Revisiting Rosenzweig-MacArthur: Towards a general approach to population dynamics incorporating individual behavior

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1 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. A classical application of game-theory is patch-choice models, where the ideal free distribution emerges to explain spatial distributions (Cressman et al., 2004; Fretwell, 1969). 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 behavorial choice involves choosing between a wide array of different habitats, in the context of intra-specific competition and outside risk. Models that can handle such systems allows for better models of habitat distribution, and represent a significant step forward in understanding natural systems (Morris, 2003).

A common simplification when including behavior in population models is to assume that at least one payoff is linear in the choice of strategy, (Krivan, 1997). Linear models are suffficient to explain simple predator-prey dynamics with optimal behavior, (Křivan, 2007), but non-linear effects in natural systems are significant (Gross et al., 2009). The population game approach advanced by (Vincent and Brown, 2005) for merging optimal behavior with population dynamics through maximizing the pr. capita growth implicitly assumes monomorphic populations, where all individuals intrinsically act as one (Malone et al., 2020; Stump and Chesson, 2017). We propose a modification of the approach from (Vincent and Brown, 2005), based on individual optimization. We assume each invidiual maximies its own instantaneous growth rate, with density dependent behavior depending on the mean population behavior. This marks a return to the ideas of playing the field, (Smith, 1982; Cressman and Křivan, 2010). If we assume that the animals of each type are indistinguishable and large populations, the game can be modeled as a static mean field game with multiple types.

The evolution of mean-field games has followed two parallel tracks, one in mathematical biology through the ideal free distribution (Fretwell, 1969; Cressman et al., 2004; Křivan et al., 2008; Cressman and Křivan, 2010), and the other in mathematical optimization based directly on anonymous actors (Lasry and Lions, 2007; Aumann, 1964; Blanchet and Carlier, 2016). The main focus in ecology has been on and specific families of games in depth Broom and Rychtár (2013), while the focus in mathematical optimization has been in establishing uniqueness and existence of Nash equilibria through the toolbox of variational inequalities (Karamardian, 1969; Gabay, 1980; Nabetani et al., 2011). We demonstrate that in certain cases, a mean-field game can be rephrased equivalently as a normal-form game. This allows us to bring the entire toolbox of variational inequalities to bear on population games.

Using the theory of variational inequalities, we show that population games based on individual optimization have a unique equilibrium under very general assumptions. Our approach allows us to handle both continuous and discrete strategy spaces, but more technical assumptions are required for existence in the continuous setting. The classical ideal free distribution emerges as a special case of our approach, providing a compelling argument the mean-field approach. We demonstrate the fundamental difference between working with direct pr. capita optimization and using the mean field approach, explicitly quantifying the difference in expected payoff for the case of the ideal free distribution. Behavior based on individual optimization appears more cautios than predicted when optimizing pr. capita consumption, which we demonstrate with an example and conjecture as a general property. We demonstrate our approach by applying it to a behaviorally modified Rosenzweig-MacArthur system in continuous space. We show that the system satisfies the criteria for existence and unique as a population game.

In addition to our theoretical advances, we implement a simple and efficient numerical method of finding Nash equilibria and equilbria of population games. The approach is applied to our case of the behaviorally modified Rosenzweig-MacArthur system. We examine the population dynamics through a phase portrait, where they appear to be asymptotically stable. We study the population levels and spatial distribution at equilibrium as a function of the carrying capacity, intraspecific predator competition and refuge quality.

2   Population games: Mean-field games and monomorphism

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.

An alternative point of view for population games is assuming monomorphic populations from the get-go instead of as an emergent phenonenom (Vincent and Brown, 2005). There is a stark difference between the Nash equilibria of a game where the monomorphism is imposed and where it emerges, (Křivan et al., 2008; Collet, 2019). We quantify this explicitly:

Proposition 1. *Consider a population game with a population of size N with payoff U given by a bilinear form U specified by a matrix A such that $U(\sigma_1, \sigma_2) = \langle \sigma_1, A\sigma_2 \rangle$. The expected payoff for a player with an inherently monomorphic population is twice that of a player in the mean-field game.*

