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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? / Acotto, Francesca; Venturino, Ezio; Viscardi, Alberto. - In: CHAOS, SOLITONS AND FRACTALS. - ISSN 0960-0779. - ELETTRONICO. - 184:(2024), pp. 1-13. [10.1016/j.chaos.2024.115050]

Availability:

This version is available at: 11583/2989333 since: 2024-06-05T09:43:20Z

Publisher:

Elsevier

Published

DOI:10.1016/j.chaos.2024.115050

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(Article begins on next page)

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

1 Funding

2 The research work has been partially supported by the project “Approxima-
3 tion Methods and Models for the Life Sciences” of the Department of Mathe-
4 matics “Giuseppe Peano” of the University of Turin.

5 1. Introduction

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

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

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

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

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

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

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

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

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

87 **2. Two models for marginal contact between periodic migrants and** 88 **residential population**

89 *2.1. Interference model*

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

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

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

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

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

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

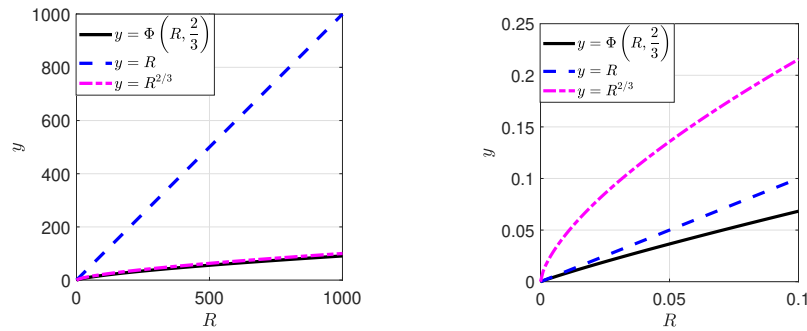


Figure 1: The graph of $\Phi(R, \frac{2}{3})$ (black solid line) is compared with the two-thirds root (magenta dash-dotted line) and the bisectrix of the first and third quadrants (blue dashed line). On the left we consider a large domain: we observe that $\Phi(R, \frac{2}{3})$ behaves as $R^{2/3}$ for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

120 We distinguish two scenarios. At first, we disregard any possible vital dy-
 121 namics for the migrants and we focus on the interference damages to the native
 122 species, neglecting possible benefits for the former population. Secondly, we con-
 123 sider also vital dynamics for the migrants and their benefit gained by feeding
 124 on the native species, without other internal resources.

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

126 [15, 52]. In these research works classical functional responses such as Holling
 127 type II (HTII) or the Beddington-DeAngelis functional form are considered
 128 to model the population interactions in their own domain. Here however we
 129 consider instead an interaction limited to the boundary of the domain. For
 130 the migrating population, no reproduction is considered because it occurs on a
 131 longer timescale than the one needed for the interference mechanism. Also, we
 132 can assume that it occurs elsewhere, in suitable reproduction sites.

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

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

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

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

138 Here r denotes the prey reproduction rate, b is the intraspecific competition
 139 of the prey and c represents the ravaging rate. Further, as mentioned before,
 140 $\frac{1}{2} \leq \alpha < 1$ is the shape index of the native species territory.

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

146 2.2. Predation model

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

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

154 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

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

155 Therefore, the model for the second scenario is

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

156 with

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

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

160 **3. Interference model analysis**

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

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

163 and

$$Y(t) = Y(0) \cos(\omega t) - \omega (M(0) - M_0) \sin(\omega t). \quad (5)$$

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

166 **Proposition 3.1.** *Let $(R(0), M(0), Y(0)) \in \mathbb{R}_{\geq 0}^2 \times \mathbb{R}$ the initial condition of (2).*

167 *Then, the corresponding solution $(R(t), M(t), Y(t))$ is bounded and contained in*
 168 *$\mathbb{R}_{\geq 0}^2 \times \mathbb{R}$ if and only if*

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

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

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

170 and

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

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

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

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

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

174 with

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

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

176 As for $R(t)$, when $R(t) > r/b$ and (6) holds, $M(t) \geq 0$ and $R'(t) < 0$, thus,
 177 $\lim_{t \rightarrow +\infty} R(t) < +\infty$. Moreover, if there exists $t_* \in \mathbb{R}$ such that $R(t_*) = 0$,
 178 then $R'(t_*) = 0$ and

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

179 which means that t_* is a local minimum for $R(t)$. Therefore, since $R(0) \geq 0$,
 180 $R(t)$ is bounded from below by 0. \square

181 The equilibrium points of the interference model (2) must have $Y = 0$ and
 182 $M = M_0$ to satisfy the last two equilibrium equations, respectively. Further,
 183 from the first equilibrium equation we have either $R = 0$ or

$$r - bR - \frac{cM_0}{1 + R^{1-\alpha}} = 0. \quad (7)$$

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

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

186 where

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

187 Moreover, on one hand E_0 is unconditionally feasible, while, on the other hand,
 188 the coexistence equilibria in \mathcal{E}_* are conditionally feasible, where $\#\mathcal{E}_* = \#\mathcal{R}_* \in$
 189 $\{0, 1, 2\}$. In particular, there are saddle-node bifurcations of the coexistence
 190 equilibrium as r , b , cM_0 and α vary.

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

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

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

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

198 and

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

199 Moreover, we can easily observe that Λ tends to zero as R increases, it satisfies
 200 $\Lambda(0) = cM_0 > 0$ and it is non-differentiable at $R = 0$ since its first derivative
 201 diverges negatively as R decreases.

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

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

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

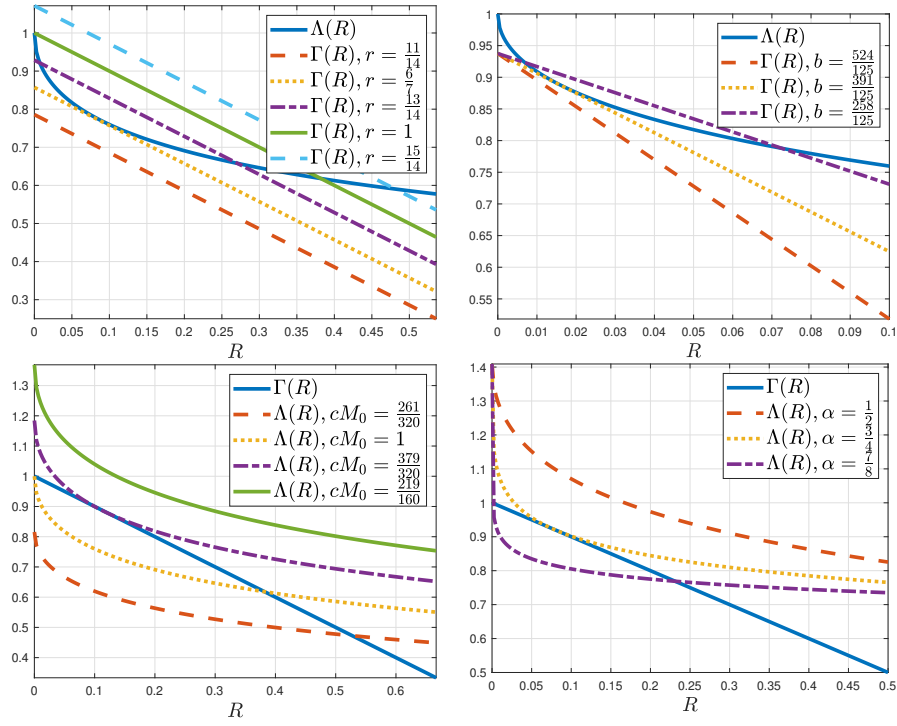


Figure 2: Different possible configurations of the functions $\Gamma(R)$ and $\Lambda(R)$ in (8). (Top-left): fixing $\Lambda(R)$ with $cM_0 = 1$ and $\alpha = 1/2$, we vary $\Gamma(R)$ with $b = 1$ and r as in the legend; (Top-right): fixing $\Lambda(R)$ with $cM_0 = 1$ and $\alpha = 1/2$, we vary $\Gamma(R)$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

