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Asymptotic Dynamics in Populations Structured by Sensitivity to Global Warming and Habitat Shrinking

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Abstract How to recast effects of habitat shrinking and global warming on evolutionary dynamics into continuous mutation/selection models? Bearing this question in mind, we consider differential equations for structured populations, which include mutations, proliferation and competition for resources. Since mutations are assumed to be small, a parameter ε is introduced to model the average size of phenotypic changes. A well-posedness result is proposed and the asymptotic behavior of the density of individuals is studied in the limit $\varepsilon \to 0$. In particular, we prove the weak convergence of the density to a sum of Dirac masses and characterize the related concentration points. Moreover, we provide numerical simulations illustrating the theorems and showing an interesting sample of solutions depending on parameters and initial data.

Keywords Structured populations · Asymptotic analysis · Concentration phenomena · Integrodifferential equations

1 Introduction

Recent scientific literature shows the spreading of mathematical models for the evolution of species under the effects of external selective pressures [8, 14, 15, 21, 24, 25, 31, 33, 34,

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36]. In this paper, we consider a population structured by two continuous variables x and y representing the sensitivity to, respectively, habitat shrinking and global warming. The density of individuals with a sensitivity level $u := (x, y)$ at time t is modeled by the real function $f(t, x, y) \geq 0$ that satisfies

$$\begin{cases} \dfrac{\partial}{\partial t} f(t, u) = M[f](t, u) + P\big(t, u, \varrho(t)\big) f(t, u) \\ \varrho(t) = \displaystyle\int_U f(t, u) du, \end{cases} \tag{1.1}$$

where:

- $t \in \mathbb{R}_+$, $x \in X := [a_X, b_X]^k \subset \mathbb{R}^k$, $y \in Y := [a_Y, b_Y]^l \subset \mathbb{R}^l$, with $-\infty < a_X, b_X, a_Y, b_Y < \infty$, integers $k, l \geq 1$ and $u \in U := X \times Y$;
- $M[f](t, u)$ describes the effects of renewal and mutations from parent to offspring;
- $P(t, u, \varrho(t))$ models the per capita net growth rate of the population at time t and it is assumed to depend on the total size of the population at the same time instant, which is identified by $\varrho(t)$.

It is worth noting that we allow dimension k to be greater than one to account for the fact that sensitivity to habitat shrinking can result from the simultaneous expression of several traits. In fact, each component of the x variable can stand for the expression level of one of those traits that yield together the sensitivity to habitat shrinking. Analogous considerations hold for dimension l, variable y and sensitivity to global warming.

Habitat-generalists are able to thrive in a wide variety of environmental conditions and can make use of a variety of different resources; therefore, they are characterized by low sensitivity to habitat shrinking and global warming. Whereas, habitat-specialists can only live within a narrow range of environmental conditions and have a limited diet; as a consequence, they are strongly sensitive to habitat shrinking and global warming. Since x and y represent the levels of sensitivity to habitat shrinking and global warming, generalists (specialists) are identified by x and y close, respectively, to a_X and a_Y (b_X and b_Y).

Before we go into mathematical details, let us give a motivation for considering this model. The fourth report by the UN Panel for Climate Change [1] foresees an increase in the average world temperature of about three degrees by the end of the 21st century and, even worse, the latest analysis support the idea that such a forecast is underestimating the actual rising rate [30].

Every single degree that the temperature rises on Earth, 7 % more water evaporates from the ground [29]. This means more floods, more droughts, more wild forest fires and more violent tropical thunderstorms. This implies a more rapid shift in the world hydrological system endangering the survival of 70 % of life species on Earth by the end of this century, according to the Intergovernmental Panel on Climate Change [1].

Current climate changes are occurring at the same time as increased soil consumption by human activities, such as the expansion of farmlands, which shrinks habitats. This promotes the loss of areas where wildlife can survive and causes the fragmentation of habitats into patches of reduced size.

This process has direct and dramatic effects on animal wildlife and increases the probability of extinction of species. In fact, narrow areas can usually host only small populations, which are more prone to extinction due to stochastic effects [18]. Furthermore, the isolation of patches can hamper migratory fluxes and recolonization, so reducing the chance for persistence and increasing the risk for extinction.

As a consequence, the rise of average temperatures and the spread of human urbanization are endangering the survival of habitat-specialist species [17]. In fact, in contrast to habitat-generalists, which are more adapted to reduced biodiversity and new environmental conditions, habitat-specialists are characterized by a stronger sensitivity to nutrition variation. Therefore, they are often forced to move poleward by global warming, in order to follow specific subsistence resources. Moreover, generalist species may take advantage of man's proximity, namely gaining resources from human foods, and they are able to live both in interiors and edges of habitat-patches. On the other hand, specialist species used to live in the interior areas of patches and avoid edges, since they are disturbed by those external factors that usually come along with civilization.

Different mathematical formalisms have been used in the recent years to model the dynamics of populations exposed to the effects of climate and habitat modifications; see for instance [2, 4, 5, 7, 10, 19, 27, 32, 35] and references therein. The model here considered relies on a continuous selection/mutation formalism [6, 9, 13, 22, 23, 28]. Since mutations are assumed to cause small phenotypic changes, a parameter ε is introduced to model the average size of mutations. In order to consider the dynamics of the population on a time scale longer than the one of a single generation, we use the same time rescaling proposed in [13] and the asymptotic behavior of the solutions to the mathematical problem is studied in the limit $\varepsilon \to 0$ (*i.e.*, in the limit of small phenotypic changes and many generations), so that the slow process of significant change in predominant traits can be captured. In particular, asymptotic analysis prove the existence of limit solutions that concentrate as Dirac masses. In fact, as it has been pointed out in [20], this kind of concentration effects provides a possible mathematical formalization of the selection principle in evolutionary biology: a population initially dispersed over several traits concentrates, for large time, along few of them, which can be interpreted as the fittest ones.

From a mathematical standpoint, we use the idea of modeling species evolution presented in [13] and we take advantage of the analytical approach proposed in [12] and extended in [11]. These two works are devoted to study the asymptotic behavior of models describing the dynamics of populations structured by a one-dimensional continuous variable. The former takes into account the effects of proliferation and death processes only, while the latter deals also with mutations and mutualistic interactions. In particular, we show how, under additional assumptions, a similar approach can be used to study the asymptotic behavior of higher-dimensional models as the one here proposed, where time dependent proliferation and death rates are included together with mutations.

From an ecological perspective, it is worth noting that the definition of a model well suited for quantitative forecasts is beyond our present scope. This work is rather meant to show how previous considerations [16, 17, 26] about the effects of habitat shrinking and global warming on the evolution of species can be recast in continuous structured populations model. In particular, we propose a possible modeling strategy to translate into mathematical terms the idea that habitat shrinking affects the growth of individuals by altering bio-diversity and space availability, while global warming diminishes available resources, thus intensifying the competition among individuals.

The contents of the paper are organized into three further sections. In more detail, Sect. 2 outlines the basic modeling assumptions and provides a precise mathematical formalization. Section 3 summarizes results about the asymptotic behavior of the solutions to the Cauchy Problem. Section 4 illustrates the obtained analytical results by means of numerical simulations.

