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Solution of a Nonlinear Integral Equation Arising in the Moment Approximation of Spatial Logistic Dynamics

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Abstract: We investigate a nonlinear integral equation derived through moment approximation from the individual-based representation of spatial logistic dynamics. The equation describes how the densities of pairs of individuals represented by points in continuous space are expected to equilibrate under spatially explicit birth–death processes characterized by constant fecundity with local natal dispersal and variable mortality determined by local competition. The equation is derived from a moment hierarchy truncated by a moment closure expressing the densities of triplets as a function of the densities of pairs. Focusing on results for individuals inhabiting two-dimensional habitats, we explore the solvability of the equation by introducing a dedicated space of functions that are integrable up to a constant. Using this function space, we establish sufficient conditions for the existence of solutions of the equation within a zero-centered ball. For illustration and further insights, we complement our analytical findings with numerical results.

Keywords: nonlinear integral equations; spatial logistic dynamics; individual-based models; fixed-point

MSC: 45G10; 92B99; 65B99

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1. Introduction

Theoretical ecology has evolved significantly since the middle of the 20th century. The discipline has transitioned from simple models that characterize populations merely by their population sizes or population densities to more complex models that are spatially explicit and/or individual-based. This transition has been prompted by the inability of simpler models to describe phenomena observed in natural populations with sufficient accuracy. Typically, the more complex models are heavily relying on computational analyses [1–3], through which the fundamental shortcomings of the simpler models have been evidenced and illustrated [4–11].

Many of the phenomena that are not accurately captured by simple models point to the importance of spatial population structure and individual-based interactions [12]. Meta-population models have offered a first step in this direction based on dividing a population's habitat into patches, which enables representing coarse-grained population structures among patches and local interactions within patches [13–16]. While meta-population models are still widely used today, they remain stylized compared with the natural world, as they cannot represent fine-grained population structures beyond patchy habitats and cannot differentiate individual-based interactions below the patch scale. The persisting need for more realistic models has been revealed, e.g., in the study of reproductive pair correlations [17,18]. Two key steps towards addressing the residual challenges involve representing habitats in terms of continuous spaces and individuals in terms of points in such spaces, which has led to the development of exceptionally complex ecological models [19–21].

These complexities notwithstanding, it has been demonstrated that the effective number of degrees of freedom in such models can be reduced [22]. Starting from representing population dynamics as spatiotemporal point processes, Dieckmann and Law showed how the analysis of spatial moments enables a natural reduction in spatial complexity through moment dynamics and moment closures, putting a spotlight on the advantages of modeling pair correlations alongside population densities [23]. The resultant moment equations describe the coupled dynamics of spatial moments such as a population's mean density and pair density based on a moment closure using these for approximating triplet densities. This approach was initially developed for discrete-space models [24–26] and has later been extended to continuous-space models [18,23,27,28].

The principal aim of the present study is to analyze and solve a nonlinear integral equation describing a population distributed in continuous space equilibrating under spatial logistic dynamics [23,29]. We rigorously derive the conditions that ensure the solvability of this equation. While a brief summary of this investigation has previously been made available [30], the present study provides the first comprehensive analysis incorporating all proofs.

This paper is structured into three primary sections followed by a conclusion section. Section 2 describes the model and frames the central question. Section 3 examines the equilibrium equation derived from the model and identifies sufficient conditions for its solvability. Section 4 introduces a numerical method for solving the equilibrium equation and exemplifies its utility by applications to various parameter combinations that meet the identified sufficient conditions.

2. Model Description

We begin by describing the individual-based representation of spatial logistic dynamics and explain how the point patterns representing the spatial distributions of individuals in continuous space are characterized by their spatial moments. We then specify the resultant moment hierarchy and consider its closure and equilibration, which together give rise to the nonlinear integral equation that is the primary focus of our investigation.

2.1. Individual-Based Model

Our individual-based model of spatial logistic dynamics [23,29] is represented by a spatiotemporal point process. Individuals are single agents such as plants, animals, humans, or firms. Each individual is represented by a point indicating its location in the continuous space called habitat and by an interval indicating its lifespan in continuous time. An individual's lifespan is specified by its birth and death events, which, thus, determine the end points of the corresponding temporal interval, while its location does not change during its lifespan, which, thus, determines the corresponding spatial point to be stationary.

For a given instant in time, the currently existing individuals form a population represented by the temporal cross-section of the spatiotemporal point process. We postulate that, over time, this cross-section converges to a stationary, homogeneous, and isotropic spatial point process. This limit point process is, thus, invariant under temporal translation, spatial translation, and spatial rotation, respectively, and can, hence, be characterized by its time-independent spatial moments.

The evolution of the spatiotemporal point process is driven by birth and death events. As death rates are dependent on the population's current spatial distribution of individuals, this introduces a coupling among individuals that renders nonlinear the integral equations determining the time-independent spatial moments.

Remark 1. *In this paper, we focus on two-dimensional habitats, which are most interesting from the perspective of practical applications, especially in ecology (see Figure 1). It is worth noting, however, that many findings of this research have the potential to be extended to other dimensionalities [31].*

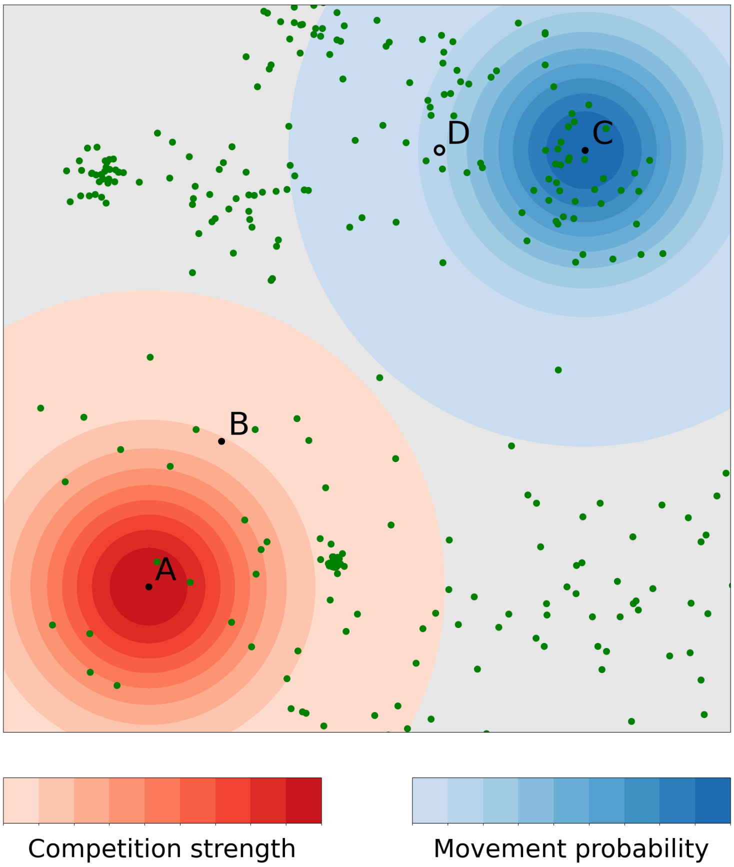

Figure 1. Visualization of the kernels describing competition and dispersal. Individuals are represented by points in a two-dimensional habitat. The strength according to which an individual A competes with individuals such as B is determined by the competition kernel, depicted here by variations in red shading. Similarly, the probability density according to which an individual C moves a newly produced offspring individual to locations such as D is determined by the dispersal kernel, depicted here by variations in blue shading.

In our model, birth events are independent of other individuals. They are characterized by the per capita birth rate $b > 0$ and the dispersal kernel $m(\Delta x)$. The latter specifies the probability density according to which an individual produces an offspring at a location shifted by the vector Δx from its own location. Consequently, the rate density for the appearance of a new individual at location x' produced by an individual at location x is $bm(x - x')$.

In our model, death events are dependent on competition with other individuals. They are characterized by the intrinsic death rate $d \in [0; b)$, the strength of competition $s \geq 0$, and the competition kernel $w(\Delta x)$. The latter specifies the probability density according to which the death rate of an individual is increased by other individuals at locations shifted by the vector Δx from its own location. Consequently, the rate density for the disappearance of an existing individual at location x under competition with other individual at location x' is

$$d + s \sum_{x' \in X \setminus \{x\}} w(x - x'),$$

where X is a set of individuals in the population.