220 bifurcation at a threshold value \tilde{b} . The coexistence equilibria are two different
 221 ones if $0 < b < \tilde{b}$, they coincide if $b = \tilde{b}$, and none exists if $b > \tilde{b}$. Finally, as the
 222 value of the parameter α varies, there exists a value $\hat{r} < cM_0$ such that there
 223 are no positive-coordinate intersection points if $0 < r \leq \hat{r}$, while if $\hat{r} < r < cM_0$
 224 there is a saddle-node bifurcation for the coexistence equilibrium at a threshold
 225 $\tilde{\alpha}$. Specifically, we have two different coexistence equilibria when $\alpha > \tilde{\alpha}$, two
 226 coincident ones if $\alpha = \tilde{\alpha}$, and there are none if $0 < \alpha < \tilde{\alpha}$. Particular examples
 227 of all these different possibilities are depicted in Figure 2. \square

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

229 $r \geq \tilde{r}$. Then,

230 (a) the system (2) presents a unique center in the plane M - Y ;

231 (b) E_0 is “stable” if and only if $r < cM_0$;

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

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

233 In particular,

234 1. for $0 < r^\dagger \leq \tilde{r}$ the feasibility condition, $r \geq \tilde{r}$, and the “stability”
235 condition (10) of E_* are never simultaneously verified;

236 2. for $\tilde{r} < r^\dagger \leq cM_0$,

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

237 3. for $r^\dagger > cM_0$,

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

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

240 *Proof.* The Jacobian of (2) is

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

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

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

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

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

250 the “stability” condition for E_0 is

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

251 while for E_* we have (10).

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

- 260 1. If $0 < r^\dagger \leq \tilde{r}$ there are no intervals of r in which the feasibility condition,
 261 $r \geq \tilde{r}$, and the “stability” condition (10) of E_* are simultaneously verified.
 262 In particular, when the condition (11) holds, we have $S_B(E_0) = 1$ and
 263 $S_B(E_*) = 0$.
- 264 2. If $\tilde{r} < r^\dagger \leq cM_0$ the coexistence is feasible and “stable” when $\tilde{r} \leq r < r^\dagger$.
 265 Thus, when $0 < r < \tilde{r}$ or when $r^\dagger \leq r < cM_0$, we have $S_B(E_0) = 1$ and
 266 $S_B(E_*) = 0$, while when $\tilde{r} \leq r < r^\dagger$, we have $S_B(E_0) \neq 0$ and $S_B(E_*) \neq 0$,
 267 such that $S_B(E_0) + S_B(E_*) = 1$. In the latter situation, there is bistability
 268 of the closed orbits around both E_0 and E_* .
- 269 3. If $r^\dagger > cM_0$ we have the same interval for r of the previous two points in
 270 which the closed orbits around E_* are feasible and stable. In this case,

271 when $0 < r < \tilde{r}$, we have $S_B(E_0) = 1$ and $S_B(E_*) = 0$; when $\tilde{r} \leq r <$
272 cM_0 , $S_B(E_0) \neq 0$ and $S_B(E_*) \neq 0$, such that $S_B(E_0) + S_B(E_*) = 1$,
273 thus bistability of the closed orbits around both E_0 and E_* ; finally, when
274 $cM_0 \leq r < r^\dagger$, $S_B(E_0) = 0$ and $S_B(E_*) = 1$.

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

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

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

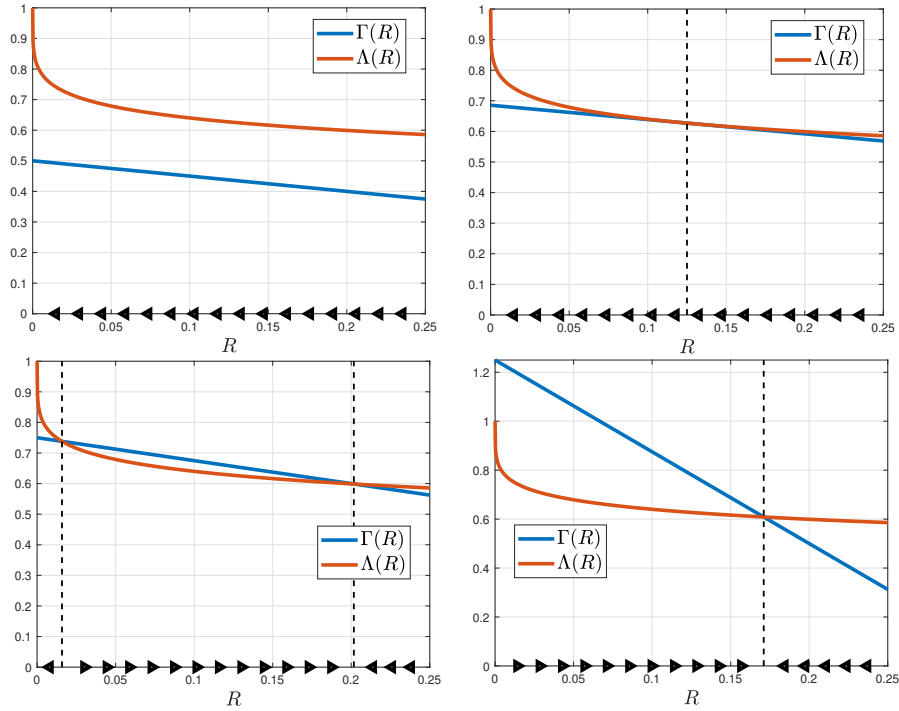


Figure 3: Different possible configurations of the functions $\Gamma(R)$ and $\Lambda(R)$ in (8) and “stability” of the arising equilibria. (Top-left): no intersection – 0 is the only “stable” equilibrium point; (Top-right): tangency – the value of R at which tangency occurs is “semistable” on the right 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.

287 **4. Predation model analysis**

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

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

$$\tilde{\mathcal{E}} := \{ \tilde{E}_0 := E_0 \} \cup \tilde{\mathcal{E}}_*, \quad \text{where} \quad \tilde{\mathcal{E}}_* := \mathcal{E}_*.$$

292 Moreover, on one hand, \tilde{E}_0 is unconditionally feasible, while, on the other one,
 293 the coexistence equilibria in $\tilde{\mathcal{E}}_*$ are conditionally feasible, where $\#\tilde{\mathcal{E}}_* = \#\mathcal{R}_* \in$
 294 $\{0, 1, 2\}$. In particular, there are saddle-node bifurcations of the coexistence
 295 equilibrium as r , b , cM_0 and α vary.

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

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

298

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

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

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

The eigenvalues of this matrix are the first diagonal element and

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

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

$$2\omega < m,$$

303 otherwise, it is a stable focus.