2 The Model

Making reference to equation (1.1), we use the following definitions of the parameter functions

$$M[f](t, x, y) = M_\varepsilon[f](t, x, y)$$

$$:= \alpha \int_X K_X(x - z; \varepsilon) f(t, z, y) dz$$

$$+ \beta \int_Y K_Y(y - z; \varepsilon) f(t, x, z) dz$$

$$- (\alpha + \beta) f(t, x, y), \qquad (2.1)$$

$$P\big(t, x, y, \varrho(t)\big) := \kappa(t, x) - \mu(t, y)\varrho(t), \qquad (2.2)$$

where:

• Kernel $K_X(x - z; \varepsilon)$, or $K_Y(y - z; \varepsilon)$, models the probability that an individual with traits (z, y), or (x, z), gives birth to individuals with traits (x, y), while parameters $\alpha, \beta \in \mathbb{R}_+$ describe the average rate of mutations in trait x and y, respectively. As a result:

$$\int_X K_X(x - z; \varepsilon) dx = 1, \quad \forall z \in X \qquad (2.3)$$

and an analogous integral identity holds for $K_Y(y - z; \varepsilon)$. First of all, it is worth noting that definition (2.1) stems from the assumption that mutations in the x and y traits are independent from one another. Moreover, following [13], we have introduced a small parameter ε to model the average size of phenotypic changes. In particular, we define

$$K_X(x - z; \varepsilon) := \prod_{i=1}^k \tilde{K}_X(x_i - z_i; \varepsilon), \qquad (2.4)$$

with

$$\tilde{K}_X(x_i - z_i; \varepsilon) := \begin{cases} \frac{1}{2}\delta(x_i - (z_i - \varepsilon)) + \frac{1}{2}\delta(x_i - (z_i + \varepsilon)), & \text{if } a_X + \varepsilon < x_i < b_X - \varepsilon, \\ \frac{1}{2}\delta(x_i - (z_i - \varepsilon)) + \frac{1}{2}\delta(x_i - z_i), & \text{if } a_X \le x_i \le a_X + \varepsilon, \\ \frac{1}{2}\delta(x_i - (z_i + \varepsilon)) + \frac{1}{2}\delta(x_i - z_i), & \text{if } b_X - \varepsilon \le x_i \le b_X \end{cases}$$

for $i = 1, \ldots, k$. Definition (2.4) implies that kernel K_X is negligibly small for x outside an ε-neighborhood of z. This translates into mathematical terms the idea that mutations are small, *i.e.*, only small variations in the phenotypic traits can occur from parent to offspring. Analogous assumptions and considerations apply to $K_Y(y - z; \varepsilon)$. Definitions of kernels K_X and K_Y implicitly rely on the assumption that mutations can be modeled as discrete jump in x and y of size ε; this is the main difference with respect to the models considered in [13].

• Definition (2.2) relies on the idea that habitat shrinking can be considered as an external pressure that affects the growth of individuals by altering bio-diversity and space availability, while global warming can be seen as acting via the competition among individuals by modifying the quantity of available resources [16, 17, 26]. In fact, functions $\kappa(t, x)$ and

$\mu(t, y)$ model, respectively, the proliferation rate and death rate due to competition for resources of individuals with phenotypic expression (x, y) at time t. Throughout the paper we assume

$$\kappa(t, x) := \kappa_3 + \kappa_1(t)\kappa_2(x) > 0, \qquad \mu(t, y) := \mu_3 + \mu_1(t)\mu_2(y) > 0, \qquad (2.5)$$

with:

$$\kappa_3, \mu_3 \geq 0, \quad \kappa_1, \mu_1 : [0, T] \to \mathbb{R}, \quad \kappa_1, \mu_1 \in W^{1,\infty}([0, T]), \qquad (2.6)$$

$$\kappa_2 : X \to \mathbb{R}_+, \quad \kappa_2 \in W^{2,\infty}(X), \qquad \mu_2 : Y \to \mathbb{R}_+, \quad \mu_2 \in W^{2,\infty}(Y). \qquad (2.7)$$

Remark 2.1 The selective forces exerted by habitat shrinking and global warming can evolve over time due, for instance, to human migratory fluxes or to oscillations in average temperatures. For this reason, functions κ and μ are assumed to depend also on variable t.

In order to consider the dynamics of the population on a time scale longer than the one of a single generation, we use the same time rescaling proposed in [13] and rewrite model (1.1) as follows:

$$\begin{cases} \dfrac{\partial}{\partial t} f_\varepsilon(t, u) = \dfrac{1}{\varepsilon} M_\varepsilon[f_\varepsilon](t, u) + \dfrac{1}{\varepsilon} P_\varepsilon\big(t, u, \varrho_\varepsilon(t)\big) f_\varepsilon(t, u), \\ \varrho_\varepsilon(t) = \displaystyle\int_U f_\varepsilon(t, u)du. \end{cases} \qquad (2.8)$$

The behavior of the solutions of the mathematical problems linked to the rescaled model (2.8) can be analyzed in the limit $\varepsilon \to 0$, *i.e.*, in the limit of large times and small mutations, so that the slow process of substantial change in predominant traits can be captured. These asymptotic analysis prove the existence of a limit solution f that concentrates over a countable subset of U as a sum of Dirac masses and, as previously noted, this provides a possible mathematical formalization for the selection principle of evolutionary biology: a population initially dispersed over several traits, concentrates, for large time, along few of them, which can be interpreted as the fittest ones.

3 Analytical Results

This section provides analytical properties for the Cauchy Problem derived by endowing model (1.1), or (2.8), with appropriate initial conditions. In more detail, we recall two theorems ensuring the well-posedness of such initial value problems and prove a third theorem characterizing the asymptotic behavior of the related solutions in the limit $\varepsilon \to 0$.

At first, we focus on the Cauchy Problem for f given hereafter:

$$\begin{cases} \dfrac{\partial}{\partial t} f(t, u) = M[f](t, u) + P\big(t, u, \varrho(t)\big) f(t, u), \quad (t, u) \in \mathbb{R}_+ \times U, \\ \varrho(t) = \displaystyle\int_U f(t, u)du, \\ f(0, u) = f^0(u) \in L^1(U), \quad f^0(\cdot) > 0 \text{ a.e. on } U. \end{cases} \qquad (3.1)$$

Making use of the assumptions previously introduced as well as of standard fixed point arguments, it can be shown that Problem (3.1) is well-posed in the sense of Hadamard (*i.e.*,

the solution exists, it is unique and depends continuously on the initial data), as stated by the following theorems, which can be proved in a similar way as those in [11, 12, 22] and so are left without proof:

Theorem 3.1 (Well-Posedness and Non-negativity) *Let assumptions* (2.3)–(2.7) *hold. Then, Problem* (3.1) *admits a unique non-negative local in time solution* $f \in C([0, T], L^1(U))$ *that satisfies*

$$\left\| f(t, \cdot) \right\|_{L^1(U)} \leq C_0 \left\| f^0(\cdot) \right\|_{L^1(U)}, \quad \forall t \in [0, T],$$

where C_0 *and* T *are positive constants depending on the initial data as well as on the model parameters.*