We assume dispersal and competition kernels to be radially symmetric, which means that their values depend only on the scalar distance between locations. We also assume the absence of a large-scale spatial structure, and thus, of long-range spatial correlations, which means that the kernels must tend to zero at infinite distance. Consequently, the functions m and w must belong to the following class:

$$\mathcal{K} = \left\{ f \in L_1(\mathbb{R}^2) : \ f(x) \geq 0, \ \|f\|_{L_1} = 1, \ f(x) = F\big(\|x\|\big), \lim_{r \to +\infty} F(r) = 0 \right\}. \tag{1}$$

2.2. Spatial Moments

Owing to the stochastic nature of the individual-based model, its direct investigation proves challenging, as the population's evolution is not deterministically predictable even when the initial locations of all individuals are known. This suggests focusing instead on expected spatial moments, which describe average characteristics of a population's spatial distribution at a given time across all possible stochastic realizations starting from given initial conditions.

We consider the first spatial moment $N(t)$, which describes the mean density at time t, i.e., the density of single individuals, also known as singlets. Even though it is a highly pertinent characteristic of a population, it fails, by its definition, to provide any information about how individuals are distributed in space. To quantify the most salient aspects of a population's spatial structure, we therefore utilize the second spatial moment $C(x, t)$ which describes the pair density at time t, i.e., the density of pairs of individuals separated by the distance vector x. Note that the radial symmetry of the kernels implies the radial symmetry of the second spatial moment. Together, these first two moments can often capture the most salient information about the current state of a spatially distributed population.

Calculating the expectation of spatial moments from the individual-based model by averaging over a sufficiently large number of stochastic realizations is a computationally intensive task. If the process is spatially ergodic, long-range spatial correlations do not emerge and cannot persist, so that averages over realizations can be replaced with averages over space. This means that the expected spatial moments can equivalently be obtained from a single stochastic realization, provided the considered habitat area is so large that it contains a sufficiently large number of essentially uncorrelated subareas.

An absence of long-range spatial correlations means that pairs at large distances are uncorrelated. The density of such long-range pairs is, thus, simply given by the square of the mean density, and the following asymptotic constraint applies [32]:

$$\lim_{\|x\| \to +\infty} C(x, t) = N^2(t). \tag{2}$$

If $C(x, t) = N^2(t)$ applies for all x, this reduces the expected dynamics of the mean density in the individual-based model to a simple closed dynamical system known as logistic dynamics [33], which has been extensively studied for decades. In contrast, when $C(x, t) = N^2(t)$ applies only for large $\|x\|$, the shape of $C(x, t)$ for $\|x\|$ not large contains salient information not captured by $N(t)$, and the dynamics of the first spatial moment then have to be studied together with those of the second spatial moment [23].

2.3. Equilibrium Equation

The equations for the dynamics of moments were originally derived by Dieckmann and Law [23] for moments of up to second order and individuals of multiple types. Subsequently, Galkin and Nikitin extended these results to cover moments of any order and individuals of a single type [34]. The most comprehensive form of these equations, covering a moment of any order and individuals of multiple types, was conjectured by Plank and Law [35] based on their derivation for moments of low order.

Here, we show the result for the n-th spatial moment M_n of a single species using the notation and assumptions introduced above:

$$\begin{aligned}\frac{1}{n}\frac{\partial M_n}{\partial t}(x_1,\ldots,x_{n-1},t) = {} & b\sum_{k=1}^{n-1} m(x_k)M_{n-1}(x_2-x_1,\ldots x_{n-1}-x_1,t) \\ & + b\int_{\mathbb{R}^2} m(x)M_n(x_1-x,\ldots,x_{n-1}-x,t)\,\mathrm{d}x \\ & - \left(d + s\sum_{k=1}^{n-1} w(x_k)\right)M_n(x_1,\ldots,x_{n-1},t) \\ & - s\int_{\mathbb{R}^2} w(x)M_{n+1}(x_1,\ldots,x_{n-1},x,t)\,\mathrm{d}x.\end{aligned} \tag{3}$$

This equation describes how the dynamics of M_n depend on M_{n-1}, M_n, and M_{n+1}, which creates a moment hierarchy [23]. In particular, the dynamics of the first spatial moment $M_1(t) = N(t)$ depend on the second spatial moment $M_2(x,t) = C(x,t)$, while the dynamics of the second spatial moment depend on the third spatial moment $M_3(x,y,t) = T(x,y,t)$. The latter describes the triplet density at time, i.e., the density of triplets of individuals separated by the distance vectors x and y. Thus, an infinite series of spatial moments of increasing order must be known in order to describe the dynamics of the first spatial moment, the mean density. An approach to truncate this moment hierarchy is to approximate the third spatial moment T in terms of N and C, a method known as moment closure [32].

In this article, we analyze the equilibrium of the resultant moment dynamics. We consider an equilibrium to have been reached when there are no further changes in a population's spatial moments of low order, which requires that the right-hand side in (3) equals zero. As our primary interest is in the dynamics of the first and second spatial moments, we set $n = 1$ and $n = 2$ in (3) and obtain

$$\begin{cases} 0 = (b-d)N - s\int_{\mathbb{R}^2} C(y)w(y)\,\mathrm{d}y, \\ 0 = bm(x)N + b\int_{\mathbb{R}^2} m(y)C(x-y)\,\mathrm{d}y \\ \quad - \big(d + sw(x)\big)C(x) - s\int_{\mathbb{R}^2} w(y)T(x,y)\,\mathrm{d}y. \end{cases} \tag{4}$$

To close this system by expressing the third spatial moment in terms of the first and second spatial moments, alternative moment closures exist [23], all of which must satisfy specific conditions [32]. In accordance with [32], we consider the following general power-2 closure:

$$T_{\alpha\beta\gamma}(x,y) = \frac{1}{\alpha+\gamma}\left(\alpha\frac{C(x)C(y)}{N} + \beta\frac{C(x)C(y-x)}{N} + \gamma\frac{C(y)C(y-x)}{N} - \beta N^3\right), \tag{5}$$

where $\alpha, \beta, \gamma \in \mathbb{R}$ and $\alpha + \gamma \neq 0$. By substituting (5) into (4), we obtain the following equilibrium equation, which is the main object of research in this article:

$$\begin{aligned} 0 = {} & bm(x)N(C) + b\int_{\mathbb{R}^2} m(y)C(x-y)\,\mathrm{d}y \\ & - \left(\frac{\alpha}{\alpha+\gamma}b + \frac{\gamma}{\alpha+\gamma}d + sw(x)\right)C(x) \\ & - \frac{\beta}{\alpha+\gamma}\cdot\frac{s}{N(C)}C(x)\int_{\mathbb{R}^2} w(y)C(y-x)\,\mathrm{d}y \\ & - \frac{\gamma}{\alpha+\gamma}\cdot\frac{s}{N(C)}\int_{\mathbb{R}^2} w(y)C(y)C(y-x)\,\mathrm{d}y \\ & + \frac{\beta}{\alpha+\gamma}\cdot sN^3(C), \end{aligned} \tag{6}$$

where

$$N(C) = \frac{s}{b-d} \int_{\mathbb{R}^2} C(y) w(y) \, \mathrm{d}y.$$

According to (2), given the lack of dependence on time, these equations are supplemented by the asymptotic condition

$$\lim_{\|x\| \to +\infty} C(x) = N^2(C). \tag{7}$$

3. Equilibrium-Equation Theory

We now proceed to analyze the solvability of the equilibrium equation. This is achieved by establishing a dedicated function space encompassing the solutions for the equation, thereby transforming the original question into one of fixed-point existence.

3.1. Auxiliary Statements

To begin, we state several well-known definitions and results that will be utilized in our subsequent investigation. The proofs of the following lemmas are readily available in standard textbooks of functional analysis.

