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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 therefor 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

- 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
- 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
- 12 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
- 15 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 notori-30 ous examples for the former class and green sea turtles (Chelonia mydas) for 31 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]. 35 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 38 resources [27], such as wildebeests (Connochaetes taurinus) and elephants (Loxodonta africana), and by big cetaceans in search of krill [20], such as minke 40 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 69 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 71 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 popu-76 lations 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. 79

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

As a starting point, consider a logistically growing residential population R.

Then, suppose that a periodically migrating population M can interact with the

89 2.1. Interference model

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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. 94 In general, the shape of the native species' territory could be very compli-95 cated, 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] 100 for interactions between individualistic predators and herding prey and later 101 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 103 the fact that interactions of an outside individual of another population with 104 a population living in herd are mainly limited to the individuals on the out-105 most positions in the herd. This assumption has been discussed in several other 106 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 108 tries to avoid such difficulties. Specifically, the function we use here is 109

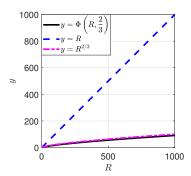
$$\Phi(R,\alpha) = \frac{R}{1 + R^{1-\alpha}} \,.$$

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 $\alpha = \frac{2}{3}$.



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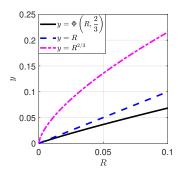


Figure 1: The graph of $\Phi\left(R,\frac{2}{3}\right)$ (black solid line) is compared with the two-thirds root (magenta dash-dotted line) and the bisectrix of the first and third quadrants (blue dashed line). On the left we consider a large domain: we observe that $\Phi\left(R,\frac{2}{3}\right)$ behaves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

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

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:

$$\frac{dR}{dt} = f_1(R, M) = R(r - bR) - c\Phi(R, \alpha)M,$$

$$\frac{dM}{dt} = f_2(Y) = Y,$$

$$\frac{dY}{dt} = f_3(M) = -\omega^2(M - M_0).$$
(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.

6 2.2. Predation model

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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

$$\frac{d^2M}{dt^2} = ecM f_1(R, M) \frac{\partial \Phi(R, \alpha)}{\partial R} + ec\Phi(R, \alpha)Y - mY - \omega^2(M - M_0).$$

Therefore, the model for the second scenario is

$$\frac{dR}{dt} = f_1(R, M) = R(r - bR) - c\Phi(R, \alpha)M,$$

$$\frac{dM}{dt} = f_2(Y) = Y,$$

$$\frac{dY}{dt} = \widetilde{f}_3(R, M, Y),$$
(3)

156 with

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$$\widetilde{f}_3(R, M, Y) = ecM f_1(R, M) \frac{\partial \Phi(R, \alpha)}{\partial R} + ec\Phi(R, \alpha)Y - mY - \omega^2(M - M_0).$$

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

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

163 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
- 168 $\mathbb{R}^2_{\geq 0} \times \mathbb{R}$ if and only if

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

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

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

170 and

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

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,

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

174 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, $M(t) \ge 0$ 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

$$R''(t_*) = r - 2bR(t_*)R'(t_*) - c\left(Y(t_*)\Phi(R(t_*),\alpha) - M(t_*)R'(t_*)\frac{\partial\Phi}{\partial R}(R(t_*),\alpha)\right)$$

= r > 0,

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

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

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

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

186 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

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

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

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

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

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

there exists a unique positive-coordinate intersection point of the graphs of Γ 205 and Λ . Thus, the condition (9) is sufficient for the feasible coexistence of the 206 native species and the migrant population. Otherwise, there may be two or 207 none. In particular, we can say that there exists a value $\tilde{r} \in (0, cM_0)$ such that, when $0 < r < \tilde{r}$, we have no intersection between the graphs of the two functions 200 of interest, when $r = \tilde{r}$, we have two coincident positive-coordinate intersection 210 points and, when $\tilde{r} < r < cM_0$, we have two different ones. Consequently, 211 there is a saddle-node bifurcation at $r = \tilde{r}$ for the coexistence equilibrium. 212 Bifurcations of this type can also be identified as the value of parameter b213 varies, fixing the graph of Λ and moving the straight line, or vice versa as 214 cM_0 and α vary. Specifically, when cM_0 varies, the situation is analogous to 215 what we have when r varies. In fact, there exists a threshold $cM_0 > r$ such 216 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 $cM_0 = cM_0$. As b varies, instead, if the condition (9) does not hold there is a saddle-node