Theorem 3.2 (Global Existence) *Let the same assumptions of Theorem* 3.1 *hold for all* $T > 0$. *Then, there exists a unique non-negative solution* $f \in C(\mathbb{R}_+, L^1(U))$ *of Problem* (3.1), *which satisfies the following a priori estimate*

$$\sup_{t \in [0,T]} \left\| f(t, \cdot) \right\|_{L^1(U)} \leq C_T, \quad \forall T \geq 0,$$

where C_T *is a given constant depending on* T, *on the initial data and on the parameters of the model.*

In particular, the proof of Theorem 3.2 relies on the following *a priori* estimate for the unique solution of Problem (3.1):

$$\left\| f(t, \cdot) \right\|_{L^1(U)} \leq \max\left(\frac{\|\kappa(t, \cdot)\|_{L^\infty(X)}}{\inf \mu(t, \cdot)}, \|f^0\|_{L^1(U)} \right), \quad \forall t \in [0, T]. \tag{3.2}$$

This is obtained by integrating over U Eqs. (1.1) and making use of assumptions (2.3)–(2.7), as well as of the non-negativity of function f, to achieve the following differential inequality

$$\frac{d}{dt} \left\| f(t, \cdot) \right\|_{L^1(U)} \leq \left(\left\| \kappa(t, \cdot) \right\|_{L^\infty(X)} - \inf \mu(t, \cdot) \left\| f(t, \cdot) \right\|_{L^1(U)} \right) \left\| f(t, \cdot) \right\|_{L^1(U)}, \tag{3.3}$$

which implies the upper bound (3.2).

Remark 3.3 Differential inequality (3.3) guarantees, besides the results established by Theorem 3.1 and Theorem 3.2, the continuity of $\| f(t, \cdot) \|_{L^1(U)}$.

Let $f(t, u)$ be the unique solution of Problem (3.1), whose existence is provided by Theorem 3.1 and Theorem 3.2; then, $f_\varepsilon(t, u)$ is the unique solution of the rescaled problem

$$\begin{cases} \dfrac{\partial}{\partial t} f_\varepsilon(t, u) = \dfrac{1}{\varepsilon} M_\varepsilon[f_\varepsilon](t, u) + \dfrac{1}{\varepsilon} P_\varepsilon\big(t, u, \varrho_\varepsilon(t)\big) f_\varepsilon(t, u), \quad (t, u) \in \mathbb{R}_+ \times U \\[2mm] \varrho_\varepsilon(t) = \displaystyle\int_U f_\varepsilon(t, u) du \\[2mm] f_\varepsilon(0, u) = f^0(u) \in L^1(U), \quad f^0(\cdot) > 0 \text{ a.e. on } U. \end{cases} \tag{3.4}$$

The results above stated for Problem (3.1) apply to Problem (3.4) as well, for any $\varepsilon > 0$. In particular, Problem (3.4) is well-posed, its unique solution is non-negative and satisfies the upper bound (3.2).

Let us introduce the definition below

$$R_\varepsilon(t, u) := \int_0^t P_\varepsilon(s, u, \varrho_\varepsilon(s)) ds$$

together with the following

Remark 3.4 Assumptions (2.5)–(2.7) imply that, for any ε greater than zero, R_ε, as well as its first and second derivatives with respect to t, x and y are bounded in $L^\infty((0, T) \times U)$. As a result, R_ε belong to $W^{2,\infty}((0, T) \times U)$.

Now we are in the position to prove the following preliminary result:

Lemma 3.5 *Let $f_\varepsilon(t, u)$ be the unique solution of Problem* (3.4). *Then, for all test functions $\varphi(u)$ belonging to the completion of $C_c^\infty(\mathring{U})$ in $W^{2,\infty}(U)$:*

$$\lim_{\varepsilon \to 0} \int_U \varphi(u) f_\varepsilon(t, u) du = \lim_{\varepsilon \to 0} \int_U \varphi(u) f^0(u) e^{\frac{R_\varepsilon(t,u)}{\varepsilon}} du,$$

for $\varepsilon > 0$ small enough and $t \in [0, T]$.

Proof For any smooth test function $\varphi \in C_c^\infty(\mathring{U})$, the definition of $M_\varepsilon[f_\varepsilon](t, x, y)$ for $(x, y) \in U$ implies, for ε small enough the following equality holds

$$\int_X \int_Y \varphi(x, y) \frac{M_\varepsilon[f_\varepsilon](t, x, y)}{\varepsilon} dx dy = \frac{\alpha}{2^k} \int_X \int_Y I_1(x, y; \varepsilon) f_\varepsilon(t, x, y) dx dy$$

$$+ \frac{\beta}{2^l} \int_X \int_Y I_2(x, y; \varepsilon) f_\varepsilon(t, x, y) dx dy, \quad (3.5)$$

with

$$I_1(x, y; \varepsilon) = \frac{\sum_{\gamma_i \in \{-1,1\}} \varphi(x + \varepsilon \sum_{i=1}^k \gamma_i e_i, y) - 2^k \varphi(x, y)}{\varepsilon},$$

$$I_2(x, y; \varepsilon) = \frac{\sum_{\gamma_i \in \{-1,1\}} \varphi(x, y + \varepsilon \sum_{i=1}^l \gamma_i e_i) - 2^l \varphi(x, y)}{\varepsilon},$$

where we write e_i for the i-th unit normal vector, in order to simplify notation. Using the Taylor expansion

$$\varphi(x + x', y) = \varphi(x, y) + (\nabla_x \varphi(x, y))^T x' + \frac{1}{2} x'^T D_x^2(\varphi(x, y)) x' + \mathcal{O}(\|x'\|^3),$$

we obtain

$$\varphi(x + x', y) - 2\varphi(x, y) + \varphi(x - x', y) = x'^T D_x^2(\varphi(x, y)) x' + \mathcal{O}(\|x'\|^3).$$

Since for every sequence $(\gamma_i)_{i=1,\dots,k}$ there are both terms

$$\varphi\left(x + \varepsilon \sum_{i=1}^k \gamma_i e_i, y\right) \quad \text{and} \quad \varphi\left(x - \varepsilon \sum_{i=1}^k \gamma_i e_i, y\right)$$

in the outer sum of expression I_1, we have

$$|I_1| \leq \varepsilon C \|D_x^2 \varphi(x, y)\| + \mathcal{O}(\varepsilon^3), \quad C \in \mathbb{R}_+. \tag{3.6}$$

In the same way we obtain

$$|I_2| \leq \varepsilon C \|D_y^2 \varphi(x, y)\| + \mathcal{O}(\varepsilon^3), \quad C \in \mathbb{R}_+. \tag{3.7}$$

Hence, since $f_\varepsilon(s, \cdot)$ is bounded for any $s \in [0, T]$, the following identity holds true:

$$\lim_{\varepsilon \to 0} \int_0^t \int_U \varphi(u) \frac{M_\varepsilon[f_\varepsilon](s, u)}{\varepsilon} du\, ds = 0.$$

By approximation, this also holds for the completion of $C_c^\infty(\mathring{U})$ in $W^{2,\infty}(U)$.

