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Partial Prey Migration as a Non-autonomous Harmonic Oscillator: Chaos-Order Transitions in a Forced Classical Lotka-Volterra Model

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ABSTRACT I investigate how partial prey migration cycles, analogous to a non-autonomous harmonic oscillator, force the classical Lotka-Volterra model and reshape predator-prey interactions. A 3D nonlinear system is introduced, into which the external forcing replicates the entry and exit of partial migrants from the ecosystem, devoid feedback loops. Numerical simulations reveal an elusive resilience contour of the species interplay under stationary migration cycles. Thus, quasi-periodic and chaotic fluctuations appear at a minimum migration magnitude, vanishing beyond a bifurcation-induced tipping point. However, resilient interactions surge in localized hotspots, i.e., narrow regions of phase space and forcing intensity. It is striking to note that the detected chaos exhibits a threefold complexity related to migration magnitude, initial conditions, and a functional response parameter, implying a basin of attraction intertwined at fractal boundaries. In contrast, the resilience non-monotonicity fades due to ascending cycles of partial prey migration involving recruitment of a cohort of migrants by its resident species. In this case, chaos is suppressed, leading to predictable oscillations and phase-locking. Even extreme predator-prey ratios (e.g., 10:1) do not endanger prey. Despite its parsimony, the framework offers a tractable prototype with broader ecological applicability for studying how exogenous forcings (e.g., climate-driven phenology), can alter ecosystems.

KEYWORDS
Non-autonomous oscillator
Classical Lotka-Volterra model
Partial migration-driven dynamics
Chaos-Order
Resilience

INTRODUCTION

Many resident wildlife species share their habitat seasonally with their migrating conspecifics, a phenomenon called partial migration (Kaitala *et al.* 1993; Chapman *et al.* 2011; Lundberg 2013; Hansen *et al.* 2019; Peller *et al.* 2022). However, the periodic grouping of residents and migrants of the same species, observed particularly for prey, intrigues ecologists (De Leenheer *et al.* 2017). A key question that has been the foci of much research is that of the existence of asymptotical stable predator-prey interactions under weak prey immigration (Tahara *et al.* 2018; Alebraheem 2021; Kangalgil and Isik 2022; Alebraheem *et al.* 2024). Nevertheless, the dual role of partial migration (*immigration and emigration*) has been largely overlooked.

Here, I investigate how periodic waves of partial prey migration, akin to oscillatory forcing, reshape predator-prey dynamics. First, I introduce a minimalist yet ecologically grounded, dynamical system based on the classical Lotka-Volterra model (Lotka 1925; Volterra 1926), explicitly designating the interacting prey and predators as resident species. Despite idealized assumptions (e.g., exponential prey growth), it offers unparalleled mathematical parsimony, considering only essential functional responses, thus avoiding being engulfed by confounding factors such as refuges, Allee effects, or density-dependence processes (De Leenheer *et al.* 2017). Consequently, the role of partial prey migration as a forcing term becomes clearly discernible. Second, I formulate migration waves determined by the fitness of partial migrants, in accordance with empirical ecological studies (Alerstam *et al.* 2007; Vergara *et al.* 2007; Briedis *et al.* 2018; Nussbaumer *et al.* 2021, 2022). Hence, for both immigration and emigration, the fastest and fittest individuals lead, followed by slower, less fit stragglers, producing a staggered and velocity-dependent migratory flow. With this in mind, I define a simple harmonic oscillator (Gottlieb and Pfeiffer

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2013) as an *ansatz*, to capture the momentum of the entry/exit dynamics of partial migration cycle related to the targeted habitat zone. Finally, I propose a parsimonious heuristic framework that encompasses the Lotka-Volterra model for resident prey and predator species and an oscillator for partially migratory prey, in a non-autonomous 3D system (Ashwin *et al.* 2017), allowing a numerical exploration of how their interplay modulates ecosystem resilience (Holling 1973; Peterson *et al.* 1998; Scheffer *et al.* 2001; Doherty *et al.* 2000; Dakos *et al.* 2015).

However, to probe its limits of sustainability, I adopt a simple definition: species interactions are resilient if they resist, absorb, or readjust to disturbances without collapsing over a specified very long period; otherwise, they are not resilient or experience precarious resilience. Specifically, I investigate whether variation in the magnitude of a stationary partial migration cycle could trigger a regime shift, along with the expected early warning signals (Guttal and Jayaprakash 2008; Scheffer *et al.* 2009; Carpenter *et al.* 2011; Evers *et al.* 2024). Using basic numerical tools (e.g., phase portraits, Poincaré maps), I characterize the resulting regime spectrum. Furthermore, I search for hotspots, i.e., regions in phase space exhibiting resilient species interactions, while the ecological ecosystem is under extreme prey migration pressure. Indeed, I test whether certain initial abundances of resident species can prevent ecosystem collapse in such a case.

Simulations of scenarios in which a net cohort of migratory prey switches to a sedentary behavior at each cycle are also performed. Indeed, flexible strategies have been observed in a significant number of species, where individuals can adopt either migratory or sedentary behavior (Brodersen *et al.* 2014). Thus, I explore the dynamical regimes induced by such partial prey migration with increasing cyclical trends, replenishing resident species. These results will be contrasted to those obtained under a stationary migratory cycle, where immigrant and emigrated prey populations are balanced, viewed through the lens of ecosystem resilience.

The paper is organized as follows. Section II introduces the heuristic framework and the tractable system, with ecological and mathematical grounds. Section III numerically explores partial migration scenarios (stationary and ascending cycles) and their implications for species interactions and ecosystem resilience. Section IV presents concluding remarks.