Proof. The payoff for a player with strategy σ in a monomorphic population of size N is

$$U(\sigma, \sigma) = \langle \sigma, AN\sigma \rangle \tag{1}$$

Conversely, if we assume that the relevant opposing strategy is the mean $\bar{\sigma}$ of an a-priori polymorphic collection strategies the payoff is

$$U(\sigma, \bar{\sigma}) = \langle \sigma, AN\bar{\sigma} \rangle \tag{2}$$

Since we assumed all agents are identical in the mean-field game, at the Nash equilibrium they must all follow the same strategy. Therefore, at the Nash equilibrium $\sigma = \bar{\sigma}$, ie.

$$\bar{\sigma} = \operatorname{argmax}_\sigma U(\sigma, \bar{\sigma}) \tag{3}$$

so we are interested in extrema where $\sigma = \bar{\sigma}$. Consider the Karush-Kuhn-Tucker (KKT) conditions at the Nash equilibrium for the monomorphic game

$$
\begin{aligned}
2AN\sigma + \mu - \lambda_1 \cdot 1 &= 0 \\
\langle \sigma, \mu \rangle &= 0 \\
\mu &\geq 0 \\
\sigma &\geq 0 \\
\int_X \sigma - 1 &= 0
\end{aligned}
\tag{4}
$$

At every point with a non-zero concentration, the payoff for the monomorphic population is λ_1. We can likewise find the pointwise payoff for the mean-field game through the KKT-conditions:

$$
\begin{aligned}
AN\sigma + \mu - \lambda_2 \cdot 1 &= 0 \\
\langle \sigma, \mu \rangle &= 0 \\
\mu &\geq 0 \\
\sigma &\geq 0 \\
\int_X \sigma - 1 &= 0
\end{aligned}
\tag{5}
$$

the payoff here is $\lambda_2 = 2\lambda_1$. In conclusion, the individual payoff for a player using the optimal strategy in a monomorphic population is twice that of an individual player in the mean-field game where the monomorphic behavior is an emergent property. □

As Proposition 1 shows, assuming a monomorphic population has a drastic effect on the expected payoff in a simple game, highlighting the necessity of considering monomorphism as an emergent property. Therefore, the approach advocated in (Vincent and Brown, 2005) of optimizing the pr. capita growth directly in a population game overestimates the possible growth if there are density-dependent effects.

In Proposition 1 we also see the connection between the ideal free distribution and mean field games, where the classical ideal free distribution emerges as the mean-field equilibrium .

The proof of Proposition 1 suggests a connection between mean-field population games and games with monomorphic populations, allowing the study of mean-field games using the tools of monomorphic games.

Definition 1. *Consider a mean-field game with populations* $N_1, \ldots, N_M$ *with individual payoffs specified by* $U_i(\sigma_i, (\bar{\sigma}_j)_{j=1}^M, (N_j)_{j=1}^M)$. *Assume* $\nabla_{\sigma_i} U_i \mid_{\sigma_i = \bar{\sigma}_i}$ *admits a primitive* U_{mon}. *We define the monomorphic equivalent game by the payoff functions* U_{mon}^i.

The game specified by the collection U_{mon}^i is a monomorphic game, and in case the Nash equilibrium is unique, the Nash equilibria of the original game and the one specified by U_i^{mon} are the same. Later on, by utilizing the toolbox of variational inequalities, we will give a sufficient criterion to check when the Nash equilibrium is unique, so Definition 1 may be used. The notion of a monomorphic equivalent game eases the analysis of mean-field games, and allows direct illustration of the difference between the emergent monomorphism in a mean-field game and imposed monomorphism.

As an example consider a habitat-choice game where a consumer in a total population of size N with a growth rate given by a Type II functional response can either stay in a refuge or go into a foraging arena. In the foraging arena there is a population of predators. The predators also have a Type II functional response, but their satiation level depends on the mean time spent in the the arena by the consumers. If we use the instantaneous growth as a fitness proxy and let σ modelling the time spent in the arena range from $[0, 1]$, this situation is modeled by the payoff function:

$$U(\sigma, \bar{\sigma}) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \frac{\sigma}{1 + c_3 N \bar{\sigma}} \tag{6}$$

Using Definition 1, we can see that Equation (6) is equivalent to the monomorphic game

$$U^{mon}(\sigma, \sigma) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \log(1 + N c_3 \sigma) \tag{7}$$

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which contrasts the naive monomorphic game,

$$U(\sigma, \sigma) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \frac{\sigma}{1 + N c_3 \sigma} \tag{8}$$

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. This example, along with Proposition 1 lets us conjecture that a monomorphic population will generally be more risk-seeking.