Since $e^{\frac{R_\varepsilon(s,u)}{\varepsilon}}$ belongs to $W^{2,\infty}((0, T), U)$ (see Remark 3.4), we are allowed to select $\varphi(u)e^{\frac{R_\varepsilon(t,u)}{\varepsilon}} e^{-\frac{R_\varepsilon(s,u)}{\varepsilon}}$ as a test function. Then, we obtain

$$\lim_{\varepsilon \to 0} \int_0^t \int_U \varphi(u)e^{\frac{R_\varepsilon(t,u)}{\varepsilon}} \frac{\partial}{\partial s} \left(f_\varepsilon(s, u)e^{-\frac{R_\varepsilon(s,u)}{\varepsilon}} \right) du\, ds = 0.$$

So performing the integration over s gives

$$\lim_{\varepsilon \to 0} \int_U \varphi(u) \left(f_\varepsilon(t, u) - f^0(u)e^{\frac{R_\varepsilon(t,u)}{\varepsilon}} \right) du = 0. \qquad \square$$

Due to Lemma 3.5, the asymptotic behavior of $f_\varepsilon(t, u)$ for $\varepsilon \to 0$, *i.e.*, in the limit of large times and small mutations, can be characterized by means of techniques similar to those that have been introduced in [12], as highlighted by the following

Theorem 3.6 (Large Times and Small Mutations Asymptotics) *Let the same assumptions of Theorem* 3.1 *hold and let*

$$\|f^0(\cdot)\|_{L^1(U)} \leq \frac{\|\kappa(t, \cdot)\|_{L^\infty(X)}}{\inf \mu(t, \cdot)}. \tag{3.8}$$

Then, there exist a subsequence of f_ε, denoted again as f_ε, and a subsequence of R_ε, denoted again as R_ε, such that:

(i) *Establishing convergence.*

$$f_\varepsilon \rightharpoonup f \text{ on } w^* - L^\infty\big((0, T), M^1(U)\big), \text{ as } \varepsilon \to 0,$$

$$R_\varepsilon \to R \quad \text{uniformly in } [0, T] \times U, \text{ as } \varepsilon \to 0,$$

where $f \in L^\infty((0, T), M^1(U))$ and

$$R(t, u) = \int_0^t P\big(s, u, \varrho(s)\big) ds \in W^{2,\infty}\big((0, T) \times U\big). \tag{3.9}$$

(ii) *Characterizing the support of the limit f.*

$$\max_{u \in U} R(t, u) = 0, \quad \forall t \in [0, T].$$

Furthermore, assume

$$f^0(\cdot) > 0 \quad \text{a.e. on } R(t, \cdot)^{-1}(0); \tag{3.10}$$

then,

$$\text{supp}\big(f(t, \cdot)\big) \neq \emptyset \quad \text{and} \quad \text{supp}\big(f(t, \cdot)\big) \subset R(t, \cdot)^{-1}(0), \quad \text{for a.e. } t \in [0, T].$$

Proof (i) *Establishing convergence.* Upper bound (3.2) along with the Banach-Alaoglu theorem lead us to conclude that, up to extraction,

$$f_\varepsilon \rightharpoonup f \quad \text{on } w^* - L^\infty\big((0, T), M^1(U)\big),$$

and

$$R_\varepsilon \to R \quad \text{pointwise in } [0, T] \times U,$$

where R is defined by (3.9). Thus, since R_ε belongs to $W^{2,\infty}((0, T), U)$ (see Remark 3.4) and $W^{2,\infty}((0, T), U) \subset\subset C([0, T], U)$, we can conclude that

$$R_\varepsilon \to R \quad \text{uniformly in } [0, T] \times U.$$

(ii) *Characterizing the support of the limit f.*

   Step 1 ($R \leq 0$ on $[0, T] \times U$). By contradiction, assume that there exists $(\hat{t}, \hat{u}) \in [0, T] \times \mathring{U}$ s.t. $R(\hat{t}, \hat{u}) > 0$. The above uniform convergence result implies that $R_\varepsilon(t, u) \geq \sigma$ for some $\sigma > 0$, as long as $|t - \hat{t}| \leq \sigma$, $|u - \hat{u}| \leq \sigma$ and $\sigma \geq \varepsilon > 0$. Introducing a smooth test function $\varphi(u)$ such that $\mathbf{1}_{B(\hat{u}, \sigma/2)}(u) \leq \varphi(u) \leq \mathbf{1}_{B(\hat{u}, \sigma)}(u)$ and making use of the weak convergence result established by Lemma 3.5, we achieve

$$\lim_{\varepsilon \to 0} \int_U \varphi(u) f_\varepsilon(t, u) du = \lim_{\varepsilon \to 0} \int_U \varphi(u) f^0(u) e^{\frac{R_\varepsilon(t,u)}{\varepsilon}} du$$

$$\geq \lim_{\varepsilon \to 0} \int_{B(\hat{u}, \sigma/2)} f^0(u) e^{\frac{\sigma}{\varepsilon}} du = \infty. \tag{3.11}$$

This contradicts upper bound (3.2). As a result, we conclude that $R \leq 0$ on $[0, T] \times U$.

   Step 2 (If $R(\hat{t}, \hat{u}) < 0$, then f vanishes in a neighborhood of $(\hat{t}, \hat{u}) \in [0, T] \times U$). Assume $(\hat{t}, \hat{u}) \in [0, T] \times \mathring{U}$ s.t. $R(\hat{t}, \hat{u}) < 0$. Then, there exists some $\sigma > 0$ s.t. $R_\varepsilon(t, u) \leq -\sigma$ for $|t - \hat{t}| \leq \sigma$, $|u - \hat{u}| \leq \sigma$ and $\sigma \geq \varepsilon > 0$. The weak convergence result provided by point (i) implies that

$$\int_0^T \int_U \varphi(u) f(t, u) du \, dt = \lim_{\varepsilon \to 0} \int_0^T \int_U \varphi(u) f_\varepsilon(t, u) du \, dt,$$

for each smooth test function $\varphi : U \to \mathbb{R}$. Thus, choosing $\mathbf{1}_{B(\hat{u},\sigma/2)}(u) \leq \varphi(u) \leq \mathbf{1}_{B(\hat{u},\sigma)}(u)$ and using the weak convergence result established by Lemma 3.5, we have

$$\int_{B(\hat{t},\sigma)} \int_U \varphi(u) f(t,u) du\, dt = \lim_{\varepsilon \to 0} \int_{B(\hat{t},\sigma)} \int_U \varphi(u) f_\varepsilon(t,u) du\, dt$$

$$\leq \lim_{\varepsilon \to 0} \int_{B(\hat{t},\sigma)} \int_{B(\hat{u},\sigma)} f_\varepsilon(t,u) du\, dt$$

$$= \lim_{\varepsilon \to 0} \int_{B(\hat{t},\sigma)} \int_{B(\hat{u},\sigma)} f^0(u) e^{\frac{R_\varepsilon(t,u)}{\varepsilon}} du\, dt$$

$$\leq 2\sigma \lim_{\varepsilon \to 0} e^{-\frac{\sigma}{\varepsilon}} \int_{B(\hat{u},\sigma)} f^0(u) du = 0. \qquad (3.12)$$

As a result, $supp(f) \subset \{(t,u) \in [0,T] \times U : R(t,u) = 0\}$, and $f(t,u) = 0$ a.e. on U if $R(t,u) < 0$ on U.