THE HEURISTIC FRAMEWORK

Several theoretical frameworks can be applied to explore the interplay of partially migratory prey with already interacting resident prey and predator species, depending on the type of inter- and intra-specific functional responses and environmental complexities. For the sake of simplicity, I selected the pioneering classical Lotka-Volterra model for my study, forcing it via a non-autonomous elementary harmonic oscillator, analogous to partial migration.

The Classical Lotka-Volterra Model: "stylized facts" of the Resident Predator-Prey Interactions

The classical Lotka-Volterra model (CLV) selected overly simplistic functional responses and idealized assumptions, but it remains relevant to illustrate the "stylized facts" of predator-prey interactions. Hence, such "idealizations may be far from the truth, without being epistemically inadequate" (Elgin 2004), and it is therefore well-grounded that the CLV constitutes a building block of a heuristic framework. It also specifically describes interactions between resident species, although the terms "resident" and "sedentary" are not used in CLV-related studies unless otherwise stated. Indeed, Volterra had clearly expressed his intention: "let us suppose we have two species living in the same environment" (Volterra 1931). Written as a pair of first-order ordinary differential equations, the CLV incorporates parameters (Table 1) describing the interactions between species as follows:

$$\begin{cases} \dfrac{dx}{dt} = x(\alpha - \beta y) \\ \dfrac{dy}{dt} = -y(\varphi - \mu x) \end{cases} \tag{1}$$

where x(t), and y(t) are the population of prey and predator, respectively.

Table 1 The Parameters of the Classical Lotka-Volterra Model

Parameter	Description
α	Per capita birth rate of prey in the absence of predators
β	Rate of fatal encounters between predator and prey
φ	Intrinsic mortality rate of predators in the absence of prey
μ	Reproduction rate of predator per prey
$\gamma = \frac{\mu}{\beta}$	Rate of converting ingested prey biomass into predator offspring

The model has two solutions:

$$S_0(x,y) = (0,0) \quad \text{and}$$
$$S_1(x,y) = \left(\frac{\varphi}{\mu}, \frac{\alpha}{\beta}\right)$$

Linearization states that S_0 is a saddle point and S_1 behaves either as a center or as a spiral point. Excluding the trivial solution S_0, and under usual initial conditions of strictly positive populations, the prey and predator populations exhibit stable oscillations without converging to S_1, thus defining a limit-cycle in the phase portrait. These interactions are inherently resilient, as they do not lead to ecological collapse. For instance, with parameters $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$, the solutions are the origin and

$$S_1(x,y) = \left(\frac{10}{3}, \frac{1}{3}\right)$$

Figure 1 illustrates these fluctuations when the model is parameterized with P_0 and the initial condition $\mathrm{IC}_0(x_0, y_0) = (0.7, 0.3)$ differs from the two solutions.

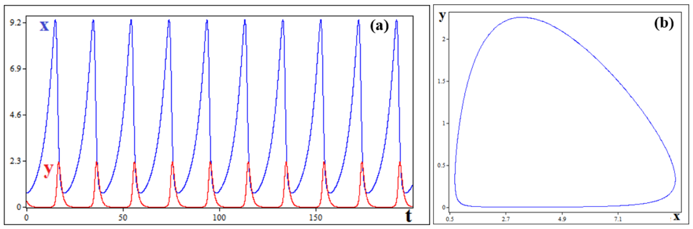

Figure 1 The Classical Lotka-Volterra prey-predator model. Parameters $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$ and initial condition $\mathrm{IC}_0(x_0, y_0) = (0.7, 0.3)$. (a) Time series of resident populations of prey x (blue line) and predator y (red line) up to t = 200, and (b) their limit-cycle in the phase portrait.

By considering these interactions as those of resident prey and predator species in an open ecosystem, I introduce the partial migration cycle of prey as an oscillatory mechanism.

A Non-autonomous Harmonic Oscillator as an Analogue of Partial Prey Migration

Inspired by empirical ecological studies, I propose a simplified non-autonomous harmonic oscillator that describes partial prey migration, where $x_m(t)$ represents the accumulation of migrants in the habitat area and $M(t)$ its velocity at time t:

$$\begin{cases} \frac{dx_m}{dt} = \lambda M \\ \frac{dM}{dt} = A\cos(\Omega t) \end{cases} \tag{2}$$

Table 2 The forcing parameters (all positive)

Parameter	Description
λ	Control parameter of the migration coupling
A	Amplitude of migration velocity
Ω	Forcing frequency

Technically, the velocity M is the derivative of the corresponding innate momentum, i.e. the increment/reduction of partial migrants within the ecosystem. Additionally, the cosine function governs the Hamiltonian flow, shaping the partial migration cycle of prey. Although it is easy to avoid such a non-autonomous velocity vector by introducing a third dependent variable, I keep time t as an explicit variable, with mathematical parsimony guiding this study. Thus, the Hamiltonian of this purely linear oscillator has the formulation:

$$H(x_m, M, t) = \frac{\lambda}{2}M^2(t) - A\cos(\Omega t)x_m$$

$H(x_m, M, t)$ represents the total energy of the oscillator, which is the sum of its kinetic energy and potential energy, respectively.

For $M = 0$, the Hamiltonian is not conserved due to time-dependent forcing, but conservative, which gives periodic orbits in the phase space (x_m, M). For values of M^+, it is also not conserved, but non-conservative with energy growth, exhibiting spirals with drift.

