lou. Advection-mediated coexistence of competing species. *Proc. Roy. Soc. Edinburgh Sect. A*, 137(3):497–518, 2007.
- [8] Robert Stephen Cantrell, Chris Cosner, and Yuan Lou. Evolution of dispersal and the ideal free distribution. *Math. Biosci. Eng.*, 7(1):17–36, 2010.
- [9] Robert Stephen Cantrell, Chris Cosner, Yuan Lou, and Daniel Ryan. Evolutionary stability of ideal free dispersal strategies: a nonlocal dispersal model. *Can. Appl. Math. Q.*, 20(1):15–38, 2012.
- [10] Xinfu Chen, Richard Hambrook, and Yuan Lou. Evolution of conditional dispersal: a reaction-diffusion-advection model. *J. Math. Biol.*, 57(3):361–386, 2008.
- [11] Chris Cosner, Juan Dávila, and Salome Martínez. Evolutionary stability of ideal free nonlocal dispersal. *J. Biol. Dyn.*, 6(2):395–405, 2012.
- [12] Eleonora Di Nezza, Giampiero Palatucci, and Enrico Valdinoci. Hitchhiker’s guide to the fractional Sobolev spaces. *Bull. Sci. Math.*, 136(5):521–573, 2012.
- [13] Serena Dipierro, Ovidiu Savin, and Enrico Valdinoci. All functions are locally s -harmonic up to a small error. *Preprint, to appear in J. Eur. Math. Soc. (JEMS)*, 2014.

- [14] Jack Dockery, Vivian Hutson, Konstantin Mischaikow, and Mark Pernarowski. The evolution of slow dispersal rates: a reaction diffusion model. *J. Math. Biol.*, 37(1):61–83, 1998.
- [15] Avner Friedman. PDE problems arising in mathematical biology. *Netw. Heterog. Media*, 7(4):691–703, 2012.
- [16] David Gilbarg and Neil S. Trudinger. *Elliptic partial differential equations of second order*. Classics in Mathematics. Springer-Verlag, Berlin, 2001. Reprint of the 1998 edition.
- [17] Nicolas E. Humphries, Nuno Queiroz, Jennifer R. M. Dyer, Nicolas G. Pade, Michael K. Musyl, Kurt M. Schaefer, Daniel W. Fuller, Juerg M. Brunnschweiler, Thomas K. Doyle, Jonathan D. R. Houghton, Graeme C. Hays, Catherine S. Jones, Leslie R. Noble, Victoria J. Wearmouth, Emily J. Southall, and David W. Sims. Environmental context explains Lévy and Brownian movement patterns of marine predators, 2010/06/24/print.
- [18] V. Hutson, S. Martinez, K. Mischaikow, and G. T. Vickers. The evolution of dispersal. *J. Math. Biol.*, 47(6):483–517, 2003.
- [19] V. Hutson, K. Mischaikow, and P. Poláčik. The evolution of dispersal rates in a heterogeneous time-periodic environment. *J. Math. Biol.*, 43(6):501–533, 2001.
- [20] Chiu-Yen Kao, Yuan Lou, and Wenxian Shen. Random dispersal vs. non-local dispersal. *Discrete Contin. Dyn. Syst.*, 26(2):551–596, 2010.
- [21] Chiu-Yen Kao, Yuan Lou, and Wenxian Shen. Evolution of mixed dispersal in periodic environments. *Discrete Contin. Dyn. Syst. Ser. B*, 17(6):2047–2072, 2012.
- [22] Eugenio Montefusco, Benedetta Pellacci, and Gianmaria Verzini. Fractional diffusion with Neumann boundary conditions: the logistic equations. *Preprint*, 2012.
- [23] Diana Stan and Juan Luis Vázquez. The Fisher-KPP equation with non-linear fractional diffusion. *SIAM J. Math. Anal.*, 46(5):3241–3276, 2014.
- [24] Enrico Valdinoci. From the long jump random walk to the fractional Laplacian. *Bol. Soc. Esp. Mat. Apl. SĒMA*, (49):33–44, 2009.
- [25] G. M. Viswanathan, V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. Lévy flight search patterns of wandering albatrosses, 1996/05/30/print.