Step 3 ($\max R(t,\cdot) = 0$ *for any* $t \in [0,T]$ *and* $\|f(t,\cdot)\|_{L^1(U)} > 0$ *a.e. on* $[0,T]$). Assume that there exists $\hat{t}$ s.t.

$$\forall t \in [0,\hat{t}], \quad \max_u R(t,u) = 0$$

and

$$\forall t \in (\hat{t},\hat{t}+\sigma), \quad \max_u R(t,u) < 0,$$

with $\sigma > 0$ and $\hat{t} + \sigma \leq T$, which allows us to state, due to Step 2 together with the continuity of $\|f(t,\cdot)\|_{L^1(U)}$ (see Remark 3.3),

$$\|f(t,\cdot)\|_{L^1(U)} = 0, \quad \text{for } t \in (\hat{t},\hat{t}+\sigma). \qquad (3.13)$$

If we take $\hat{u}$ s.t. $R(\hat{t},\hat{u}) = 0$, identity (3.13) implies

$$\int_{\hat{t}}^{\hat{t}+\sigma} P\big(t,\hat{u},\varrho(t)\big) dt \geq \sigma \inf \kappa > 0,$$

which is equivalent, because of definition (3.9), to

$$\frac{R(\hat{t}+\sigma,\hat{u}) - R(\hat{t},\hat{u})}{\sigma} > 0.$$

Since R is continuous, we can infer that $R(\hat{t}+\sigma,\hat{u}) > R(\hat{t},\hat{u}) = 0$. The latter conclusion contradicts the ones drawn in Step 1. Therefore, it follows that $\|f(t,\cdot)\|_{L^1(U)} > 0$ a.e. on $(\hat{t},\hat{t}+\sigma)$ and $\max R(t,\cdot) = 0$ for any $t \in (\hat{t},\hat{t}+\sigma)$. $\square$

Remark 3.7 Under the time rescaling here considered, another possible strategy to develop asymptotic analysis for $\varepsilon \to 0$ could be the one used in [3, 13, 22, 28], which relies on the ansatz $f_\varepsilon(t,u) = e^{\varphi(t,u)/\varepsilon}$. However, due to the particular shape of our mutation kernel, the present strategy seems to be more efficient in the case at hand. In fact, plugging in this ansatz we obtain

$$\partial_t \varphi(t,u) = P\big(t,u,\varrho(t)\big) + \big(e^{(\varphi(t,u+\varepsilon)-\varphi(t,u))/\varepsilon} + e^{(\varphi(t,u-\varepsilon)-\varphi(t,u))/\varepsilon} - 2\big).$$

In the limit $\varepsilon \to 0$, it follows formally that

$$\partial_t \varphi(t, u) = P\big(t, u, \varrho(t)\big) + \big(e^{\nabla_u \varphi(t,u)} + e^{-\nabla_u \varphi(t,u)} - 2\big),$$

so that the assumptions made in [3, 13, 22, 28] are not fulfilled.

A characterization of the measure f is provided by the following propositions, which rely on some technical assumptions that allow the emergence of different asymptotic scenarios, such as:

- the formation of one single Dirac mass, or even several Dirac masses (Proposition 3.8),
- the formation of multiple Dirac masses that then merge into a single one (Proposition 3.9 and Proposition 3.10).

These results are illustrated by the numerical simulations presented in the last section. In all cases, as established by Theorem 3.6, the concentration points correspond to the maximum points of functional $R(t, \cdot)$.

Proposition 3.8 *Let assumptions* (2.3)–(2.7) *and* (3.8) *hold true. If*

$$\kappa_3 = \mu_3 = 0, \qquad \kappa_1(t) > 0, \quad \forall t \in [0, T], \ \mu_1(t) > 0, \ \forall t \in [0, T] \tag{3.14}$$

and

$$\max_{(x,y) \in U} \big(\kappa_2(x)\mu_2^{-1}(y)\big) = \kappa_2(\overline{x}_n)\mu_2^{-1}(\underline{y}_n), \quad \big\{(\overline{x}_n, \underline{y}_n)\big\}_{n=1}^{N} \in U, \tag{3.15}$$

then the measure f results as follows:

$$f(t, x, y) = \sum_{n=1}^{N} \varrho_n(t)\delta(x - \bar{x}_n)\delta(y - \underline{y}_n), \quad \varrho_n(t) \geq 0. \tag{3.16}$$

Proof The following identity holds true:

$$\frac{R(t, x, y)}{\mu_2(y)} = \frac{\kappa_2(x)}{\mu_2(y)} \int_0^t \kappa_1(s)ds - \int_0^t \mu_1(s)\varrho(s)ds,$$

where the second term on the right hand side does not depend on (x, y). Then, making use of the result established by step 3 of point (ii) in Theorem 3.6 together with assumption (3.15), we can conclude that

$$R(t, x, y) = 0 \Leftrightarrow (x, y) \in \big\{(\hat{x}_n, \hat{y}_n)\big\}_{n=1}^{N}$$

and

$$R(t, x, y) < 0, \quad \forall (x, y) \notin \big\{(\hat{x}_n, \hat{y}_n)\big\}_{n=1}^{N},$$

which imply identity (3.16). □

Proposition 3.9 *Let assumptions* (2.3)–(2.7) *and* (3.8) *hold true. If*

$$\mu_1(t) > 0 \quad \forall t \in [0, T], \qquad \mu_3 = 0, \tag{3.17}$$

$$\int_0^t \kappa_1(s)\,ds \geq 0, \quad \forall t \in [0, \tau], \qquad \int_0^t \kappa_1(s)\,ds < 0, \quad \forall t \in (\tau, T] \qquad (3.18)$$

and there exist $\{\overline{x}_n\}_{n=1}^N, \{\underline{x}_n\}_{n=1}^N \in X, \{\underline{y}_n\}_{n=1}^N \in Y$ *such that*

$$\min_{x \in X} \kappa_2(x) = \kappa_2(\underline{x}_n), \qquad \max_{x \in X} \kappa_2(x) = \kappa_2(\overline{x}_n), \qquad \min_{y \in Y} \mu_2(y) = \mu_2(\underline{y}_n), \qquad (3.19)$$

then the measure f *can be written as follows*:

$$f(t, x, y) = \sum_{n=1}^N \varrho_n(t)\delta(x - \overline{x}_n)\delta(y - \underline{y}_n), \quad \varrho_n(t) \geq 0, \text{ for } 0 < t \leq \tau, \qquad (3.20)$$

$$f(t, x, y) = \sum_{n=1}^N \varrho_n(t)\delta(x - \underline{x}_n)\delta(y - \underline{y}_n), \quad \varrho_n(t) \geq 0, \text{ for } \tau < t \leq T. \qquad (3.21)$$

