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Does a marginal contact with a native species living in a complex domain with a fractional dimension boundary represent a sufficient invasive mechanism for the establishment of a migrating population?

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Abstract

Animal migrations are dynamic phenomena that can change rapidly or even be lost entirely over time. In particular, when a migrant population finds favorable conditions in a region, it can settle there permanently. Since biological invasions represent a serious threat to biodiversity, we are interested in determining if and when a marginal contact of a moving population with a territory occupied by other populations is sufficient to trigger an invasion mechanism. The interaction problem of a migrant population with a residential one is considered, where the contact occurs just on the boundary of the region occupied by the native population. To study whether and how the migrants induce changes in the ecosystem subject to their transit, two models are considered. The former accounts only for damage on the native species, with no gain for the migrant population. In the second one, migrants are assumed to be predators and therefore gaining an advantage for survivability. The comparison of the two models' behaviors gives insights on the invasion process. The theoretical analysis of the two models is complemented by numerical simulations. The models suggest that, even without a direct benefit for the migratory population, these kinds of

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interactions can have serious ecological consequences for the native population that can even lead to its extinction. Comparing the results, it is instead found that if the migrating species is a predator, even this very reduced interaction on the boundary is enough to trigger invasion and migrants permanently settle in the territory.

Keywords:
periodic migration, migratory disturbance, migrating predator, residential prey, marginal interactions, border fractional dimension, fractal boundary geometry, biological invasion, bistability, bSTAB

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1. Introduction

Biological invasions refer to spontaneous or human-mediated introductions of species into new regions, other than their native territories, in which they begin to spread and reproduce, successfully establishing themselves [36]. The arrival of an alien species in a geographical area can lead to the local disappearance of one or more native species. The impact of invasive populations on native ones can be expressed at different levels, such as direct predation, competition for trophic niche and environmental resources, disease transmission, habitat alteration and species hybridization, e.g., see [5, 13, 26, 34, 46]. For this reason, biological invasions represent one of the most serious threats to biodiversity worldwide, second only to the loss and fragmentation of habitats induced mainly by profound human-caused land changes [8]. In addition, biological invaders also have a significant socio-economic impact. In particular, alien species settlings can entail large economic losses in sectors such as agriculture, fishing, tourism, and even public health. For specific examples, refer to [25, 31, 47].

Invasive species are found outside their natural habitat due primarily to human activities. Their introduction into a territory may have been intentional, for example for hunting or ornamental purposes, or accidental, for example through freight shipments. On the other hand, the introduction of a new species into a geographical area may be spontaneous, that is, not carried out directly by humans. It may be due to secondary spread by natural dispersal from a neighboring territory previously invaded or, focusing on the animal kingdom, to migratory movements, see for instance [4, 10, 21, 42]. In this paper, we want to concentrate on the last mentioned possible cause.

The most well-known migratory movements are those of birds [28] and reptiles [40]. Swallows (*Hirundo rustica*) and storks (*Ciconia ciconia*) are notorious examples for the former class and green sea turtles (*Chelonia mydas*) for the latter. However, the migrations of some fish, insects and mammals are also noteworthy. Many fish species migrate regularly, particularly clupeids and scombrids, either for trophic resources or for reproduction, leading to the concentration of large shoals in some marine areas at certain times of the year [37]. Then, among insects that move seasonally, we have some species of aphids, beetles, dipterans and lepidopterans [18]. Finally, as for mammals, periodic movements are mainly accomplished by large herbivores in search of plant food resources [27], such as wildebeests (*Connochaetes taurinus*) and elephants (*Loxodonta africana*), and by big cetaceans in search of krill [20], such as minke whales (*Balaenoptera physalus*).

As highlighted in [6], animal migrations are dynamic phenomena over space and time, varying substantially among closely related species, subspecies and even among individuals in a single population, which can change rapidly or even be lost entirely. In particular, a migrant population may settle permanently in a region, the final destination of its migratory movement or in an area encountered along the route, following the discovery of favorable conditions. In this sense, migratory movements can be counted among the possible causes of biological invasions. Among the animals that have lost or are losing their migratory behavior by settling in certain areas, we have many bird species. We

can mention, for example, European blackbirds (Turdus merula) in Estonia and Latvia [24] and white storks (Ciconia ciconia) in southern Spain [45]. Other known examples are monarch butterflies (*Danaus plexippus*) in the southern United States [39], which have become nonmigratory and breed year-round on tropical milkweeds (*Asclepias curassavica*), and in Australia the grey-headed flying foxes (*Pteropus poliocephalus*) with their establishment of a permanent camp in urban Melbourne [49].

In this paper, without focusing on a particular animal species, we consider a migrating population that, during its migratory movements, transits along the boundary of a certain territory. In particular, we are interested to determine if and when such marginal contact is sufficient to trigger an invasion mechanism, since biological invasions can have numerous negative consequences. As mentioned above, these pose a serious threat to biodiversity and can also result in significant socio-economic losses. To carry out an initial study, we consider here only one residential population that can interact significantly with the migrant population in the region subject to migration transit.

Similarly to what was done in [1], we focus on two specific scenarios. In the first one, the migrating population disturbs the residential one by ravaging its territorial boundary, but does not obtain any significant benefit in so doing. In the second one, we assume that the moving population acts as a predator of the native species, getting a reward from hunting. We consider both scenarios to identify the differences between final outcomes of the two behaviors of the migrants. In [1], the affected territory is fully crossed by the migratory flow. Two residential populations, a prey and its predator, able to interact significantly with the migratory population are presented in the region. Two situations are envisaged. In the first scenario, the moving population disturbs the two populations of the primary ecosystem. In the second one, it preys on both, acting as a superpredator. In the current work, the contact is only marginal, but the very same two situations are considered.

The paper is organized in six sections. In the next one, we present two models related to marginal contact between a migrating population and a residential

one, considering the two different migratory behaviors of interest. Then, in Section 3 and 4, these two systems are analyzed in terms of equilibria and their stability, the interference model in the former and the predation one in the latter, respectively. Section 5 contains numerical simulations. The paper ends with a discussion of the results and conclusive remarks.

2. Two models for marginal contact between periodic migrants and residential population

2.1. Interference model

As a starting point, consider a logistically growing residential population R. Then, suppose that a periodically migrating population M can interact with the first one on the boundary of the territory it occupies. The residential population will here be considered as either being only damaged by the migrants or else being their prey.

In general, the shape of the native species' territory could be very complicated, depending on its physical and geographical characteristics. Consequently, in principle, its boundary cannot be represented by a smooth line. Assuming a fractional dimension for the portion of the perimeter along which contact occurs, we introduce a function $\Phi(R, \alpha)$, with $\frac{1}{2} \leq \alpha < 1$, to model the situation. This function is a generalization of the power function R^α, proposed in [12] for interactions between individualistic predators and herding prey and later used also in other works, see, e.g., [2, 9, 22]. The introduction of square root response function [3] or the more generic power function [12] is motivated by the fact that interactions of an outside individual of another population with a population living in herd are mainly limited to the individuals on the outmost positions in the herd. This assumption has been discussed in several other papers [3, 9, 11, 12, 50] to which we refer the reader for a more detailed explanation. In [51] some shortcomings are discussed and the form we choose here tries to avoid such difficulties. Specifically, the function we use here is

$$\Phi(R, \alpha) = \frac{R}{1 + R^{1-\alpha}} \, .$$

This function is constructed in such a way as to behave as R^α for large values of R and as R for small values of R, in a manner to prevent singularity problems, a construction similar to the one of [11, 50]. The biological meaning is rooted in the remark that two or three individuals do not constitute a herd. Then their interactions with a single member of the external species occur on one to one basis, as in the classical multiple population models. The first and second derivatives of $\Phi(R,\alpha)$, respectively

$$\frac{\partial\Phi(R,\alpha)}{\partial R}=\frac{1+\alpha R^{1-\alpha}}{(1+R^{1-\alpha})^2}\quad\text{and}\quad\frac{\partial^2\Phi(R,\alpha)}{\partial R^2}=\frac{(1-\alpha)(\alpha-2-\alpha R^{1-\alpha})}{R^\alpha(1+R^{1-\alpha})^3},$$

are positive the former and negative the latter, for every positive value of R. Consequently, this is an increasing concave function. Its graphical behavior is shown in Figure 1, by way of example with $\alpha=\frac{2}{3}$.