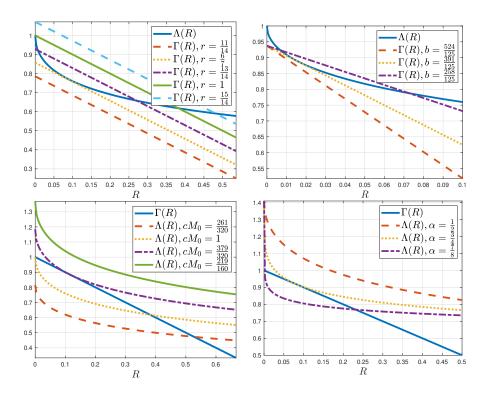


Figure 2: Different possible configurations of the functions $\Gamma(R)$ and $\Lambda(R)$ in (8). (Top-left): fixing $\Lambda(R)$ with $cM_0=1$ and $\alpha=1/2$, we vary $\Gamma(R)$ with b=1 and r as in the legend; (Top-right): fixing $\Lambda(R)$ with $cM_0=1$ and $\alpha=1/2$, we vary $\Gamma(R)$ with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

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 $0 < r \le \widehat{r}$, 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 $\#\mathcal{R}_* \ge 1$ 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

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

In particular,

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

2. for $\widetilde{r} < r^{\dagger} \le cM_0$,

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

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

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

(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

$$J = \left(\begin{array}{ccc} r - 2bR - cM \frac{\partial \Phi}{\partial R} & -c\Phi & 0 \\ 0 & 0 & 1 \\ 0 & -\omega^2 & 0 \end{array} \right).$$

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

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

the "stability" condition for E_0 is

$$r < cM_0, (11)$$

while for E_* we have (10).

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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 $0 < \tilde{r} < cM_0$. Depending on the position of r^{\dagger} with respect to \tilde{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.

- If 0 < r[†] ≤ r
 there are no intervals of r in which the feasibility condition,
 r ≥ r
 , and the "stability" condition (10) of E_{*} are simultaneously verified.
 In particular, when the condition (11) holds, we have S_B(E₀) = 1 and
 S_B(E_{*}) = 0.
- 264 2. If $\tilde{r} < r^{\dagger} \le cM_0$ the coexistence is feasible and "stable" when $\tilde{r} \le r < r^{\dagger}$.

 Thus, when $0 < r < \tilde{r}$ or when $r^{\dagger} \le r < cM_0$, we have $S_B(E_0) = 1$ and $S_B(E_*) = 0$, while when $\tilde{r} \le r < r^{\dagger}$, we have $S_B(E_0) \ne 0$ and $S_B(E_*) \ne 0$, 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,

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when 0 < r < \widetilde{r}, we have S_B(E_0) = 1 and S_B(E_*) = 0; when \widetilde{r} \le r < cM_0, S_B(E_0) \ne 0 and S_B(E_*) \ne 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 \le 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.
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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.

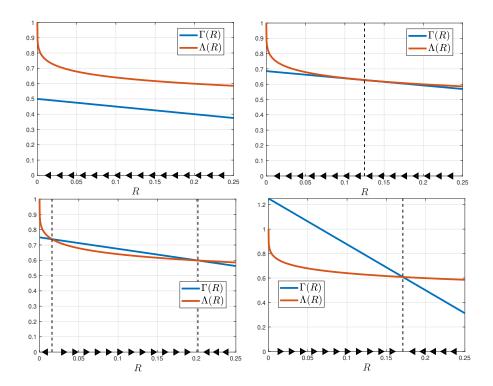


Figure 3: Different possible configurations of the functions $\Gamma(R)$ and $\Lambda(R)$ in (8) and "stability" of the arising equilibria. (Top-left): no intersection – 0 is the only "stable" equilibrium point; (Top-right): tangency – the value of R at which tangency occurs is "semistable" on the right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

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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

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

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

$$\operatorname{tr}\left(\widetilde{J}(\widetilde{E}_{*})\right) < 0, \quad \det\left(\widetilde{J}(\widetilde{E}_{*})\right) < 0, \quad \operatorname{tr}\left(\widetilde{J}(\widetilde{E}_{*})\right)\widetilde{M}_{2} < \det\left(\widetilde{J}(\widetilde{E}_{*})\right).$$
 (12)

