

Revisiting the Rosenzweig-MacArthur model with fast adaptive behavior through mean-field games

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Introduction

Game theory is the natural tool to model the behavior of animals, who must respond to the behavior of other animals as well as complex and rapidly shifting environments. The application of game theory game theory, has led to theoretical strides in understanding the complex interplay between behavior and population dynamics ?. Applying game-theory to patch-choice models gives an understanding of why animals are not all clustered at the best spot, (Cressman et al., 2004; Abrams et al., 2007). Even a simple Lotka-Volterra predator-prey system with optimal behavior changes radically, becoming asymptotically stable instead of oscillating, (Křivan, 2007). A game theoretical approach has been fruitful in studying simple ecosystems under the assumption of a few monomorphic populations or limited choices, but real-life behavioral choice involves choosing between a wide array of different strategies, in the context of intra-specific competition and outside risk. Constructing robust models that can handle such systems would allow for an integration of ecosystem function and behavior, a long-standing ambition (Schmitz et al., 2008).

We believe the way optimal behavior is included in studies of ecosystem function is usually oversimplified, due to computational and modelling limitations. A common simplification is to assume that at least one payoff is linear in the choice of strategy, (Genkai-Kato, 2007). There are computational and conceptual advantages to studying linear models, and a lot of insight can be gleaned from them, (?), but the non-linear effects in natural systems are often significant. Models framed in terms of individual choice involving a non-linear payoff, usually work with implicit assumption that the optimization happens with the prior knowledge that all other members will follow the same strategy, by optimizing the raw pr. capita growth, (Malone et al., 2020; Stump and Chesson, 2017). We believe that the correct approach is to assume that each animal optimizes individually, only taking into account the mean behavior of all other individuals, as in the ideal free distribution. Assuming very large populations,

this situation can be modeled as a static mean-field game, the generalization of the ideal free distribution, where all animals of a single type follow the mean-field strategy at the Nash equilibrium.

We demonstrate an efficient numerical approach to finding Nash equilibria in games with both linear and non-linear payoffs, handling the mean-field case as a natural side-effect. The example we work from is a classic predator-prey game. We illustrate each aspect of our approach by gradually increasing the complexity of the model, from a simple Lotka-Volterra model with a refuge to a predator-prey system with Type II functional responses in a continuous habitat. The theoretical underpinnings of our method is the well-developed theory of finding Nash equilibria by recasting the problem as a variational inequality, which has had limited applications in biology. Having developed the general method, we use it to examine the population dynamics and the patch distribution at equilibrium as a function of changing refuge quality, intraspecific predator competition and

Add references to krivan and cressmans other articles, including the empirical one by krivan.

Methods

Population games: The ideal free distribution, mean field games and monomorphism

move to introduction?

The study of population games through the ideal free distribution has had great success in the ecological literature, but it has the weakness of being unable to handle games with non-linear interactions. Here we solve this problem by introducing results from the study of mean field games in mathematical optimization.

In the study of habitat-choice games, the ideal free distribution is the correct choice, in contrast to full population optimization (cite monroe), with exceptions where inherently monomorphic populations are a reasonable assumption.

The essential assumption in population games is that we have types of different agents playing a game against each other, where the agents of each type are internally indistinguishable. The payoff for a single individual depends on the behavior of the rest of the population, as well as the other populations and its own choice. The populations are assumed to be so large that the choice of a single individual does not change the mean.

Since all agents of each type are indistinguishable, when they all play the optimal strategy simultaneously, by interchangeability the Nash equilibrium must be that they follow the same strategy.

The theory of population games has developed in the area of mathematical optimization, (?) and mathematical biology simultaneously (???). In the field of mathematical optimization, it is typically described as static mean field game

theory and is characterized by arriving at the ideal free distribution mathematical biology.

An alternative point of view for population games is assuming monomorphic populations from the get-go instead of as an emergent phenomenon (?) (also monroe). There is a stark difference between the Nash equilibria of a game where the monomorphism is imposed and where it emerges, (). We quantify this explicitly: Consider a population game with a single type where the payoff U is bilinear, given by a matrix A , the payoff for a player in an inherently monomorphic population is

$$U(\sigma, \sigma) = \langle \sigma, A\sigma \rangle \quad (1)$$

and, denoting the mean strategy by \bar{p} , the mean-field payoff is

$$U(\sigma, \bar{\sigma}) = \langle p, A\bar{p} \rangle \quad (2)$$

At the Nash equilibrium σ^* , the payoff function must satisfy:

$$\nabla_{\sigma} U(\sigma, \sigma) = 2A\sigma = \gamma_m \nabla_{\sigma} U(\sigma, \bar{\sigma})|_{\bar{\sigma}=\sigma} = A\sigma = \gamma_m \quad (3)$$