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

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

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

$$\text{tr}(\tilde{J}(\tilde{E}_*)) < 0, \quad \det(\tilde{J}(\tilde{E}_*)) < 0, \quad \text{tr}(\tilde{J}(\tilde{E}_*))\tilde{M}_2 < \det(\tilde{J}(\tilde{E}_*)). \quad (12)$$

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

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

308 and

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

309 Accordingly, we can rewrite (12) as

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

310 with

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

$$311 \quad B = \left(\frac{ecR_*}{1 + R_*^{1-\alpha}} - m \right)^2 - r^\dagger \left(\frac{ecR_*}{1 + R_*^{1-\alpha}} - m \right) + mr^\dagger - \frac{2bceR_*^2}{1 + R_*^{1-\alpha}},$$

$$312 \quad C = \left(-r^\dagger + \frac{ecR_*}{1 + R_*^{1-\alpha}} - m \right) \left(mr^\dagger + \omega^2 - \frac{2bceR_*^2}{1 + R_*^{1-\alpha}} \right) + \omega^2 r^\dagger.$$

313 *Remark.* Note that at the equilibrium \tilde{E}_0 , the residential population is wiped
314 out while M_0 represents the average number of migrants that are in the territory
315 at every time, that feed and reproduce elsewhere. Instead, at \tilde{E}_* , both $R(t)$ and
316 $M(t)$ are non-zero which means that the migrant population M settles in the
317 territory.

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

320 *Remark.* However, in contrast to the pure interference model, in this case, \tilde{E}_0
 321 is no longer a center, it rather becomes an attractor. Thus, this represents an
 322 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

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

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

330 **5. Numerical simulations**

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

$$r = b = c = e = m = \omega = 1, \quad \alpha = M_0 = 1/2, \quad (14)$$

335 and

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

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

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

355 The basins of attraction and the basin stability values corresponding to
 356 the left and right panels of Figure 7 are shown in Figures 8 and 9, respec-
 357 tively. In Figures 8 and 9 the bistability has been explored using the MATLAB
 358 toolbox bSTAB, introduced in [41]. Refer to [32, 33, 41] for the basin stabil-
 359 ity value definition. In particular, in the squares $Q_1 = [0, 0.012] \times [0, 1]$ and
 360 $Q_2 = [0, 0.025] \times [0, 1]$, $n = 5000$ uniformly distributed initial conditions were
 361 considered. The two basin stability values obtained are $S_B(E_0) \simeq 0.297$ and
 362 $S_B(E_*) \simeq 0.703$, in the first case, and $S_B(E_0) \simeq 0.52$ and $S_B(E_*) \simeq 0.48$, in the
 363 second one. By increasing the side of the squares Q_1 and Q_2 , $S_B(E_0)$ decreases
 364 and consequently $S_B(E_*)$ increases; the converse is obtained by decreasing the
 365 side of the two squares.

366 For the system (3) instead, the first observation arising from Figure 12–15
 367 is that the added term to the equation for dY/dt dampens the oscillations of
 368 the migrating population M and, thus, also the oscillations of the residential
 369 population R . Moreover, we have the following behaviors for the projection
 370 $\tilde{E}_p = (M_0, 0)$ of \tilde{E}_0 (and \tilde{E}_* when it exists) in the M – Y plane:

- 371 (i) when $2\omega > m$ and $r > cM_0$, \tilde{E}_p is a stable focus (Figure 12);
- 372 (ii) when $2\omega > m$ and $r < cM_0$, \tilde{E}_p is a stable focus (Figure 13);
- 373 (iii) when $2\omega < m$ and $r > cM_0$, \tilde{E}_p is a stable node (Figure 14);
- 374 (iv) when $2\omega < m$ and $r < cM_0$, \tilde{E}_p is a stable node (Figure 15).

375 We recall though that \tilde{E}_0 is a stable equilibrium for the whole system only when
 376 $r < cM_0$, and in this case the residential population R goes to extinction.

377 As far as bistability is concerned, using the same set of parameters (14) and
 378 the same initial conditions as for the previous model, we obtain the same exact
 379 results shown in Figure 6 and Figure 7. Thus, bistability can occur also in
 380 this case, where again both \tilde{E}_0 and the equilibrium of $\tilde{\mathcal{E}}_*$ associated to R_+ are
 381 involved. However, the basins of attraction are different, as we can see in Figures
 382 10 and 11. Again, we consider $n = 5000$ uniformly distributed initial conditions
 383 in the squares Q_1 and Q_2 . The basin stability values are $S_B(\tilde{E}_0) \simeq 0.327$ and

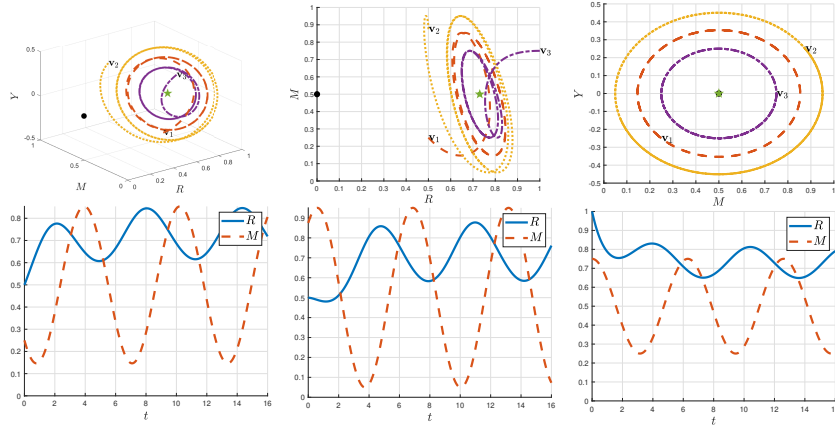


Figure 4: Orbits (top) and temporal series (bottom) of the system (2) with parameters given by (14) and initial values (15). The equilibria $E_0 = (0, M_0, 0)$ and $E_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, E_0 is unstable, E_* is a center and all orbits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

384 $S_B(\tilde{E}_*) \simeq 0.673$, in the first case, and $S_B(\tilde{E}_0) \simeq 0.563$ and $S_B(\tilde{E}_*) \simeq 0.437$, in
 385 the second one.

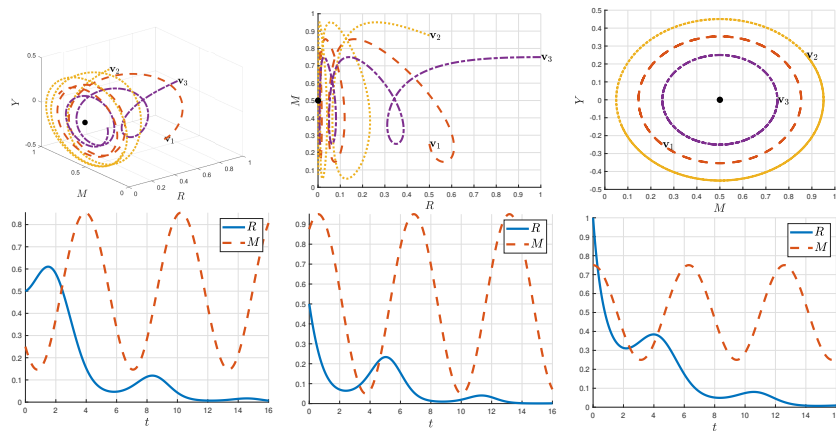


Figure 5: Orbits (top) and temporal series (bottom) of the system (2) with parameters given by (14), but $c = 3$, and initial values (15). The unique equilibrium $E_0 = (0, M_0, 0)$ is shown with a black dot. It is a center, where all the orbits are pushed towards the plane $R = 0$.