The trace, the determinant and the sum of the two-order principal minors in

307 (12) are respectively

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

308 and

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

309 Accordingly, we can rewrite (12) as

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

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

Remark. Note that at the equilibrium \tilde{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 \tilde{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 \tilde{E}_0 and \tilde{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,

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

 $_{35}$ and

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

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 trans-337 ferred, via (2), to the residential population R, when it does not vanish. All 338 trajectories tend to closed orbits around E_0 or E_* lying on the M-Y plane or 339 a plane that passes through the coexistence equilibrium E_* . This is the case 340 of Figure 4 where we also observe periodic orbits around a center in the M-Y341 plane. When R goes to extinction (see, e.g., Figure 5) the pattern on the M-Y342 plane is kept, but the system tends to periodic orbits on the plane R=0. 343 If instead we eliminate the oscillations, choosing $(M(0), Y(0)) = (M_0, 0)$, 344 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 347 that, while the inequality (9) changes at r = 0.5 and c = 2, respectively, the 348 transcritical bifurcation occurs at a different parameter value depending on the 349 initial conditions. R_{-} is always unstable: the orbit of R either goes to 0 or to 350 R_{+} , depending on which of the two domains of attraction of these equilibria 35 the initial conditions lie. On the other hand, there is a region in the parameter 352 space where both $E_0 = (0, M_0, 0)$ and $E_* = (R_+, M_0, 0)$ are feasible and stable. 353 This happens for instance in the cases depicted in Figure 7.

The basins of attraction and the basin stability values corresponding to 355 the left and right panels of Figure 7 are shown in Figures 8 and 9, respec-356 tively. 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 stabil-358 ity value definition. In particular, in the squares $Q_1 = [0, 0.012] \times [0, 1]$ and 359 $Q_2 = [0, 0.025] \times [0, 1], n = 5000$ uniformly distributed initial conditions were 360 considered. The two basin stability values obtained are $S_B(E_0) \simeq 0.297$ and 361 $S_B(E_*) \simeq 0.703$, 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 363 and consequently $S_B(E_*)$ increases; the converse is obtained by decreasing the 364 side of the two squares. 365 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 368 population R. Moreover, we have the following behaviors for the projection 369 $\widetilde{E}_p=(M_0,0)$ of \widetilde{E}_0 (and \widetilde{E}_* when it exists) in the M–Y plane: 370

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

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

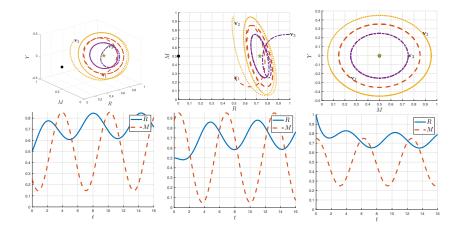


Figure 4: Orbits (top) and temporal series (bottom) of the system (2) with parameters given by (14) and initial values (15). The equilibria $E_0 = (0, M_0, 0)$ and $E_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, E_0 is unstable, E_* is a center and all orbits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

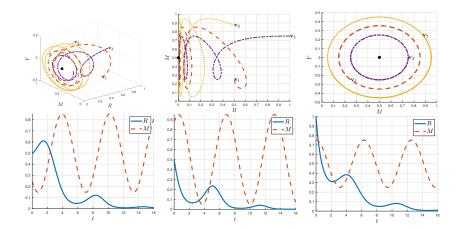


Figure 5: Orbits (top) and temporal series (bottom) of the system (2) with parameters given by (14), but c=3, and initial values (15). The unique equilibrium $E_0=(0,M_0,0)$ is shown with a black dot. It is a center, where all the orbits are pushed towards the plane R=0.