A monomorphic player gets twice the payoff of a player playing against the population mean, highlighting the necessity of considering monomorphism as an emergent property. In case $U(\sigma, \bar{\sigma})$ is concave as a function of σ , we can characterize the relationship between monomorphic population and mean field population games exactly. The optima of $U(\sigma, \bar{\sigma})$ are given by the zeros of $d_{\sigma} U(\sigma, \bar{\sigma})|_{\sigma=\bar{\sigma}}$. This is equivalent to maximizing the functional

$$U^{mon}(\sigma, \sigma) = \int d_{\sigma} U(\sigma, \bar{\sigma})|_{\sigma=\bar{\sigma}} \sigma' \quad (4)$$

As an example, letting σ range from $[0, 1]$ consider the game:

$$U(\sigma, \bar{\sigma}) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \frac{\sigma}{1 + c_3 \bar{\sigma}} \quad (5)$$

which models a predator-prey interaction where the consumers have access to a refuge. Both prey and predators have a Type II functional response, and the satiation of the predators is given by the mean-field of the consumers. Using Equation (4), we can see that Equation (5) is equivalent to the monomorphic game

$$U^{mon}(\sigma, \sigma) = \frac{\sigma r}{\sigma c_1 + 1} - \log(1 + c_3 \sigma) \quad (6)$$

which contrasts the naive monomorphic game,

$$U(\sigma, \sigma) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \frac{\sigma}{1 + c_3 \sigma} \quad (7)$$

As the growth of $c_2 \frac{\sigma}{1+c_3\sigma}$ is smaller than that of $c_2 \log(1+c_3\sigma)$, the maximum of $U(\sigma, \sigma)$ will be attained at a larger value of σ . This corresponds to an inherently monomorphic population being more risk-seeking, as individuals will sacrifice themselves for the greater good.

Nash equilibria and variational inequalities

Given N players with strategies $\sigma_i, i = 1, \dots, N$ and payoff functions $U_i((\sigma_i)_{i=1}^N)$, the problem of finding a Nash equilibrium is that of simultaneously maximizing all U_i with respect to σ_i , keeping the strategies of the other players fixed.

To handle the infinite dimensional setting, it is necessary to fix a probability space (X, μ) and assume that all σ_i are probability distributions in $L^p(X, \mu), p > 1$. The assumption on p is to ensure reflexivity of the solution space. In our setting we consider the case $p = 2$, ie. $L^2(X, \mu)$. In case the payoff-functions σ_i are pseudoconvex, the machinery of variational inequalities can be applied to show existence and uniqueness of the Nash equilibrium. We start by recalling the definition of pseudo-convexity and pseudomonotonicity.

Definition 1. *The operator $T : K \rightarrow H$ is strictly pseudomonotone if for every pair $x \neq y$ we have*

$$\langle x - y, Ty \rangle \geq 0 \Rightarrow \langle x - y, Tx \rangle > 0 \quad (8)$$

The corresponding notion of convexity is

Definition 2. *Let $\Omega \subset H$ be an open subset of H , and let $f : \Omega \rightarrow \mathbb{R}$ be G -differentiable. The function f is strictly pseudoconvex if*

$$\langle y - x, (\nabla f)(x) \rangle \geq 0 \Rightarrow f(y) > f(x) \quad (9)$$

Proving strict pseudomonotonicity in itself can be hard, but thankfully the notions of strict pseudomonotonicity and strict pseudoconvexity are related.

Theorem 1. *Let $\Omega \subset H$ be an open convex subset, and let $f : \Omega \rightarrow \mathbb{R}$ be G -differentiable. Then f is strictly pseudoconvex if and only if ∇f is strictly pseudomonotone.*

Minimizing a differentiable pseudoconvex f function over a convex set K is then equivalent to solving the variational inequality

$$\langle (\nabla f)(x), x - y \rangle \quad (10)$$

Thus finding the Nash equilibrium of the game G corresponds to solving the variational inequality:

$$\left\langle \begin{pmatrix} \nabla_{\sigma_1} U_1 \\ \vdots \\ \nabla_{\sigma_N} U_N \end{pmatrix} \begin{pmatrix} \sigma_1 \\ \vdots \\ \sigma_N \end{pmatrix}, \begin{pmatrix} \sigma_1 - \sigma'_1 \\ \vdots \\ \sigma_N - \sigma'_N \end{pmatrix} \right\rangle \geq 0, \quad \forall y \in K \quad (11)$$

over the closed convex set $K = \int \sigma_i dx = 1$.

