Eco-Evolutionary Dynamics: Surveying how predation and cyclical temperature forcing influence emergent community structure

Empirical data and theory agree that the introduction of predation can facilitate a greater number of species coexisting within a guild (Paine, 1966; Holt, 1977; Holt et al., 1994; Chesson, 2000; Leibold et al., 2017). However, a thorough mechanistic grasp of the fundamental physical constraints, the intermediate causal relationships – such as the ways in which predation may promote guild diversity – and the overall system behavior, remains crucial for understanding biological systems. Ecological theory is increasingly being translated into real world application (Anderson et al., 2021; Mouquet et al., 2015). Navigating such applications under a warming climate, and other intensifying anthropogenic pressures necessitates more accurate forecasting and a detailed understanding of individual mechanisms. This study examines one such system by looking at the role, if any, that predation plays in guild diversity. Our approach models the number of species which can stably coexist with and without predation.

Our line of inquiry follows an approach which showed that cyclical temperature forcing in species coexistence models allows for greater species trait diversity (Kremer and Klausmeier, 2017). Without temperature forcing, trait evolution is optimized for whichever species has the trait which is equal to the constant temperature value. Our periodic setup prevents any one species from being optimal at all times, allowing seasonal specialists to coexist. Prior models include regional migration – preventing true extinction – or do not introduce predation. We explore whether this increase in *species packing* – "the study of the co-occurrence of different species of organisms in a particular sampling area (Slobodkin, 2001)" – holds under more stringent modeling conditions. Hence, we have no regional migration and introduce predator-prey dynamics. We ask the question: Does top-down predation increase species packing in closed systems? We believe that predation may compress realized niche widths, reducing absolute niche overlap – *limiting similarity* – which could create space for increased guild diversity.

Methods

This project focuses on coupling ecological and evolutionary model dynamics under periodic environmental forcing, a computationally demanding, yet technically feasible extension of existing population density models (Kremer and Klausmeier, 2017). This joint approach facilitates quantitative descriptions of individual mechanisms, species competition, and long term community structure using computer simulation assisted by analytical methods.

Trait based predator-prey dynamics

$$\frac{dP}{dt} = a\sum_{i=1}^{\mathcal{N}} n_i P - m_P P \qquad \text{(Predator)}$$

$$\frac{dn_i}{dt} = \left(\mu(x_i)R - aP - m\right) n_i \quad \text{(Prey } i\text{)}$$

$$R = R_{\text{tot}} - \sum_{i=1}^{\mathcal{N}} n_i - P \qquad \text{(Resource)}$$

$$T(t) = \bar{T} + A\sin\left(\frac{2\pi t}{\tau}\right) \quad \text{(Temperature)}$$

P	predator density
n_i	density of prey species i
a	predator attack rate
m_P	predator mortality rate
$\mu(x_i)$	growth rate of species i
R	resource availability
R_{tot}	total resource
m	prey mortality rate
$\mathcal{N}$	number of prey species
x_i	temperature trait of species i
$\bar{T}$	mean temperature
A	temperature amplitude
τ	period (1 year)

We use a system of differential equations, including one equation for each prey species coupled with a predator equation. The trait we focus on is thermal optimum, such that populations have a set temperature which facilitates their fastest growth. The temperature is periodically forced using sine waves; this emulates real world temperature fluctuations in varying climate regimes, smaller amplitude being analogous to the tropics, larger to more temperate regions.

We use canonical adaptive dynamics frameworks, especially the formulation outlined in Brännström et al. 2013, to simulate community trait evolution. Our methods rely heavily on numerical solutions due to ecological systems' tendency to exhibit non-linear interactions, high dimensionality, and sensitivity to initial conditions, making closed form solutions difficult to obtain, exceedingly so in biologically realistic parameter regimes (Lorenz, 1963; Beckage et al., 2011). We avoid some of these pitfalls by utilizing numerical tools and mathematical techniques which were developed to scrutinize long-term dynamics, simplify system analysis, and constrain complicated models. These approaches have been invaluable in deepening our understanding of emergent processes as well as the mechanisms which drive them across ecological systems (Mouquet et al., 2015).