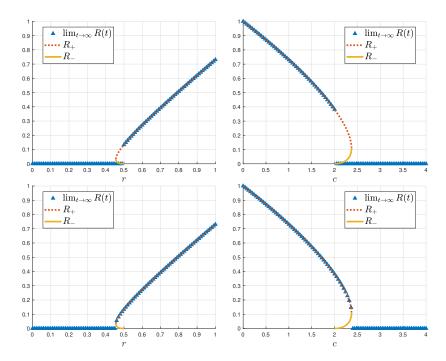


Figure 6: Values of $\lim_{t\to\infty} R(t)$ for (2) with parameters (14) for specific non-oscillating orbits compared with the (two) solution(s) R_{\pm} of (7), where (Top) the initial value is $(10^{-4}, M_0, 0)$, (Bottom) the initial value is $(1, M_0, 0)$, (Left) r varies uniformly in [0, 1], (Right)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

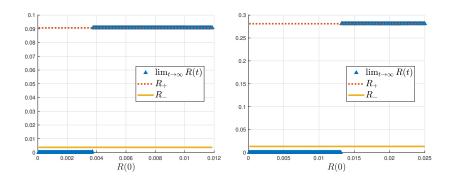


Figure 7: Bistability of 0 and R_+ for non-oscillating orbits of (2) with parameters (14), where (Left) r = 0.475 and R(0) varies uniformly in [0,0.012] and (Right) c = 2.2 and R(0) varies uniformly in [0,0.025]. Note that the horizontal orange line represents the unstable manifold R_0 . The same result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

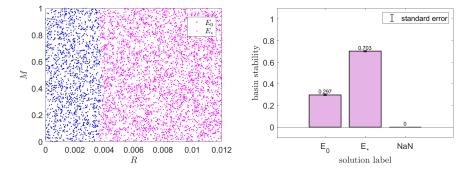


Figure 8: The basin of attraction in the Y=0 subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the left panel of Figure 7 for model (2). The parameter values are given in (14), with r=0.475. The initial conditions are n=5000 uniformly distributed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

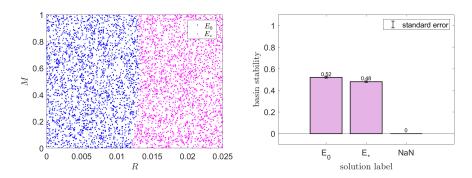


Figure 9: The basin of attraction in the Y=0 subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the right panel of Figure 7 for model (2). The parameter values are given in (14), with c=2.2. The initial conditions are n=5000 uniformly distributed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

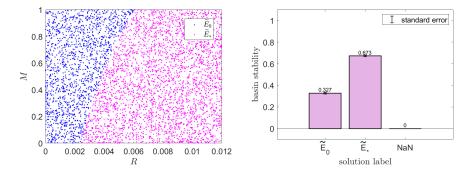


Figure 10: The basin of attraction in the Y=0 subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the left panel of Figure 7 for model (3). The parameter values are given in (14), with r=0.475. The initial conditions are n=5000 uniformly distributed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

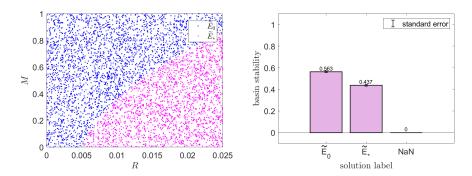


Figure 11: The basin of attraction in the Y=0 subspace of the space of states, on the left, and the basin stability values, on the right, corresponding to the right panel of Figure 7 for model (3). The parameter values are given in (14), with c=2.2. The initial conditions are n=5000 uniformly distributed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

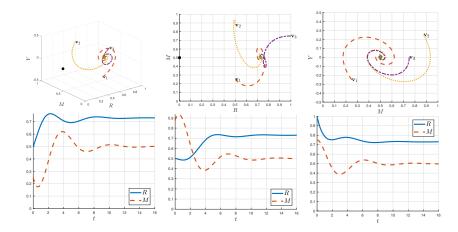


Figure 12: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14) and initial values (15). The equilibria $\widetilde{E}_0 = (0, M_0, 0)$ and $\widetilde{E}_* = (R_*, M_0, 0)$ are shown with a black dot and a green star, respectively. In this case, \widetilde{E}_0 is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

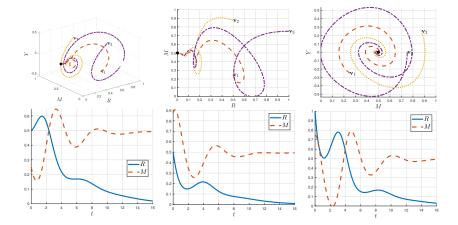


Figure 13: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but c=3, and initial values (15). The unique equilibrium $\widetilde{E}_0=(0,M_0,0)$ is shown with a black dot and it is a stable focus. Here only the migrating population M survives, reaching a fixed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