The problem of existence and uniqueness of a Nash equilibrium has been reduced to a problem of existence and uniqueness of a variational inequality. Whether a variational inequality given by a pseudomonotone operator has a solution can be determined by the following theorem:

Theorem 2. Let $K \subset H$ be a closed convex set and $T : K \rightarrow H$ a pseudomonotone operator which is lower hemicontinuous along line segments. Assume that there exists $u_0 \in K$ and $R > \|u_0\|$ such that

$$\langle Tv, v - u_0 \rangle \geq 0, \forall v \in K \cap \{v \in H : \|v\| = R\} \quad (12)$$

then the variational inequality specified by T has a solution.

The question of uniqueness is solved by the strict pseudomonotonicity:

Theorem 3. Let $K \subset H$ be a non-empty subset of H . If T is strictly pseudomonotone, then the problem $VI(T, K)$ has at most one solution.

We can gather these results and their application to game theory in the following theorem:

Theorem 4. Consider a game with N players with strictly pseudoconvex payoff functions U_i and strategies σ_i . The game has a unique Nash equilibrium if

$$S = \begin{pmatrix} \nabla_{\sigma_1} U_1 \\ \vdots \\ \nabla_{\sigma_N} U_N \end{pmatrix} \quad (13)$$

satisfies the criterion of Theorem 2.

As a corollary, we can add:

Corollary 1. A population game with N populations and dynamics specified by f_i , with strictly pseudoconvex functions payoff U_i and strategies σ_i has a unique fixed point with a unique Nash equilibrium if f_i/x_i are strictly pseudomonotone and coercive, which can be found by solving a single variational inequality.

Proof. The game specified by σ_i has a unique Nash equilibrium, given by a variational inequality with operator specified by $(\nabla_{\sigma_i} U_i)_{i=1}^N$. For each vector σ , the variational inequality $\langle (f_i/x_i)_{i=1}^N(x), x - y \rangle$ has a unique solution, by the coerciveness and pseudomonotonicity of f_i/x_i . Therefore the simultaneous problem $\langle ((\nabla_{\sigma_i} U_i)_{i=1}^N)(\sigma), \sigma - \sigma' \rangle, \langle (f_i/x_i)_{i=1}^N(x), x - y \rangle$ has a unique solution. If we append the two operators $(f_i)_{i=1}^N$ and $\nabla_{\sigma_i} U_i$, we get a single variational inequality. \square

Having established the existence and uniqueness via variational inequalities, we can go back to the complementarity formulation based on the Karush-Kuhn-Tucker conditions. At the Nash equilibrium, each payoff function U_i must satisfy the Karush-Kuhn-Tucker (KKT) conditions with respect to σ_i .

$$\nabla_{\sigma_i} U_i((\sigma_j)_{j=1}^N) + \mu_i - \lambda \cdot 1 = 0 \quad \langle \sigma_i, \mu_i \rangle = 0 \quad \mu_i \geq 0 \quad \sigma_i \geq 0 \quad \int_X \sigma_i - 1 = 0 \quad (14)$$

The Nash equilibrium of the game specified by the family (U_i) corresponds to finding a system σ_i^* satisfying the KKT conditions simultaneously for every pair $U_i, (?)$. Thus the total condition for a Nash equilibrium is:

$$\begin{pmatrix} \nabla_{\sigma_1} U_1 \\ \vdots \\ \nabla_{\sigma_N} U_N \end{pmatrix} + \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_N \end{pmatrix} + \begin{pmatrix} \lambda_1 \cdot 1_k \\ \vdots \\ \lambda_N \cdot 1_k \end{pmatrix} = 0 \left\langle \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_N \end{pmatrix}, \begin{pmatrix} \sigma_1 \\ \vdots \\ \sigma_N \end{pmatrix} \right\rangle = 0 \mu_i \geq 0 \sigma_i \geq 0 \int \sigma_i dx = 1?? \quad (15)$$

The formulation as a KKT-system allows for solving the problem numerically with simple tools, since we now have a feasibility problem rather than a minimization problem.