It follows that, in general cases, the exact solutions of (2) are:

$$x_m(t) = \lambda M_0(t) + \lambda\frac{A}{\Omega^2}(1 - \cos(\Omega t))M(t) = M_0 + \frac{A}{\Omega}\sin(\Omega t)$$

By setting $A = \Omega = 1$, and the initial condition $(x_m, M_0) = (0, 0)$, i.e., zero population of migrants, and a null increment at t_0, $x_m(t)$ varies sensitively with λ:

$$x_m(t) = \lambda(1 - \cos(t)), M(t) = \sin(t)$$

The series of regular migratory waves encapsulates the transient occupancy of the habitat area according to the stable period of these oscillations, regardless of the parameter λ. More precisely, the increment M varying in the interval [-1, 1] drives both facets of the cycle, i.e. immigration and emigration, by its positive and negative ranges respectively. First, strictly positive M values govern the entry of partial migrants in the habitat area in two steps. As M increases from 0 to 1, the number of immigrants rises at an increasing pace. Conversely, as M decreases from 1 to 0, it also rises, but at a decreasing pace, reaching zero. The immigrant population has thus reached its maximum level, marking the end of migratory entry into the ecosystem and thus the first facet of the cycle. Second, strictly negative M values govern the exit of partial migrants from the habitat area, also in two steps. When M varies from 0 to -1, and given its absolute value, the number of emigrants rises at an increasing velocity. On the other hand, when M varies from -1 to 0, and also given its absolute value, it rises but at a decreasing velocity until reaching zero. Thus, the withdrawal process is fully realized, signaling that all emigrants have left the ecosystem. With this second facet, the entire migratory cycle is completed (Figure 2).

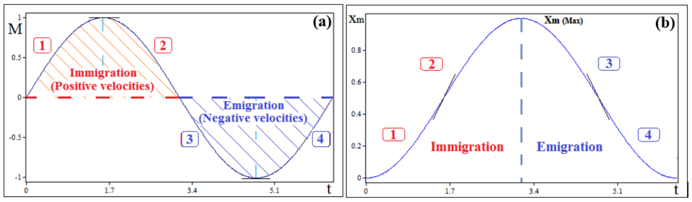

Figure 2 The M-velocity waveform shapes both facets of the migration cycle. Illustration with the initial condition $(x_m(0), M_0) = (0, 0)$ for the cycle n°1. a) Positive values of M drive the migrant population $x_m(t)$ into the ecosystem at an increasing (box 1) and then decreasing (box 2) pace. Conversely, negative values withdraw migrants xm(t) from the ecosystem at an increasing (box 3) and then decreasing (box 4) velocities given their absolute values. (b) Bell-curve of partial migrants $x_m(t)$ in the habitat area. After reaching its maximum number, the migration process reverses and all have left the ecosystem at the end of the cycle.

With momentum kept unchanged, with M_0 = 0 and A = Ω = 1 the partial migrant population increases significantly with magnitude λ. Indeed, for several values of λ ϵ $\in$ {0.1, 0.2, 0.5, 0.7, 1}, the migratory cycle exhibits higher amplitudes (Figure 3a). Therefore, the phase portrait of the accumulation of partial migrants x_m as a function of the velocity M, with the corresponding λ value, exhibits periodic orbits. Figure 3b illustrates, for the selected set of λ, these cycles in phase space, where the (M, x_m) plot moves in counterclockwise orbits from the origin.

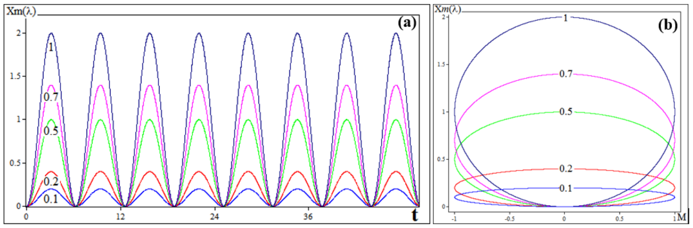

Figure 3 Partial prey migration cycles with A = Ω = 1, and the initial condition $(M_0, x_m(0)) = (0, 0)$ up to t = 50. (a) Accumulation of partial migrants x_m vs. time for selected values of the magnitude λ $\in$ {0.1, 0.2, 0.5, 0.7, 1}. (b) Their phase portraits where (M, x_m) plot rotates 2π counterclockwise from the origin to complete a partial migration cycle.

The Unified Model

Consider the non-autonomous 3D system where x(t) and y(t) are the abundances of prey and predators respectively, and M(t) the velocity/displacement of migratory prey within the ecosystem. It is formulated as follows:

$$\begin{cases} \frac{dx}{dt} = x\left(\alpha - \beta y\right) + \lambda M \\ \frac{dy}{dt} = -y\left(\varphi - \mu x\right) \\ \frac{dM}{dt} = A\cos(\Omega t) \end{cases} \tag{3}$$

where α, β, φ and μ, parameters identical to those of the CLV (see Table 1), and λ, A, and Ω, parameters of the forcing oscillator. (see Table 2). When $\lambda = 0$, the system is reduced to the unforced CLV, exhibiting neutral oscillations around an equilibrium. For $\lambda > 0$, prey migration driven by oscillatory forcing is enabled in the first equation by the term λM, where λ adapts its impact. From then on, the system becomes non-autonomous via $\cos(\Omega t)$ according to the mechanism introduced in the previous sub-section. For small λ, the system can be approximated using perturbation methods. I obtain:

$$\frac{dx}{dt} \approx x(\alpha - \beta y) + \lambda \frac{A}{\Omega} \sin(\Omega t)$$

, where

$$M(t) = M_0 + \frac{A}{\Omega} \sin(\Omega t)$$

As formulated in the first equation, the migrants avoid lethal encounters with predators upon entering the ecosystem and are therefore not affected by the parameter β. They are expected to be moving targets, more vigilant in their new environment, and it will inevitably be difficult for a predator to surprise them. Although studies have reported greater predation avoidance in partial migrants than in residents (Skov *et al.* 2013; Zúñiga *et al.* 2017; Berg *et al.* 2023), in the presented system, this immediate survival of migrants within the ecosystem is lost at the next step, i.e., the iteration at t+1. This cohort is then faced with a lethal encounter rate β and a predator conversion rate μ identical to those of resident prey, as indicated in the second equation. Regarding the third equation, technically, the forcing injects/removes prey periodically into the CLV without a feedback loop from its state variables. Therefore, the system no longer distinguishes between migratory prey and residents that interact together with the resident predator. In the following, I numerically simulate the non-autonomous three-dimensional ODE system in order to evaluate its resilience with the 4th-order Runge-Kutta method.