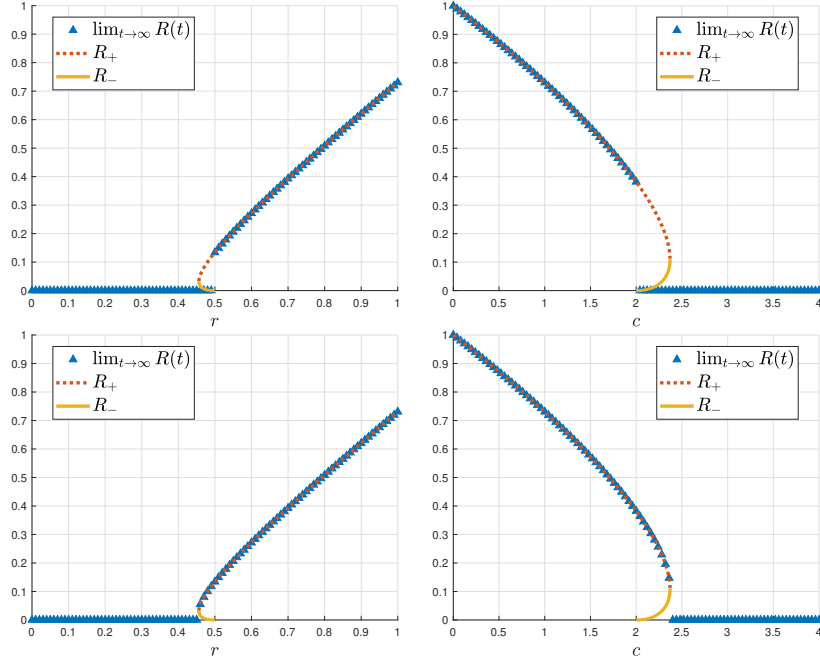


Figure 6: Values of $\lim_{t \rightarrow \infty} R(t)$ for (2) with parameters (14) for specific non-oscillating orbits compared with the (two) solution(s) R_{\pm} of (7), where (Top) the initial value is $(10^{-4}, M_0, 0)$, (Bottom) the initial value is $(1, M_0, 0)$, (Left) r varies uniformly in $[0, 1]$, (Right) c varies uniformly in $[0, 4]$. Comparing the values of $\lim_{t \rightarrow \infty} R(t)$, 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.

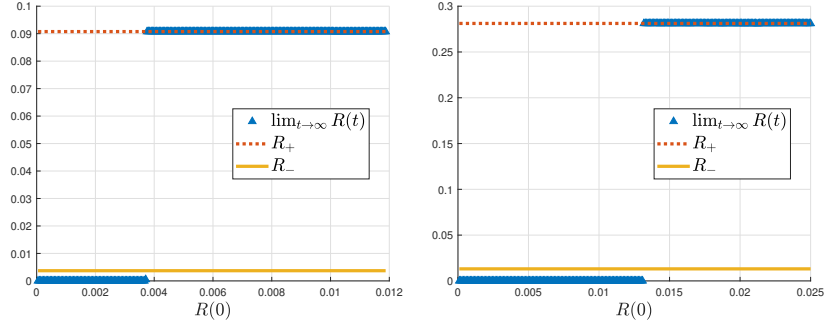


Figure 7: Bistability of 0 and R_+ for non-oscillating orbits of (2) with parameters (14), where (Left) $r = 0.475$ and $R(0)$ varies uniformly in $[0, 0.012]$ and (Right) $c = 2.2$ and $R(0)$ varies uniformly in $[0, 0.025]$. Note that the horizontal orange line represents the unstable manifold R_0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

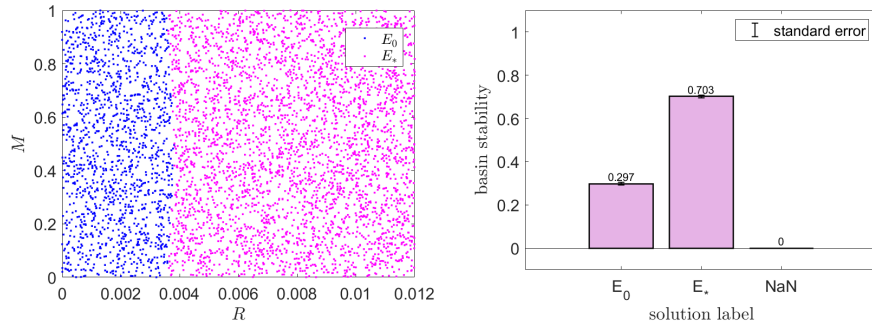


Figure 8: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the left panel of Figure 7 for model (2). The parameter values are given in (14), with $r = 0.475$. The initial conditions are $n = 5000$ uniformly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

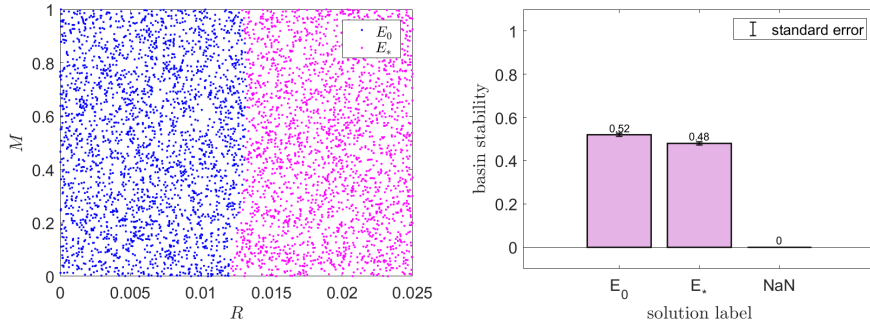


Figure 9: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the right panel of Figure 7 for model (2). The parameter values are given in (14), with $c = 2.2$. The initial conditions are $n = 5000$ uniformly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

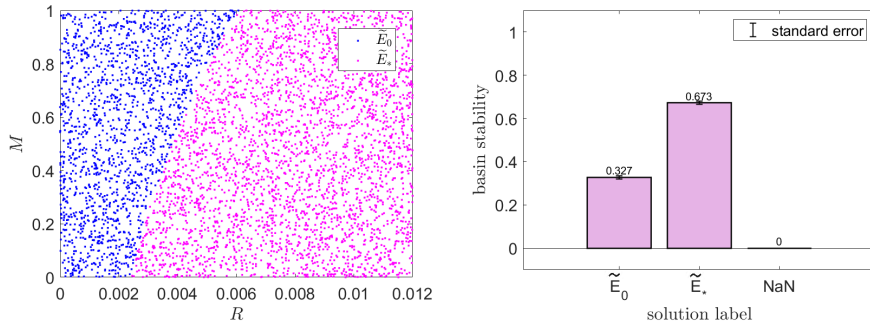


Figure 10: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the left panel of Figure 7 for model (3). The parameter values are given in (14), with $r = 0.475$. The initial conditions are $n = 5000$ uniformly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

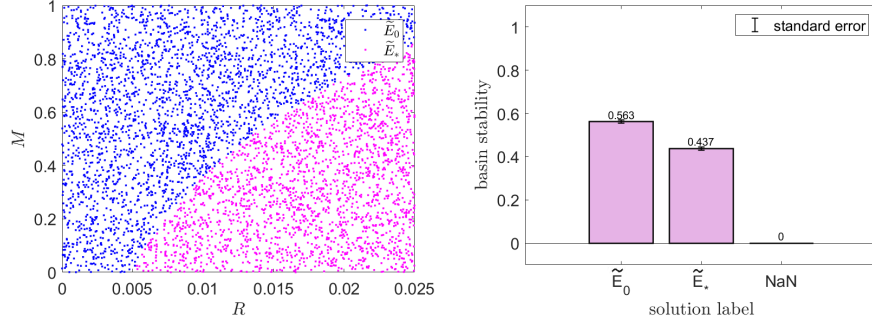


Figure 11: The basin of attraction in the $Y = 0$ subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the right panel of Figure 7 for model (3). The parameter values are given in (14), with $c = 2.2$. The initial conditions are $n = 5000$ uniformly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