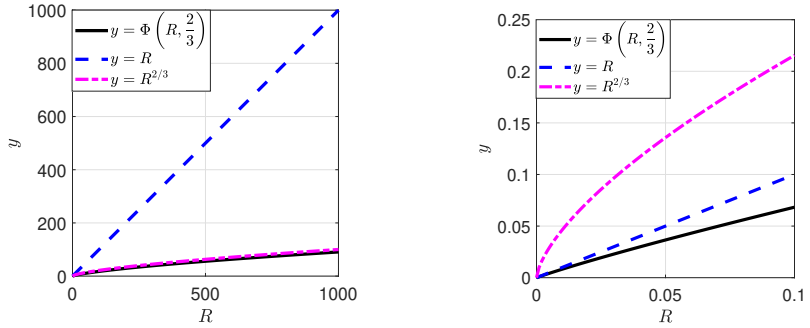


Figure 1: The graph of $\Phi\left(R,\frac{2}{3}\right)$ (black solid line) is compared with the two-thirds root (magenta dash-dotted line) and the bisectrix of the first and third quadrants (blue dashed line). On the left we consider a large domain: we observe that $\Phi\left(R,\frac{2}{3}\right)$ behaves as $R^{2/3}$ for large values of R. On the right we focus on a zoom near the origin: we see that $\Phi\left(R,\frac{2}{3}\right)$ behaves as R for small values of R.

We distinguish two scenarios. At first, we disregard any possible vital dynamics for the migrants and we focus on the interference damages to the native species, neglecting possible benefits for the former population. Secondly, we consider also vital dynamics for the migrants and their benefit gained by feeding on the native species, without other internal resources.

In the literature there are many papers on more classical formulations such as

[15, 52]. In these research works classical functional responses such as Holling type II (HTII) or the Beddington-DeAngelis functional form are considered to model the population interactions in their own domain. Here however we consider instead an interaction limited to the boundary of the domain. For the migrating population, no reproduction is considered because it occurs on a longer timescale than the one needed for the interference mechanism. Also, we can assume that it occurs elsewhere, in suitable reproduction sites.

In the first case, we simply model the migrating population via

$$\frac{d^2M}{dt^2} + \omega^2(M - M_0) = 0\,. \tag{1}$$

In the above equation, M_0 is the value around which the migrants oscillate and ω is the pulsation of this oscillation. Thus, by introducing the auxiliary variable Y, we have the following minimal model for the migratory disturbance on the border of a residential population:

$$\begin{aligned} \frac{dR}{dt} &= f_1(R, M) = R(r - bR) - c\Phi(R, \alpha)M, \\ \frac{dM}{dt} &= f_2(Y) = Y, \\ \frac{dY}{dt} &= f_3(M) = -\omega^2(M - M_0). \end{aligned} \tag{2}$$

Here r denotes the prey reproduction rate, b is the intraspecific competition of the prey and c represents the ravaging rate. Further, as mentioned before, $\frac{1}{2} \leq \alpha < 1$ is the shape index of the native species territory.

Note that in this formulation no dispersion is considered, although it may occur. However, dispersion has already been investigated by several other researchers [14, 19, 23, 29, 30, 35, 48, 53]. Furthermore, we neglect it because we want to focus on the initial phase of the invasion and not on what happens when the species settles in the environment.

2.2. Predation model

Here we assume that the migrating process still holds, as in the previous model, and the migrant population is able to thrive independently from the

native population, getting resources from other places. In addition, in this model, the migrant exhibits demographic features, by predating on the native population and possibly spends more time in the territory that is encountered in the migration, and thus being subject to mortality. The predator is supposed to be a specialist only in the area of invasion, having no other internal resources.

We model the population M via

$$\frac{dM}{dt} = ec\Phi(R,\alpha)M - mM,$$

where m is the predator natural mortality rate, e denotes the prey into predator conversion rate, expressing the benefit they gain, and c, unlike the previous case, represents the hunting rate. However, to take the migratory behavior into account, we have to differentiate the above equation and add the contribution of the periodic migration. In this way we get

$$\frac{d^2M}{dt^2} = ecMf_1(R,M)\frac{\partial\Phi(R,\alpha)}{\partial R} + ec\Phi(R,\alpha)Y - mY - \omega^2(M - M_0).$$

Therefore, the model for the second scenario is

$$\begin{aligned} \frac{dR}{dt} &= f_1(R,M) = R(r - bR) - c\Phi(R,\alpha)M, \\ \frac{dM}{dt} &= f_2(Y) = Y, \\ \frac{dY}{dt} &= \widetilde{f}_3(R,M,Y), \end{aligned} \tag{3}$$

with

$$\widetilde{f}_3(R,M,Y) = ecMf_1(R,M)\frac{\partial\Phi(R,\alpha)}{\partial R} + ec\Phi(R,\alpha)Y - mY - \omega^2(M - M_0).$$

In the two following sections, we will separately study in detail the models (2) and (3). For notational convenience, from here on, we omit the variable and parameter dependencies of all the functions we have introduced so far.

3. Interference model analysis

In this case, we actually have the explicit solutions for the dynamics of M and Y, namely

$$M(t) \;=\; (M(0)-M_0)\cos(\omega t) \;+\; \frac{Y(0)}{\omega}\sin(\omega t) \;+\; M_0, \tag{4}$$

and

$$Y(t) \;=\; Y(0)\cos(\omega t) \;-\; \omega\,(M(0)-M_0)\sin(\omega t). \tag{5}$$

Therefore, the following result for forward invariance of the positive cone and boundedness of the solutions hold.

Proposition 3.1. *Let $(R(0),M(0),Y(0)) \in \mathbb{R}^2_{\geq 0}\times\mathbb{R}$ the initial condition of (2). Then, the corresponding solution $(R(t),M(t),Y(t))$ is bounded and contained in $\mathbb{R}^2_{\geq 0}\times\mathbb{R}$ if and only if*

$$(M(0)-M_0)^2 \;+\; \left(\frac{Y(0)}{\omega}\right)^2 \;\leq\; M_0^2. \tag{6}$$

Proof. Due to (4) and (5), we have that, for every $t\in\mathbb{R}$,

$$|M(t)| \;\leq\; |M(0)-M_0| \;+\; \frac{|Y(0)|}{\omega} \;+\; M_0,$$

and

$$|Y(t)| \;\leq\; |Y(0)| \;+\; \omega|M(0)-M_0|.$$

Moreover, subtracting M_0 in (4), dividing (5) by ω, and then summing the squares of the resulting equations, we obtain

$$(M(t)-M_0)^2 \;+\; \left(\frac{Y(t)}{\omega}\right)^2 \;=\; (M(0)-M_0)^2 \;+\; \left(\frac{Y(0)}{\omega}\right)^2,$$

for every $t\in\mathbb{R}$. Therefore,

$$M_0 \;-\; \rho \;\leq\; M(t) \;\leq\; M_0+\rho$$

with

$$\rho \;:=\; \sqrt{(M(0)-M_0)^2 \;+\; \left(\frac{Y(0)}{\omega}\right)^2}.$$

Hence (6) is a necessary and sufficient condition for $M(t) \geq 0$.

As for $R(t)$, when $R(t) > r/b$ and (6) holds, $M(t) \geq 0$ and $R'(t) < 0$, thus, $\lim_{t\to+\infty} R(t) < +\infty$. Moreover, if there exists $t_* \in \mathbb{R}$ such that $R(t_*) = 0$, then $R'(t_*) = 0$ and

$$\begin{aligned} R''(t_*) &= r - 2bR(t_*)R'(t_*) - c\left(Y(t_*)\Phi(R(t_*),\alpha) - M(t_*)R'(t_*)\tfrac{\partial\Phi}{\partial R}(R(t_*),\alpha)\right) \\ &= r \;>\; 0, \end{aligned}$$

which means that t_* is a local minimum for $R(t)$. Therefore, since $R(0) \geq 0$, $R(t)$ is bounded from below by 0. □

The equilibrium points of the interference model (2) must have $Y = 0$ and $M = M_0$ to satisfy the last two equilibrium equations, respectively. Further, from the first equilibrium equation we have either $R = 0$ or

$$r - bR - \frac{cM_0}{1 + R^{1-\alpha}} = 0\,. \tag{7}$$

Theorem 3.1. *Let $\mathcal{R}_* \subset \mathbb{R}_{\geq 0}$ be the set of solutions of the non-linear equation* (7)*. Then, the set of equilibria of* (2) *is*

$$\mathcal{E} \;:=\; \{\; E_0 := (0, M_0, 0)\;\} \;\cup\; \mathcal{E}_*,$$

where

$$\mathcal{E}_* \;:=\; \{\; (R_*, M_0, 0) \;:\; R_* \in \mathcal{R}_*\;\}.$$

Moreover, on one hand E_0 is unconditionally feasible, while, on the other hand, the coexistence equilibria in $\mathcal{E}_*$ are conditionally feasible, where $\#\mathcal{E}_* = \#\mathcal{R}_* \in \{0, 1, 2\}$. In particular, there are saddle-node bifurcations of the coexistence equilibrium as r, b, cM_0 and α vary.