NUMERICAL RESULTS

To scrutinize the dynamical regimes of the system, predator-prey interactions are considered resilient if they persist until at least $t = 10^5$. Otherwise, they are not resilient if they collapse before $t = 10^4$, and resilience is precarious for $t \in [10^4, 10^5]$. In the first analysis, the magnitude λ serves as the control parameter for the stationary partial migration cycle. Specifically, λ is categorized as follows: low migration intensity for $0 < \lambda \leq 0.5$, moderate intensity for $0.5 < \lambda \leq 2$, and massive intensity for $\lambda > 2$. The second analysis examines partial prey migration cycles with a positive trend. All simulations use fixed parameters $A = \Omega = 1$.

Stationary Cycles of Partial Prey Migration Imply Elusive Ecosystem Resilience

By setting $M_0 = 0$, the partial prey migration adheres to a stationary cycle fully anchored in recurring dates, exhibiting identical waveform movements. Hence, the number of immigrants and emigrants must be roughly balanced. This constraint implies that losses of partial migrants due to predation within the ecosystem are compensated either by reproduction or by recruitment of a cohort of residents.

Figure 4 provides a direct comparison of partial migrating prey $X_m(\lambda)$ for selected λ magnitudes and resident prey abundance when the CLV and the partial prey migration oscillator are not yet connected. I find that a single cycle of resident prey-predator interactions encompasses three migration pulses, allowing us to explore the resilience limits of the system. Further studies should consider A and Ω as control parameters.

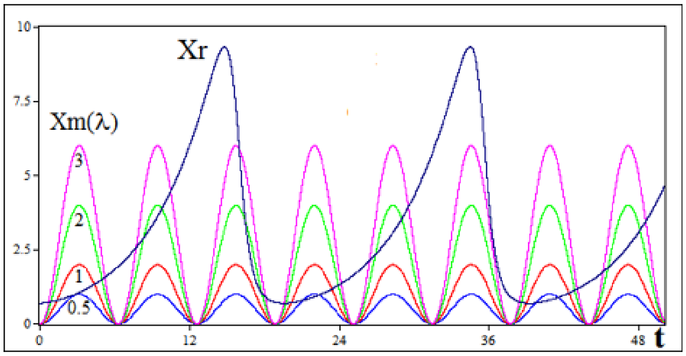

Figure 4 Accumulations of partially migratory prey $X_m(\lambda)$ for the magnitudes $\lambda \in \{0.5, 1, 2, 3\}$ and of resident prey X_r before forcing the CLV by the oscillator up to $t = 50$. CLV parameters $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$, and initial condition $IC_0(x_0, y_0) = (0.7, 0.3)$. Initial condition of the partial migration oscillator $(M_0, X_m(0)) = (0, 0)$.

Dependence on the magnitude parameter λ

In the first set of simulations, the weak coupling of the oscillator leads to immediate non-periodic fluctuations in species populations. As shown in Figure 5, for $\lambda = 0.1$ and 0.2, the time series of $x(t)$ and $y(t)$, and in particular the phase portraits of the state variables (x, y) suggest asymptotically unstable oscillations under parameters $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$ and the initial condition $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$.

Furthermore, the Poincaré sections, plotted when $M = 0$ (i.e., at the precise moments of the beginning and end of the partial migration cycles, as well as at the moments separating immigration and emigration), illustrate the complex trajectory of species populations.

These fluctuations persist resiliently for λ in the interval $]0, 0.22[$. However, a slight increase in coupling, i.e., a partial migration magnitude varying only by $\Delta\lambda = 0.01$, results in an almost immediate vanishing of predator-prey interactions, signaling a critical transition. Since the catastrophic event results from the continuous change in λ, the system has crossed a bifurcation-induced tipping point (or B-tipping).

Starting with the sudden and drastic change at the critical value $\lambda_c = 0.23$ and for slightly higher values, interactions exhibit volatile dynamics and therefore do not even reach the threshold of precarious resilience. For example, at $\lambda = 0.5$, species become extinct around $t \approx 170$ as shown in Figure 6. The upward alignment of the last four prey population peaks may suggest an early warning signal of impending ecosystem collapse.

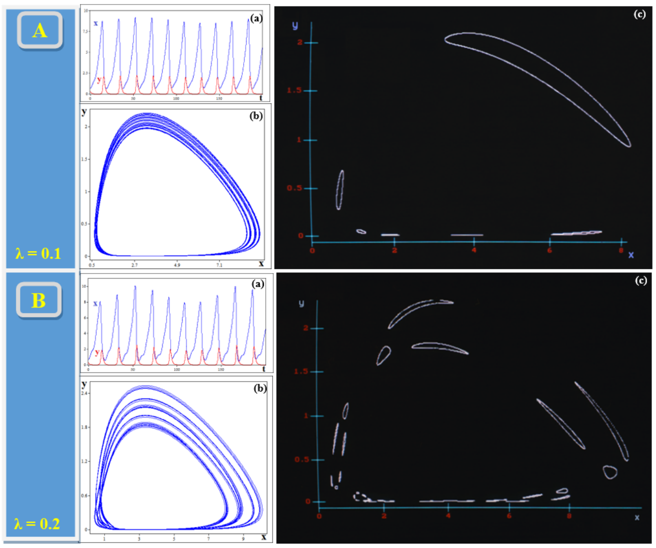

Figure 5 Numerical simulations with parameters $P_0(\alpha, \beta, \lambda, \varphi, \mu) = (0.2, 0.6, \lambda, 1, 0.3)$ and initial condition $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$. (a) Time series of x and y (prey and predator abundances respectively) first $t = 200$ (b) Phase portrait of state variables x and y (c) Poincaré maps ($M = 0$) Panel A: $\lambda = 0.1$. Panel B: $\lambda = 0.2$.