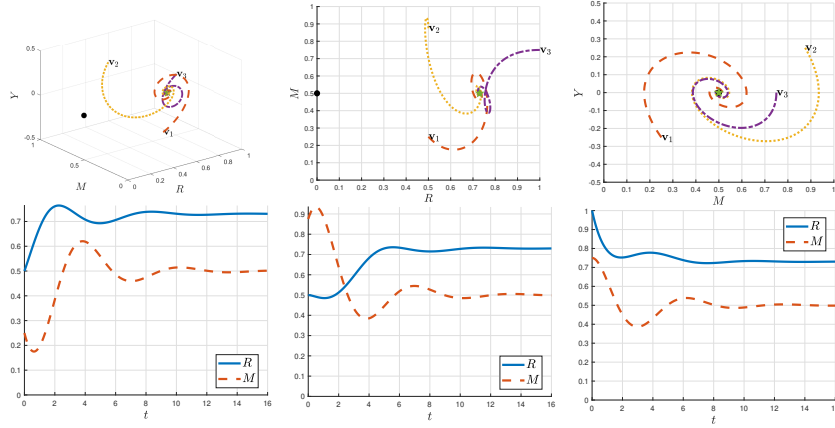


Figure 12: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14) and initial values (15). The equilibria $\tilde{E}_0 = (0, M_0, 0)$ and $\tilde{E}_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, \tilde{E}_0 is unstable, while \tilde{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.

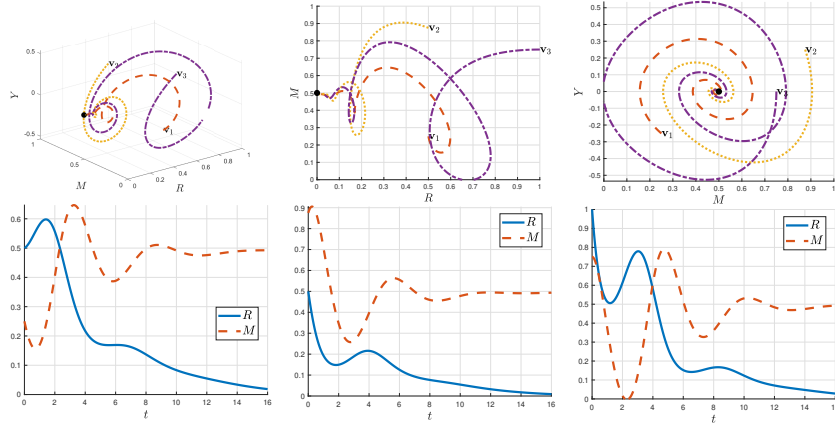


Figure 13: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but $c = 3$, and initial values (15). The unique equilibrium $\tilde{E}_0 = (0, M_0, 0)$ is shown with a black dot and it is a stable focus. Here only the migrating population M survives, reaching a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

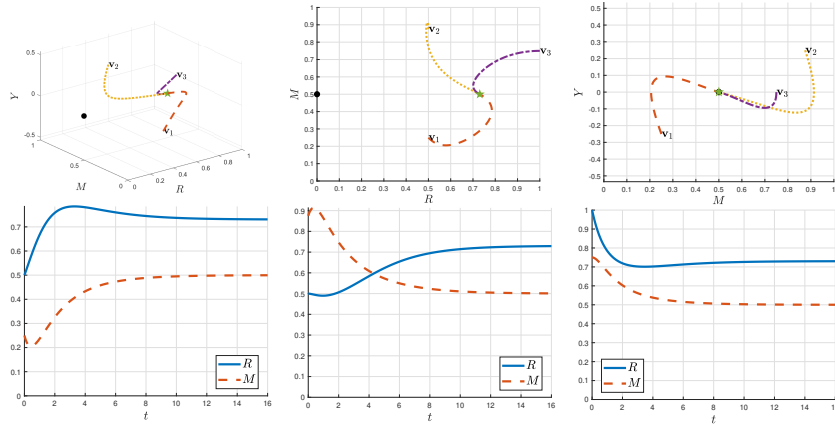


Figure 14: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but $m = 3$, and initial values (15). The equilibria $\tilde{E}_0 = (0, M_0, 0)$ and $\tilde{E}_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, \tilde{E}_0 is unstable, while \tilde{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.

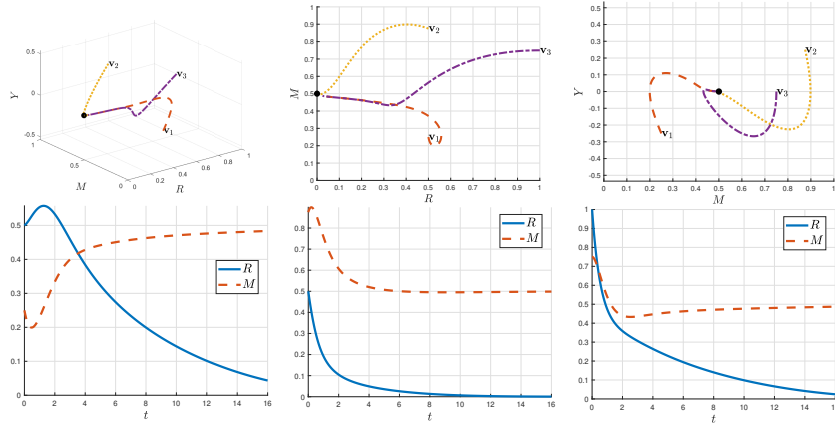


Figure 15: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but $c = m = 3$, and initial values (15). The unique equilibrium $\tilde{E}_0 = (0, M_0, 0)$ is shown with a black dot and it is a stable node. Here only the migrating population M survives, reaching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

386 6. Conclusion

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

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

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

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

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

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

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

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

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

448 In a similar recent investigation where instead the interference occurs within
449 the resident territory, [1], we discovered that when the migrant predators find
450 favorable conditions, they settle in the environment traversed in their journey.
451 Our goal here is to understand if the same can occur when the population in-
452 termingling is limited only to a marginal area, the perimeter of the residential
453 species habitat. We find that indeed this is the case. Our major finding is
454 that even a minor predatory interaction may induce the migrants to invade and
455 colonize the so-found new territory. Although the model has been intention-
456 ally kept at a minimal level, to highlight the basic mechanisms underlying this
457 phenomenon, in our opinion, this may give another clue on the phenomenon of
458 exotic species that find good harboring conditions at temperate latitudes. Their
459 settling into regions in which they are not native has negative consequences on
460 the autochthonous species, putting them at threat of extinction, perhaps also
461 with the importation of diseases against which the indigenous populations are
462 defenseless. Some current examples are the grey squirrels invasions in Italy
463 and Great Britain, where in the last case also they carry a lethal virus for
464 the European red squirrels [7, 44, 46, 54]. Also, the cottontails originating in
465 America settling in Italy, possibly carrying the EBHS (European Brown Hares
466 Syndrome) virus are causing a hyperpredation of foxes on the resident hares
467 [13, 16, 17]. These examples do not fall within the present analysis, but are just
468 reported to highlight the possible very negative consequences of these invasions.
469 Thus, as a final word, our results indicate that, if possible, it is best to prevent
470 even the slightest possibility of populations intermingling when the migratory
471 species could represent a threat for the native one.