Proof. We can rewrite the equation (7) moving the last term on the left to the right of the equal sign. Thus, $\#\mathcal{E}_* = \#\mathcal{R}_*$ is equal to the number of intersections in the first quadrant of the graphs of the two functions

$$y = \Gamma(R) = r - bR \qquad \text{and} \qquad y = \Lambda(R) = \frac{cM_0}{1 + R^{1-\alpha}}. \tag{8}$$

The first one is a straight line with a positive intercept and a negative angular coefficient. The second one is a nonlinear function that is strictly positive, decreasing and convex throughout its domain since, for all positive values of R, we have

$$\frac{\partial \Lambda}{\partial R} = -\frac{cM_0(1-\alpha)}{R^{\alpha}(1+R^{1-\alpha})^2} < 0,$$

and

$$\frac{\partial^2 \Lambda}{\partial R^2} = \frac{cM_0(1-\alpha)((2-\alpha)R^{1-\alpha}+\alpha)}{R^{1+\alpha}(1+R^{1-\alpha})^3} > 0.$$

Moreover, we can easily observe that Λ tends to zero as R increases, it satisfies $\Lambda(0) = cM_0 > 0$ and it is non-differentiable at $R = 0$ since its first derivative diverges negatively as R decreases.

Since the qualitative behavior of the two functions is known, we can conclude that when the intercept of Γ is greater than or equal to the height of the intersection point of Λ with the vertical axis, i.e., when

$$r \geq cM_0, \tag{9}$$

there exists a unique positive-coordinate intersection point of the graphs of Γ and Λ. Thus, the condition (9) is sufficient for the feasible coexistence of the native species and the migrant population. Otherwise, there may be two or none. In particular, we can say that there exists a value $\widetilde{r} \in (0, cM_0)$ such that, when $0 < r < \widetilde{r}$, we have no intersection between the graphs of the two functions of interest, when $r = \widetilde{r}$, we have two coincident positive-coordinate intersection points and, when $\widetilde{r} < r < cM_0$, we have two different ones. Consequently, there is a saddle-node bifurcation at $r = \widetilde{r}$ for the coexistence equilibrium. Bifurcations of this type can also be identified as the value of parameter b varies, fixing the graph of Λ and moving the straight line, or vice versa as cM_0 and α vary. Specifically, when cM_0 varies, the situation is analogous to what we have when r varies. In fact, there exists a threshold $\widetilde{cM_0} > r$ such that, if $cM_0 > \widetilde{cM_0}$, we have no positive intersections and, if $r < cM_0 < \widetilde{cM_0}$, we have two different positive intersections that coincide when $cM_0 = \widetilde{cM_0}$. As b varies, instead, if the condition (9) does not hold there is a saddle-node

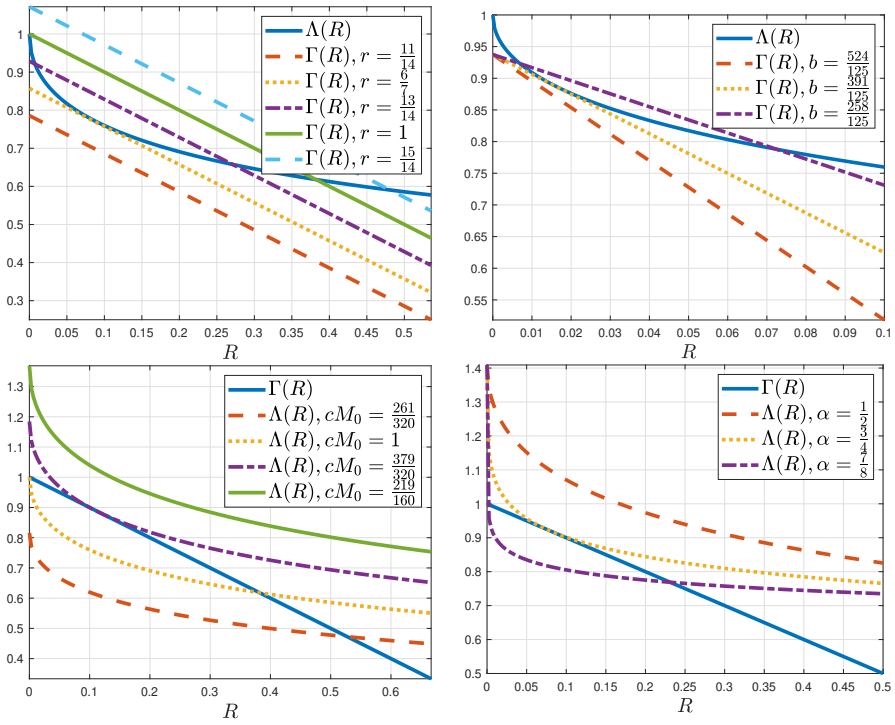


Figure 2: Different possible configurations of the functions $\Gamma(R)$ and $\Lambda(R)$ in (8). (Top-left): fixing $\Lambda(R)$ with $cM_0 = 1$ and $\alpha = 1/2$, we vary $\Gamma(R)$ with $b = 1$ and r as in the legend; (Top-right): fixing $\Lambda(R)$ with $cM_0 = 1$ and $\alpha = 1/2$, we vary $\Gamma(R)$ with $r = 15/16$ and b as in the legend; (Bottom-left): fixing $\Gamma(R)$ with $r = 1$ and $b = 1$, we vary $\Lambda(R)$ with $\alpha = 1/2$ and cM_0 as in the legend; (Bottom-right): fixing $\Gamma(R)$ with $r = 1$ and $b = 1$, we vary $\Lambda(R)$ with $cM_0 = 31/22$ and α as in the legend.

bifurcation at a threshold value $\widetilde{b}$. The coexistence equilibria are two different ones if $0 < b < \widetilde{b}$, they coincide if $b = \widetilde{b}$, and none exists if $b > \widetilde{b}$. Finally, as the value of the parameter α varies, there exists a value $\widehat{r} < cM_0$ such that there are no positive-coordinate intersection points if $0 < r \leq \widehat{r}$, while if $\widehat{r} < r < cM_0$ there is a saddle-node bifurcation for the coexistence equilibrium at a threshold $\widetilde{\alpha}$. Specifically, we have two different coexistence equilibria when $\alpha > \widetilde{\alpha}$, two coincident ones if $\alpha = \widetilde{\alpha}$, and there are none if $0 < \alpha < \widetilde{\alpha}$. Particular examples of all these different possibilities are depicted in Figure 2. □

Theorem 3.2. *Let $\widetilde{r} \in (0, cM_0]$ such that $\mathcal{R}_* = \emptyset$ for $r < \widetilde{r}$ and $\#\mathcal{R}_* \geq 1$ for*

$r \geq \widetilde{r}$. *Then,*

(a) the system (2) *presents a unique center in the plane* M*–*Y*;*

(b) E_0 *is "stable" if and only if* $r < cM_0$*;*

(c) for $r \geq \widetilde{r}$, $E_* = (R_*, M_0, 0) \in \mathcal{E}_*$ *is "stable" if and only if*

$$r \;<\; r^{\dagger} \;:=\; 2bR_* \;+\; \frac{cM_0(1+\alpha R_*^{1-\alpha})}{(1+R_*^{1-\alpha})^2}. \tag{10}$$

In particular,

1. *for* $0 < r^{\dagger} \leq \widetilde{r}$ *the feasibility condition,* $r \geq \widetilde{r}$*, and the "stability" condition* (10) *of* E_* *are never simultaneously verified;*
2. *for* $\widetilde{r} < r^{\dagger} \leq cM_0$*,*

$$\begin{cases} E_0 \text{ is the unique "stable" equilibrium,} & \text{if } r \in (0, \widetilde{r}) \cup \left[r^{\dagger}, cM_0\right], \\ \text{bistability of } E_0 \text{ and } E_*, & \text{if } r \in \left[\widetilde{r}, r^{\dagger}\right); \end{cases}$$