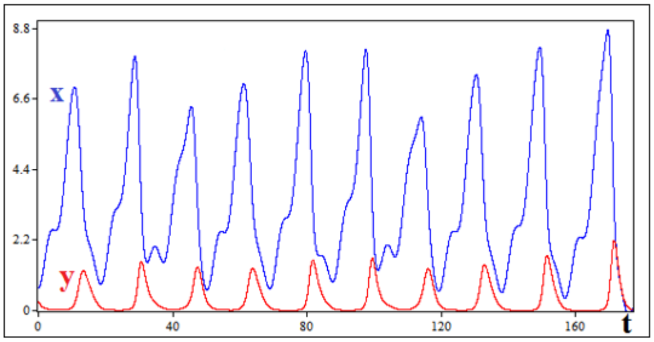

Figure 6 Time series of prey and predator accumulations, x and y respectively, for magnitude $\lambda = 0.5$ of partial prey migration. The collapse occurs at $t \approx 170$. Parameters $P_0(\alpha, \beta, \lambda, \varphi, \mu) = (0.2, 0.6, 0.5, 1, 0.3)$, and the initial condition $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$.

Surprisingly, resilient interactions are restored within very narrow windows of λ. These hotspots are scattered and detected in small numbers under the aforementioned parameters $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$, and the initial condition $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$. Figure 7 presents time series of prey and predator accumulations, x and y respectively, phase portraits and Poincaré maps ($M = 0$) for some of the identified magnitudes, e.g., $\lambda \in \{0.7, 1, 1.5\}$, which exhibit rare resilient interactions. Indeed, to avoid prey extinction and therefore predator starvation, a key condition to ensure ecosystem resilience must be met: $\lambda M(t) > x(\alpha - \beta y)$.

Dependence on initial conditions of the species populations and parameter α

The proposed system also exhibits extreme sensitivity to the initial sizes of resident species, as interactions can abruptly disappear even after small changes. Indeed, the resilient regimes shown in Figure 7 rapidly collapse when $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$ is adjusted to $IC_1(x_0, y_0, M_0) = (0.6, 0.2, 0)$, while the parameters remain unchanged. Conversely, the volatile dynamics illustrated in Figure 6 for $\lambda = 0.5$ becomes resilient when the initial conditions are slightly shifted from $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$ to $IC_2(x_0, y_0, M_0) = (0.9, 0.3, 0)$, as illustrated in Figure 8, panel A. It is also worth mentioning the significant dependence on prey birth rate, the parameter α. For example, the collapsed regime mentioned in Figure 6 becomes resilient when only the parameter α varies from 0.2 to 0.5 (Figure 8, Panel B).

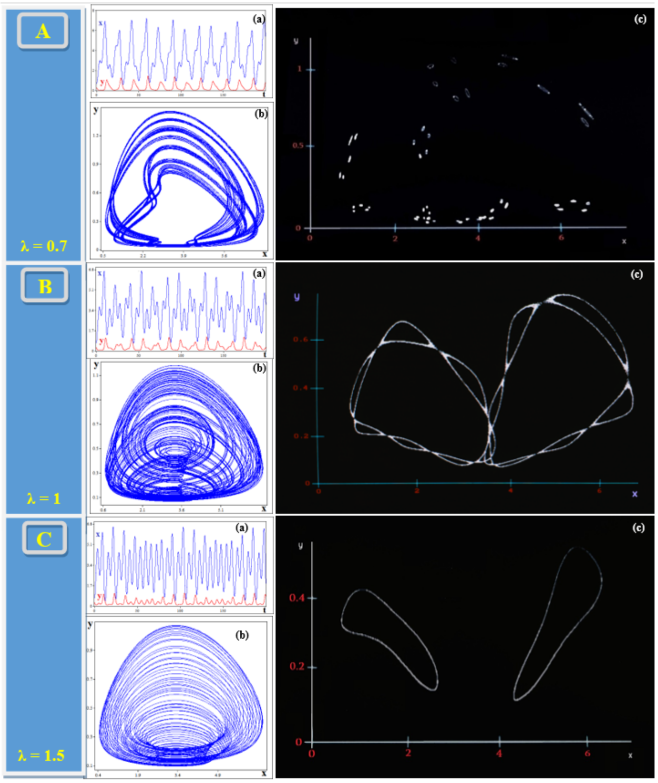

Figure 7 Hotspots of resilient quasi-periodic or chaotic dynamics in a very narrow window of magnitude λ. Numerical simulations with parameters $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$ and initial condition $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$. (a) Time series of x and y, the abundances of prey and predators, respectively, for the first 200 iterations. (b) Phase portrait of x and y. (c) Their Poincaré map ($M = 0$). Panel A: $\lambda = 0.7$, Panel B: $\lambda = 1$, Panel C: $\lambda = 1.5$

A threefold complexity of chaos

To characterize the chaotic nature of the system, the largest Lyapunov exponent (LLE) is computed. Thus, the detection of a single positive exponent among the three for a three-dimensional system confirms the signature of chaos. As shown in Figure 9, the LLE spectra computed for $\lambda \in [0, 1.7]$ and the same P_0 parameters, but under two distinct initial conditions, namely $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$ and $IC_1(x_0, y_0, M_0) = (0.9, 0.3, 0)$, state the hallmark of chaos.