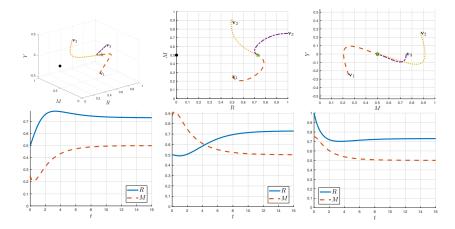


Figure 14: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but m=3, and initial values (15). The equilibria $\widetilde{E}_0=(0,M_0,0)$ and $\widetilde{E}_*=(R_*,M_0,0)$ are shown with a black dot and a green star, respectively. In this case, \widetilde{E}_0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

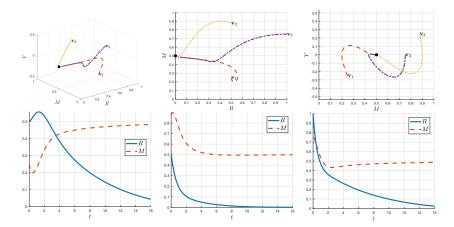


Figure 15: Orbits (top) and temporal series (bottom) of the system (3) with parameters given by (14), but c=m=3, and initial values (15). The unique equilibrium $\widetilde{E}_0=(0,M_0,0)$ is shown with a black dot and it is a stable node. Here only the migrating population M survives, reaching the equilibrium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

6. Conclusion

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

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. 419 However, the main focus of the paper is to provide an interpretation of the 420 invasion mechanism which occurs if the migrant touching only (but not crossing) 421 an environment finds a suitable prey, which is the case in model (3) and not in 422 the disruption model (2). Clearly, the outcome in bistable scenarios depends on 423 the initial condition. But the equilibria that are attained are either the point in 424 which the migrants thrive by wiping out the prey or alternatively the point in 425 which the two populations coexist. In both scenarios, the migrating predators 426 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 429 is very different from what it is being discussed here. Indeed in [1] the migrants 430 are not limited to marginal contact but interfere with the whole residential 431 ecosystem, composed by a predator-prey system. In [1] we consider also a model 432 for pure interference and another one with the migrant being superpredator of 433 both native species. The possible equilibria in [1] are more numerous because 434 each one of the two native species could be wiped out. However, the main point 435 is that coexistence is a center or an attractor exactly as in the model proposed 436 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 438 that the migrants cross the environment but even a marginal contact would lead 439 to an invasion in suitable circumstances. 440

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

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475 References

- [1] Acotto, F., Bardi, L., Manzini, A., Sarfatti, O., Viscardi, A., Venturino,
 E., (to be published in) 2024. An exploration of the effects of periodic top
 predator interference and hunting on a predator-prey system, in: Mondaini,
 R.P. (Ed.), Trends in Biomathematics Selected Works from the BIOMAT
 Consortium Lectures. Springer International Publishing, Springer Nature,
 Cham, Switzerland.
- [2] Acotto, F., Bulai, I.M., Venturino, E., 2023. Prey herding and predators' feeding satiation induce multiple stability. Communications in Nonlinear Science and Numerical Simulation 127, 107564. URL:

 https://www.sciencedirect.com/science/article/pii/S1007570423004859, doi:https://doi.org/10.1016/j.cnsns.2023.107564.
- [3] Ajraldi, V., Pittavino, М., Venturino, Ε., 2011.Model-487 herd behavior in population systems. Nonlinear Anal-488 World Applications 12, 2319 - 2338.URL: ysis: Real 489 https://www.sciencedirect.com/science/article/pii/S1468121811000149, 490 doi:https://doi.org/10.1016/j.nonrwa.2011.02.002. 491
- T., [4] Alerstam, Bäckman, J., 2018. Ecology of ani-492 Biology 28, R968-R972. URL: mal migration. Current 493 https://www.sciencedirect.com/science/article/pii/S0960982218305153, doi:https://doi.org/10.1016/j.cub.2018.04.043. 495
- 496 [5] Atkinson, M.S., Savage, A.E., 2023. Invasive amphibians al497 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.
- [6] Atwell, J.M., O'Neal, D.M., Ketterson, E.D., 2011. Animal migration as a moving target for conservation: intra-species variation