3. *for* $r^{\dagger} > cM_0$*,*

$$\begin{cases} E_0 \text{ is the unique "stable" equilibrium,} & \text{if } r \in (0, \widetilde{r}), \\ \text{bistability of } E_0 \text{ and } E_*, & \text{if } r \in [\widetilde{r}, cM_0), \\ E_* \text{ is the unique "stable" equilibrium,} & \text{if } r \in \left[cM_0, r^{\dagger}\right); \end{cases}$$

(d) if $\mathcal{R}_* = \{R_{\pm}\}$ *with* $0 < R_- < R_+$*, the "stable" equilibrium in* $\mathcal{E}_*$ *is the one associated to* R_+*.*

Proof. The Jacobian of (2) is

$$J = \begin{pmatrix} r - 2bR - cM\frac{\partial \Phi}{\partial R} & -c\Phi & 0 \\ 0 & 0 & 1 \\ 0 & -\omega^2 & 0 \end{pmatrix}.$$

The structure of J implies that in the $M - Y$ subspace the system behaves as a center, as expected. In particular, the matrix has two conjugate pure imaginary eigenvalues, $\pm i\omega$. Thus, we have neutral oscillations of the migrating

population M, that, in turn, also affect the residential population R, unless this one vanishes.

The "stability" of the equilibrium points, whereby the trajectories in the three-dimensional phase space approach those relative to the center in the $M-Y$ subspace and the system settles there on persistent neutrally stable oscillations, depends on the remaining eigenvalue of the matrix, namely $J_{1,1}$. Since

$$J_{1,1}(E_0) = r - cM_0 \qquad \text{and} \qquad J_{1,1}(E_*) = r - 2bR_* - \frac{cM_0(1+\alpha R_*^{1-\alpha})}{(1+R_*^{1-\alpha})^2}\,,$$

the "stability" condition for E_0 is

$$r < cM_0\,, \tag{11}$$

while for E_* we have (10).

In general, when the condition (11) is satisfied E_0 is feasible and "stable", since this equilibrium is unconditionally feasible. For coexistence, we remember that $0 < \widetilde{r} < cM_0$. Depending on the position of $r^\dagger$ with respect to $\widetilde{r}$ and cM_0 considered below, we have different possibilities. Let us focus on the following four options for $r^\dagger$. Refer to [32] and [33] for the definition of the basin stability value $S_B(A)$ of an attractor A. In this case, the attractors are closed orbits. We therefore use $A \in \{E_0, E_*\}$ to refer to the attractive closed orbits that have the point A as their center.

1. If $0 < r^\dagger \leq \widetilde{r}$ there are no intervals of r in which the feasibility condition, $r \geq \widetilde{r}$, and the "stability" condition (10) of E_* are simultaneously verified. In particular, when the condition (11) holds, we have $S_B(E_0) = 1$ and $S_B(E_*) = 0$.
2. If $\widetilde{r} < r^\dagger \leq cM_0$ the coexistence is feasible and "stable" when $\widetilde{r} \leq r < r^\dagger$. Thus, when $0 < r < \widetilde{r}$ or when $r^\dagger \leq r < cM_0$, we have $S_B(E_0) = 1$ and $S_B(E_*) = 0$, while when $\widetilde{r} \leq r < r^\dagger$, we have $S_B(E_0) \neq 0$ and $S_B(E_*) \neq 0$, such that $S_B(E_0) + S_B(E_*) = 1$. In the latter situation, there is bistability of the closed orbits around both E_0 and E_*.
3. If $r^\dagger > cM_0$ we have the same interval for r of the previous two points in which the closed orbits around E_* are feasible and stable. In this case,

when $0 < r < \widetilde{r}$, we have $S_B(E_0) = 1$ and $S_B(E_*) = 0$; when $\widetilde{r} \leq r < cM_0$, $S_B(E_0) \neq 0$ and $S_B(E_*) \neq 0$, such that $S_B(E_0) + S_B(E_*) = 1$, thus bistability of the closed orbits around both E_0 and E_*; finally, when $cM_0 \leq r < r^\dagger$, $S_B(E_0) = 0$ and $S_B(E_*) = 1$.

Lastly, we observe that bistability of E_0 and E_* and (d) can be obtained by a simple graphical proof, see Figure 3. □

Remark. Note that at the equilibrium E_0, the residential population is wiped out while M_0 represents the average number of migrants that are in the territory at every time, that feed and reproduce elsewhere.

In all cases where the system converges towards the center E_0, the migrants keep on periodically ravaging the territorial boundary and lead to the extinction of the native population. On the other hand, if the system evolves toward the closed trajectories around the point E_*, see Figure 4, it means that the original population is not completely eliminated, although the migrants do harm it. Thus, in any case, these migratory interactions on the border cause a negative consequences for the native species.

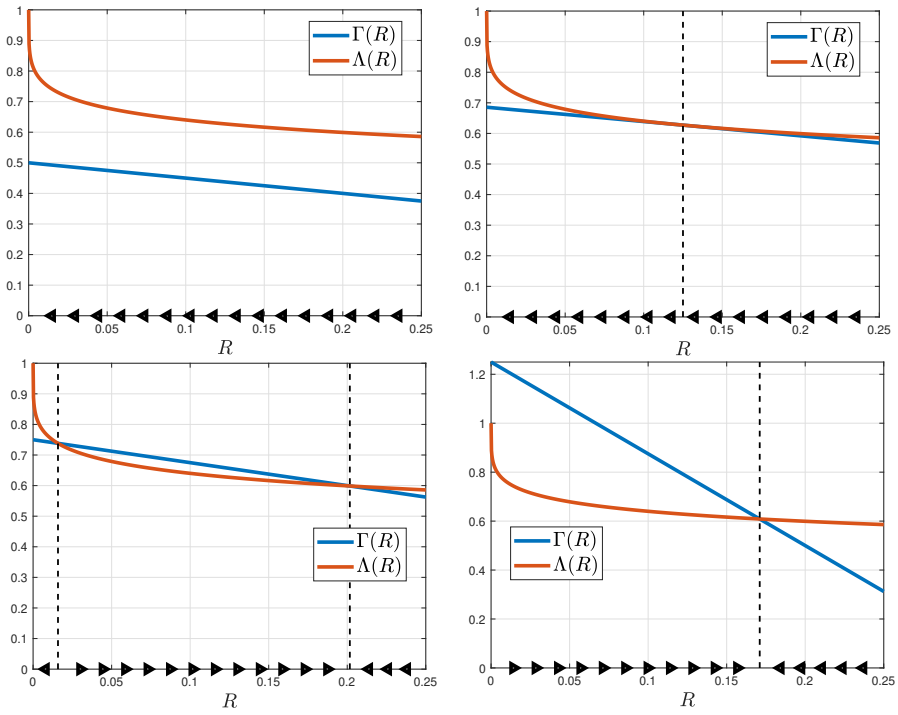


Figure 3: Different possible configurations of the functions $\Gamma(R)$ and $\Lambda(R)$ in (8) and "stability" of the arising equilibria. (Top-left): no intersection – 0 is the only "stable" equilibrium point; (Top-right): tangency – the value of R at which tangency occurs is "semistable" on the right and unstable on the left; (Bottom-left): two intersections – denoted by $R_- < R_+$ the two solutions of (7), we have that 0 and R_+ are both "stable" and R_- is a saddle; (Bottom-right): one intersection – the unique solution of (7) is the only "stable" equilibrium point.

4. Predation model analysis

The equilibria of the predation model (3) coincide with those of the interference model since the first and second equilibrium equations are the same and the third one can be easily reduced to $M = M_0$ using the first two.

Theorem 4.1. *The set of equilibria of* (3) *is*

$$\widetilde{\mathcal{E}} \;:=\; \{\, \widetilde{E}_0 := E_0 \,\} \,\cup\, \widetilde{\mathcal{E}}_*, \qquad \textit{where} \qquad \widetilde{\mathcal{E}}_* \;:=\; \mathcal{E}_*.$$

Moreover, on one hand, $\widetilde{E}_0$ is unconditionally feasible, while, on the other one, the coexistence equilibria in $\widetilde{\mathcal{E}}_*$ are conditionally feasible, where $\#\widetilde{\mathcal{E}}_* = \#\mathcal{R}_* \in \{0, 1, 2\}$. In particular, there are saddle-node bifurcations of the coexistence equilibrium as r, b, cM_0 and α vary.