Alongside this, the dissimilarity of LLE spectra provides compelling evidence of sensitive dependence on initial conditions. Furthermore, sawtooth-shaped spectra with steep peaks and dips are likely indicators of tipping points and thus express regime shifts (Nazarimehr *et al.* 2017), either in response to the variation of the parameter λ or to the initial conditions. The three dependencies of the system under λ, the initial conditions, and the

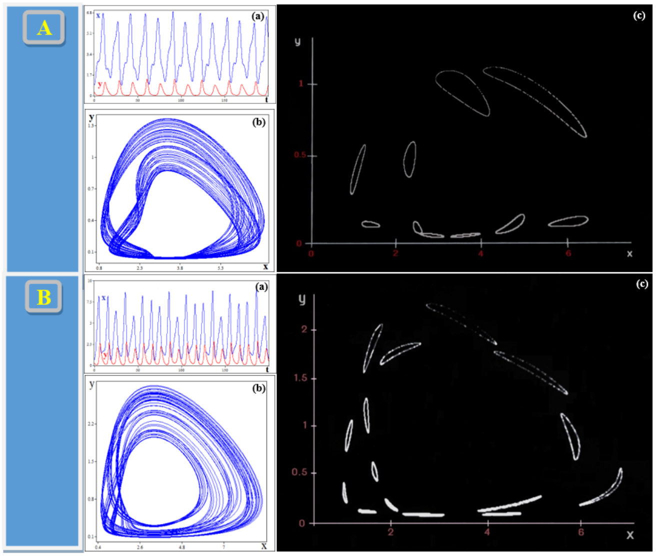

Figure 8 Sensitive dependencies on the initial sizes of species and the parameter α. (a) Time series of state variables x and y, the prey and predator populations, respectively; first $t = 200$, (b) the corresponding phase portrait, and (c) Poincaré map after transients died down. Panel A: Parameters $P_0(\alpha, \beta, \lambda, \varphi, \mu) = (0.2, 0.6, 0.5, 1, 0.3)$ and $IC_1(x_0, y_0, M_0) = (0.9, 0.3, 0)$. Compare with collapsed regime in Figure 6 with $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$. Panel B: Parameters $P_0(\alpha, \beta, \lambda, \varphi, \mu) = (0.5, 0.6, 0.5, 1, 0.3)$ and $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$. Compare with the same collapsed regime in Figure 6 where $\alpha = 0.2$.

functional response parameters α might be expected to entail an intertwined and highly entangled basin of attraction, delimited by fractal boundaries.

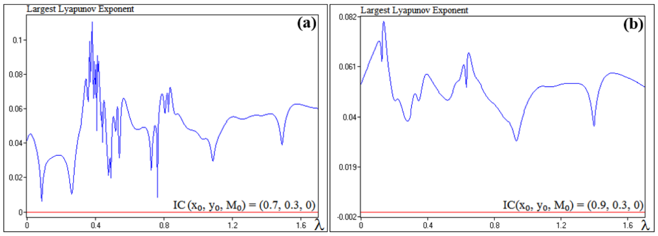

Figure 9 Largest Lyapunov exponent (LLE) spectra computed for migration magnitude λ varying in the range $[0, 1.7]$. $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$, and two distinct initial conditions. (a) LLE spectrum with $IC_0(x_0, y_0, M_0) = (0.7, 0.3, 0)$. (b) LLE spectrum recomputed with $IC_1(x_0, y_0, M_0) = (0.9, 0.3, 0)$.

Upward Cycles of Partial Prey Migration Preserve Ecosystem Resilience

In scenarios where M_0 has strictly positive values, and $\lambda = A = \Omega = 1$, partial prey migrations exhibit upward cycles. Thus, a number of partially migratory prey are recruited by its resident species in the habitat area during each cycle (Figure 10).

The velocity $M(t)$, or augmentation/reduction of migrants, varies in the range $[-1 + M_0, 1 + M_0]$, as shown for example in Figure 11a for several values of $M_0 \in \{0, 0.5, 1, 2\}$. Furthermore, Figure 11b illustrates the cycles of partial migrants $X_m(M_0)$ for the selected values of M_0 compared to the abundance of resident prey X_r, already interacting with the predator, before coupling. In the following, still with $\lambda = 1$ and considering M_0 as a control parameter, I examine how ascending cycles of partial prey migration shape overall ecosystem dynamics and thus its resilience. Here, the recruitment is considered low for $0 < M_0 \leq 0.2$, moderate for $0.2 < M_0 \leq 1$, and massive for higher values.

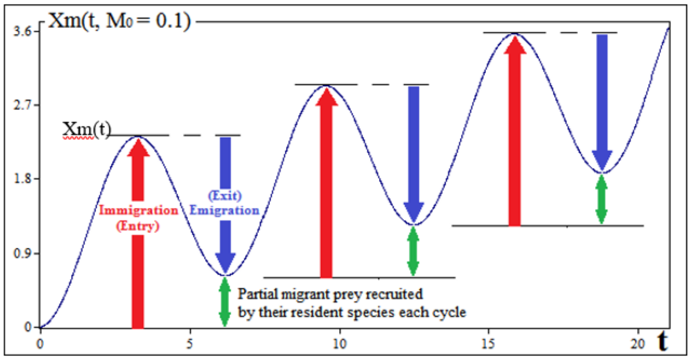

Figure 10 A net cohort of migrants settles in the ecosystem each cycle. Time series of partial prey migration up to $t \approx 22$. $\lambda = 1$ and initial condition $\text{Xm}(t, M_0) = (0, 0.1)$.