Definition 1. *Let a function f be measurable on a set X with a measure μ and let*

$$U_f(M) = \{x \in X : \; f(x) > M\}.$$

Then, we call the value

$$\operatorname*{ess\,sup}_X f = \inf \left\{ M \in \mathbb{R} : \; \mu\big(U_f(M)\big) = 0 \right\}$$

the essential supremum of the function f.

Definition 2. *We call a function $f : \mathbb{R}^2 \to \mathbb{R}$ essentially bounded if* $\operatorname{ess\,sup}_{\mathbb{R}^2} |f| < +\infty$.

Definition 3. *For an essentially bounded function $f \in L_1(\mathbb{R}^2)$ (i.e., Lebesgue-integrable on the whole plane $\mathbb{R}^2$), we define*

$$\|f\|_{BL_1} = \max \left\{ \|f\|_{L_1}, \operatorname*{ess\,sup}_{\mathbb{R}^2} |f| \right\}.$$

Remark 2. *If $f \in L_1(\mathbb{R}^2)$ and g is essentially bounded, then $fg \in L_1(\mathbb{R}^2)$.*

Remark 3. *In further calculations, we will use the obvious fact that for any $f \in L_1(\mathbb{R}^2)$ and any $y \in \mathbb{R}^2$,*

$$\int_{\mathbb{R}^2} f(x+y) \, \mathrm{d}x = \int_{\mathbb{R}^2} f(x) \, \mathrm{d}x.$$

Lemma 1. *If $f \in L_1(\mathbb{R}^2)$, then, for any $\varepsilon > 0$, there exists $\delta = \delta(\varepsilon) > 0$ such that for any $h \in \mathbb{R}^2$ of which the norm is less or equal to δ,*

$$\int_{\mathbb{R}^2} |f(x+h) - f(x)| \, \mathrm{d}x \le \varepsilon.$$

Proof. See, for example, ([36], p. 216). □

Lemma 2. *If f, $g \in L_1(\mathbb{R}^2)$ then the convolution*

$$[f * g](x) = \int_{\mathbb{R}^2} f(x-y) g(y) \, \mathrm{d}y$$

exists and belongs to $L_1(\mathbb{R}^2)$.

Proof. The proof is similar to ([37], p. 503) with the obvious exchange of $\mathbb{R}$ by $\mathbb{R}^2$. □

Theorem 1 (Fubini)**.** *If for almost all* $y \in \mathbb{R}^2$*, there exists an integral*

$$\int_{\mathbb{R}^2} |f(x,y)|\,\mathrm{d}x = F(y)$$

and

$$\int_{\mathbb{R}^2} F(y)\,\mathrm{d}y < +\infty,$$

then, there exist integrals

$$\int_{\mathbb{R}^2\times\mathbb{R}^2} f(x,y)\,\mathrm{d}x\,\mathrm{d}y \quad \text{and} \quad \int_{\mathbb{R}^2}\left(\int_{\mathbb{R}^2} f(x,y)\,\mathrm{d}y\right)\mathrm{d}x$$

and the following equality is true:

$$\int_{\mathbb{R}^2}\left(\int_{\mathbb{R}^2} f(x,y)\,\mathrm{d}x\right)\mathrm{d}y = \int_{\mathbb{R}^2}\left(\int_{\mathbb{R}^2} f(x,y)\,\mathrm{d}y\right)\mathrm{d}x = \int_{\mathbb{R}^2\times\mathbb{R}^2} f(x,y)\,\mathrm{d}x\,\mathrm{d}y.$$

Proof. See, for example, ([38], p. 318). □

3.2. Space of Functions Integrable up to a Constant

Prior to venturing further into the investigation of the equilibrium equation, we will first elaborate on a dedicated function space we define in order to facilitate this investigation. We will subsequently demonstrate that the solution to the equilibrium equation can be located in this space.

We examine a set of functions of the form $f = F + \eta$, where $F \in L_1(\mathbb{R}^2)$ and $\eta \in \mathbb{R}$. We refer to F as the functional part of the element f and denote it by $\mathcal{F}f$. Similarly, we refer to η as the numerical part of the element f and denote it by $\mathcal{N}f$. The set under consideration is evidently linear concerning the operations of addition and scalar multiplication, which are defined in accordance with the following rules:

$$f + g = (\mathcal{F}f + \mathcal{F}g) + (\mathcal{N}f + \mathcal{N}g),$$
$$\alpha f = (\alpha\mathcal{F}f) + (\alpha\mathcal{N}f),$$

where f and g are arbitrary elements of the considered set and $\alpha \in \mathbb{R}$.

We elevate the aforementioned space to a normed vector space by defining the norm of an element $f = \mathcal{F}f + \mathcal{N}f$ by

$$\|f\| = \|\mathcal{F}f\|_{L_1} + |\mathcal{N}f|. \tag{8}$$

This emerging space is denoted by $\widehat{L_1}(\mathbb{R}^2)$ and is referred to as the space of functions integrable up to a constant. Further on, we will use $\|f\|_{\widehat{L_1}}$ to denote the norm (8).

Remark 4. $L_1(\mathbb{R}^2)$ *is a closed linear subspace of the space* $\widehat{L_1}(\mathbb{R}^2)$.

Remark 5. *The elements* f *and* g *of the space* $\widehat{L_1}(\mathbb{R}^2)$ *are identical if and only if their functional and numerical parts are identical.*

Lemma 3. *The space* $\widehat{L_1}(\mathbb{R}^2)$ *is complete.*

Proof. The validity of the lemma stems from the property that $\widehat{L_1}(\mathbb{R}^2)$ is isomorphic to the direct sum of the complete spaces $L_1(\mathbb{R}^2)$ and $\mathbb{R}$. □

We now delve into a detailed analysis of the various operators acting in $\widehat{L_1}(\mathbb{R}^2)$ that are relevant for our investigation. As our discussion progresses, it will become clear how the equilibrium Equation (6) can be expressed in the form of an operator equation, and how this restructured equation can be derived through the composition of the aforementioned operators.

3.3. Convolution Operator

We consider an essentially bounded function $\varphi \in L_1(\mathbb{R}^2)$ and define the convolution operator $\mathcal{C}_\varphi$ acting on functions from $\widehat{L_1}(\mathbb{R}^2)$ by the rule

$$\mathcal{C}_\varphi f = [\varphi * f] = \int_{\mathbb{R}^2} \varphi(x-y) f(y)\, \mathrm{d}y = [\varphi * \mathcal{F}f] + \mathcal{N}f \int_{\mathbb{R}^2} \varphi(y)\, \mathrm{d}y.$$

Since the convolution of two functions from $L_1(\mathbb{R}^2)$ is a function from $L_1(\mathbb{R}^2)$ and the expression $\mathcal{N}f \int_{\mathbb{R}^2} \varphi(y)\, \mathrm{d}y$ is a constant, the considered operator acts in $\widehat{L_1}(\mathbb{R}^2)$.

Lemma 4. *The operator $\mathcal{C}_\varphi$ is a bounded linear operator with a norm equal to $\|\varphi\|_{L_1}$.*

Proof. The linearity of the operator $\mathcal{C}_\varphi$ is obvious. Let us consider any element $f \in \widehat{L_1}(\mathbb{R}^2)$ and evaluate the norm of $\mathcal{C}_\varphi f$:

$$\begin{aligned}
\|\mathcal{C}_\varphi f\|_{\widehat{L_1}} &= \int_{\mathbb{R}^2} \left| \int_{\mathbb{R}^2} \varphi(x-y) \mathcal{F}f(y)\, \mathrm{d}y \right| \mathrm{d}x + \left| \mathcal{N}f \int_{\mathbb{R}^2} \varphi(y)\, \mathrm{d}y \right| \\
&\le \int_{\mathbb{R}^2} \int_{\mathbb{R}^2} |\varphi(x-y)| \cdot |\mathcal{F}f(y)|\, \mathrm{d}y\, \mathrm{d}x + |\mathcal{N}f| \int_{\mathbb{R}^2} |\varphi(y)|\, \mathrm{d}y \\
&= \int_{\mathbb{R}^2} \int_{\mathbb{R}^2} |\varphi(x-y)|\, \mathrm{d}x \cdot |\mathcal{F}f(y)|\, \mathrm{d}y + |\mathcal{N}f| \int_{\mathbb{R}^2} |\varphi(y)|\, \mathrm{d}y \\
&= \|\varphi\|_{L_1} \cdot \|\mathcal{F}f\|_{L_1} + |\mathcal{N}f| \cdot \|\varphi\|_{L_1} = \|\varphi\|_{L_1} \cdot \|f\|_{\widehat{L_1}}.
\end{aligned}$$