Only the entries of the third row change in the Jacobian $\widetilde{J}$ of (3) with respect to the corresponding one of J. In particular, we find

$$\widetilde{J}_{3,1} = ecM\left(f_1\frac{\partial^2\Phi}{\partial R^2} + \frac{\partial f_1}{\partial R}\frac{\partial\Phi}{\partial R}\right) + ecY\frac{\partial\Phi}{\partial R},$$

$$\widetilde{J}_{3,2} = ec\frac{\partial\Phi}{\partial R}\left(f_1 + M\frac{\partial f_1}{\partial M}\right) - \omega^2, \qquad \widetilde{J}_{3,3} = ec\Phi - m.$$

To discuss the stability of $\widetilde{E}_0$, evaluating $\widetilde{J}$ at $\widetilde{E}_0$, we get

$$\widetilde{J}(\widetilde{E}_0) = \begin{pmatrix} r - cM_0 & 0 & 0 \\ 0 & 0 & 1 \\ ecM_0(r - cM_0) & -\omega^2 & -m \end{pmatrix}.$$

The eigenvalues of this matrix are the first diagonal element and

$$\lambda_\pm = \frac{-m \pm \sqrt{m^2 - 4\omega^2}}{2}.$$

Consequently, we do not have a center in the $M - Y$ subspace, but we have again the stability condition (11). Specifically, the equilibrium point $\widetilde{E}_0$ is a stable node in the $M - Y$ subspace if

$$2\omega < m,$$

otherwise, it is a stable focus.

In contrast, the Jacobian evaluated at $\widetilde{E}_* \in \widetilde{\mathcal{E}}_*$ is

$$\widetilde{J}(\widetilde{E}_*) = \begin{pmatrix} r - r^\dagger & -\frac{cR_*}{1+R_*^{1-\alpha}} & 0 \\ 0 & 0 & 1 \\ e(r-r^\dagger)(r^\dagger - 2bR_*) & -\frac{ecR_*(r^\dagger - 2bR_*)}{1+R_*^{1-\alpha}} - \omega^2 & \frac{ecR_*}{1+R_*^{1-\alpha}} - m \end{pmatrix}.$$

Thus, the coexistence stability is given by the Routh-Hurwitz conditions

$$\mathrm{tr}\left(\widetilde{J}(\widetilde{E}_*)\right) < 0, \quad \det\left(\widetilde{J}(\widetilde{E}_*)\right) < 0, \quad \mathrm{tr}\left(\widetilde{J}(\widetilde{E}_*)\right)\widetilde{M}_2 < \det\left(\widetilde{J}(\widetilde{E}_*)\right). \tag{12}$$

The trace, the determinant and the sum of the two-order principal minors in (12) are respectively

$$\mathrm{tr}\left(\widetilde{J}(\widetilde{E}_*)\right) = r - r^\dagger + \frac{ecR_*}{1+R_*^{1-\alpha}} - m\,, \quad \det\left(\widetilde{J}(\widetilde{E}_*)\right) = \omega^2(r-r^\dagger)$$

and

$$\widetilde{M}_2 = r\left(\frac{ecR_*}{1+R_*^{1-\alpha}} - m\right) + mr^\dagger + \omega^2 - \frac{2bceR_*^2}{1+R_*^{1-\alpha}}.$$

Accordingly, we can rewrite (12) as

$$r < \min\left\{r^\dagger, r^\dagger - \frac{ecR_*}{1+R_*^{1-\alpha}} + m\right\}, \quad Ar^2 + Br + C < 0\,, \tag{13}$$

with

$$A = \frac{ecR_*}{1+R_*^{1-\alpha}} - m\,,$$

$$B = \left(\frac{ecR_*}{1+R_*^{1-\alpha}} - m\right)^2 - r^\dagger\left(\frac{ecR_*}{1+R_*^{1-\alpha}} - m\right) + mr^\dagger - \frac{2bceR_*^2}{1+R_*^{1-\alpha}}\,,$$

$$C = \left(-r^\dagger + \frac{ecR_*}{1+R_*^{1-\alpha}} - m\right)\left(mr^\dagger + \omega^2 - \frac{2bceR_*^2}{1+R_*^{1-\alpha}}\right) + \omega^2 r^\dagger\,.$$

Remark. Note that at the equilibrium $\widetilde{E}_0$, the residential population is wiped out while M_0 represents the average number of migrants that are in the territory at every time, that feed and reproduce elsewhere. Instead, at $\widetilde{E}_*$, both $R(t)$ and $M(t)$ are non-zero which means that the migrant population M settles in the territory.

Again, also in this second model, the equilibrium $\widetilde{E}_0$ is feasible and stable when the condition (11) is satisfied.

Remark. However, in contrast to the pure interference model, in this case, $\widetilde{E}_0$ is no longer a center, it rather becomes an attractor. Thus, this represents an invasion mechanism.

For coexistence we may have different possibilities. In particular, in the case where (13) yields in a condition of the form $r < r^{\ddagger}$, with

$$r^{\ddagger} = \min\left\{\bar{r}, r^{\dagger}, r^{\dagger} - \frac{ecR_*}{1+R_*^{1-\alpha}} + m\right\} > 0\,,$$

where $\bar{r}$ depends on the second condition in (13), the same considerations proposed at the end of Section 3 for the interference model are also valid here, with $r^{\ddagger}$ instead of $r^{\dagger}$, and, again, bistability of $\widetilde{E}_0$ and $\widetilde{E}_*$ can occur. Also in this case this entails negative consequences for the native species leading in some cases even to their extinction. However, the major finding is that the marginal contacts between the migrant and residential populations trigger a mechanism of biological invasion that leads to the settlement of the migrant predators.

5. Numerical simulations

The simulations here presented were obtained via the `ode23t` MATLAB routine (release 2023a) for moderately stiff problems. When not otherwise specified, the benchmark values for the parameters and the initial conditions used for the simulations are, respectively,

$$r = b = c = e = m = \omega = 1, \qquad \alpha = M_0 = 1/2, \tag{14}$$

and

$$\begin{bmatrix} R(0) \\ M(0) \\ Y(0) \end{bmatrix} \in \left\{ \mathbf{v}_1 := \begin{bmatrix} 1/2 \\ 1/4 \\ -1/4 \end{bmatrix}, \mathbf{v}_2 := \begin{bmatrix} 1/2 \\ 7/8 \\ 1/4 \end{bmatrix}, \mathbf{v}_3 := \begin{bmatrix} 1 \\ 3/4 \\ 0 \end{bmatrix} \right\}. \tag{15}$$

For the system (2), in view of (4), when $(M(0), Y(0)) \neq (M_0, 0)$, we have an explicitly oscillating behavior for the migrating population M that is transferred, via (2), to the residential population R, when it does not vanish. All trajectories tend to closed orbits around E_0 or E_* lying on the M–Y plane or a plane that passes through the coexistence equilibrium E_*. This is the case of Figure 4 where we also observe periodic orbits around a center in the M–Y plane. When R goes to extinction (see, e.g., Figure 5) the pattern on the M–Y plane is kept, but the system tends to periodic orbits on the plane $R = 0$.

If instead we eliminate the oscillations, choosing $(M(0), Y(0)) = (M_0, 0)$, and we vary, e.g., the parameters r and c, crossing the condition (9) the situation we obtain is depicted in Figure 6. In particular, we are in presence of transcritical bifurcations from E_0 to E_* and vice versa. Moreover, we observe that, while the inequality (9) changes at $r = 0.5$ and $c = 2$, respectively, the transcritical bifurcation occurs at a different parameter value depending on the initial conditions. R_- is always unstable: the orbit of R either goes to 0 or to R_+, depending on which of the two domains of attraction of these equilibria the initial conditions lie. On the other hand, there is a region in the parameter space where both $E_0 = (0, M_0, 0)$ and $E_* = (R_+, M_0, 0)$ are feasible and stable. This happens for instance in the cases depicted in Figure 7.