Population model with continuous habitat

We consider a predator-prey system in a spatially heterogonous habitat, where the predators are specialized so that their hunting success is maximal in the most productive zone of the habitat. We assume that predators (P) and consumers (C) share a heterogonous habitat ??, modeled as the interval $[0, 1]$. The mean strategy of the consumer population is $\bar{\sigma}_c$ and the mean strategy of the predator population is $\bar{\sigma}_p$. The population dynamics are given by a behaviorally modified Rosenzweig-MacArthur system. The predator clearance rate is $\beta_p = \beta_l + \beta_0$ where β_l varies locally and β_0 is the minimal clearance rate. The function β_p is normalized to a constant value of 5. Consumption events are assumed local, so the expected encounter rate between predators and prey is $\langle \beta_p \bar{\sigma}_p, \bar{\sigma}_c \rangle$. To model intraspecific predator competition, we have added a term $c \langle \beta_p \bar{\sigma}_p, \bar{\sigma}_p \rangle$ where c describes the level of competition. In addition there is a constant metabolic loss μ_c for the consumers. The carrying capacity is given by $K\varphi + K_0$, where K varies, φ is a distribution, and K_0 is the minimal carrying capacity. Denoting the maximal predator growth rate by F_p , the consumer clearance rate by β_c , the dynamics are given by:

$$\dot{C} = f_c = C \left(\left\langle \beta_c \bar{\sigma}_c, 1 - \frac{\beta_c}{K\varphi + K_0} \bar{\sigma}_c C \right\rangle - \frac{F_p \langle \beta_p \bar{\sigma}_p, \bar{\sigma}_p \rangle P}{F_p + \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle C} - \mu_c \right) \quad (16)$$

$$\dot{P} = f_p = P \left(\varepsilon \frac{F_p \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle C}{F_p + \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle C} - c \langle \bar{\sigma}_p, \beta_p \bar{\sigma}_p \rangle - \mu_p \right) \quad (17)$$

Introducing the quality (q) of the habitat as a parameter, the functions β_p and φ are given by

$$\beta_p = 5 \frac{\exp(-(qx)^2) + \beta_0}{\int_0^1 \exp(-(qx)^2) + \beta_0 dx} \quad (18)$$

$$\varphi = \frac{\exp(-qx) + K_0}{\int_0^1 \exp(-qx) + K_0 dx} \quad (19)$$

where the normalization is to keep a constant total encounter rate and carrying capacity of K when varying q . The choice of functions reflect a predator specialized in hunting the most productive zones, and a heterogonous productivity.

The parameters for the model are:

Name	Value	Meaning
q	Varies	Refuge quality
K	Varies	Carrying capacity
c	Varies	Predator competition
K_0	10^{-4}	Minimal carrying capacity
β_c	1	Consumer clearance rate
μ_c	0.001	Consumer metabolic rate
μ_p	0.15	Predator metabolic rate
F_p	100	Predator maximum growth rate
ε	0.1	Trophic efficiency <

Population game

We model predator and consumer movement as instantaneous, with each predator and consumer seeking to maximize its fitness at each instant. The fitness of an individual depends on the mean strategy of its conspecifics and that of either the predators, or consumers, respectively. Denoting the individual consumer and predator strategies by σ_c and σ_p respectively, the instantaneous fitness U_c of a consumer and a predator U_p are:

$$U_c(\sigma_c, \bar{\sigma}_c, \bar{\sigma}_p) = \left\langle \beta_c \sigma_c, 1 - \frac{\beta_c}{K\varphi + K_0} \bar{\sigma}_c C \right\rangle - \frac{F_p \langle \beta_p \sigma_c, \bar{\sigma}_p \rangle P}{F_p + \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle C} - \mu_c \quad (20)$$

$$U_p(\sigma_p, \bar{\sigma}_c, \bar{\sigma}_p) = \varepsilon \frac{F_p \langle \beta_p \bar{\sigma}_c, \sigma_p \rangle C}{F_p + \langle \beta_p \bar{\sigma}_c, \sigma_p \rangle C} - c \langle \sigma_p, \beta_p \bar{\sigma}_p \rangle - \mu_p \quad (21)$$

Denoting the optimum by $*$, at the Nash equilibrium $\sigma_c^* = \bar{\sigma}_c$ and $\sigma_p^* = \bar{\sigma}_p$. We use the method of Equation (4) to convert both mean-field payoffs into a monomorphic equivalent form,

$$U_c^{mon}(\sigma_c, \sigma_p) = \left\langle \beta_c \sigma_c, 1 - \frac{1}{2} \frac{\beta_c}{K\varphi + K_0} \sigma_c C \right\rangle - P \log(F_p + \langle \beta_p \sigma_c, \sigma_p \rangle C) - \mu_c \quad (22)$$

$$U_p^{mon}(\sigma_p, \sigma_c) = \varepsilon \frac{F_p \langle \beta_p \sigma_c, \sigma_p \rangle C}{F_p + \langle \beta_p \sigma_c, \sigma_p \rangle C} - \frac{1}{2} c \langle \sigma_p, \beta_p \sigma_p \rangle - \mu_p \quad (23)$$

We need to verify that $-U_c^{mon}$ and $-U_p^{mon}$ are strictly pseudoconvex, as well as show existence. To this end, we state a characterization of strict pseudomonotonicity for differentiable functions.