472 **Acknowledgements**

473 All authors are members of the INdAM research group GNCS and of the
474 Research ITalian network on Approximation (RITA).

475 **References**

- 476 [1] Acotto, F., Bardi, L., Manzini, A., Sarfatti, O., Viscardi, A., Venturino,
477 E., (to be published in) 2024. An exploration of the effects of periodic top
478 predator interference and hunting on a predator-prey system, in: Mondaini,
479 R.P. (Ed.), Trends in Biomathematics - Selected Works from the BIOMAT
480 Consortium Lectures. Springer International Publishing, Springer Nature,
481 Cham, Switzerland.
- 482 [2] Acotto, F., Bulai, I.M., Venturino, E., 2023. Prey herding and preda-
483 tors' feeding satiation induce multiple stability. Communications
484 in Nonlinear Science and Numerical Simulation 127, 107564. URL:
485 <https://www.sciencedirect.com/science/article/pii/S1007570423004859>,
486 doi:<https://doi.org/10.1016/j.cnsns.2023.107564>.
- 487 [3] Ajraldi, V., Pittavino, M., Venturino, E., 2011. Model-
488 ing herd behavior in population systems. Nonlinear Anal-
489 ysis: Real World Applications 12, 2319–2338. URL:
490 <https://www.sciencedirect.com/science/article/pii/S1468121811000149>,
491 doi:<https://doi.org/10.1016/j.nonrwa.2011.02.002>.
- 492 [4] Alerstam, T., Bäckman, J., 2018. Ecology of ani-
493 mal migration. Current Biology 28, R968–R972. URL:
494 <https://www.sciencedirect.com/science/article/pii/S0960982218305153>,
495 doi:<https://doi.org/10.1016/j.cub.2018.04.043>.
- 496 [5] Atkinson, M.S., Savage, A.E., 2023. Invasive amphibians al-
497 ter host-pathogen interactions with primarily negative outcomes
498 for native species. Biological Conservation 286, 110310. URL:
499 <https://www.sciencedirect.com/science/article/pii/S0006320723004111>,
500 doi:<https://doi.org/10.1016/j.biocon.2023.110310>.
- 501 [6] Atwell, J.M., O'Neal, D.M., Ketterson, E.D., 2011. Animal mi-
502 gration as a moving target for conservation: intra-species variation

- 503 and responses to environmental change, as illustrated in a sometimes
504 migratory songbird. *Environmental law* 41 (2), 289–316. URL:
505 <http://www.jstor.org/stable/43267492>.
- 506 [7] Barbara, F., La Morgia, V., Parodi, V., Toscano, G., Venturino,
507 E., 2018. Analysis of the Incidence of Poxvirus on the Dynam-
508 ics between Red and Grey Squirrels. *Mathematics* 6. URL:
509 <https://www.mdpi.com/2227-7390/6/7/113>, doi:10.3390/math6070113.
- 510 [8] Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a
511 driver of recent extinctions. *Biology Letters* 12, 20150623. URL:
512 <https://royalsocietypublishing.org/doi/abs/10.1098/rsbl.2015.0623>,
513 doi:10.1098/rsbl.2015.0623.
- 514 [9] Berardo, C., Bulai, I.M., Venturino, E., 2021. Interactions Ob-
515 tained from Basic Mechanistic Principles: Prey Herds and Predators.
516 *Mathematics* 9. URL: <https://www.mdpi.com/2227-7390/9/20/2555>,
517 doi:10.3390/math9202555.
- 518 [10] Blakeslee, A.M., Canning-Clode, J., Lind, E.M., Quilez-Badia,
519 G., 2011. Biological invasions in the 21st century: Eco-
520 logical impacts, predictions, and management across land
521 and sea. *Environmental Research* 111, 891–892. URL:
522 <https://www.sciencedirect.com/science/article/pii/S0013935111002179>,
523 doi:<https://doi.org/10.1016/j.envres.2011.09.005>.
- 524 [11] Borgogni, D., Losero, L., Venturino, E., 2020. A More Realistic
525 Formulation of Herd Behavior for Interacting Populations. Springer
526 International Publishing, Cham. chapter 2. pp. 9–21. URL:
527 https://doi.org/10.1007/978-3-030-46306-9_2, doi:10.1007/978-
528 3-030-46306-9_2.
- 529 [12] Bulai, I.M., Venturino, E., 2017. Shape effects on herd be-
530 havior in ecological interacting population models. *Math-*
531 *ematics and Computers in Simulation* 141, 40–55. URL:

- 532 <https://www.sciencedirect.com/science/article/pii/S0378475417301696>,
533 doi:<https://doi.org/10.1016/j.matcom.2017.04.009>.
- 534 [13] Camattari, F., Acotto, F., Venturino, E., 2023. Z-Type Control
535 Methods on a Three-Species Model with an Invasive Prey. *Math-*
536 *ematics* 11. URL: <https://www.mdpi.com/2227-7390/11/19/4182>,
537 doi:10.3390/math11194182.
- 538 [14] Cantrell, R.S., Cosner, C., Lewis, M.A., Lou, Y., 2020. Evo-
539 lution of dispersal in spatial population models with multiple
540 timescales. *Journal of Mathematical Biology* 80, 3–37. URL:
541 [https://doi.org/10.1007/s00285-](https://doi.org/10.1007/s00285-018-1302-2)
542 [018-1302-2](https://doi.org/10.1007/s00285-018-1302-2), doi:10.1007/s00285-
018-1302-2.
- 543 [15] Castillo-Alvino, H., Marva, M., 2020. The competition
544 model with Holling type II competitive response to inter-
545 fering time. *Journal of Biological Dynamics* 14, 222–244.
546 URL: <https://doi.org/10.1080/17513758.2020.1742392>,
547 doi:10.1080/17513758.2020.1742392. pMID: 32266869.
- 548 [16] Caudera, E., Viale, S., Bertolino, S., Cerri, J., Venturino, E.,
549 2021. A Mathematical Model Supporting a Hyperpredation Ef-
550 fect in the Apparent Competition Between Invasive Eastern Cot-
551 tontail and Native European Hare. *Bulletin of Mathematical Bi-*
552 *ology* 83. URL: [https://doi.org/10.1007/s11538-](https://doi.org/10.1007/s11538-021-00873-9)
553 [021-00873-9](https://doi.org/10.1007/s11538-021-00873-9), doi:10.1007/s11538-021-00873-9.
- 554 [17] Caudera, E., Viale, S., Bertolino, S., Venturino, E., 2020. A European
555 Brown Hare Syndrome model within a foxes-cottontails-hares interaction
556 system. Special Issue of the Journal “Annals of the Alexandru Ioan Cuza
557 University of Iași (New Series) - Mathematics”, devoted to recent applica-
558 tions of Mathematics in Life Sciences 66, 347–384.
- 559 [18] Chapman, J.W., Drake, V.A., 2019. Insect Migration, in:

- 560 Choe, J.C. (Ed.), *Encyclopedia of Animal Behavior* (Sec-
561 ond Edition). Academic Press, Oxford, pp. 573–580. URL:
562 <https://www.sciencedirect.com/science/article/pii/B9780128096338012486>,
563 doi:<https://doi.org/10.1016/B978-0-12-809633-8.01248-6>.
- 564 [19] Codling, E.A., Plank, M.J., Benhamou, S., 2008. Random walk models
565 in biology. *Journal of The Royal Society Interface* 5, 813–834. URL:
566 <https://royalsocietypublishing.org/doi/abs/10.1098/rsif.2008.0014>,
567 doi:[10.1098/rsif.2008.0014](https://doi.org/10.1098/rsif.2008.0014).
- 568 [20] Corkeron, P.J., Van Parijs, S.M., Adamczak, S.K., 2019. Marine
569 Mammal Migrations and Movement Patterns, in: Cochran, J.K.,
570 Bokuniewicz, H.J., Yager, P.L. (Eds.), *Encyclopedia of Ocean Sci-*
571 *ences* (Third Edition). Academic Press, Oxford, pp. 563–571. URL:
572 <https://www.sciencedirect.com/science/article/pii/B9780124095489113934>,
573 doi:<https://doi.org/10.1016/B978-0-12-409548-9.11393-4>.
- 574 [21] Costello, K.E., Lynch, S.A., McAllen, R., O’Riordan, R.M., Cul-
575 loty, S.C., 2022. Assessing the potential for invasive species
576 introductions and secondary spread using vessel movements in
577 maritime ports. *Marine Pollution Bulletin* 177, 113496. URL:
578 <https://www.sciencedirect.com/science/article/pii/S0025326X22001783>,
579 doi:<https://doi.org/10.1016/j.marpolbul.2022.113496>.
- 580 [22] Djilali, S., Cattani, C., Guin, L.N., 2021. Delayed predator-prey
581 model with prey social behavior. *The European Physical Journal*
582 *Plus* 136. URL: <https://doi.org/10.1140/epjp/s13360-021-01940-9>,
583 doi:[10.1140/epjp/s13360-021-01940-9](https://doi.org/10.1140/epjp/s13360-021-01940-9).
- 584 [23] Eigentler, L., Sherratt, J.A., 2023. Long-range seed dis-
585 persal enables almost stationary patterns in a model for
586 dryland vegetation. *Journal of Mathematical Biology* 86,
587 15. URL: <https://doi.org/10.1007/s00285-022-01852-x>,
588 doi:<https://doi.org/10.1007/s00285-022-01852-x>.

- 589 [24] Evans, K.L., Newton, J., Gaston, K.J., Sharp, S.P., McGowan,
590 A., Hatchwell, B.J., 2012. Colonisation of urban environments
591 is associated with reduced migratory behaviour, facilitating di-
592 vergence from ancestral populations. *Oikos* 121, 634–640. URL:
593 <https://nsojournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1600-0706.2011.19722.x>,
594 doi:<https://doi.org/10.1111/j.1600-0706.2011.19722.x>.
- 595 [25] Fantle-Lepczyk, J.E., Haubrock, P.J., Kramer, A.M., Cuthbert,
596 R.N., Turbelin, A.J., Crystal-Ornelas, R., Diagne, C., Courchamp,
597 F., 2022. Economic costs of biological invasions in the United
598 States. *Science of The Total Environment* 806, 151318. URL:
599 <https://www.sciencedirect.com/science/article/pii/S0048969721063968>,
600 doi:<https://doi.org/10.1016/j.scitotenv.2021.151318>.
- 601 [26] Fortuna, T.M., Le Gall, P., Mezdour, S., Calatayud, P.A.,
602 2022. Impact of invasive insects on native insect communi-
603 ties. *Current Opinion in Insect Science* 51, 100904. URL:
604 <https://www.sciencedirect.com/science/article/pii/S2214574522000396>,
605 doi:<https://doi.org/10.1016/j.cois.2022.100904>.
- 606 [27] Fryxell, J., Sinclair, A., 1988. Causes and consequences of migration
607 by large herbivores. *Trends in Ecology & Evolution* 3, 237–241. URL:
608 <https://www.sciencedirect.com/science/article/pii/0169534788901668>,
609 doi:[https://doi.org/10.1016/0169-5347\(88\)90166-8](https://doi.org/10.1016/0169-5347(88)90166-8).
- 610 [28] Gauthreaux, S., 2010. Bird Migration, in: Breed,
611 M.D., Moore, J. (Eds.), *Encyclopedia of Animal Be-*
612 *havior*. Academic Press, Oxford, pp. 211–219. URL:
613 <https://www.sciencedirect.com/science/article/pii/B9780080453378003624>,
614 doi:<https://doi.org/10.1016/B978-0-08-045337-8.00362-4>.
- 615 [29] Giuggioli, L., Bartumeus, F., 2010. Animal movement, search
616 strategies and behavioural ecology: a cross-disciplinary way
617 forward. *Journal of Animal Ecology* 79, 906–909. URL:

- 618 <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2656.2010.01682.x>,
619 doi:<https://doi.org/10.1111/j.1365-2656.2010.01682.x>.
- 620 [30] Levin, S.A., Cohen, D., Hastings, A., 1984. Dispersal strategies in
621 patchy environments. *Theoretical Population Biology* 26, 165–191. URL:
622 <https://www.sciencedirect.com/science/article/pii/0040580984900285>,
623 doi:[https://doi.org/10.1016/0040-5809\(84\)90028-5](https://doi.org/10.1016/0040-5809(84)90028-5).
- 624 [31] Li, Y., Yu, F.H., 2023. Managing the risk of bi-
625 ological invasions. *iScience* 26, 108221. URL:
626 <https://www.sciencedirect.com/science/article/pii/S2589004223022988>,
627 doi:<https://doi.org/10.1016/j.isci.2023.108221>.
- 628 [32] Menck, P.J., Heitzig, J., Kurths, J., Joachim Schellnhuber, H., 2014. How
629 dead ends undermine power grid stability. *Nature Communications* 5, 3969.
630 URL: <https://doi.org/10.1038/ncomms4969>, doi:10.1038/ncomms4969.
- 631 [33] Menck, P.J., Heitzig, J., Marwan, N., Kurths, J., 2013. How basin stability
632 complements the linear-stability paradigm. *Nature Physics* 9, 89–92. URL:
633 <https://doi.org/10.1038/nphys2516>, doi:10.1038/nphys2516.
- 634 [34] Márquez, F., Zabala, S., Bökenhans, V., Cumplido, M., Espinosa, F.,
635 Bigatti, G., Averbuj, A., 2024. Predation of the invasive green crab
636 *Carcinus maenas* on the edible snail *Buccinastrum deforme*, targeted
637 as the most important nearshore marine gastropod fishery from Patag-
638 onia, Argentina. *Regional Studies in Marine Science* 69, 103299. URL:
639 <https://www.sciencedirect.com/science/article/pii/S2352485523004899>,
640 doi:<https://doi.org/10.1016/j.rsma.2023.103299>.
- 641 [35] Owen-Smith, N., Fryxell, J.M., Merrill, E.H., 2010. For-
642 aging theory upscaled: the behavioural ecology of herbi-
643 vore movement. *Philosophical Transactions of the Royal
644 Society B: Biological Sciences* 365, 2267–2278. URL:
645 <https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2010.0095>,
646 doi:10.1098/rstb.2010.0095.