Proof The following identity is verified:

$$\frac{R(t, x, y)}{\kappa_2(x)} = \frac{\kappa_3 t - \mu_2(y) \int_0^t \mu_1(s)\varrho(s)\,ds}{\kappa_2(x)} + \int_0^t \kappa_1(s)\,ds.$$

The second term of the right hand side does not depend on x and y and it is greater than or equal to zero for $0 \leq t \leq \tau$ and smaller than zero for $\tau < t \leq T$. Then, step 3 of point (ii) in Theorem 3.6 implies that the first term of the right hand side is smaller than or equal to zero for $0 \leq t \leq \tau$ and greater than zero for $\tau < t \leq T$. As a result, identities (3.20) and (3.21) directly follow. □

Proposition 3.10 *Let assumptions* (2.3)–(2.7) *and* (3.8) *hold true. If*

$$\kappa_3 = 0, \qquad \frac{d\kappa_1(t)}{dt} \geq 0, \quad \forall t \in [0, T], \qquad \frac{d\mu_1(t)}{dt} \leq 0, \quad \forall t \in [0, T], \qquad (3.22)$$

$$\int_0^t \mu_1(s)\,ds \geq 0, \quad \forall t \in [0, \tau], \qquad \int_0^t \mu_1(s)\,ds < 0, \quad \forall t \in (\tau, T], \qquad (3.23)$$

and there exist $\{\overline{x}_n\}_{n=1}^N \in X, \{\underline{y}_n\}_{n=1}^N, \{\overline{y}_n\}_{n=1}^N \in Y$ *such that*

$$\max_{x \in X} \kappa_2(x) = \kappa_2(\overline{x}_n), \qquad \min_{y \in Y} \mu_2(y) = \mu_2(\underline{y}_n), \qquad \max_{y \in Y} \mu_2(y) = \mu_2(\overline{y}_n), \qquad (3.24)$$

then the measure f *can be written as follows*:

$$f(t, x, y) = \sum_{n=1}^N \varrho_n(t)\delta(x - \overline{x}_n)\delta(y - \underline{y}_n), \quad \varrho_n(t) \geq 0, \text{ for } 0 < t \leq \tau, \qquad (3.25)$$

$$f(t, x, y) = \sum_{n=1}^N \varrho_n(t)\delta(x - \overline{x}_n)\delta(y - \overline{y}_n), \quad \varrho_n(t) \geq 0, \text{ for } \tau < t \leq T. \qquad (3.26)$$

Proof The following identity holds:

$$\frac{R(t, x, y)}{\mu_2(y)} = \frac{\kappa_2(x) \int_0^t \kappa_1(s)ds - \mu_3 \int_0^t \varrho(s)ds}{\mu_2(y)} - \int_0^t \mu_1(s)\varrho(s)ds. \tag{3.27}$$

The second term of the right hand side does not depend on x and y and, because of assumptions (3.23), it is greater than or equal to zero for $0 \leq t \leq \tau$. Furthermore, since $\varrho(t)$ is monotonically increasing over $[0, T]$ due to assumptions (3.8) and (3.22), we can state

$$\int_0^t \mu_1(s)\varrho(s)ds \leq \varrho(\tau) \int_0^t \mu_1(s)ds < 0, \quad \text{for } \tau < t \leq T,$$

where the last inequality follows from assumptions (3.23). As a result, step 3 of point (ii) in Theorem 3.6 implies that the first term of the right hand side in (3.27) is greater than or equal to zero for $0 \leq t \leq \tau$ and smaller than zero for $\tau < t \leq T$, and this allows us to conclude that identities (3.25) and (3.26) hold true. □

4 Computational Results

This section summarizes the results of numerical simulations of the initial value problem (3.4), which illustrate the analytical results established by Theorem 3.6, Propositions 3.8, 3.9 and 3.10. In particular, we consider different definitions of functions κ and μ such that:

- one single Dirac mass arises both under the hypothesis of still concentrated and uniformly distributed initial data;
- a function mainly concentrated in one single point at time $t = 0$ can split, over time, into four Dirac masses;
- considering a single Dirac mass at time $t = 0$, this splits into two masses that afterwards merge back into a single one.

Numerical computations are performed in MATLAB making use of an implicit-explicit finite difference scheme with 200 points on the square $[-0.5, 1.5] \times [-0.5, 1.5]$. Interval $[0, T]$ with T an integer multiple of the unit time $dt = 0.005$ is selected as time domain. We look for concentration points belonging to the set $[0, 1] \times [0, 1]$; thus, the set $[-0.5, 1.5] \times [-0.5, 1.5]$ is selected as computational domain in order to highlight that the obtained results are not affected by boundary effects.

Since we assume only small mutations to occur, we fix $\varepsilon = 0.005$, while, as the focus is on situations where mutations that lead to a greater or lower expression level of the phenotypic traits related to x and y occur at the same rate, we set $\alpha = \beta = 0.5$. Initial data are chosen among the ones given hereafter:

$$f^0(x, y) = e^{-\frac{(x-0.5)^2}{0.1} - \frac{(y-0.5)^2}{0.1}}, \tag{4.1}$$

$$f^0(x, y) = 1. \tag{4.2}$$

The former mimics an evolutionary scenario where most of the individuals are characterized by an intermediate level of sensitivity to habitat shrinking and global warming at the beginning of observations, *i.e.*, $f^0(x, y)$ is mainly concentrated in $(x, y) = (0.5, 0.5)$. On the other hand, the latter reproduces the case where all possible traits are expressed by the same number of individuals at time $t = 0$, *i.e.*, $f^0(x, y)$ is uniformly distributed.
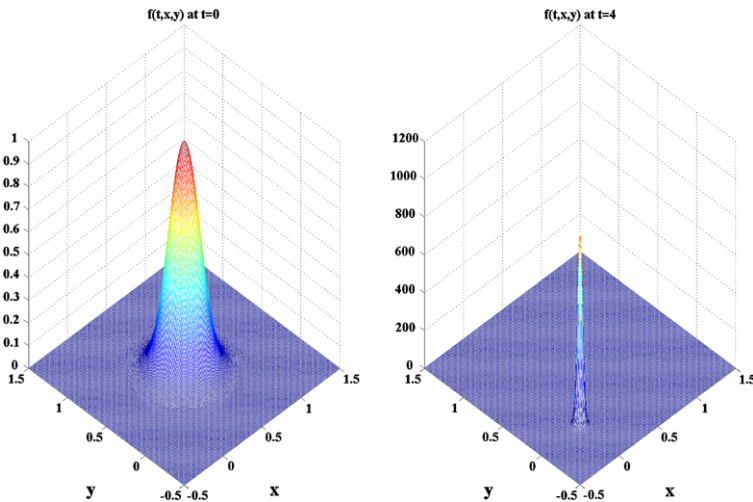
Fig. 1 Dynamics of $f(t, x, y)$ under the assumptions of Proposition 3.8 with (4.3) and initial conditions (4.1). The figure illustrates the concentration from Gaussian-like initial data into a Dirac mass. Plot of $f(t, x, y)$ for $t = 0$ is on the *left* and for $t = T = 4$ on the *right*