Here, the change in the integration order is correct because of Fubini's theorem. Hence, the norm $\mathcal{C}_\varphi$ is less or equal to $\|\varphi\|_{L_1}$. To see whether we can tighten this upper bound, we consider the function

$$f_\delta(x) = \begin{cases} \dfrac{1}{\pi\delta^2}, & \|x\| \le \delta, \\ 0, & \|x\| > \delta, \end{cases}$$

for an arbitrary $\delta > 0$. This function is obviously an element of $L_1(\mathbb{R}^2)$. Using standard evaluations, we can show that

$$\|\mathcal{C}_\varphi f_\delta\|_{\widehat{L_1}} \xrightarrow[\delta \to 0+0]{} \|\varphi\|_{L_1}.$$

Since $\|f_\delta\|_{L_1} = 1$ for all $\delta > 0$, we can deduce that the upper bound of the norm $\|\mathcal{C}_\varphi\|$ cannot be tightened. Therefore, $\|\mathcal{C}_\varphi\| = \|\varphi\|_{L_1}$. □

3.4. Self-Convolution Operator

We now consider nonlinear operators acting in $\widehat{L_1}(\mathbb{R}^2)$ that are relevant to the equilibrium problem. We need to estimate norms of these operators images; hence, we prove the following lemma:

Lemma 5. *For a function $\varphi \in L_1(\mathbb{R}^2)$ that is essentially bounded and any pair of functions $f, g \in \widehat{L_1}(\mathbb{R}^2)$,*

$$\Big\| [f\varphi * g] \Big\|_{\widehat{L_1}} \le \|\varphi\|_{BL_1} \|f\|_{\widehat{L_1}} \|g\|_{\widehat{L_1}}.$$

Proof. We start from

$$[f\varphi * g] = \int_{\mathbb{R}^2} \mathcal{F}f(x-y)\varphi(x-y)\mathcal{F}g(y)\,\mathrm{d}y + \mathcal{N}f\int_{\mathbb{R}^2}\varphi(x-y)\mathcal{F}g(y)\,\mathrm{d}y \\ + \mathcal{N}g\int_{\mathbb{R}^2}\varphi(y)\mathcal{F}f(y)\,\mathrm{d}y + \mathcal{N}f\mathcal{N}g\int_{\mathbb{R}^2}\varphi(y)\,\mathrm{d}y. \tag{9}$$

Using Fubini's theorem, we obtain

$$\int_{\mathbb{R}^2}\left|\int_{\mathbb{R}^2}\mathcal{F}f(x-y)\varphi(x-y)\mathcal{F}g(y)\,\mathrm{d}y\right|\mathrm{d}x \le \operatorname*{ess\,sup}_{\mathbb{R}^2}|\varphi|\cdot\|\mathcal{F}f\|_{L_1}\cdot\|\mathcal{F}g\|_{L_1}.$$

Combining the second and fourth terms of (9), we obtain

$$\mathcal{N}f\int_{\mathbb{R}^2}\varphi(x-y)\mathcal{F}g(y)\,\mathrm{d}y + \mathcal{N}f\mathcal{N}g\int_{\mathbb{R}^2}\varphi(y)\,\mathrm{d}y = \mathcal{N}f\cdot\mathcal{C}_\varphi g,$$

which, according to Lemma 4, has an $\widehat{L_1}$-norm less or equal to $|\mathcal{N}f|\cdot\|\varphi\|_{L_1}\cdot\|g\|_{\widehat{L_1}}$. Finally,

$$\left|\mathcal{N}g\int_{\mathbb{R}^2}\varphi(y)\mathcal{F}f(y)\,\mathrm{d}y\right| \le |\mathcal{N}g|\cdot\operatorname*{ess\,sup}_{\mathbb{R}^2}|\varphi|\cdot\|\mathcal{F}f\|_{L_1}.$$

Putting all this together, we deduce the inequality

$$\begin{aligned}\big\|[f\varphi * g]\big\|_{\widehat{L_1}} &\le \operatorname*{ess\,sup}_{\mathbb{R}^2}|\varphi|\cdot\|\mathcal{F}f\|_{L_1}\cdot\|\mathcal{F}g\|_{L_1} + |\mathcal{N}f|\cdot\|\varphi\|_{L_1}\cdot\|g\|_{\widehat{L_1}} \\ &\quad + |\mathcal{N}g|\cdot\operatorname*{ess\,sup}_{\mathbb{R}^2}|\varphi|\cdot\|\mathcal{F}f\|_{L_1} \\ &\le \|\varphi\|_{BL_1}\|f\|_{\widehat{L_1}}\cdot\|g\|_{\widehat{L_1}}.\end{aligned}$$

□

We now define the self-convolution $\mathcal{S}_\varphi$ acting on functions from $\widehat{L_1}(\mathbb{R}^2)$ by the rule

$$\begin{aligned}\mathcal{S}_\varphi f = [f\varphi * f] &= \int_{\mathbb{R}^2} f(x-y)\varphi(x-y)f(y)\,\mathrm{d}y \\ &= \int_{\mathbb{R}^2}\mathcal{F}f(x-y)\varphi(x-y)\mathcal{F}f(y)\,\mathrm{d}y + \mathcal{N}f\int_{\mathbb{R}^2}\varphi(x-y)\mathcal{F}f(y)\,\mathrm{d}y \\ &+ \mathcal{N}f\int_{\mathbb{R}^2}\varphi(y)\mathcal{F}f(y)\,\mathrm{d}y + \mathcal{N}f^2\int_{\mathbb{R}^2}\varphi(y)\,\mathrm{d}y.\end{aligned}$$

According to Lemma 2, the first two terms in this expression are functions from $L_1(\mathbb{R}^2)$. The last two terms are constants. Thus, $\mathcal{S}_\varphi$ acts in $\widehat{L_1}(\mathbb{R}^2)$.

Lemma 6. *For any pair of functions $f, g \in \widehat{L_1}(\mathbb{R}^2)$, the following inequality holds:*

$$\|\mathcal{S}_\varphi f - \mathcal{S}_\varphi g\|_{\widehat{L_1}} \le \|\varphi\|_{BL_1}\left(\|f\|_{\widehat{L_1}} + \|g\|_{\widehat{L_1}}\right)\|f-g\|_{\widehat{L_1}}.$$

Proof. For any functions $f, g \in \widehat{L_1}(\mathbb{R}^2)$, we have

$$\begin{aligned}\mathcal{S}_\varphi f - \mathcal{S}_\varphi g &= [f\varphi * f] - [g\varphi * g] \\ &= [f\varphi * f] - [f\varphi * g] + [f\varphi * g] - [g\varphi * g] \\ &= \big[f\varphi * (f-g)\big] + \big[(f-g)\varphi * g\big].\end{aligned}$$

According to Lemma 5,

$$\left\| \left[f\varphi * (f-g) \right] \right\|_{\widehat{L_1}} \leq \|\varphi\|_{BL_1} \|f\|_{\widehat{L_1}} \|f-g\|_{\widehat{L_1}},$$
$$\left\| \left[(f-g)\varphi * g \right] \right\|_{\widehat{L_1}} \leq \|\varphi\|_{BL_1} \|f-g\|_{\widehat{L_1}} \|g\|_{\widehat{L_1}}.$$