The basins of attraction and the basin stability values corresponding to the left and right panels of Figure 7 are shown in Figures 8 and 9, respectively. In Figures 8 and 9 the bistability has been explored using the MATLAB toolbox bSTAB, introduced in [41]. Refer to [32, 33, 41] for the basin stability value definition. In particular, in the squares $Q_1 = [0, 0.012] \times [0, 1]$ and $Q_2 = [0, 0.025] \times [0, 1]$, $n = 5000$ uniformly distributed initial conditions were considered. The two basin stability values obtained are $S_B(E_0) \simeq 0.297$ and $S_B(E_*) \simeq 0.703$, in the first case, and $S_B(E_0) \simeq 0.52$ and $S_B(E_*) \simeq 0.48$, in the second one. By increasing the side of the squares Q_1 and Q_2, $S_B(E_0)$ decreases and consequently $S_B(E_*)$ increases; the converse is obtained by decreasing the side of the two squares.

For the system (3) instead, the first observation arising from Figure 12–15 is that the added term to the equation for dY/dt dampens the oscillations of the migrating population M and, thus, also the oscillations of the residential population R. Moreover, we have the following behaviors for the projection $\widetilde{E}_p = (M_0, 0)$ of $\widetilde{E}_0$ (and $\widetilde{E}_*$ when it exists) in the M–Y plane:

(i) when $2\omega > m$ and $r > cM_0$, $\widetilde{E}_p$ is a stable focus (Figure 12);

(ii) when $2\omega > m$ and $r < cM_0$, $\widetilde{E}_p$ is a stable focus (Figure 13);

(iii) when $2\omega < m$ and $r > cM_0$, $\widetilde{E}_p$ is a stable node (Figure 14);

(iv) when $2\omega < m$ and $r < cM_0$, $\widetilde{E}_p$ is a stable node (Figure 15).

We recall though that $\widetilde{E}_0$ is a stable equilibrium for the whole system only when $r < cM_0$, and in this case the residential population R goes to extinction.

As far as bistability is concerned, using the same set of parameters (14) and the same initial conditions as for the previous model, we obtain the same exact results shown in Figure 6 and Figure 7. Thus, bistability can occur also in this case, where again both $\widetilde{E}_0$ and the equilibrium of $\widetilde{\mathcal{E}}_*$ associated to R_+ are involved. However, the basins of attraction are different, as we can see in Figures 10 and 11. Again, we consider $n = 5000$ uniformly distributed initial conditions in the squares Q_1 and Q_2. The basin stability values are $S_B(\widetilde{E}_0) \simeq 0.327$ and

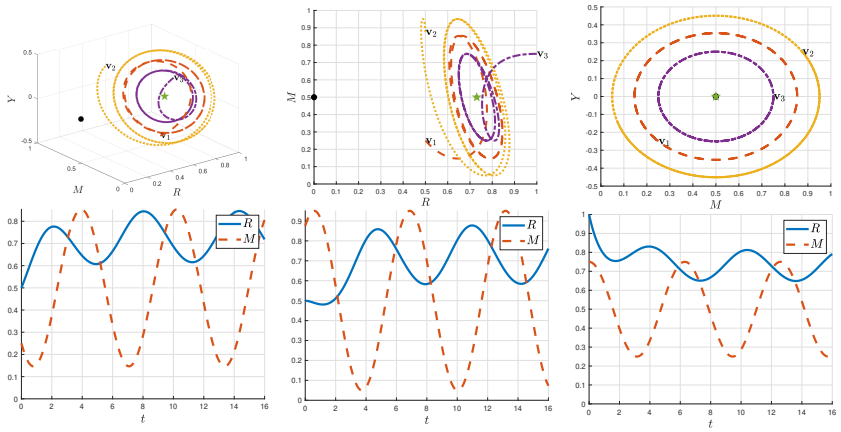


Figure 4: Orbits (top) and temporal series (bottom) of the system (2) with parameters given by (14) and initial values (15). The equilibria $E_0 = (0, M_0, 0)$ and $E_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, E_0 is unstable, E_* is a center and all orbits are pushed towards a plane passing through E_*.

$S_B(\widetilde{E}_*) \simeq 0.673$, in the first case, and $S_B(\widetilde{E}_0) \simeq 0.563$ and $S_B(\widetilde{E}_*) \simeq 0.437$, in the second one.

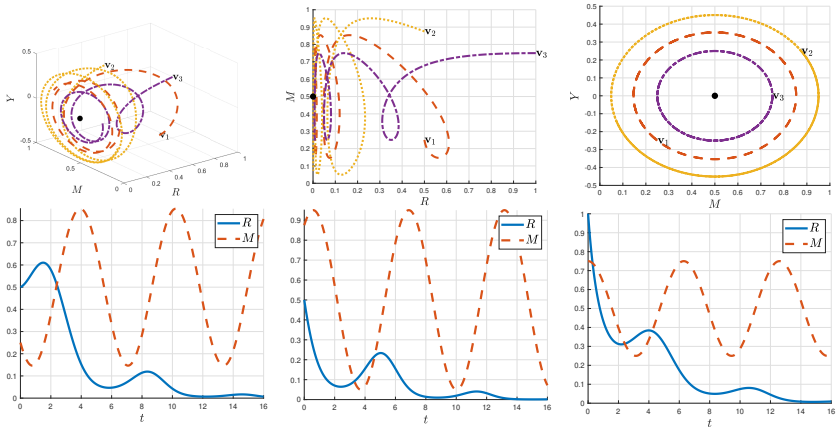


Figure 5: Orbits (top) and temporal series (bottom) of the system (2) with parameters given by (14), but $c = 3$, and initial values (15). The unique equilibrium $E_0 = (0, M_0, 0)$ is shown with a black dot. It is a center, where all the orbits are pushed towards the plane $R = 0$.

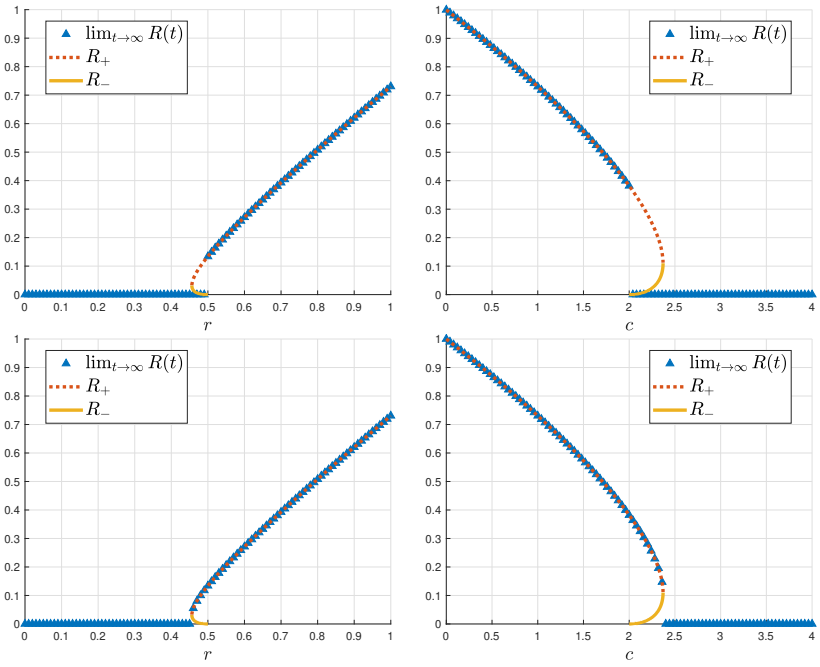


Figure 6: Values of $\lim_{t\to\infty} R(t)$ for (2) with parameters (14) for specific non-oscillating orbits compared with the (two) solution(s) $R_\pm$ of (7), where (Top) the initial value is $(10^{-4}, M_0, 0)$, (Bottom) the initial value is $(1, M_0, 0)$, (Left) r varies uniformly in $[0, 1]$, (Right) c varies uniformly in $[0, 4]$. Comparing the values of $\lim_{t\to\infty} R(t)$, one observes that, varying only r, there exists $z_r \in (0.4, 0.5)$ such that, for $r \in (z_r, 0.5)$ there is bistability of 0 and R_+. Similarly, varying only c, there exists $z_c \in (2, 2.5)$ such that, for $c \in (2, z_c)$ there is bistability of 0 and R_+. The same result is obtained for model (3) using the same parameters and initial conditions and the corresponding figure is not shown.