- 647 [36] Pearson, D.E., 2024. Biological Invasions: An Overview,
648 in: Scheiner, S.M. (Ed.), Encyclopedia of Biodiversity (Third
649 Edition). Academic Press, Oxford, pp. 667–679. URL:
650 <https://www.sciencedirect.com/science/article/pii/B9780128225622000372>,
651 doi:<https://doi.org/10.1016/B978-0-12-822562-2.00037-2>.
- 652 [37] Piczak, M.L., Binder, T.R., Cooke, S.J., 2022. The biology of fish
653 migration, in: Reference Module in Life Sciences. Elsevier. URL:
654 <https://www.sciencedirect.com/science/article/pii/B9780323908016000082>,
655 doi:<https://doi.org/10.1016/B978-0-323-90801-6.00008-2>.
- 656 [38] Righton, D.A., Verhelst, P., Westerberg, H., 2023. Fish
657 migrations - migration of the European eel (*Anguilla an-*
658 *guilla*), in: Reference Module in Life Sciences. Elsevier. URL:
659 <https://www.sciencedirect.com/science/article/pii/B9780323908016001026>,
660 doi:<https://doi.org/10.1016/B978-0-323-90801-6.00102-6>.
- 661 [39] Satterfield, D.A., Maerz, J.C., Altizer, S., 2015. Loss of migratory
662 behaviour increases infection risk for a butterfly host. Proceedings
663 of the Royal Society B: Biological Sciences 282, 20141734. URL:
664 <https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2014.1734>,
665 doi:[10.1098/rspb.2014.1734](https://doi.org/10.1098/rspb.2014.1734).
- 666 [40] Southwood, A., 2007. 29.3. Physiology and behavior of migra-
667 tion in reptiles. Comparative Biochemistry and Physiology Part
668 A: Molecular & Integrative Physiology 148, S127–S128. URL:
669 <https://www.sciencedirect.com/science/article/pii/S1095643307013785>,
670 doi:<https://doi.org/10.1016/j.cbpa.2007.06.318>.
- 671 [41] Stender, M., Hoffmann, N., 2022. bSTAB: an open-source
672 software for computing the basin stability of multi-stable dy-
673 namical systems. Nonlinear Dynamics 107, 1451–1468. URL:
674 <https://doi.org/10.1007/s11071-021-06786-5>, doi:[10.1007/s11071-](https://doi.org/10.1007/s11071-021-06786-5)
675 [021-06786-5](https://doi.org/10.1007/s11071-021-06786-5).

- 676 [42] Strickman, D., 2020. Chapter 10 - Invasive Mosquito Species
677 and Potential Introductions, in: Debboun, M., Nava, M.R.,
678 Rueda, L.M. (Eds.), Mosquitoes, Communities, and Pub-
679 lic Health in Texas. Academic Press, pp. 307–315. URL:
680 <https://www.sciencedirect.com/science/article/pii/B9780128145456000109>,
681 doi:<https://doi.org/10.1016/B978-0-12-814545-6.00010-9>.
- 682 [43] Thorpe, J.E., 1988. Salmon migration. *Science Progress* (1933-) 72, 345–
683 370. URL: <http://www.jstor.org/stable/43420999>.
- 684 [44] Tompkins, D.M., White, A.R., Boots, M., 2003. Ecolog-
685 ical replacement of native red squirrels by invasive greys
686 driven by disease. *Ecology Letters* 6, 189–196. URL:
687 <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1461-0248.2003.00417.x>,
688 doi:<https://doi.org/10.1046/j.1461-0248.2003.00417.x>.
- 689 [45] Tortosa, F.S., Caballero, J.M., Reyes-López, J., 2002. Ef-
690 fect of Rubbish Dumps on Breeding Success in the White
691 Stork in Southern Spain. *Waterbirds* 25, 39–43. URL:
692 [https://doi.org/10.1675/1524-4695\(2002\)025\[0039:EORDOB\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2002)025[0039:EORDOB]2.0.CO;2),
693 doi:[10.1675/1524-4695\(2002\)025\[0039:EORDOB\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2002)025[0039:EORDOB]2.0.CO;2).
- 694 [46] Travaglia, E., Morgia, V.L., Venturino, E., 2020. Poxvirus, red and
695 grey squirrel dynamics: Is the recovery of a common predator affecting
696 system equilibria? Insights from a predator-prey ecoepidemic model.
697 *Discrete and Continuous Dynamical Systems - B* 25, 2023–2040. URL:
698 <https://www.aims sciences.org/article/id/982a449d-916b-4da4-bcff-8f3b5b44b4d0>,
699 doi:[10.3934/dcdsb.2019200](https://doi.org/10.3934/dcdsb.2019200).
- 700 [47] Turbelin, A.J., Cuthbert, R.N., Essl, F., Haubrock, P.J., Ricciardi,
701 A., Courchamp, F., 2023. Biological invasions are as costly as natural
702 hazards. *Perspectives in Ecology and Conservation* 21, 143–150. URL:
703 <https://www.sciencedirect.com/science/article/pii/S2530064423000214>,
704 doi:<https://doi.org/10.1016/j.pecon.2023.03.002>.

- 705 [48] Turchin, P., 1998. Quantitative Analysis of Movement:
706 Measuring and Modeling Population Redistribution in Ani-
707 mals and Plants. Weimar and Now; 13, Sinauer. URL:
708 <https://books.google.it/books?id=ZbdmQgAACAAJ>.
- 709 [49] Van Der Ree, R., McDonnell, M.J., Temby, I., Nelson, J., Whit-
710 tingham, E., 2006. The establishment and dynamics of a recently
711 established urban camp of flying foxes (*Pteropus poliocephalus*) out-
712 side their geographic range. Journal of Zoology 268, 177–185. URL:
713 <https://zslpublications.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-7998.2005.00005.x>
714 doi:<https://doi.org/10.1111/j.1469-7998.2005.00005.x>.
- 715 [50] Venturino, E., Caridi, Y., Dos Anjos, V., D’Ancona, G., 2023.
716 On some methodological issues in mathematical modeling of in-
717 teracting populations. Journal of Biological Systems 31, 169–
718 184. URL: <https://doi.org/10.1142/S0218339023500080>,
719 doi:[10.1142/S0218339023500080](https://doi.org/10.1142/S0218339023500080).
- 720 [51] Venturino, E., Petrovskii, S., 2013. Spatiotemporal be-
721 havior of a prey-predator system with a group de-
722 fense for prey. Ecological Complexity 14, 37–47. URL:
723 <https://www.sciencedirect.com/science/article/pii/S1476945X1300007X>,
724 doi:<https://doi.org/10.1016/j.ecocom.2013.01.004>. Special Issue on the
725 occasion of Horst Malchow’s 60th birthday.
- 726 [52] Vera, M.C., Marva, M., Garcıa-Garrido, V.J., Escalante, R.,
727 2024. The Beddington-DeAngelis Competitive Response: Intra-
728 Species Interference Enhances Coexistence in Species Competition.
729 Mathematics 12. URL: <https://www.mdpi.com/2227-7390/12/4/562>,
730 doi:[10.3390/math12040562](https://doi.org/10.3390/math12040562).
- 731 [53] Viswanathan, G.M., da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
732 2011. The Physics of Foraging: An Introduction to Random

733 Searches and Biological Encounters. Cambridge University Press.

734 doi:<https://doi.org/10.1017/CBO9780511902680>.

735 [54] White, A., Bell, S.S., Lurz, P.W.W., Boots, M., 2014. Con-
736 servation management within strongholds in the face of

737 disease-mediated invasions: red and grey squirrels as a case
738 study. *Journal of Applied Ecology* 51, 1631–1642. URL:

739 <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12274>,

740 doi:<https://doi.org/10.1111/1365-2664.12274>.