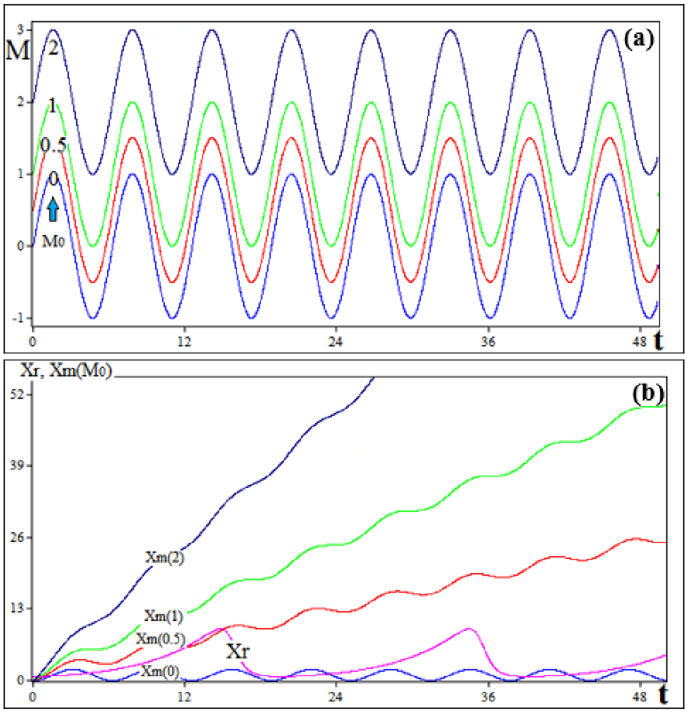

Figure 11 Upward cycles for several M_0 values and corresponding abundances of partial migratory prey. The migratory prey population is governed by a stationary cycle when $M_0 = 0$, and by upward cycles when $M_0 > 0$. Parameters: $\lambda = A = \Omega = 1$, and initial condition $(X_m, M_0) = (0, M_0)$, till $t = 50$. (a) $M(t)$ for $M_0 \in \{0, 0.5, 1, 2\}$, and (b) time series of $X_m(M_0)$ for the selected M_0 compared with the resident prey population X_r already interacting with predators, before coupling. Parameters $P_0(\alpha, \beta, \varphi, \mu) = (0.2, 0.6, 1, 0.3)$, and the initial condition $IC_0(x_0, y_0) = (0.7, 0.3)$.

Double-peaked fluctuations and phase-locking

Numerical computations reveal pronounced periodic double-peaked fluctuations in the prey population for $M_0 \in \{0.1, 0.2\}$, resulting in characteristic orbits in the phase portraits (Figure 12). This pattern is derived from the asynchrony between the waxing and waning of resident and partially migratory prey populations, associated to the recruitment of a cohort of migrants by the resident population each cycle. As M_0 increases from 0.1 to 0.2, both prey and predator populations show slow but steady growth, observed across the entire range of $M_0 \in [0, 0.2]$.

In the next, broader range of $M_0 \in [0.2, 1]$, and after transients died down, the populations of both species increase and maintain stable fluctuations, adopting regular wave patterns. These partial migration cycles with moderate recruitment introduce a significant stabilizing effect on intrinsic species interactions. Indeed, for M_0 equal to 0.5 and 1, phase portraits exhibit periodic orbits, confirming that newly settled migrants do not jeopardize the ecosystem resilience (Figure 13). More specifically, the time series reveal a characteristic phase locking, with the predator population peak lagging at approximately a quarter cycle (90°) compared to that of the prey. This type of asynchronous fluctuations is consistent with the literature on in-phase, anti-phase, and phase-locking synchronizations in coupled-species oscillators (Winfree 1967; Vandermeer 2006; Vasseur and Fox 2009; Smirnov and Pikovsky 2024).

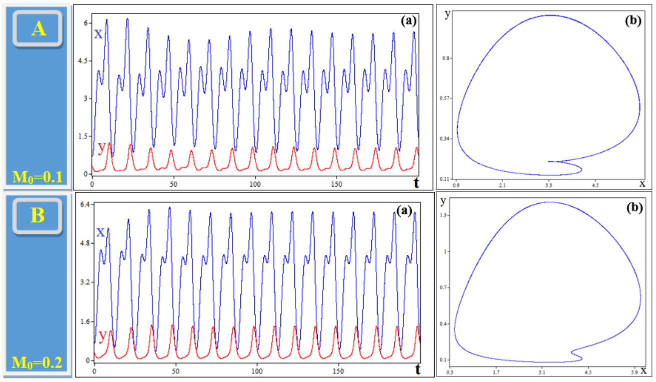

Figure 12 Double-peaked prey and predator populations with low recruitment. Dynamical regimes with weak ascending cycles of the partial migration. $P_0(\alpha, \beta, \lambda, \varphi, \mu) = (0.2, 0.6, 1, 1, 0.3)$ and initial condition $(x_0, y_0, M_0) = (0.7, 0.3, M_0)$. (a) Time series of the prey and predator populations up to $t = 200$, and (b) their phase portraits after transients died down. Panel A: $M_0 = 0.1$. Panel B: $M_0 = 0.2$.

"Catching up" and overtaking game for massive recruitment

The partial migration of prey exhibiting extreme upward cycles stabilizes, as in the previous cases, the species populations and induces limit cycles (Figure 14). It is noteworthy that a "catching up" process between the prey and predator populations occurs, balancing them at $M_0 = 6.05$.

The predator species experiences a phenomenal increase in abundance due to the recurrent and strong recruitment of immigrant prey, via the conversion rate of ingested prey into predatory offspring. This process, observed for example at the invasive level of $M_0 = 80$, leads to a predator population exceeding tenfold that of the prey. Although this ratio may suggest that the resident prey is an endangered species, the settlement of partially migratory prey replenishes the residents each cycle and thus prevents their extinction.