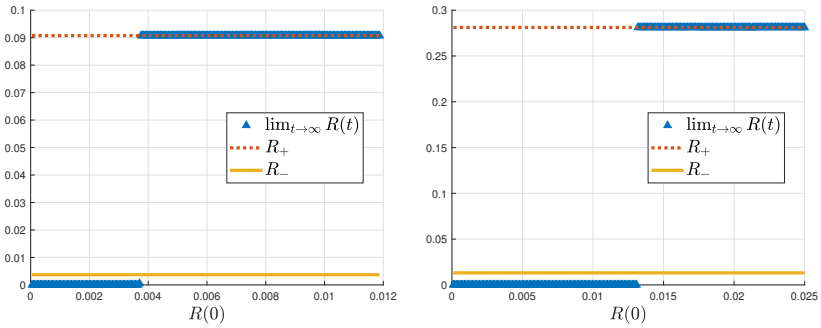


Figure 7: Bistability of 0 and R_+ for non-oscillating orbits of (2) with parameters (14), where (Left) $r = 0.475$ and $R(0)$ varies uniformly in $[0, 0.012]$ and (Right) $c = 2.2$ and $R(0)$ varies uniformly in $[0, 0.025]$. Note that the horizontal orange line represents the unstable manifold R_0. The same result is obtained for model (3) using the same parameters and initial conditions and the corresponding figure is not shown

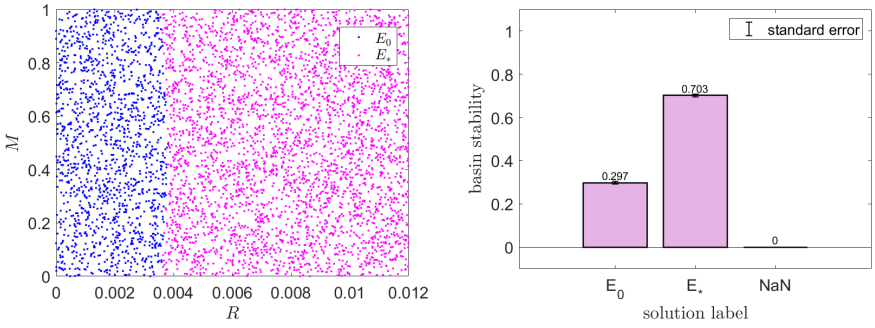


Figure 8: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the left panel of Figure 7 for model (2). The parameter values are given in (14), with $r = 0.475$. The initial conditions are $n = 5000$ uniformly distributed points in $Q_1 = [0, 0.012] \times [0, 1]$.

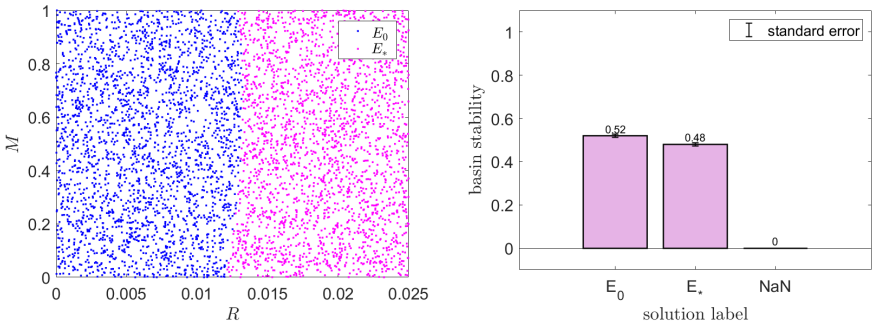


Figure 9: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the right panel of Figure 7 for model (2). The parameter values are given in (14), with $c = 2.2$. The initial conditions are $n = 5000$ uniformly distributed points in $Q_2 = [0, 0.025] \times [0, 1]$.

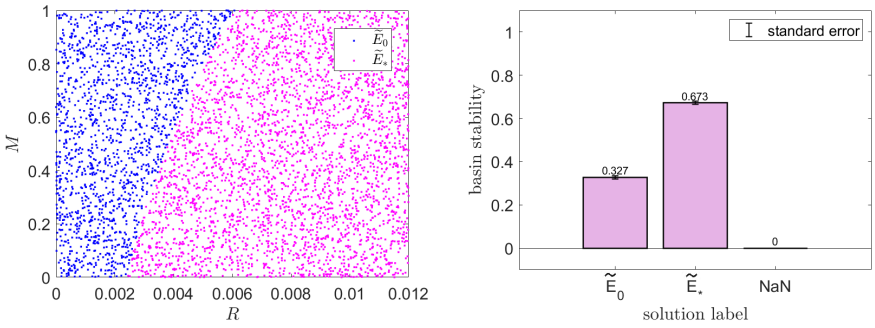


Figure 10: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the left panel of Figure 7 for model (3). The parameter values are given in (14), with $r = 0.475$. The initial conditions are $n = 5000$ uniformly distributed points in $Q_1 = [0, 0.012] \times [0, 1]$.

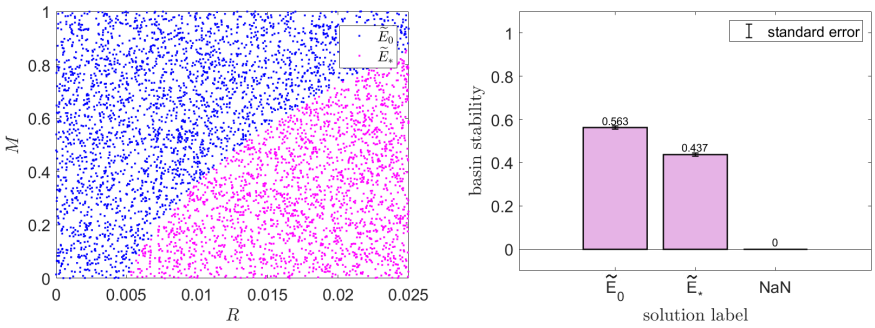


Figure 11: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the right panel of Figure 7 for model (3). The parameter values are given in (14), with $c = 2.2$. The initial conditions are $n = 5000$ uniformly distributed points in $Q_2 = [0, 0.025] \times [0, 1]$.

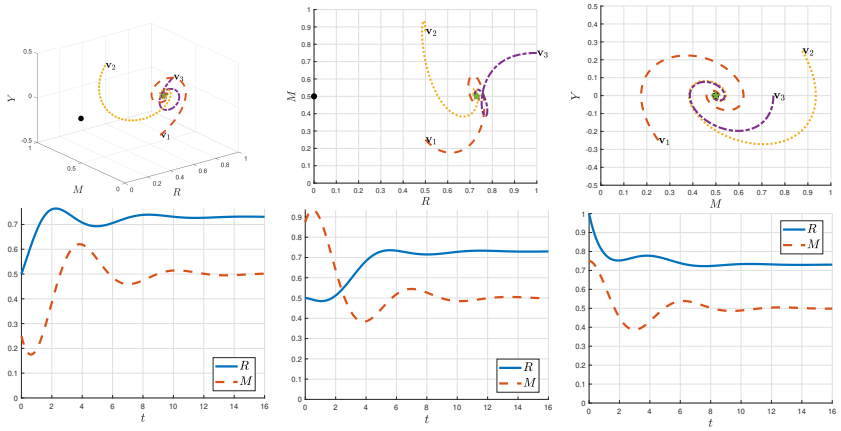


Figure 12: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14) and initial values (15). The equilibria $\widetilde{E}_0 = (0, M_0, 0)$ and $\widetilde{E}_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, $\widetilde{E}_0$ is unstable, while $\widetilde{E}_*$ is a stable focus. Here both populations survive, reaching the coexistence equilibrium via more and more dampened oscillations, i.e., with the population M invading the territory of population R and permanently settling in it.

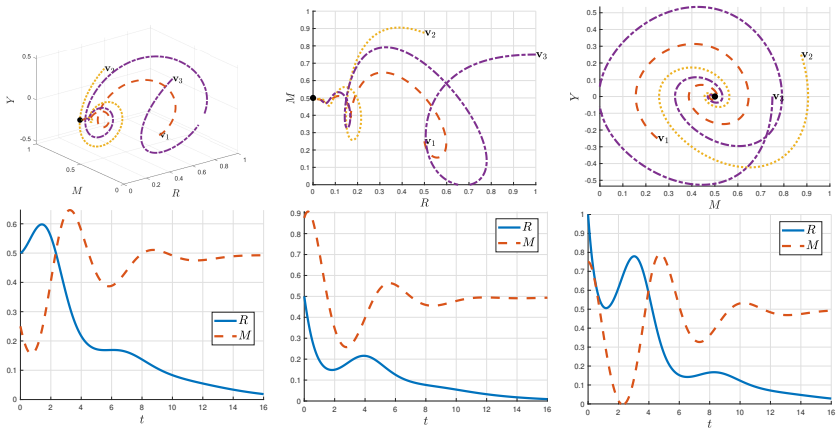


Figure 13: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but $c = 3$, and initial values (15). The unique equilibrium $\widetilde{E}_0 = (0, M_0, 0)$ is shown with a black dot and it is a stable focus. Here only the migrating population M survives, reaching a fixed limit via more and more dampened oscillations, i.e., invading the territory of population R and permanently settling in it.