Summing up these estimates, we obtain the inequality stated in the lemma. □

3.5. Product-Convolution Operator

We again consider an essentially bounded function $\varphi \in L_1(\mathbb{R}^2)$ and define the product-convolution operator $\mathcal{P}_\varphi$ acting on functions from $\widehat{L_1}(\mathbb{R}^2)$ by the rule

$$\begin{aligned}\mathcal{P}_\varphi f = f[\varphi * f] &= f(x) \int_{\mathbb{R}^2} \varphi(x-y) f(y)\, \mathrm{d}y \\ &= \mathcal{F}f(x) \int_{\mathbb{R}^2} \varphi(x-y)\mathcal{F}f(y)\, \mathrm{d}y + \mathcal{N}f \int_{\mathbb{R}^2} \varphi(x-y)\mathcal{F}f(y)\, \mathrm{d}y \\ &+ \mathcal{N}f\mathcal{F}f(x) \int_{\mathbb{R}^2} \varphi(y)\, \mathrm{d}y + (\mathcal{N}f)^2 \int_{\mathbb{R}^2} \varphi(y)\, \mathrm{d}y.\end{aligned}$$

According to Lemma 2, the function $g(x) = \int_{\mathbb{R}^2} \varphi(x-y)\mathcal{F}f(y)\, \mathrm{d}y$ belongs to $L_1(\mathbb{R}^2)$ and is essentially bounded since

$$\operatorname*{ess\,sup}_{\mathbb{R}^2} |g| \leq \operatorname*{ess\,sup}_{\mathbb{R}^2} |\varphi| \cdot \|\mathcal{F}f\|_{L_1}.$$

Hence, the first three terms on the right-hand side of the equation above are functions from $L_1(\mathbb{R}^2)$, while the last term is a constant. Thus, the operator $\mathcal{P}_\varphi$ acts in $\widehat{L_1}(\mathbb{R}^2)$.

Using similar techniques as for the self-convolution operator $\mathcal{S}_\varphi$, we can prove the following lemma.

Lemma 7. *For any pair of functions $f, g \in \widehat{L_1}(\mathbb{R}^2)$,*

$$\|\mathcal{P}_\varphi f - \mathcal{P}_\varphi g\|_{\widehat{L_1}} \leq \|\varphi\|_{BL_1} \left(\|f\|_{\widehat{L_1}} + \|g\|_{\widehat{L_1}} \right) \|f-g\|_{\widehat{L_1}}.$$

3.6. Equilibrium Operator

Remark 6. *Below, we assume that the dispersal kernel and competition kernel are essentially bounded.*

Now, we are ready to continue investigating of the equilibrium Equation (6). First, we introduce

$$Q(x) = \frac{C(x)}{N(C)} \tag{10}$$

and assume $Q \in \widehat{L_1}(\mathbb{R}^2)$. From (7), it follows that

$$\lim_{\|x\| \to +\infty} Q(x) = N(C) \Longrightarrow \mathcal{N}Q = N(C).$$

By dividing both sides of (6) by $N(C)$, we obtain

$$\begin{aligned} 0 = bm(x) &+ b \int_{\mathbb{R}^2} m(y) Q(x-y)\,\mathrm{d}y \\ &- \left(\frac{\alpha}{\alpha+\gamma} b + \frac{\gamma}{\alpha+\gamma} d + sw(x) \right) Q(x) \\ &- \frac{\beta}{\alpha+\gamma} \cdot sQ(x) \int_{\mathbb{R}^2} w(y) Q(y-x)\,\mathrm{d}y \\ &- \frac{\gamma}{\alpha+\gamma} \cdot s \int_{\mathbb{R}^2} w(y) Q(y) Q(y-x)\,\mathrm{d}y \\ &+ \frac{\beta}{\alpha+\gamma} \cdot s(\mathcal{N}Q)^2. \end{aligned} \tag{11}$$

This equation can be expressed in the operator form $Q = \mathcal{E}Q$, where we define the equilibrium operator $\mathcal{E}$ acting on functions from $\widehat{L_1}(\mathbb{R}^2)$ by the rule

$$\mathcal{E}f = \frac{bm + b\mathcal{C}_{\mathrm{m}} f - swf - \dfrac{\beta s}{\alpha+\gamma} \mathcal{P}_{\mathrm{w}} f - \dfrac{\gamma s}{\alpha+\gamma} \mathcal{S}_{\mathrm{w}} f + \dfrac{\beta s}{\alpha+\gamma} (\mathcal{N} f)^2}{d + \dfrac{\alpha(b-d)}{\alpha+\gamma}}. \tag{12}$$

For context, we recall that $b > 0$ and $s \geq 0$ are constants specifying the considered population's birth rate and competition strength; $d \in [0; b)$ is a constant specifying the population's intrinsic death rate; α, β, and γ are constants specifying the closure such that $\alpha + \gamma \neq 0$; and $m(x)$ and $w(x)$ are essentially bounded functions specifying the dispersal kernel and competition kernel from the class (1).

Using the properties of the components of this operator, we can show that for any $f \in \widehat{L_1}(\mathbb{R}^2)$, $\mathcal{E}f \in \widehat{L_1}(\mathbb{R}^2)$. Thus, the operator $\mathcal{E}$ acts in $\widehat{L_1}(\mathbb{R}^2)$. We have, therefore, reduced the problem of solving (6) to the problem of finding the fixed point of the operator (12).

3.7. Fixed Point of Equilibrium Operator

For our further investigation, we utilize a well-known principle for analyzing fixed-point existence in complete metric spaces.

Theorem 2 (Banach)**.** *If an operator $\mathcal{A}$ acting in a complete metric space (X, ρ) is a contraction, i.e.,*

$$\exists q \in [0; 1)\ \forall x, y \in X \quad \rho(\mathcal{A}x, \mathcal{A}y) \leqslant q\rho(x, y),$$

then, there is one and only one element $z \in X$ such that

$$z = \mathcal{A}z.$$

Considering the lemmas above elucidating the properties of the operators $\mathcal{C}_{\mathrm{m}}$, $\mathcal{S}_{\mathrm{w}}$, and $\mathcal{P}_{\mathrm{w}}$, it becomes feasible to identify the necessary conditions that make the equilibrium operator $\mathcal{E}$ a contraction within a closed ball of the space $\widehat{L_1}(\mathbb{R}^2)$ centered at zero. Given such conditions, utilizing the Banach fixed-point theorem allows us to infer that the equilibrium operator possesses a unique fixed point within that ball, as a closed ball of a complete metric space is a complete metric space in its own right.

Theorem 3. *Assume the following conditions are met:*

$$\begin{aligned} &\gamma < 0, \\ &\alpha b + \gamma d > 0, \\ &2\beta - \gamma > 0, \\ &b - d > \frac{\alpha+\gamma}{-\gamma} s \|w\|_{BL_1}. \end{aligned} \tag{13}$$

Then, the equilibrium operator (12) *is a contraction in a closed ball of radius R centered at zero, where R is a positive number satisfying the double inequality*

$$-\frac{1}{2}\cdot\frac{\alpha+\gamma}{2\beta-\gamma}\leq R<\frac{1}{2}\left(\frac{-\gamma}{2\beta-\gamma}\cdot\frac{b-d}{s\|w\|_{BL_1}}-\frac{\alpha+\gamma}{2\beta-\gamma}\right).$$

Proof. We denote the expression $\frac{\beta}{\alpha+\gamma}(\mathcal{N}f)^2 - wf$ by $\mathcal{T}f$. Then,

$$\mathcal{E}f-\mathcal{E}g=\frac{b\Big(\mathcal{C}_{\mathrm{m}}f-\mathcal{C}_{\mathrm{m}}g\Big)-\frac{\beta s}{\alpha+\gamma}\Big(\mathcal{P}_{\mathrm{w}}f-\mathcal{P}_{\mathrm{w}}g\Big)-\frac{\gamma s}{\alpha+\gamma}\Big(\mathcal{S}_{\mathrm{w}}f-\mathcal{S}_{\mathrm{w}}g\Big)+s\Big(\mathcal{T}f-\mathcal{T}g\Big)}{d+\frac{\alpha(b-d)}{\alpha+\gamma}}.$$

