Extended Abstracts

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Exploring the principles of coexistence in invader-driven replicator dynamics

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Resum *(CAT)*
En aquest treball, utilitzem la "replicator equation" per explorar una de les qüestions fonamentals de la biologia evolutiva i l'ecologia: com es genera i es manté la biodiversitat? Centrant-nos en els sistemes "invader-driven", en què les interaccions o "fitnesses" de les espècies estan determinades per l'espècie invasora independentment de l'espècie envaïda, busquem relacionar les "fitnesses" amb les espècies que coexisteixen als estats finals d'equilibri. Descobrim el mecanisme que regeix la selecció d'espècies supervivents i que maximitza la resistència del sistema envers les invasions externes, i trobem que el nombre mitjà d'espècies que coexisteixen creix amb el nombre inicial d'espècies.

Keywords: *biological modelling, replicator equation, pairwise invasion fitness matrix, multi-species system, coexistence, invasion resistance.*

Abstract

Studying the non-linear and often complex dynamics of large systems of interacting species, competing or cooperating between them, can help to discover the principles that, in ecosystems, lead some species to survive and coexist, while others go extinct, to better understand of one of the central questions in ecology and evolutionary biology that remains unsolved, which is how biodiversity is generated and maintained. In the early 1970s, ecologists widely accepted that the stability and resilience observed in rich ecosystems were enhanced by complexity and biodiversity, until in 1972 the paradigm shifted completely when Robert May mathematically showed that random complexity tends to destabilise system dynamics [3]. This raised a contradiction between observation and theory known as the ecology paradox or diversity-stability debate, highlighting the need for some hidden structure or pattern in nature, such as the antisymmetric prey-predator interactions [1]. In this work, we study invader-driven interactions as a potential mechanism for the stabilization of large complex systems and we find that, under certain assumptions, invader-driven systems lead to the coexistence of species.

We use the replicator equation as a theoretical framework [4], which originated in game theory but has been widely applied to biology and epidemiology [2]. Given a system with N species, $S = \{1, 2, \dots, N\}$, consider the pairwise invasion fitness λ_i^j from species i to j, with $i, j \in S$ and $\lambda_i^i = 0$, and the invasion fitness matrix $\Lambda = (\lambda_i^j)_{i,j\in S}$. Then, the replicator equation models the time evolution of the species frequencies $\mathbf{z} = (z_1, z_2, \dots, z_N)$, with $\sum_{i\in S} z_i = 1$ and $0 \le z_i \le 1 \ \forall\, i \in S$, as

$$\dot{z}_i = \Theta z_i((\Lambda \mathbf{z})_i - \mathbf{z}^\top \Lambda \mathbf{z}) = \Theta z_i \left(\sum_{j\neq i} \lambda_i^j z_j - Q(\mathbf{z}) \right), \quad i \in S,$$

where the constant $\Theta \geq 0$ is the speed of dynamics and $Q(\mathbf{z})$ is the global mean fitness or system resistance to external invasion. In particular, we focus on invader-driven systems, in which pairwise interactions are determined by the invading species regardless of the invaded one, i.e., $\lambda_i^j = \lambda_i(1-\delta_i^j)\ \forall\, i,j \in S$, so each species i is characterized by its active trait λ_i. We study the equilibrium states $\mathbf{z}^*$ to understand how fitnesses in the case $\lambda_i > 0\ \forall\, i \in S$ relate to the set of surviving or coexisting species at equilibrium, $S^* = \{i \in S \mid z_i^* > 0\} \subseteq S$, finding that $Q^* = Q(\mathbf{z}^*)$ plays a crucial role in the species selection process.

We prove that locally asymptotically stable equilibria are always composed of the top $n = |S^*|$ species without gaps, with fitnesses $\lambda_N \leq \cdots \leq \lambda_n \leq \cdots \leq \lambda_2 \leq \lambda_1$ and $2 \leq n \leq N$, and, furthermore, we find numerical evidence that each system contains just one of these equilibria, which in turn is a global attractor (any initial condition with all species present tends asymptotically towards it). Therefore, for each S there is a unique S^* that can be asymptotically reached by the dynamics and, hence, a unique set of species characterized by n that end up coexisting. We discover the mechanism ruling the species selection (see Figure 1), which starting with two species iteratively adds a species $i \in S$ if $Q_{i-1}^* < \lambda_i$, that is, if it can invade the previous $i-1$, until some species n meets the condition $\lambda_{n+1} < Q_n^* < \lambda_n$. Moreover, we prove that in each step Q^* increases, $Q_{i-1}^* < Q_i^*$, so this biological process tends to maximize the system resistance to invasion.

Lastly, using this mechanism we create an algorithm that allows to find n for several invader-driven systems generated randomly with $\lambda_i \sim \mathcal{U}[0,1]$, from $N = 5$ to $N = 500$. Fitting the data we find that the mean number of coexisting species increases according to $\bar{n} = 1.381\sqrt{N}$, suggesting that invader-driven interactions could be a potential mechanism through which ecosystems stabilize and maintain biodiversity.

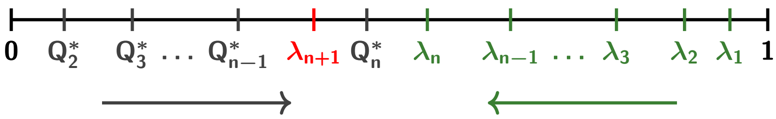

Figure 1: Species selection mechanism in invader-driven systems, $0 < \lambda_N \leq \cdots \leq \lambda_n \leq \cdots \leq \lambda_2 \leq \lambda_1 \leq 1$.

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References

[1] T. Chawanya, K. Tokita, Large-dimensional replicator equations with antisymmetric random interactions, *J. Phys. Soc. Japan* **71(2)** (2002), 429–431.

[2] S. Madec, E. Gjini, Predicting *N*-strain coexistence from co-colonization interactions: epidemiology meets ecology and the replicator equation, *Bull. Math. Biol.* **82(11)** (2020), Paper no. 142, 26 pp.

[3] R.M. May, Will a large complex system be stable?, *Nature* **238(5364)** (1972), 413–414.

[4] P.D. Taylor, L.B. Jonker, Evolutionarily stable strategies and game dynamics, *Math. Biosci.* **40(1-2)** (1978), 145–156.