4.1 Concentration in One Single Dirac Mass

We start by performing simulations under the assumptions of Proposition 3.8 with

$$\kappa_1(t) = \mu_1(t) = 1, \quad \forall t \in [0, T], \qquad \mu(t, y) = \mu_2(y),$$

$$\max \kappa_2 = \kappa_2(0), \quad \frac{d}{dx} k_2(x) \leq 0, \qquad \min \mu_2 = \mu_2(0), \quad \frac{d}{dy} \mu_2(y) \geq 0, \tag{4.3}$$

in order to consider an evolutionary scenario where the selective pressures exerted by habitat shrinking and global warming are constant over time and make the living conditions of specialist individuals harsher. In particular, we define

$$\kappa_2(x) = \frac{1}{1 + x^2}, \qquad \mu_2(y) = 1 + y^2. \tag{4.4}$$

The obtained results are summarized by Figs. 1 and 2, which refer to initial conditions (4.1) and (4.2), respectively, and show that $f(t, x, y)$ tends to concentrate as a Dirac mass centered in $(x, y) = (0, 0)$. Since $(0, 0)$ is the maximum point of $\kappa_2(x)\mu_2^{-1}(y)$, these numerical results illustrate the analytical ones stated by Proposition 3.8. Let us point out that such a dynamics is consistent with the considerations drawn in [22]. In fact, assumptions (3.14) and (4.3) make function $P(t, x, y, \varrho(t))$ concave in (x, y); thus, no more than one single Dirac mass can be sustained by the present model.

4.2 Formation of Four Dirac Masses

Then, we choose initial conditions (4.1) and make again the assumptions of Proposition 3.8 with

$$\kappa_1(t) = \mu_1(t) = 1, \quad \forall t \in [0, T], \qquad \mu(t, y) = \mu_2(y),$$

$$\max \kappa_2 = \kappa_2(0) = \kappa_2(1) > 0, \qquad \min \mu_2 = \mu_2(0) = \mu_2(1) > 0, \tag{4.5}$$
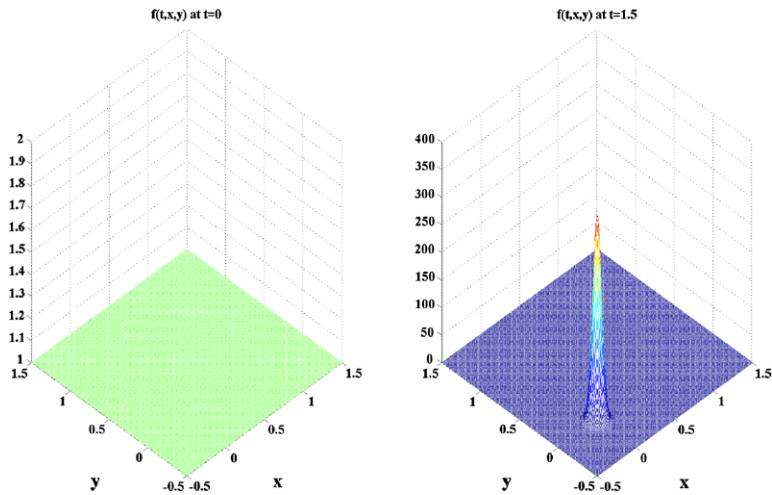
Fig. 2 Dynamics of $f(t, x, y)$ under the assumptions of Proposition 3.8 with (4.3) and initial conditions (4.2). The figure illustrates the concentration from uniform constant initial data into a Dirac mass. Plot of $f(t, x, y)$ for $t = 0$ is on the *left* and for $t = T = 1.5$ on the *right*
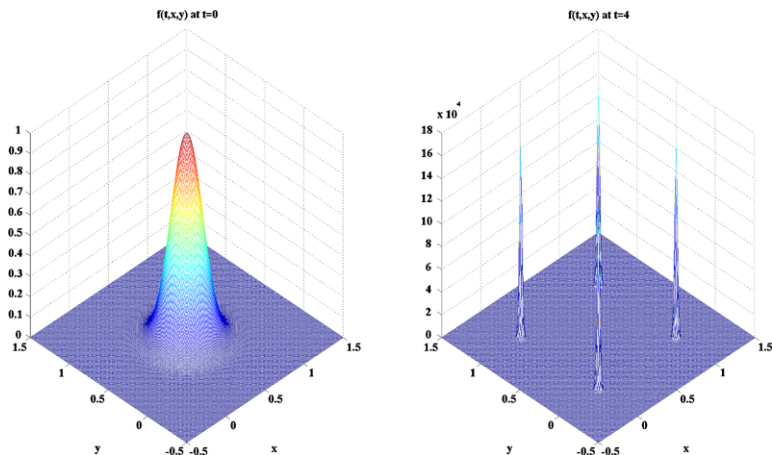
Fig. 3 Dynamics of $f(t, x, y)$ under the assumptions of Proposition 3.8 with (4.5) and initial conditions (4.1). The figure illustrates the splitting up of Gaussian-like initial data into four Dirac masses. Plot of $f(t, x, y)$ for $t = 0$ is on the *left* and for $t = T = 4$ on the *right*

which mimic an evolutionary scenario where the selective forces under consideration allow the survival of both habitat-generalists and habitat-specialists. Simulations are performed under the following particular definitions:

$$\kappa_2(x) = 30 - 100x^2(1 - x)^2, \qquad \mu_2(y) = 0.3 + y^2(1 - y)^2. \tag{4.6}$$

In agreement with Proposition 3.8, Fig. 3 shows that function f concentrates into four Dirac masses located in the vertexes of the square $[0, 1] \times [0, 1]$. In fact, $(0, 0)$, $(1, 0)$, $(0, 1)$ and $(1, 1)$ are the maximum points of $\kappa_2(x)\mu_2^{-1}(y)$.

4.3 Splitting and Merging of Dirac Masses

Here, the idea is that by going from a non-convex back to a convex parameter function R, we can start with one Dirac, split it up in two and then merge them again. The function R either satisfies Proposition 3.9, implying splitting in the x-direction, or Proposition 3.10 implying splitting in the y-direction. More precisely, at first, we select initial conditions (4.1) and parameter functions fulfilling the assumptions of Proposition 3.9

$$\min \kappa_2 = \kappa_2(0.5), \qquad \max \kappa_2 = \kappa_2(0) = \kappa_2(1),$$
$$\mu_1(t) = A_1, \quad \forall t \in [0, T], \qquad \min \mu_2 = \mu_2(0.5), \tag{4.7}$$

with:

$$\kappa_3 = 4, \qquad \kappa_1(t) = 10\left(\frac{\tau}{2} - t\right), \qquad \tau = 1,$$

$$\kappa_2(x) = \begin{cases} 1 - x^2(1 - x)^2, & \text{if } 0 \leq x \leq 1, \\ 1 - \min(0.06, x^2(1 - x)^2), & \text{otherwise}, \end{cases} \tag{4.8}$$

$$A_1 = 0.005, \qquad \mu_2(y) = 1 + (y - 0.5)^2, \qquad \mu_3 = 0.$$

From an evolutionary perspective, assumptions (4.7) model a scenario where the selective pressure exerted by global warming is constant in time and confers a competitive advantage to individuals in the state $y = 0.5$, while habitat shrinking selects individuals in the states $x = 0$ and $x = 1$ on the time interval $[0, \tau]$ and individuals in the state $x = 0.5$ on $(\tau, T]$.