Let $f,\, g\in\widehat{L_1}(\mathbb{R}^2)$ with $\|f\|_{\widehat{L_1}}\leq r$ and $\|g\|_{\widehat{L_1}}\leq r$. Using the Lemmas 4, 6, and 7, we obtain

$$\begin{aligned}
&\|\mathcal{C}_{\mathrm{m}}f-\mathcal{C}_{\mathrm{m}}g\|_{\widehat{L_1}}=\|\mathcal{C}_{\mathrm{m}}(f-g)\|_{\widehat{L_1}}\leq\|f-g\|_{\widehat{L_1}},\\
&\|\mathcal{P}_{\mathrm{w}}f-\mathcal{P}_{\mathrm{w}}g\|_{\widehat{L_1}}\leq\|w\|_{BL_1}\left(\|f\|_{\widehat{L_1}}+\|g\|_{\widehat{L_1}}\right)\|f-g\|_{\widehat{L_1}}\leq 2r\|w\|_{BL_1}\|f-g\|_{\widehat{L_1}},\\
&\|\mathcal{S}_{\mathrm{w}}f-\mathcal{S}_{\mathrm{w}}g\|_{\widehat{L_1}}\leq\|w\|_{BL_1}\left(\|f\|_{\widehat{L_1}}+\|g\|_{\widehat{L_1}}\right)\|f-g\|_{\widehat{L_1}}\leq 2r\|w\|_{BL_1}\|f-g\|_{\widehat{L_1}},\\
&\|\mathcal{T}f-\mathcal{T}g\|_{\widehat{L_1}}\leq\|w\|_{BL_1}\left(1+\frac{2r\beta}{\alpha+\gamma}\right)\|f-g\|_{\widehat{L_1}}.
\end{aligned}$$

Considering that $\gamma<0$, we thus obtain

$$\|\mathcal{E}f-\mathcal{E}g\|_{\widehat{L_1}}\leq\frac{\left(1+\frac{2\beta-\gamma}{\alpha+\gamma}2r\right)s\|w\|_{BL_1}+b}{d+\frac{\alpha(b-d)}{\alpha+\gamma}}\|f-g\|_{\widehat{L_1}}.$$

Hence, $\mathcal{E}$ is a contraction if

$$q=\frac{\left(1+\frac{2\beta-\gamma}{\alpha+\gamma}2r\right)s\|w\|_{BL_1}+b}{d+\frac{\alpha(b-d)}{\alpha+\gamma}}\in[0;1).$$

It is easy to show that this condition is equivalent to

$$-\frac{1}{2}\cdot\frac{\alpha+\gamma}{2\beta-\gamma}\leq r<\frac{1}{2}\left(\frac{-\gamma}{2\beta-\gamma}\cdot\frac{b-d}{s\|w\|_{BL_1}}-\frac{\alpha+\gamma}{2\beta-\gamma}\right)=M,$$

and, therefore, it just remains to check when M is positive:

$$M>0\Longleftrightarrow b-d>\frac{\alpha+\gamma}{-\gamma}s\|w\|_{BL_1}.$$

□

Theorem 4. *If the conditions* (13) *are met, and additionally,*

$$b-d>\frac{4b(2\beta-\gamma)}{-\gamma},\tag{14}$$

and if R is a positive number satisfying the double inequality

$$\frac{\gamma(b-d)-\sqrt{D}}{2s\|w\|_{BL_1}(2\beta-\gamma)} \le R \le \frac{\gamma(b-d)+\sqrt{D}}{2s\|w\|_{BL_1}(2\beta-\gamma)},$$

with

$$D = \gamma^2(b-d)^2 - 4bs(\alpha+\gamma)(2\beta-\gamma)\|w\|_{BL_1},$$

then $\mathcal{E}[B_R] \subset B_R$*, where* B_R *is a closed ball of radius R centered at zero.*

Proof. Suppose that $f \in B_R$. Given that $\gamma < 0$ and taking into account Lemmas 4, 6, and 7, we obtain

$$\|\mathcal{E}f\|_{\widehat{L_1}} \le \frac{b + b\|f\|_{\widehat{L_1}} + \frac{\beta s}{\alpha+\gamma}\|w\|_{BL_1}\|f\|^2_{\widehat{L_1}} - \frac{\gamma s}{\alpha+\gamma}\|w\|_{BL_1}\|f\|^2_{\widehat{L_1}} + \frac{\beta s}{\alpha+\gamma}(\mathcal{N}f)^2}{d + \frac{\alpha(b-d)}{\alpha+\gamma}}$$
$$\le \frac{b + b\|f\|_{\widehat{L_1}} + \frac{2\beta-\gamma}{\alpha+\gamma}s\|w\|_{BL_1}\|f\|^2_{\widehat{L_1}}}{d + \frac{\alpha(b-d)}{\alpha+\gamma}} \le \frac{b + bR + \frac{2\beta-\gamma}{\alpha+\gamma}s\|w\|_{BL_1}R^2}{d + \frac{\alpha(b-d)}{\alpha+\gamma}}.$$

If we can show that the last expression in this inequality chain does not exceed R, then the theorem is proved. Using the theorem's conditions, we can show that

$$\frac{b + bR + \frac{2\beta-\gamma}{\alpha+\gamma}s\|w\|_{BL_1}R^2}{d + \frac{\alpha(b-d)}{\alpha+\gamma}} \le R \iff$$
$$b(\alpha+\gamma) + \gamma(b-d)R + (2\beta-\gamma)s\|w\|_{BL_1}R^2 \le 0.$$

The discriminant of the last inequality (with respect to the variable R) is

$$D = \gamma^2(b-d)^2 - 4b(\alpha+\gamma)(2\beta-\gamma)s\|w\|_{BL_1}.$$

The inequality is solvable only if $D > 0$. However, it is obvious that

$$D > 0 \iff -\gamma(b-d)^2 > \frac{\alpha+\gamma}{-\gamma}s\|w\|_{BL_1}4b(2\beta-\gamma).$$

According to (13), $b - d > \frac{\alpha+\gamma}{-\gamma}s\|w\|_{BL_1}$, so the last inequality is equivalent to

$$-\gamma(b-d) > 4b(2\beta-\gamma),$$

which is true according to (14). Applying the well-known formula for the roots of quadratic equations, we obtain

$$\|\mathcal{E}f\|_{\widehat{L_1}} \le R \Longleftarrow \frac{\gamma(b-d)-\sqrt{D}}{2s\|w\|_{BL_1}(2\beta-\gamma)} \le R \le \frac{\gamma(b-d)+\sqrt{D}}{2s\|w\|_{BL_1}(2\beta-\gamma)}.$$

□

Combining the statements of Theorems 3 and 4, we deduce our following main result.

Theorem 5. *If* (13) *and* (14) *are met and a positive number R satisfies the system of inequalities*

$$\begin{cases} -\dfrac{\alpha+\gamma}{4\beta-2\gamma} \le R < -\dfrac{\gamma}{s\|w\|_{BL_1}(4\beta-2\gamma)}(b-d) - \dfrac{\alpha+\gamma}{4\beta-2\gamma}, \\ \dfrac{\gamma(b-d)-\sqrt{D}}{2s\|w\|_{BL_1}(2\beta-\gamma)} \le R \le \dfrac{\gamma(b-d)+\sqrt{D}}{2s\|w\|_{BL_1}(2\beta-\gamma)}, \end{cases}$$

with

$$D = \gamma^2(b-d)^2 - 4b(\alpha+\gamma)(2\beta-\gamma)s\|w\|_{BL_1},$$

then the equilibrium operator (12) *has a single fixed point in a ball of radius R centered at zero.*

Lemma 8. *The fixed point of the equilibrium operator is not the zero function.*

Proof. Suppose that the zero function θ were the solution of the equation $f = \mathcal{E}f$. Then,

$$\theta = \mathcal{E}\theta = \frac{bm + b[m*\theta] - sw\theta - \dfrac{\beta s}{\alpha+\gamma}\theta[w*\theta] - \dfrac{\gamma s}{\alpha+\gamma}[\theta w*\theta] + \dfrac{\beta s}{\alpha+\gamma}0^2}{d + \dfrac{\alpha(b-d)}{\alpha+\gamma}} = \frac{bm}{d + \dfrac{\alpha(b-d)}{\alpha+\gamma}}.$$

Thus, $bm = \theta$, which contradicts $\int_{\mathbb{R}^2} m(x)\,\mathrm{d}x = 1$ and $b > 0$. □

4. Computational Implementation

In this section, we provide a numerical application of the analytical results derived above. After devising a computationally efficient numerical method suitable for this application, we present a collection of solutions of the equilibrium equation for different parameter combinations. These solutions adhere to the conditions stipulated in Theorem 5.