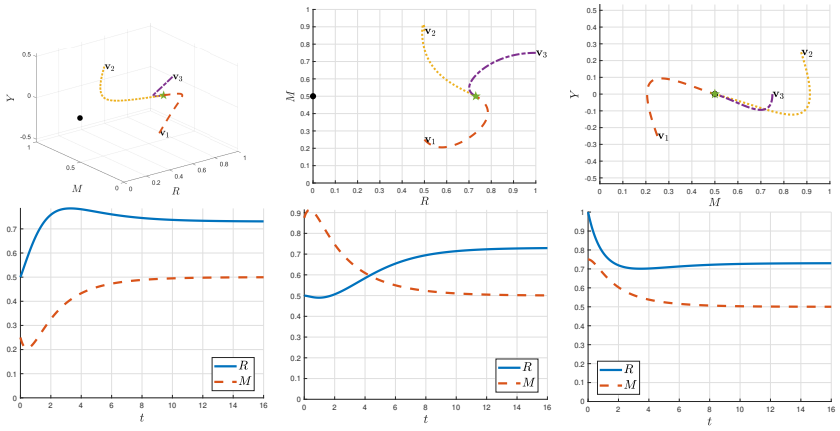


Figure 14: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but $m = 3$, and initial values (15). The equilibria $\widetilde{E}_0 = (0, M_0, 0)$ and $\widetilde{E}_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, $\widetilde{E}_0$ is unstable, while $\widetilde{E}_*$ is a stable node. Here both the resident and the migrating populations survive, reaching the coexistence equilibrium without oscillations, i.e., with the population M invading the territory of population R and permanently settling in it.

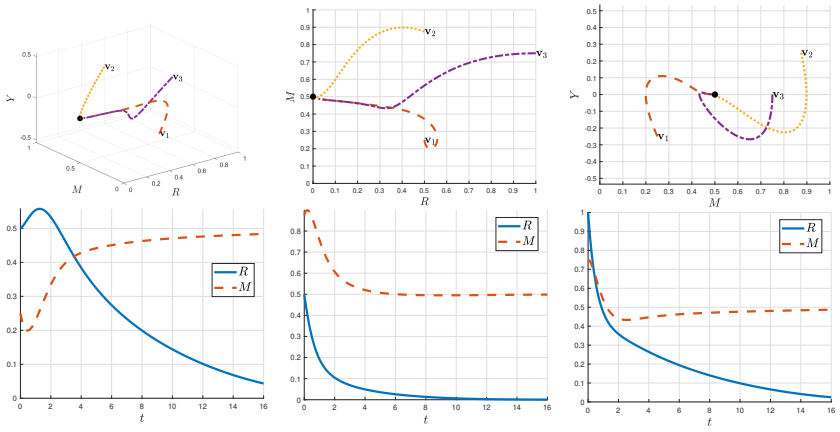


Figure 15: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but $c = m = 3$, and initial values (15). The unique equilibrium $\widetilde{E}_0 = (0, M_0, 0)$ is shown with a black dot and it is a stable node. Here only the migrating population M survives, reaching the equilibrium without oscillations, i.e., invading and permanently settling in the territory of the population R, wiping the prey out and replacing it.

6. Conclusion

Migrations of animal populations in search of better living conditions are a fact in nature [4]. In particular, it is well known that numerous bird species travel long distances among continents to settle during the good season in the favorable landing nesting places [28]. This is by no means restricted to flying animals, as in the aquatic medium, it is well known that during the reproducing season eels travel also across oceans [38], and salmons swim upstream even overcoming natural obstacles such as waterfalls [43].

The models considered in this paper are general enough to account for such situations, although the main focus is on terrestrial habitats. In the systems' formulation, this is possible by the use of a very general expression for the shape of the territory touched but not traversed by the migrants. Assuming that in this habitat a residential population thrives, the shape of their territorial boundary is expressed by the fractional parameter α that precisely takes into account its complexity. The migrants are supposed to travel just along this boundary, not really disturbing the interior of the residential population habitat.

The two models presented here share the fact that a migrant species touches the boundary of a certain territory where a native species thrives. The migrant is assumed to exhibit demographic features only in places other than this territory and not explicitly modeled. Hence in the first model the interaction with the native species is of disruptive nature causing damages to the autochtonous population with no gain for the migrant. In the second model instead, we assume that the residential population represents a prey for the migrant, which takes advantages from this situation and possibly settles into the environment, exhibiting a local demography. The residential population still suffers from the interaction.

The two models have the same equilibria, E_0 and $\mathcal{E}_*$. However, in the first model these points are centers while in the second one they became attractors. This is an important difference because in the first model the migrants do not find a favorable settling environment and continue to migrate back and forth and

in so doing damaging the environment. In the second case they discover that the native population is a palatable prey and hence they invade the territory by permanently settling into it.

Both models exhibit bistability features that are mathematically interesting. However, the main focus of the paper is to provide an interpretation of the invasion mechanism which occurs if the migrant touching only (but not crossing) an environment finds a suitable prey, which is the case in model (3) and not in the disruption model (2). Clearly, the outcome in bistable scenarios depends on the initial condition. But the equilibria that are attained are either the point in which the migrants thrive by wiping out the prey or alternatively the point in which the two populations coexist. In both scenarios, the migrating predators still have external resources to survive. In any case, the important result is that they invade the territory.

The idea of a migrant crossing an ecosystem has been presented in [1] but it is very different from what it is being discussed here. Indeed in [1] the migrants are not limited to marginal contact but interfere with the whole residential ecosystem, composed by a predator-prey system. In [1] we consider also a model for pure interference and another one with the migrant being superpredator of both native species. The possible equilibria in [1] are more numerous because each one of the two native species could be wiped out. However, the main point is that coexistence is a center or an attractor exactly as in the model proposed here. This means that the migrants settle in a favorable environment when they cross it. The results of this investigation show instead that it is not necessary that the migrants cross the environment but even a marginal contact would lead to an invasion in suitable circumstances.

In other recent papers such as [15, 52] a probabilistic mechanism for the formation of the Holling type II functional response is described. But no migrating species appear, thus the models cannot be really compared. Since we consider migrations touching only the border of the territory of the native species, the scenarios of [1] and of the model presented here are more general. The difference distinguishing the model in [1] and [15, 52] is once more given by the fact that

the superpredator exhibits a periodic dynamics since it is a migrant.

In a similar recent investigation where instead the interference occurs within the resident territory, [1], we discovered that when the migrant predators find favorable conditions, they settle in the environment traversed in their journey. Our goal here is to understand if the same can occur when the population intermingling is limited only to a marginal area, the perimeter of the residential species habitat. We find that indeed this is the case. Our major finding is that even a minor predatory interaction may induce the migrants to invade and colonize the so-found new territory. Although the model has been intentionally kept at a minimal level, to highlight the basic mechanisms underlying this phenomenon, in our opinion, this may give another clue on the phenomenon of exotic species that find good harboring conditions at temperate latitudes. Their settling into regions in which they are not native has negative consequences on the autochthonous species, putting them at threat of extinction, perhaps also with the importation of diseases against which the indigenous populations are defenseless. Some current examples are the grey squirrels invasions in Italy and Great Britain, where in the last case also they carry a lethal virus for the European red squirrels [7, 44, 46, 54]. Also, the cottontails originating in America settling in Italy, possibly carrying the EBHS (European Brown Hares Syndrome) virus are causing a hyperpredation of foxes on the resident hares [13, 16, 17]. These examples do not fall within the present analysis, but are just reported to highlight the possible very negative consequences of these invasions. Thus, as a final word, our results indicate that, if possible, it is best to prevent even the slightest possibility of populations intermingling when the migratory species could represent a threat for the native one.

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