3 Nash equilibria and variational inequalities

Calculating Nash equilibria is generally a hard problem. A fruitful approach to calculating Nash equilibria is via. the theory of complementarity problems and variational inequalities (**?**). We unite the approach of variational inequalities and mean-field games, and by using relatively modern theory, we can characterize a rather general setup that guarantees uniqueness and existence of Nash equilibria for population games in both a finite and infinite dimensional setting.

Definition 2. *Define H as the real Hilbert space $L^2(X)$, where X is either a finite set of points or the union of the interval $[0, 1]$ and a finite set of points. Define $H_+ \subset H$ as the a.e. positive functions in H.*

Finding Nash equilibria is one of the oldest applications of (linear) complementarity theory. We define a complementarity problem:

Definition 3. *Let H be a real Hilbert space, and $K \subset H$ be a closed convex cone. Define $K^* = \{x \in H : \langle x, y \rangle = 0, \quad \forall y \in K\}$. Assume $T : K \to H$. The complementarity problem $CP(T, K)$ is the problem of finding an element x^* such that*

$$\langle x^*, Tx^* \rangle = 0$$
$$Tx \in K^*, \quad x \in K \tag{9}$$

However, showing existence and uniqueness for complementarity problems is generally hard, which is where their relationship to variational inequalities comes in handy.

Definition 4. *Let H be a real Hilbert space and $K \subset H$ be a non-empty subset of H. Let $T : K \to H$. The variational inequality $VI(T, K)$ is the following system*

$$x \in K, \langle y - x, Tx \rangle \geq 0, \quad \forall y \in K \tag{10}$$

and a solution is an x satisfying the inequality.

If K is a convex cone, the problems $VI(T, K)$ and $CP(T, K)$ have the same solutions, which can be seen by setting $y = 2x$ and $y = 0$ respectively.

To motivate the approach based on complementarity and variational inequalities, assume that we have a game with M players and payoff functions U_i and strategies σ_i. At the Nash equilibrium, each payoff function U_i must satisfy the Karush-Kuhn-Tucker (KKT) conditions with respect to σ_i.

$$\nabla_{\sigma_i} U_i((\sigma_j)_{j=1}^N) + \mu_i - \lambda \cdot 1 = 0 \quad \langle \sigma_i, \mu_i \rangle = 0 \quad \mu_i \geq 0 \quad \sigma_i \geq 0 \int_X \sigma_i - 1 = 0 \quad (11)$$

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, (Deimling, 2010). Thus the total condition for a Nash equilibrium is:

$$\begin{pmatrix} \nabla_{\sigma_1} U_1 \\ \vdots \\ \nabla_{\sigma_N} U_N \end{pmatrix} + \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_N \end{pmatrix} + \begin{pmatrix} \lambda_1 \cdot 1_k \\ \vdots \\ \lambda_N \cdot 1_k \end{pmatrix} = 0$$

$$\left\langle \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_N \end{pmatrix}, \begin{pmatrix} \sigma_1 \\ \vdots \\ \sigma_N \end{pmatrix} \right\rangle = 0 \qquad (12)$$

$$\mu_i \geq 0$$

$$\sigma_i \geq 0$$

$$\int \sigma_i dx = 1$$

To simplify Equation (12), we define $dU = \begin{pmatrix} \nabla_{\sigma_1} U_1 \\ \vdots \\ \nabla_{\sigma_N} U_N \end{pmatrix}$, $S = (\sigma_i)_{i=1}^M$, and $\lambda = (\lambda_i)_{i=1}^M$. Then the problem can be restated as

$$\langle dU(S) + \lambda, S \rangle = 0 \, \langle S_i - 1, 1 \rangle \, \lambda = 0 - dU(S) - \lambda \geq 0 \, \langle S_i - 1, 1 \rangle \in \{0\} S \geq 0 \lambda \in \mathbb{R}$$
$$(13)$$

which is a complementarity problem with $K = (H_+ \oplus \mathbb{R})^n$, $K^* = (H_+ \oplus \{0\})^n$ and

$$T(S, \lambda) = \begin{pmatrix} dU(S) + \lambda \\ (\langle \sigma_i, 1 \rangle - 1)_{i=1}^M \end{pmatrix} \qquad (14)$$