- and responses to environmental change, as illustrated in a sometimes migratory songbird. Environmental law 41 (2), 289–316. URL: http://www.jstor.org/stable/43267492.
- [7] Barbara, F., La Morgia, V., Parodi, V., Toscano, G., Venturino, E., 2018. Analysis of the Incidence of Poxvirus on the Dynamics between Red and Grey Squirrels. Mathematics 6. URL: https://www.mdpi.com/2227-7390/6/7/113, doi:10.3390/math6070113.
- [8] Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. Biology Letters 12, 20150623. URL: https://royalsocietypublishing.org/doi/abs/10.1098/rsbl.2015.0623, doi:10.1098/rsbl.2015.0623.
- [9] Berardo, C., Bulai, I.M., Venturino, E., 2021. Interactions Obtained from Basic Mechanistic Principles: Prey Herds and Predators.
 Mathematics 9. URL: https://www.mdpi.com/2227-7390/9/20/2555,
 doi:10.3390/math9202555.
- [10] Blakeslee, A.M., Canning-Clode, J., Lind, E.M., Quilez-Badia, 518 2011. Biological invasions in the 21st century: G.. Eco-519 logical impacts, predictions, and management across land 520 Environmental Research 111, 891-892. and sea. URL: 521 https://www.sciencedirect.com/science/article/pii/S0013935111002179, 522 doi:https://doi.org/10.1016/j.envres.2011.09.005. 523
- [11] Borgogni, D., Losero, L., Venturino, E., 2020. A More Realistic Formulation of Herd Behavior for Interacting Populations. Springer International Publishing, Cham. chapter 2. pp. 9–21. URL: https://doi.org/10.1007/978-3-030-46306-9_2, doi:10.1007/978-3-030-46306-9_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:

- https://www.sciencedirect.com/science/article/pii/S0378475417301696, doi:https://doi.org/10.1016/j.matcom.2017.04.009.
- [13] Camattari, F., Acotto, F., Venturino, E., 2023. Z-Type Control

 Methods on a Three-Species Model with an Invasive Prey. Mathematics 11. URL: https://www.mdpi.com/2227-7390/11/19/4182,
 doi:10.3390/math11194182.
- [14] Cantrell, R.S., Cosner, C., Lewis, M.A., Lou, Y., 2020. Evolution of dispersal in spatial population models with multiple timescales. Journal of Mathematical Biology 80, 3–37. URL: https://doi.org/10.1007/s00285-018-1302-2, doi:10.1007/s00285-018-1302-2.
- Н., 2020. The [15] Castillo-Alvino, Marvá, М., competition 543 model with Holling type Π competitive response tointerfering time. Journal of Biological Dynamics 14. 222 - 244.545 URL: https://doi.org/10.1080/17513758.2020.1742392, 546 doi:10.1080/17513758.2020.1742392. pMID: 32266869. 547
- [16] Caudera, E., Viale, S., Bertolino, S., Cerri, J., Venturino, E.,
 2021. A Mathematical Model Supporting a Hyperpredation Effect in the Apparent Competition Between Invasive Eastern Cottontail and Native European Hare. Bulletin of Mathematical Biology 83. URL: https://doi.org/10.1007/s11538-021-00873-9,
 doi:10.1007/s11538-021-00873-9.
- [17] Caudera, E., Viale, S., Bertolino, S., Venturino, E., 2020. A European
 Brown Hare Syndrome model within a foxes-cottontails-hares interaction
 system. Special Issue of the Journal "Annals of the Alexandru Ioan Cuza
 University of Iaşi (New Series) Mathematics", devoted to recent applications of Mathematics in Life Sciences 66, 347–384.
- [18] Chapman, J.W., Drake, V.A., 2019. Insect Migration, in:

- Choe, J.C. (Ed.), Encyclopedia of Animal Behavior (Second Edition). Academic Press, Oxford, pp. 573–580. URL:
- https://www.sciencedirect.com/science/article/pii/B9780128096338012486, doi:https://doi.org/10.1016/B978-0-12-809633-8.01248-6.
- [19] Codling, E.A., Plank, M.J., Benhamou, S., 2008. Random walk models
 in biology. Journal of The Royal Society Interface 5, 813-834. URL:
 https://royalsocietypublishing.org/doi/abs/10.1098/rsif.2008.0014,
 doi:10.1098/rsif.2008.0014.
- [20] Corkeron, P.J., Van Parijs, S.M., Adamczak, S.K., 2019. Marine

