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Population viability in three trophic-level food chains

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Abstract

The perpetuation of three-trophic level ecosystems where the three species exhibit unpredictable time-varying survival strategies is described by a specific set, the viability kernel, gathering all states from which there exists at least one trajectory safeguarding each species over a given density threshold. The strategies permitting this property are delineated and called viable strategies. All solutions starting outside the viability kernel lead to too low densities or extinction. The viability approach highlights the timing of strategy changes necessary for a system to perpetuate itself or alternatively to lead one species to extinction.

The study of the dependence of the viability kernel on the admissible sets of strategies reveals the minimal flexibilities necessary for the existence of the system. The shape of the viability kernel determines whether the exogenous addition or substraction of prey or predator will endanger the system or not, thus gathering different experiments with opposite results. The comparison of the coexistence kernel with viability kernels for one, two or three species points out the importance of repeated strategies, not necessarily in a periodic manner, thus emphasizing the concept of repetitions in ecosystems instead of cycles as a key feature of coexistence.

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1. Introduction

Which three-trophic food chains can perpetuate themselves, and if so, how should interactions vary between the three levels, as the dynamics could sometimes lead a species to the verge of extinction? We suggest to explore this question, completing the concomitant question of persistence, which has been an important theme in population dynamics [11,12,14,13,10,9,18–20,23]. We discuss permanence, persistence and viability in Appendix A.3.

Co-evolution was presented as a dynamical game, where each individual was thought to adopt a "fitness-maximizing strategy" [6,7]. A species can then be identified to its strategy [1], or by a whole strategy set, benefiting to individuals who are not evolutionary identical [8,38,39]. Brown and Vincent [8] pointed out that the fitness of an individual in a community is bounded by evolutionary constraints. Strategies are allowed to vary only within a closed set, representing admissible bio-diversity, so that a prey species is defined by its strategy u, the predator by v, and the super-predator by w, within the constraints:

$$u(t) \in U, \quad v(t) \in V, \quad w(t) \in W, \tag{1}$$

where U, V, and W are closed sets included in $[0, \infty[$. In this formulation, any predator characterized by $v \in V$ can hunt a prey of strategy $u \in U$, and any super-predator $w \in W$ can hunt a predator $v \in V$. Sih et al. [37, p. 296] for example concluded that "environmental stress can either increase or decrease the importance of predation", and that "the outcome depends on the relative effects of stress on predation rates and on prey growth rate". Hickman [17] showed that plants of annual species *Polygonum cascadense* allocate proportionally more resources to reproduction in harsh open habitats than in more moderate habitats, and that these differences are developmentally plastic, adapting to short-term environmental unpredictability. Giesel [15, p.75], from studies of passerine birds, concludes that the variability in fertility is an "important adaptation to account for environmentally induced unpredictability of the major selective forces". Wilbur [41,43] observes the plastic growth rate and variable size at metamorphosis of amphibians as adaptations to the uncertain environment of temporary ponds, knowing that these morphological variations are induced defenses rather than a genetic polymorphism [29].

The assumption that strategies can vary within certain fixed bounds changes the kind of results to be expected: beside asymptotic patterns, all trajectories issued from all states in finite time are also worth studying. As pointed out by Law and Morton [24, p. 763] indeed, "it is not clear that local asymptotic stability is an appropriate condition for coexistence, for species may coexist