4.1. Normalization and Centralization

To implement our numerical method, we bound and discretize the space of distance vectors x over which the pair density $C(x)$ is represented. This involves approximations, which are computationally aggravated by the fact that, according to (7), the unknown function C is expected to approach a non-zero constant N^2 as $\|x\| \to +\infty$. To mitigate this computational challenge and minimize the error, we transform the function C together with the equation characterizing its equilibrium.

Through normalization and centralization, we define a new unknown function q that approaches zero at infinity:

$$q(x) = \frac{C(x)}{N^2(C)} - 1. \tag{15}$$

With this substitution, the equilibrium Equation (6) becomes

$$\begin{aligned} q(x) = {} & \frac{\alpha+\gamma}{D(q,x)}\left(\frac{bm(x)}{N(q)} + b[m*q](x) - sw(x)\right) \\ & - \frac{sN(q)}{D(q,x)}\left(\Big(\beta\big(q(x)+1\big)+\gamma\Big)[w*q](x) + \gamma[qw*q](x)\right), \end{aligned} \tag{16}$$

where $[\cdot * \cdot]$ notation is used for a convolution and

$$N(q) = \frac{b-d}{s + s\int_{\mathbb{R}^2} w(y)q(y)\,\mathrm{d}y},$$
$$D(q,x) = (\alpha+\gamma)\big(d + sw(x)\big) + \big(\alpha(b-d) + \beta s N(q)\big).$$

To solve Equation (16) numerically, we employ the Neumann method, also known as the simple-iteration method. Starting from any initial function q_0, this method generates the sequence

$$q_{k+1} = \mathcal{A}q_k, \quad k \in \mathbb{N},$$

where k denotes the iteration number and the operator $\mathcal{A}$ is defined by equating the right-hand side of (16) with $\mathcal{A}q$. The Banach fixed-point theorem ensures that, if $\mathcal{A}$ acts within a complete metric space and is a contraction, then, there exists a function q^* such that

$$\lim_{k\to+\infty} q_k = q^*.$$

Therefore, with a sufficient number of iterations, it is possible to obtain a function closely approximating the solution of the equilibrium Equation (16), assuming $q \in L_1(\mathbb{R}^2)$ is equivalent to $C \in \widehat{L_1}(\mathbb{R}^2)$ and ensuring that the method can be applied to (16).

4.2. Acceleration of Convolution Calculation

In this subsection, we briefly review the findings presented in [39] for two-dimensional habitats.

The most computationally demanding aspect of solving the equilibrium Equation (16) is the convolution operation. The conventional algorithm computes convolutions directly according to their definition and exhibits a computational complexity of $O(G^2)$, where G is the number of grid points on which the involved functions are represented. It is, therefore, important that the convolution theorem, stated below, enables a significant streamlining of this algorithm's computational complexity.

The convolution theorem uses the Fourier transform $\mathfrak{F}$ and its inverse $\mathfrak{F}^{-1}$. Here we utilize the following definitions applied to n-dimensional functions f and g:

$$\mathfrak{F}f(\omega_1, \omega_2, \ldots, \omega_n) = \int_{\mathbb{R}^n} f(x_1, x_2, \ldots, x_n) \cdot \exp\left(-i \sum_{j=1}^{n} x_j \omega_j\right) \mathrm{d}x_1 \mathrm{d}x_2 \cdots \mathrm{d}x_n,$$

$$\mathfrak{F}^{-1}g(\omega_1, \omega_2, \ldots, \omega_n) = \frac{1}{(2\pi)^n} \int_{\mathbb{R}^n} g(x_1, x_2, \ldots, x_n) \cdot \exp\left(i \sum_{j=1}^{n} x_j \omega_j\right) \mathrm{d}x_1 \mathrm{d}x_2 \cdots \mathrm{d}x_n.$$

Theorem 6 (on convolutions)**.** *If functions f and g are from $L_1(\mathbb{R}^n)$,*

$$[f * g](x_1, x_2, \ldots, x_n) = \mathfrak{F}^{-1}\Big[\mathfrak{F}f(\omega_1, \omega_2, \ldots, \omega_n) \cdot \mathfrak{F}g(\omega_1, \omega_2, \ldots, \omega_n)\Big](x_1, x_2, \ldots, x_n).$$

This theorem enables the reduction of a convolution operation to three separate Fourier transforms, two direct and one inverse. To elucidate the significance of this, we first consider the discrete direct and inverse Fourier transforms for vectors f and F that represent one-dimensional functions:

$$F_j = \sum_{k=0}^{G-1} f_k \exp\left(-\frac{2\pi i}{G} kj\right) \quad \text{and} \quad f_k = \frac{1}{G} \sum_{j=0}^{G-1} F_j \exp\left(\frac{2\pi i}{G} kj\right), \tag{17}$$

where G is the number of points in a uniform grid. While the computational complexity $O(G^2)$ of (17) is again quadratic, the convolution theorem enables the application of the fast Fourier transform algorithm, which has a lower computational complexity of just $O(G \ln G)$. The computation of one-dimensional convolutions can, thus, be accomplished at the same lower level of computational complexity, $O(G \ln G)$.

For two dimensional habitats, the functions q, m, and w in (16) are two-dimensional. When such functions are discretized, they are represented by matrices f and F, for which the discrete direct and inverse Fourier transforms defined as follows:

$$
\begin{aligned}
F_{mn} &= \sum_{k,j=0}^{G-1} f_{kj} \exp\left(-\frac{2\pi i}{G}(km + jn)\right),\\
f_{kj} &= \frac{1}{G^2} \sum_{m,n=0}^{G-1} F_{mn} \exp\left(\frac{2\pi i}{G}(km + jn)\right).
\end{aligned} \tag{18}
$$

The computational complexity of (18) is $O(G^4)$, resulting from determining G^2 values at each of G^2 points of the quadratic uniform grid. By transforming (18), we obtain

$$
\begin{aligned}
F_{mn} &= \sum_{k=0}^{G-1} \left[\sum_{j=0}^{G-1} f_{kj} \exp\left(-\frac{2\pi i}{G} km\right)\right] \exp\left(-\frac{2\pi i}{G} jn\right),\\
f_{kj} &= \frac{1}{G} \sum_{m=0}^{G-1} \frac{1}{G} \left[\sum_{n=0}^{G-1} F_{mn} \exp\left(\frac{2\pi i}{G} km\right)\right] \exp\left(\frac{2\pi i}{G} jn\right).
\end{aligned} \tag{19}
$$

By comparing (17) and (19), it becomes evident that the computation of the two-dimensional Fourier transform can be reduced to the computation of the one-dimensional Fourier transform. Again employing the fast Fourier transform algorithm, we obtain a computational complexity of $O\left(G^3 \ln G\right)$.

We now discuss strategies for further expediting the computation of two-dimensional convolutions. For this, we examine the continuous Fourier transform in two dimensions:

$$
\mathfrak{F} f(\omega_1, \omega_2) = \iint_{\mathbb{R}^2} f(x, y) e^{-i(x\omega_1 + y\omega_2)} \mathrm{d}x\mathrm{d}y.
$$

A function f is radially symmetric if we can express it as $f(x, y) = h(r)$ with $r = \sqrt{x^2 + y^2}$. Since we are considering only radially symmetric kernels m and w, the solution q of our equilibrium equation is also radially symmetric. Therefore, we consider the polar coordinates

$$
\omega_1 = \rho \cos \psi, \quad \omega_2 = \rho \sin \psi, \quad x = r \cos \varphi, \quad y = r \sin \varphi,
$$

where $r, \rho \in [0; +\infty)$ and $\phi, \psi \in [0; 2\pi)$, with which the two-dimensional continuous Fourier transform can be expressed as

$$
\mathfrak{F} f(\rho, \psi) = \int_0^{+\infty} r h(r) \mathrm{d}r \int_{-\pi}^{\pi} e^{-ir\rho \cos(\psi - \varphi)} \mathrm{d}\varphi.
$$