Lemma 1. *A function $f : K \subset H \rightarrow \mathbb{R}$ is strictly pseudoconvex if*

$$\langle f(x), u \rangle = 0 \Rightarrow \langle (\nabla_x f(x))h, h \rangle > 0 \quad (24)$$

Proposition 1. *The functions $-U_c^{mon}$ and $-U_p^{mon}$ are strictly pseudconvex, and their derivatives $\begin{pmatrix} -\nabla_{\sigma_c} - U_c^{mon} \\ -\nabla_{\sigma_p} U_p^{mon} \end{pmatrix}$ satisfy the criteria of ??.*

Proof. We start by showing the strict pseudoconvexity. The function U_p^{mon} is strictly concave, as it has strictly negative second derivative, so the derivative with respect to σ_p is strictly monotone, therefore strictly pseudomonotone. Note that on K a function g is strictly pseudomonotone if and only if $g + \lambda$ is strictly pseudomonotone for any $g \in \mathbb{R}$, since $\langle g(x) + \lambda, x - y \rangle = \langle g(x), x - y \rangle + \lambda \int x d\mu + \lambda \int y d\mu = \langle g(x), x - y \rangle$. If we consider $f(x) = \nabla_{\sigma_c} U_c^{mon}(x) + 1$ and assume $\langle f(x), u \rangle = 0$, then

$$-\langle x, u \rangle \frac{C\beta_c}{K\varphi + K_0} - \frac{\langle \sigma_p, h \rangle}{F_p + \langle \sigma_p, x \rangle} = 0 \quad (25)$$

Since K consists of positive functions, $\langle x, u \rangle = 0$ and $\langle \sigma_p, h \rangle = 0$. If we consider

$$H(x, u) = \langle (\nabla_x f)(x)u, u \rangle = \langle u, u \rangle \frac{C\beta_c}{K\varphi + K_0} - \frac{\langle \sigma_p, u \rangle \langle \sigma_p, h \rangle}{F_p + \langle \sigma_p, x \rangle} \quad (26)$$

then $H(x, u) > 0$ since $\langle \sigma_p, u \rangle = 0$, so S is strictly pseudomonotone. To show that there exists a solution, consider $u_0 = [1, 1]$ and $R = 1 + \varepsilon$. Then we wish to show that

$$\langle S(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle \geq 0 \quad (27)$$

for $\|(\sigma_c, \sigma_p)\| = 1$. It is sufficient to show that each term is positive. We start with the consumer term, where we utilize that $\langle \sigma_c, 1 \rangle = 1$

$$1 - \langle \sigma_c, \sigma_c - 1 \rangle \frac{C\beta_c}{K\varphi + K_0} - \frac{\langle \sigma_p, \sigma_c - 1 \rangle}{F_p + \langle \sigma_p, \sigma_c \rangle} = 1 - (1 - \|\sigma_c\|^2) \frac{C\beta_c}{K\varphi + K_0} + (1 - \langle \sigma_p, \sigma_c \rangle) \frac{1}{F_p + \langle \sigma_p, \sigma_c \rangle} \quad (28)$$

The terms $1 - \|\sigma_c\|^2$ and $1 - \langle \sigma_p, \sigma_c \rangle$ are bounded above by $\varepsilon^2 + 2\varepsilon$. If we define $\xi = \frac{C\beta_c}{K\varphi + K_0}$ and $\eta = \frac{1}{F_p + \langle \sigma_p, \sigma_c \rangle}$, ε can be determined by solving the inequality

$$(\varepsilon^2 + 2\varepsilon)(\xi + \eta) \leq 1 \quad (29)$$

Proceeding in the same fashion with the second term, we arrive at a pair of constants $\varepsilon, \varepsilon'$. We can then pick the minimum of these two, showing the desired. \square

Since we are also interested in the fixed-points of the population dynamics Equation (17), we are also interested in showing that the fixed-point of the dynamics exists and is unique. An interior fixed-point C^*, P^* must necessarily satisfy:

$$\left\langle \begin{pmatrix} f_c/C(C^*) \\ f_p/P(P^*) \end{pmatrix}, \begin{pmatrix} C^* \\ P^* \end{pmatrix} \right\rangle = 0 \quad (30)$$

$$\begin{pmatrix} C^* \\ P^* \end{pmatrix} \geq 0 \quad (31)$$

$$f_1 \geq 0, f_2 \geq 0 \quad (32)$$

The functions f_1/C and f_2/P are strictly monotone, and coercive. Therefore, by ?? there is a unique equilibrium for the population game.