Analyzing adaptive dynamics

We begin our analysis by solving for ecological dynamics with empirically motivated parameter values. This requires finding a stable attractor, in our model taking the form of a limit cycle which begins and ends on the same value. This can be imagined as representing the conditions late on December 31st leading to the dynamics early the following morning, January 1st. This analysis simulates τ or one year of population densities over time. (fig 1)

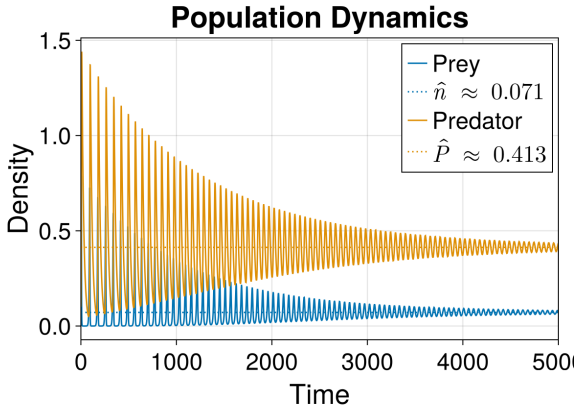

Figure 1: Constant temperature conceptual model: Population density of a predator P, and prey n, approach ecological equilibrium over time.

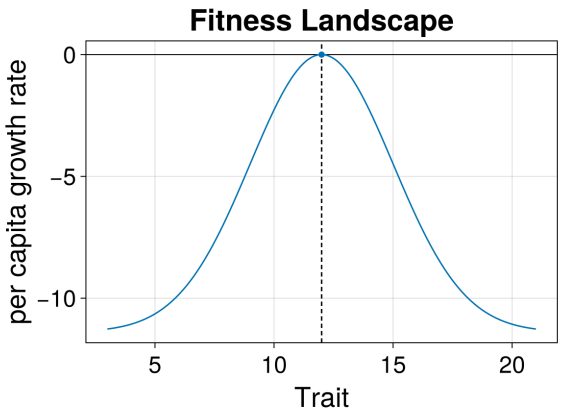

Figure 2: Single species fitness landscape at eco-evolutionary equilibrium.

After obtaining our limit cycle we introduce trait based evolution, tracking thermal optimum at the ecological attractor. This is justified by a separation of timescales between ecological and evolutionary dynamics, that is, the ecological system has stabilized before evolution enters the picture. To do this we use game theoretic framing to find our communities *evolutionarily stable strategy* (ESS) – a community structure where the population has adopted a trait which out-competes all other traits in a given environment under natural selection (fig 2). Species possessing these optimal traits are *uninvasible*, since no mutant species can invade

in their presence. This is followed by finding those ESS which are perturbation stable – also known as an *evolutionarily stable community* (ESC) – Once this is done for our starting species, we find fitness landscapes representing local minima and introduce new species where they can stably coexist, computing their ESS and ESC using the prior techniques. We then sweep our parameter space using numerical continuation and generate a bifurcation diagram showing how communities structure themselves as our temperature amplitude grows (fig 3).

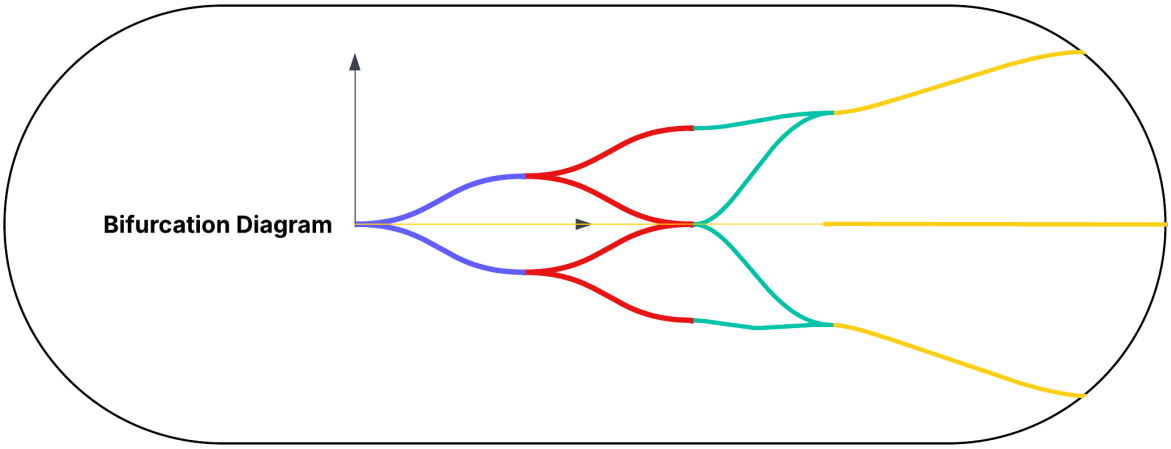

Figure 3: Conceptual sketch of a community structure bifurcation diagram. If our hypothesis is true then we would expect the diagram with a predator to show greater diversity than the one with predators absent.

Key takeaway

Comparing the maximum number of and the general trend in species diversity which emerges from our model, against a baseline without predation will shed light on whether predation facilitates species packing, decreases diversity, or has no effect on the number of species which can coexist on a shared resource.

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