If we do not include the criterion $\int \sigma_i dx = 1$ explicitly, but instead consider the convex set $K = \{f \in H : \int f dx = 1\}$. Then we are looking for a vector $S = (\sigma_i)_{i=1}^M$ that minimizes

$$\langle dU(S), S - T \rangle \geq 0 \forall T \in K^n \qquad (15)$$

which is more tractable for theoretical considerations, while the complementarity formulation is preferable for solving the problem numerically.

In case the payoff-functions σ_i are sufficiently nice, the machinery of variational inequalities can be applied to show existence and uniqueness of the Nash

equilibrium. Asking for strict convexity is too strong, but we can relax the requirement to the related weaker notion of strict pseudoconvexity. See **??** for further details. We can gather the results on pseudoconvex functions and their application to game theory in the following theorem:

Theorem 1. *Cnosider a game with N players with strictly pseudoconvex payoff functions U_i and strategies σ_i in H. The game has a unique Nash equilibrium if*

$$dU = \begin{pmatrix} \nabla_{\sigma_1} U_1 \\ \vdots \\ \nabla_{\sigma_N} U_N \end{pmatrix} \tag{16}$$

*satisfies the criterion of **??** or H is finite dimensional.*

Proof. If $\nabla_{\sigma_i} U_i$ is strictly pseudomonotone, then so is their direct sum dU by linearity of the inner product. By **??** this solution is unique since dU is strictly pseudomonotone. So if the solution exists, it is unique. By assumption **??** gives existence of a solution of $VI(dU, K)$ in case H is infinite dimensional. If H is finite-dimensional then K is compact and there exists a solution **??**. $\qquad\square$

With this result, we can show that there exist unique fixed points of population games with strictly pseudoconvex payoff functions and bounded dynamics.

Theorem 2. *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 satisfy **??**, and the set of fixed points of f_i is uniformly bounded in σ.*

Proof. The game specified by σ_i has a unique Nash equilibrium for each $x \in \mathbb{R}^N$, given by a complementarity problem over K with operator specified by $dU = (\nabla_{\sigma_i} U_i)_{i=1}^N$. The solution specifies a continuous mapping $G : K^N \to \mathbb{R}^N$, (Barbagallo and Cojocaru, 2009, Theorem 4.2). Likewise, due to the assumptions on f_i the complementarity problem $\left\langle (f_i)_{i=1}^N(x), x \right\rangle$ has a unique solution for every σ. Denote this solution function by F.

Finding a fixed point of the dynamical system along with a Nash equilibrium then corresponds to finding a fixed point of $F \circ H : \mathbb{R}_+^N \to \mathbb{R}_+^N$. Since F is assumed to be uniformly bounded, hence has compact range, $F \circ H$ has compact range. Therefore $F \circ H$ has a fixed point by Schauders fixed point theorem.

For uniqueness, note that for each vector σ, the variational inequality

$$x \in \mathbb{R}_+^n, \left\langle (f_i/x_i)_{i=1}^N(x), y - x \right\rangle \geq 0 \quad y \in \mathbb{R}_+^n \tag{17}$$

has a unique solution, by strict pseudomonotonicity of f_i/x_i. If we append the two operators $(f_i)_{i=1}^N$ and $\nabla_{\sigma_i} U_i$, we get a single strictly pseudomonotone variational inequality, where there exists a unique solution, since all terms are strictly pseudomonotone. Therefore the simultaneous problem

$$\begin{aligned} S \in K^n, \langle dU(S) \rangle, S' - S \rangle \geq 0, \quad S' \in K^n \\ x \in \mathbb{R}_+^n, \left\langle (f_i/x_i)_{i=1}^N(x), y - x \right\rangle \geq 0 \quad y \in \mathbb{R}_+^n \end{aligned} \tag{18}$$

has a unique solution, showing the existence and uniqueness of a fixed point for a population game. □

Remark that the assumption of uniformly bounded fixed-point space as a function of the strategies is biologically reasonable, since e.g. Type II growth functions are uniformly bounded and a metabolic loss is usually constant.