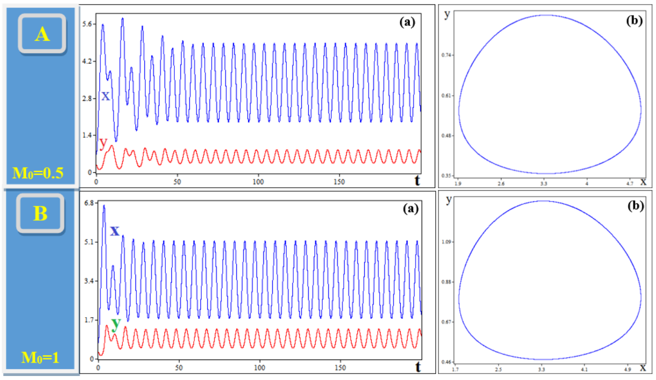

Figure 13 Phase locking of predator and prey populations by approx. one-quarter cycle (90°) for moderate recruitment. Parameters $P_0(\alpha, \beta, \lambda, \varphi, \mu) = (0.2, 0.6, 1, 1, 0.3)$ and the initial condition $(x_0, y_0, M_0) = (0.7, 0.3, M_0)$. (a) Time series of prey and predator populations up to $t = 200$, and (b) their limit cycle in phase space. Panel A: $M_0 = 0.5$. Panel B: $M_0 = 1$.

This result is consistent with the seminal contribution of Levins (1969), and the source-sink habitats of the metapopulation approach (Holt 1985; Hanski 1999; Taylor and Hall 2012). Indeed, Pulliam (1988) notes that in sink areas: "the population may persist in such habitats, being locally maintained by continued immigration from more productive 'source' areas nearby." Here, no discontinuity in ecosystem resilience is detected for $M_0 > 0$ of partial prey migration cycles since the domain of attraction envelops the entire phase space.

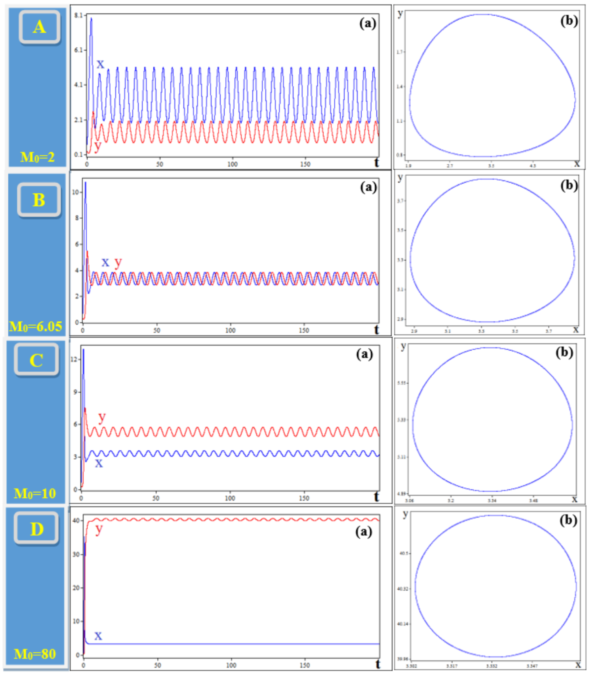

Figure 14 The predator population approaches, catches up with, and then overtakes the prey population. Parameters $P_0(\alpha, \beta, \lambda, \varphi, \mu) = (0.2, 0.6, 1, 1, 0.3)$ and initial condition $(x_0, y_0, M_0) = (0.7, 0.3, M_0)$. (a) Time series of prey and predator populations up to $t = 200$, and (b) associated limit cycle in the phase space after transients died down. Panel A: $M_0 = 2$. Panel B: $M_0 = 6.05$. Panel C: $M_0 = 10$. Panel D: $M_0 = 80$.

CONCLUSION

In this study, I focused on the magnitude and trend of the cycle, two key dimensions of partial prey migration, conceptualized as an oscillatory mechanism. Thus, the proposed system uncovered a striking dichotomy: partial migration acts as a *dual* driver of chaos and order in open ecological ecosystems. Hence, even a low magnitude of stationary migratory cycles inject critical instability into predator-prey interactions, fostering resilient chaos that persists until the migration magnitude crosses a bifurcation-induced threshold. Beyond this B-tipping, collapse ensues, yet chaos resurges in localized hotspots, suggesting fractal basin boundaries and a non-monotonic dependence on magnitude, initial conditions and α parameter.

Such behavior mirrors the sensitive dependence of driven oscillators, where minute parameter shifts precipitate phase transitions. Conversely, upward-trending cycles suppress the risk of ecosystem collapse, stabilizing interactions in predictable limit cycles even leading to phase synchronizations. This chaos-to-order transition challenges conventional views on the destabilizing role of immigration, positioning flexible migratory behavior as a key ecological parameter. Indeed, the route from chaotic regimes, ecosystem extinction, and elusive resilience to the realm of order is simply unlocked when the trend in partial prey migration cycles becomes strictly positive, even slightly. This dichotomy echoes a critical phenomenon in oscillatory systems, where the sign of the trend (positive or neutral) determines whether dynamics converge toward equilibrium or diverge into turbulence.

Mainly, I acknowledge deliberate simplifications of the introduced heuristic framework, such as multiple waves of partial migration for a single predator-prey interaction cycle. It nevertheless provides a preliminary and tractable prototype for a valuable approximation of how exogenous pulses trigger bifurcation-like behaviors (e.g., climate-induced phenological changes). Framing migration as a forced oscillator underscores its capacity to reconfigure entire food webs, including protected habitats. The tractable system is also fully valid for being forced via its second equation by the oscillator of a partially migratory predator with a similar or delayed cycle. In further studies, incorporating a latency period to account for resident species interactions outside of partial migration cycles may prove more realistic. Therefore, future works could potentially unveil new complex regimes.

Ethical standard

The author has no relevant financial or non-financial interests to disclose.

Availability of data and material

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of interest

The author declares that there is no conflict of interest regarding the publication of this paper.

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