 Mammal Migrations and Movement Patterns, in: Cochran, J.K.,

 Bokuniewicz, H.J., Yager, P.L. (Eds.), Encyclopedia of Ocean Sciences (Third Edition). Academic Press, Oxford, pp. 563-571. URL:

 https://www.sciencedirect.com/science/article/pii/B9780124095489113934,

 doi:https://doi.org/10.1016/B978-0-12-409548-9.11393-4.
- [21] Costello, K.E., Lynch, S.A., McAllen, R., O'Riordan, R.M., Cul-574 loty, S.C., 2022.Assessing the potential for invasive species 575 introductions and secondary spread using vessel movements in 576 Marine Pollution Bulletin 177, 113496. maritime ports. 577 https://www.sciencedirect.com/science/article/pii/S0025326X22001783, 578 doi:https://doi.org/10.1016/j.marpolbul.2022.113496. 579
- [22] Djilali, S., Cattani, C., Guin, L.N., 2021. Delayed predator-prey
 model with prey social behavior. The European Physical Journal
 Plus 136. URL: https://doi.org/10.1140/epjp/s13360-021-01940-9,
 doi:10.1140/epjp/s13360-021-01940-9.
- 2023.[23] Eigentler, L., Sherratt, J.A., Long-range seed dis-584 enables almoststationary patterns persal in model for 585 dryland vegetation. Journal of Mathematical Biology 86, 586 15. URL: https://doi.org/10.1007/s00285-022-01852-x, 587 doi:https://doi.org/10.1007/s00285-022-01852-x. 588

- 589 [24] Evans, K.L., Newton, J., Gaston, K.J., Sharp, S.P., McGowan,
- A., Hatchwell, B.J., 2012. Colonisation of urban environments
- is associated with reduced migratory behaviour, facilitating di-
- vergence from ancestral populations. Oikos 121, 634–640. URL:
- https://nsojournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1600-0706.2011.19722.x,
- 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,
- R.N., Turbelin, A.J., Crystal-Ornelas, R., Diagne, C., Courchamp,
- F., 2022. Economic costs of biological invasions in the United
- States. Science of The Total Environment 806, 151318. URL:
- https://www.sciencedirect.com/science/article/pii/S0048969721063968,
- 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-
- ties. Current Opinion in Insect Science 51, 100904. URL:
- https://www.sciencedirect.com/science/article/pii/S2214574522000396,
- doi:https://doi.org/10.1016/j.cois.2022.100904.
- 606 [27] Fryxell, J., Sinclair, A., 1988. Causes and consequences of migration
- by large herbivores. Trends in Ecology & Evolution 3, 237–241. URL:
- https://www.sciencedirect.com/science/article/pii/0169534788901668,
- doi:https://doi.org/10.1016/0169-5347(88)90166-8.
- 610 [28] Gauthreaux, S., 2010. Bird Migration, in: Breed,
- M.D., Moore, J. (Eds.), Encyclopedia of Animal Be-
- havior. Academic Press, Oxford, pp. 211–219. URL:
- https://www.sciencedirect.com/science/article/pii/B9780080453378003624,
- doi:https://doi.org/10.1016/B978-0-08-045337-8.00362-4.
- 615 [29] Giuggioli, L., Bartumeus, F., 2010. Animal movement, search
- strategies and behavioural ecology: a cross-disciplinary way
- forward. Journal of Animal Ecology 79, 906–909. URL:

- https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2656.2010.01682.x, doi:https://doi.org/10.1111/j.1365-2656.2010.01682.x.
- [30] Levin, S.A., Cohen, D., Hastings, A., 1984. Dispersal strategies in patchy environments. Theoretical Population Biology 26, 165–191. URL:

 https://www.sciencedirect.com/science/article/pii/0040580984900285,
 doi:https://doi.org/10.1016/0040-5809(84)90028-5.
- [31] Li, F.H., 2023. Y.. Yu. Managing the risk of bi-624 ological invasions. iScience 26, 108221. URL: 625 https://www.sciencedirect.com/science/article/pii/S2589004223022988, 626 doi:https://doi.org/10.1016/j.isci.2023.108221.
- [32] Menck, P.J., Heitzig, J., Kurths, J., Joachim Schellnhuber, H., 2014. How dead ends undermine power grid stability. Nature Communications 5, 3969.
 URL: https://doi.org/10.1038/ncomms4969, doi:10.1038/ncomms4969.
- [33] Menck, P.J., Heitzig, J., Marwan, N., Kurths, J., 2013. How basin stability complements the linear-stability paradigm. Nature Physics 9, 89–92. URL: https://doi.org/10.1038/nphys2516, doi:10.1038/nphys2516.
- [34] Márquez, F., Zabala, S., Bökenhans, V., Cumplido, M., Espinosa, F.,
 Bigatti, G., Averbuj, A., 2024. Predation of the invasive green crab
 Carcinus maenas on the edible snail Buccinastrum deforme, targeted
 as the most important nearshore marine gastropod fishery from Patagonia, Argentina. Regional Studies in Marine Science 69, 103299. URL:
 https://www.sciencedirect.com/science/article/pii/S2352485523004899,
 doi:https://doi.org/10.1016/j.rsma.2023.103299.
- [35] Owen-Smith, Ν., Fryxell, J.M., Merrill, E.H., 2010. For-641 aging theory upscaled: the behavioural ecology herbi-642 Philosophical Transactions movement. the Royal vore 643 Society В: Biological Sciences 365, 2267 - 2278.URL: 644 https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2010.0095, 645 doi:10.1098/rstb.2010.0095. 646

- [36] Pearson, D.E., 2024. Biological Invasions: Overview, 647 in: Scheiner, S.M. (Ed.), Encyclopedia of Biodiversity (Third 648 Oxford, 667 - 679.Edition). Academic Press. pp. URL: https://www.sciencedirect.com/science/article/pii/B9780128225622000372, 650 doi:https://doi.org/10.1016/B978-0-12-822562-2.00037-2. 651
- [37] Piczak, M.L., Binder, T.R., Cooke, S.J., 2022. The biology of fish
 migration, in: Reference Module in Life Sciences. Elsevier. URL:
 https://www.sciencedirect.com/science/article/pii/B9780323908016000082,
 doi:https://doi.org/10.1016/B978-0-323-90801-6.00008-2.
- [38] Righton, D.A., Verhelst, Р., Westerberg, Н., 2023. Fish migrations migration of the European eel (Anguillaan-657 Reference Module in Life Sciences. Elsevier. URL: quilla), in: 658 https://www.sciencedirect.com/science/article/pii/B9780323908016001026, 659 doi:https://doi.org/10.1016/B978-0-323-90801-6.00102-6.660
- [39] Satterfield, D.A., Maerz, J.C., Altizer, S., 2015. Loss of migratory
 behaviour increases infection risk for a butterfly host. Proceedings
 of the Royal Society B: Biological Sciences 282, 20141734. URL:
 https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2014.1734,
 doi:10.1098/rspb.2014.1734.
- [40] Southwood, A., 2007. 29.3. Physiology and behavior of migration in reptiles. Comparative Biochemistry and Physiology Part
 A: Molecular & Integrative Physiology 148, S127-S128. URL:
 https://www.sciencedirect.com/science/article/pii/S1095643307013785,
 doi:https://doi.org/10.1016/j.cbpa.2007.06.318.
- [41] Stender, Μ., Hoffmann, N., 2022. bSTAB: an open-source 671 for computing the basin stability of multi-stable dy-672 namical systems. Nonlinear Dynamics 107, 1451–1468. 673 https://doi.org/10.1007/s11071-021-06786-5, doi:10.1007/s11071-674 021 - 06786 - 5.675

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

[48] Turchin, 1998. P., Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution Aniin706 mals and Plants. Sinauer. URL: Weimar and Now; 13. https://books.google.it/books?id=ZbdmQgAACAAJ.

708

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

- Searches and Biological Encounters. Cambridge University Press. doi:https://doi.org/10.1017/CBO9780511902680.
- [54] White, A., Bell, S.S., Lurz, P.W.W., Boots, M., 2014. Con-735 servation management within strongholds inthe face of 736 disease-mediated invasions: red and grey squirrels as a case 737 Journal of Applied Ecology 51, 1631 - 1642.URL: 738
- ${\tt https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12274},$
- doi:https://doi.org/10.1111/1365-2664.12274.