Numerical approach and implementation

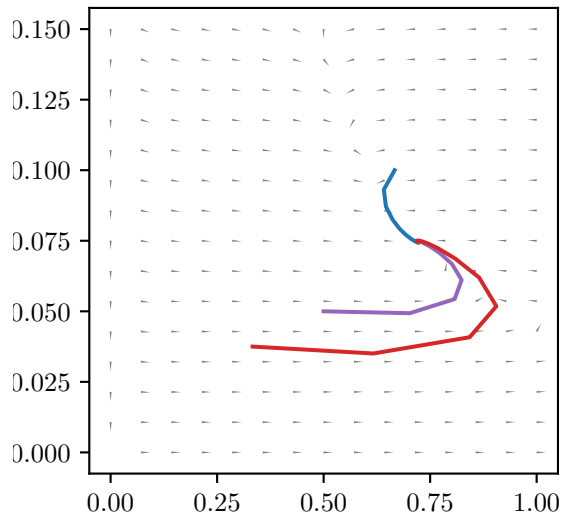
By rephrasing the population into a variational inequality, we unlock the full arsenal of tools available for the solution of variational inequalities. We discretize space uniformly, using the trapezoidal rule to evaluate the integrals. By using the trapezoidal rule, we keep a banded sparsity pattern in the coupling of the locations.

We formulate the optimization problem as a feasibility problem via. the optimization framework casadi (). To solve the problems the solver IPOPT () is invoked, using the Haswell linear algebra routines (). This approach to solving variational inequalities is state-of-the-art, and the solver was both robust and fast. Keywords: Casadi, IPOPT, state-of-the-art, simple to expand and scalable.

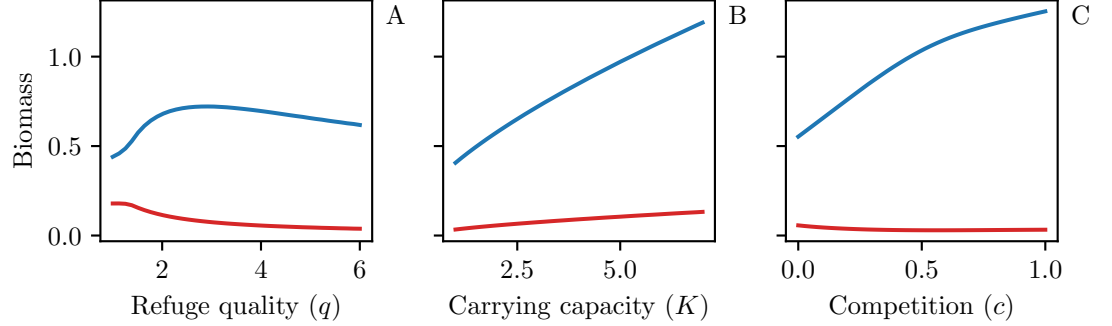
1. Introduce the theory of Variational inequalities, simple game
2. Introduce mean field game, modify predator-prey to the mean field case
3. Introduce continuous setting

Results

Populations



The plot ?? shows the general phase-portrait and the trajectories of the population dynamics for three different starting points. The dynamics have been stabilized in contrast to the Hopf bifurcation in the Rosenzweig-MacArthur model under the paradox of enrichment, but the direction of the flow is consistent with the usual Rosenzweig-MacArthur model.