Second, we choose parameter functions satisfying the assumptions of Proposition 3.10

$$\kappa_1(t) = A_2, \quad \forall t \in [0, T], \qquad \max \kappa_2 = \kappa_2(0.5),$$
$$\min \mu_2 = \mu_2(0) = \mu_2(1), \qquad \max \mu_2 = \mu_2(0.5), \tag{4.9}$$

with:

$$A_2 = 2, \qquad \kappa_2(x) = 1 - 0.1(x - 0.5)^2, \qquad \kappa_3 = 0,$$

$$\mu_3 = 0.1, \qquad \mu_1(t) = 10\left(\frac{\tau}{2} - t\right), \qquad \tau = 1,$$

$$\mu_2(y) = \begin{cases} 1 - y^2(1 - y)^2, & \text{if } 0 \leq y \leq 1, \\ 1 - \min(0.06, y^2(1 - y)^2), & \text{otherwise}. \end{cases} \tag{4.10}$$

From a biological point of view, assumptions (4.9) model a context where the selective forces exerted by habitat shrinking do not change over time and favor the selection of individuals in the state $x = 0.5$, while the selective pressure induced by global warming evolves in time and confers a competitive advantage to individuals in the states $y = 0$ and $y = 1$ on $[0, \tau]$ and to individuals in the state $y = 0.5$ on $(\tau, T]$.

On the basis of Proposition 3.9 and Proposition 3.10, we can foresee the formation of two Dirac masses located in $(0, 0.5)$ and $(1, 0.5)$, under definitions (4.7), or $(0.5, 0)$ and $(0.5, 1)$, under definitions (4.9), over the time interval $[0, \tau]$. On the other hand, for $t \in (\tau, T]$, we expect the two Dirac masses to merge into a single one centered in the point $(0.5, 0.5)$. These are exactly the behaviors highlighted by Figs. 4 and 5, respectively.
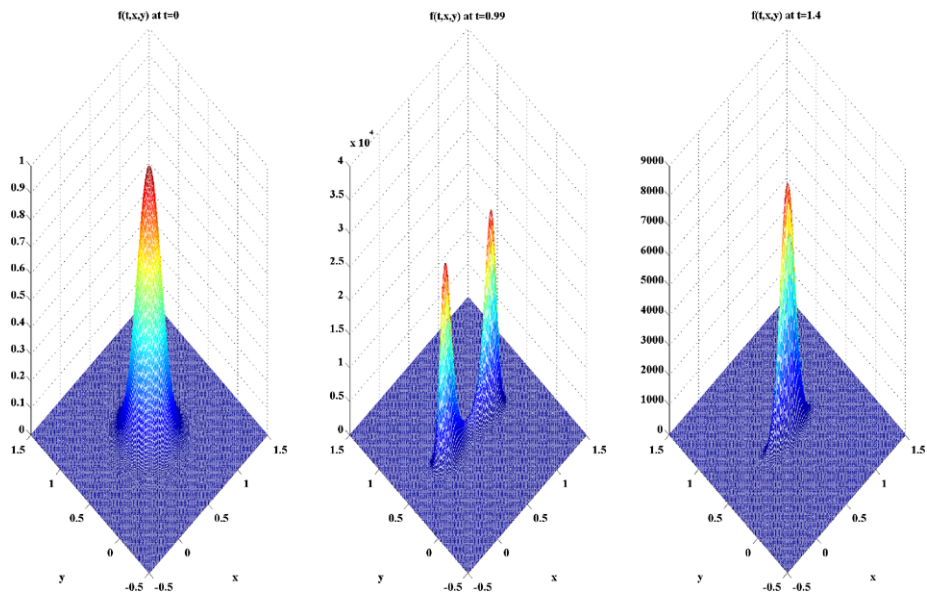
Fig. 4 Dynamics of $f(t, x, y)$ under the assumptions of Proposition 3.9 with (4.7) and initial conditions (4.1). The figure illustrates the splitting and remerging in the x-direction. Plot of $f(t, x, y)$ for $t = 0$ is on the *left*, for $t = 0.99 < \tau$ in the *centre* and for $t = T = 1.4$ on the *right*
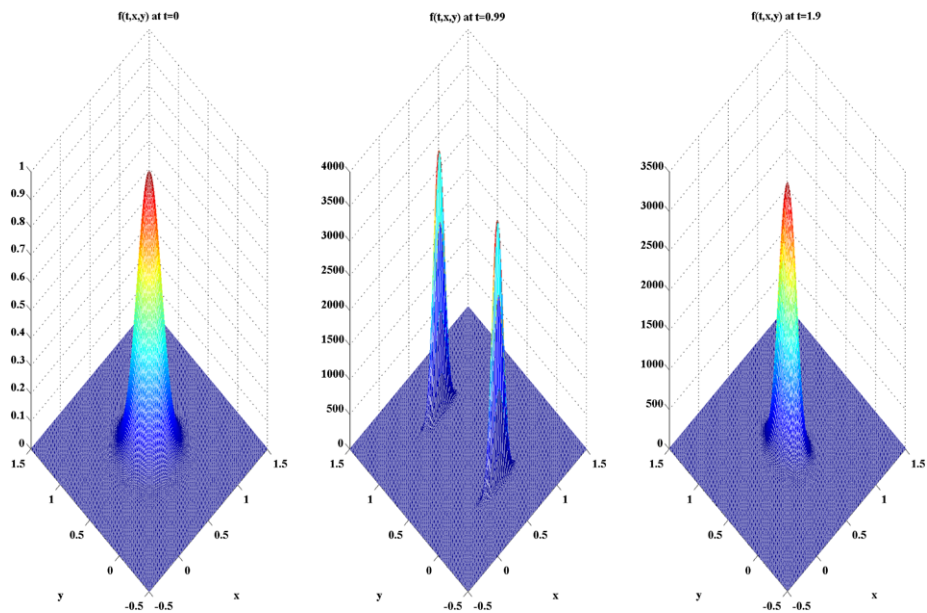
Fig. 5 Dynamics of $f(t, x, y)$ under the assumptions considered by Proposition 3.10 with (4.9) and initial conditions (4.1). The figure illustrates the splitting and remerging in the y-direction. Plot of $f(t, x, y)$ for $t = 0$ is on the *left*, for $t = 0.99 < \tau$ in the *centre* and for $t = T = 1.9$ on the *right*

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