Using

$$
\int_{-\pi}^{\pi} e^{-ir\rho \cos(\psi - \varphi)} \mathrm{d}\varphi = \int_{-\pi}^{\pi} e^{-ir\rho \cos \varphi} \mathrm{d}\varphi = 2\pi J_0(r\rho),
$$

where $J_0(x)$is the zeroth-order Bessel function of the first kind, the two-dimensional continuous Fourier transform of a radially symmetric function $f(x, y) = h(r)$ becomes

$$
\mathfrak{F} f(\rho, \psi) = 2\pi \int_0^{+\infty} r h(r) J_0(r\rho) \mathrm{d}r.
$$

As $\mathfrak{F} f$ is independent of the angle ψ, it is a radially symmetric function, too. The result can be expressed in terms of the zeroth-order Hankel transform. In general, the direct and inverse Hankel transforms of order α is defined by

$$
\mathfrak{H}_\alpha f(\rho) = \int_0^{+\infty} r f(r) J_\alpha(r\rho) \mathrm{d}r \quad \text{and} \quad \mathfrak{H}_\alpha^{-1} g(r) = \int_0^{+\infty} \rho g(\rho) J_\alpha(r\rho) \mathrm{d}\rho, \tag{20}
$$

where J_α is the Bessel function of the first kind of order α. For radially symmetric functions, the Fourier transform in $\mathbb{R}^2$ thus becomes reduced to the Hankel transform in $\mathbb{R}^1$. With an exponential change of variables, $r = r_0 e^x$ and $\rho = \rho_0 e^y$, Equation (20) gives the direct zeroth-order Hankel transform

$$\mathfrak{H}_0 f(\rho_0 e^y) = \int_{-\infty}^{+\infty} r_0^2 e^{2x} f(r_0 e^x) J_0(r_0 \rho_0 e^{x+y})\, \mathrm{d}x. \tag{21}$$

As this is a one-dimensional convolution of two functions, its computational complexity is $O(G \ln G)$. When computing two-dimensional convolutions of radially symmetric functions by using the convolution theorem and two-dimensional Fourier transforms, we can, thus, use the Hankel transform to reduce each two-dimensional Fourier transform to a one-dimensional convolution. Hence, the computational complexity of two-dimensional convolutions of radially symmetric functions is the same as that of one-dimensional convolutions, $O(G \ln G)$.

4.3. Numerical Results

Figure 2 shows three solutions of the equilibrium Equation (6) resulting for dispersal and competition kernels of Gaussian shape,

$$m(x) = \frac{1}{\sigma_\mathrm{m}\sqrt{2\pi}} \exp\left(-\frac{\|x\|^2}{2\sigma_\mathrm{m}^2}\right) \quad \text{and} \quad w(x) = \frac{1}{\sigma_\mathrm{w}\sqrt{2\pi}} \exp\left(-\frac{\|x\|^2}{2\sigma_\mathrm{w}^2}\right),$$

where σ_m and σ_w denote the standard deviations of the two kernels.

The three solutions in Figure 2 illustrate how the solutions of the equilibrium Equation (6) depend on the ratio of these standard deviations, with all other parameters kept constant. In case (a), the dispersal kernel is twice as wide as the competition kernel, enabling offspring to disperse far from their parents. In case (b), both kernels possess the same width. In case (c), the competition kernel is twice as wide as the dispersal kernel, restricting the ability of offspring to evade their parents' competitive influence.

The variation in relative kernel widths has two closely related effects. In terms of the first spatial moment, it characteristically influences the mean density, which decreases progressively from (a) to (b) to (c). In terms of the second spatial moment, it characteristically influences the pair density, which changes from locally segregated or over-dispersed in (a), to uniform in (b), to locally aggregated or clustered in (c). Naturally, the first effect follows from the second: Local segregation decreases the competitive pressure on individuals and, thus, increases the mean density, whereas local aggregation increases the competitive pressure on individuals and, thus, decreases the mean density.

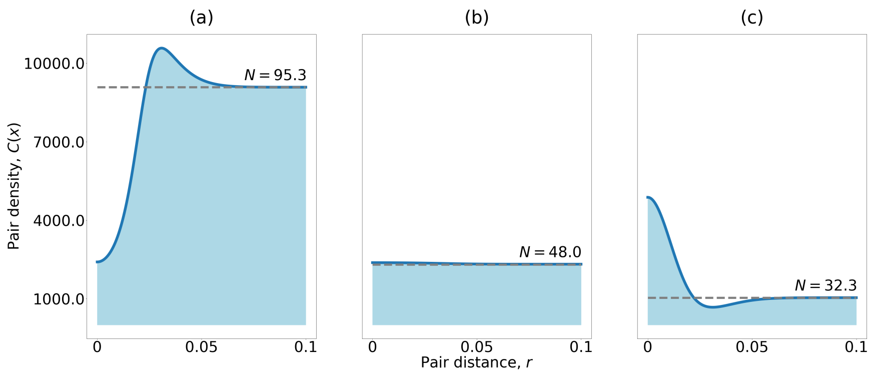

Figure 2. Solutions of the equilibrium equation. The continuous blue curves show the pair density $C(x)$ as a function of the pair distance $r = \|x\|$. The dashed gray lines indicate N^2, i.e., the limit of $C(x)$ as r approaches infinity. (**a**) $\sigma_\mathrm{m} = 0.02$, $\sigma_\mathrm{w} = 0.01$; (**b**) $\sigma_\mathrm{m} = \sigma_\mathrm{w} = 0.02$; and (**c**) $\sigma_\mathrm{m} = 0.01$, $\sigma_\mathrm{w} = 0.02$. The smaller the ratio $\sigma_\mathrm{m}/\sigma_\mathrm{w}$, the smaller the mean density N. Other parameters: $b = 0.5$, $d = 0.01$, $s = 0.01$, $\alpha = \beta = 1$, and $\gamma = -0.5$.

5. Conclusions

In this study, we have explored the equilibrium of an individual-based model describing a population living in a two-dimensional habitat whose dynamics are governed by spatial logistic dynamics. This equilibrium is defined as the solution of a system of linear integral equations, which can be transformed into a nonlinear integral equation through the application of a moment closure for the third spatial moment. We refer to this transformed equation as the equilibrium equation and have derived conditions under which its solvability can be assured. In the present work, we expand upon the analysis provided in [30] by including all necessary proofs, which were absent in the earlier outline.

Specifically, we have demonstrated that solving the equilibrium equation can be formulated as a fixed-point problem in the dedicated space of functions that are integrable up to a constant, which we have introduced for our analyses and denoted by $\widehat{L_1}(\mathbb{R}^2)$. Applying the Banach fixed-point theorem, we have established sufficient conditions for the solvability of this fixed-point problem, which are defined in terms of the model parameters describing birth, natal dispersal, death, and competition, on the one hand, and those describing the moment closure, on the other hand.

Furthermore, we have devised, presented, implemented, and illustrated a simple iterative numerical method for solving the equilibrium equation under the analytically derived conditions. Drawing upon findings from [39], we have shown how the computational complexity of this method can be substantially reduced by exploiting the radial symmetry inherent in the functions under consideration. Our numerical results draw attention to the crucial importance of the ratio between the standard deviations of the dispersal kernel and the competition kernel. The smaller this ratio, the smaller are the mean densities. Moreover, as the ratio is decreased, the spatial distribution of individuals gradually changes from clustered or locally aggregated to over-dispersed or locally segregated.

Future research endeavors may serve to extend the findings presented here in a variety of directions. First, it will be interesting to compare our results for two-dimensional habitats with those for one- or three-dimensional habitats. Assessing the impact of dimensionality on population dynamics offers a rich and promising avenue for further investigation. Second, while we have focused our numerical investigations on dispersal and competition kernels of Gaussian shape, it will be interesting to extend our corresponding findings to a greater variety of kernel shapes. Third, our results for populations in which all individuals are of a single type can be complemented by additional research efforts that explore analogously defined moment dynamics, equilibrium equations, and solvability conditions for populations with multiple types, thereby extending our findings from the realm of spatial population dynamics to that of spatial community dynamics. We hope that our work here, together with its future extensions, will further broaden the applicability of spatial logistic dynamics to a rich variety of real-world phenomena.

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