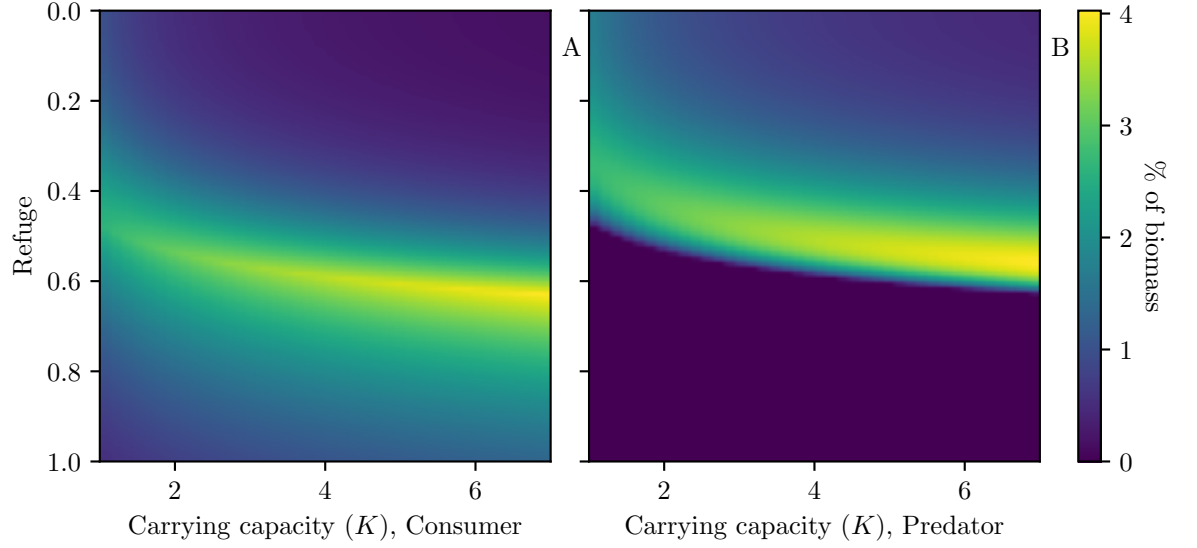


?? reveals how the population levels of consumers and predators change at equilibrium with varying refuge quality (?? (A)), carrying capacity (?? (B)) and intraspecific predator competition (?? (C)). Increasing the quality of the refuge (?? (A)) initially causes an increase in consumer populations (?? (A, blue)) and a decrease in predator populations. The refuge quality reaches a point (?? ($q \approx 2.2$)) where the availability of a better refuge causes the population of consumers to go down, presumably since staying in the refuge is individually more advantageous but overall causes lower population levels.

A higher carrying capacity causes higher populations of both consumers and predators populations at equilibrium (??). The increase in both populations is in contrast to the expected conclusion from the ecosystem exploitation hypothesis, and is probably because the behavioral choice allows the consumers to avoid the risk of predation, while achieving the same fitness.

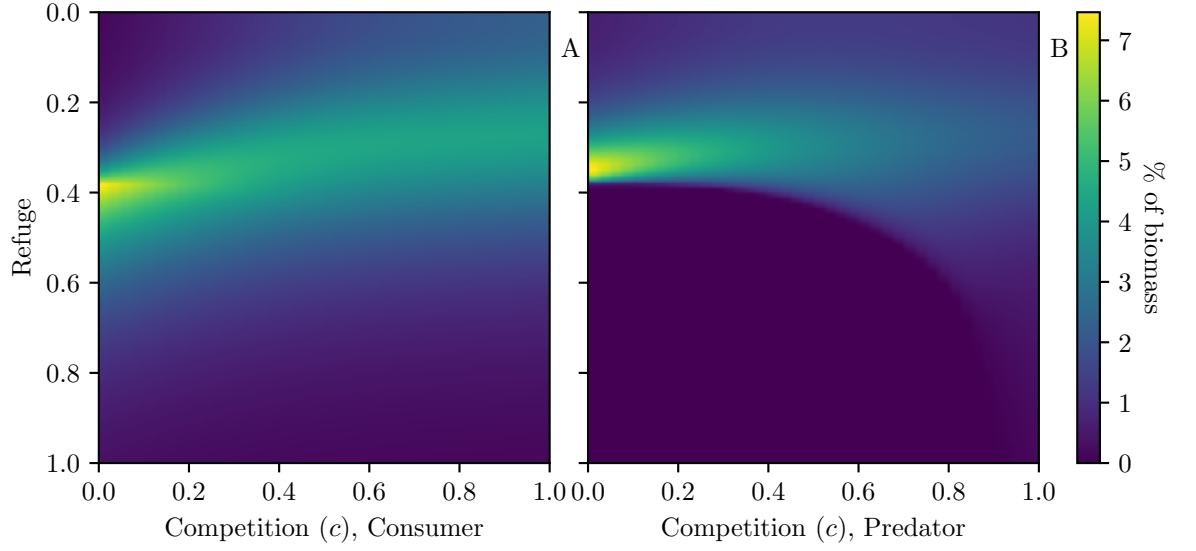
Varying the intraspecific predator competition causes a decrease in the population of predators (?? (C, red)) until a point where the population stabilizes (?? ($c \approx 1/3$)), while the population of consumers continues to increase (?? (C, blue)). The increasing quantity of consumers available must compensate for the intraspecific losses.

Strategies

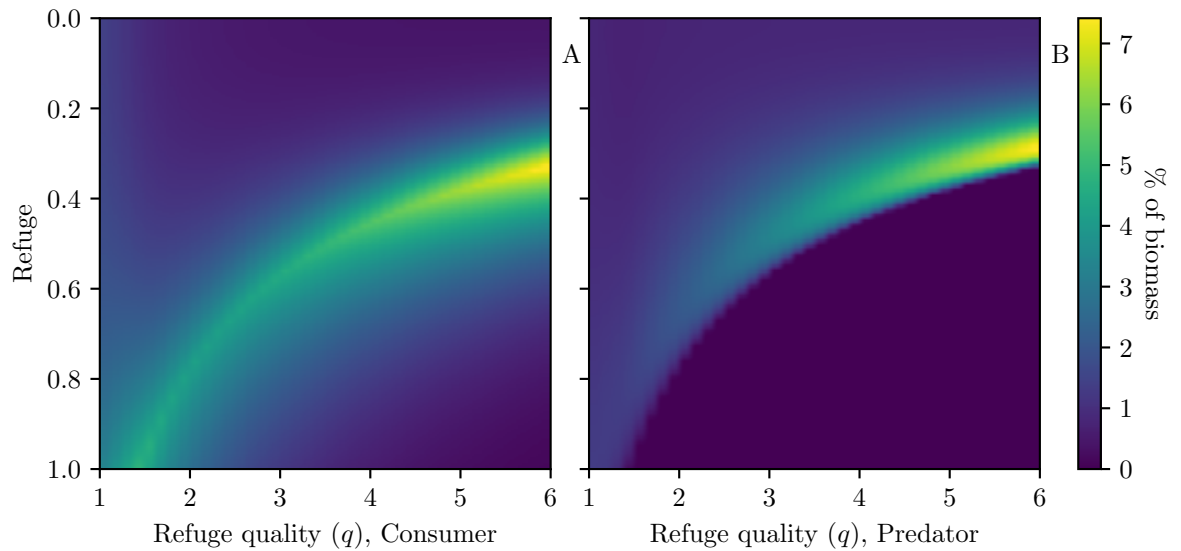


The plots in (??) illustrate the strategies of the consumers (?? (A)) and predators (??) at equilibrium when carrying capacity varies. At low carrying capacities, both consumers and predators are relatively spread out, with the peak concentration about halfway to the refuge. As the carrying capacity increases, the distribution becomes more concentrated and clusters closer to the refuge. The increase in concentration is most marked for the predators. Predators are almost uniformly distributed in the space 0.5-1 at low carrying capacity, while the majority forms a cluster just above the consumer layer at a carrying capacity of 7. Thus the gain from clustering gradually outweighs the loss from the intraspecific predator competition. That both predator and consumer population increase must be the driving factor behind the peak population concentration moving to less productive areas.

A higher carrying capacity leads to more concentrated populations, but the increase in populations leads to greater risk-aversion from the consumers so they concentrate in less desirable zones.



In ?? the intraspecific predator competition is varied and we see the emergent equilibrium strategy of the consumers (?? (A)) and predators (?? (B)). When there is no intraspecific predator competition, both consumers and predators are highly concentrated at about 0.4. The equilibrium distribution of predators spreads out as we increase the intraspecific predator competition. The previous equilibrium becomes unstable, since the gain from clustering on the consumers is outweighed by the risk of encountering other predators. As the predators gradually spread, it is echoed by the consumers spreading out as well, further incentivizing predator-spread. When the consumer population spreads out, the distribution trends towards the more productive layers. Summarizing, highly competitive predators leads to dispersed populations.



?? shows the strategy of consumers (?? (A)) and predators (?? (B)) at equilibrium with varying carrying capacity.

Discussion

1. What did we find?
2. What do our results mean?
3. Perspectives in VI for NE in ecology Compare to literature also the stuff by Patrizio. remark well-known that worse for species than population-thingy
4. MFG as approach for games, refer to papers where the distinction is not clear, note that Krivan and Cressman write it is the correct way
5. Remark taht Sandholm is reinventing field of VI - badly -
6. Scalability?
7. Generalize to "True" continuous time MFG

Habitat selection: Continuous and discrete

There are fundamentally two different types of habitat selection that an animal can undertake. One is moving from one habitat to another, totally disconnected habitat, eg. by migration (), and another is choosing exactly the placement in

a continuous setting such as a water column or landscape (). The two are often conflated, (??), but they are fundamentally different, and care must be taken to distinguish between the situations. Picking a discrete probability distribution over a finite set and a continuous distribution are radically different and can lead to different outcomes, since neighbors are modelled as being infinitely far away in the discrete setting. The toolbox of Nash equilibria and mean-field games we have introduced works equally well over finite sets and continuous spaces, allowing a direct comparison ().

Maybe move this to the discussion section...

0.1 Variational inequalities

Optimal control

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