Having established the general theory for Nash equilibria, and demonstrated how to handle mean-field games as monomorphic games, we are ready to apply the theory to a Rosenzweig-MacArthur system with fast adaptive behavior.

4   Revisiting the Rosenzweig-MacArthur model

We consider a predator-prey system modeled as a Rosenzweig-MacArthur system in a spatially heterogeneous 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 heterogeneous 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 $c \langle \beta \bar{\sigma}_p, \bar{\sigma}_p \rangle$ 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:

$$\dot{C} = f_c = C \left(\left\langle \beta_c \bar{\sigma}_c, 1 - \frac{\beta_c}{K\varphi + K_0} \bar{\sigma}_c C \right\rangle - \frac{F_p \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle P}{F_p + \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle C} \right) \tag{19}$$

$$\dot{P} = f_p = P \left(\varepsilon \frac{F_p \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle C}{F_p + \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle C} - c \langle \bar{\sigma}_p, \beta_p \bar{\sigma}_p \rangle - \mu_p \right) \tag{20}$$

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

$$\beta_p = 5 \frac{\exp(-(qx)^2) + \beta_0}{\int_0^1 \exp(-(qx)^2) + \beta_0 dx} \tag{21}$$

$$\varphi = \frac{\exp(-qx) + K_0}{\int_0^1 \exp(-qx) + K_0 dx} \tag{22}$$

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 heterogeneous productivity.

4.1 Existence and uniqueness of the equilibrium

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 own type 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:

$$U_c(\sigma_c, \bar{\sigma}_c, \bar{\sigma}_p) = \left\langle \beta_c \sigma_c, 1 - \frac{\beta_c}{K\varphi + K_0} \bar{\sigma}_c C \right\rangle - \frac{F_p \left\langle \beta_p \sigma_c, \bar{\sigma}_p \right\rangle P}{F_p + \left\langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \right\rangle C} \tag{23}$$

$$U_p(\sigma_p, \bar{\sigma}_c, \bar{\sigma}_p) = \varepsilon \frac{F_p \left\langle \beta_p \bar{\sigma}_c, \sigma_p \right\rangle C}{F_p + \left\langle \beta_p \bar{\sigma}_c, \sigma_p \right\rangle C} - c \left\langle \sigma_p, \beta_p \bar{\sigma}_p \right\rangle - \mu_p \tag{24}$$

Denoting the optimum by *, at the Nash equilibrium $\sigma_c^* = \bar{\sigma}_c$ and $\sigma_p^* = \bar{\sigma}_p$. We use the method of Definition 1 to convert both mean-field payoffs into a monomorphic equivalent form Definition 1

$$U_c^{mon}(\sigma_c, \sigma_p) = \left\langle \beta_c \sigma_c, 1 - \frac{1}{2} \frac{\beta_c}{K\varphi + K_0} \frac{1}{2} \sigma_c C \right\rangle - P \log\left(F_p + \left\langle \beta_p \sigma_c, \sigma_p \right\rangle C \right) - \mu_c \tag{25}$$

$$U_p^{mon}(\sigma_p, \sigma_c) = \varepsilon \frac{F_p \left\langle \beta_p \bar{\sigma}_c, \sigma_p \right\rangle C}{F_p + \left\langle \beta_p \sigma_c, \sigma_p \right\rangle C} - \frac{1}{2} c \left\langle \sigma_p, \beta_p \sigma_p \right\rangle - \mu_p \tag{26}$$

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 charactirization of strict pseudomonotonicity for differentiable functions.

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

$$\langle f(x), u \rangle = 0 \Rightarrow \langle (\nabla_x f(x)) h, h \rangle > 0 \tag{27}$$

A proof can be found in (Hadjisavvas et al., 2006, Proposition 2.8, p.96)

Proposition 2. *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 convex, as it has strictly positive 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

$$\langle x, u \rangle \frac{C\beta_c}{K\varphi + K_0} + \frac{\langle \sigma_p, h \rangle}{F_p + \langle \sigma_p, x \rangle} = 0 \tag{28}$$

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

$$H(x, u) = \langle (\nabla_x f)(x)u, u \rangle = \langle u, u \rangle \frac{C\beta_c}{K\varphi + K_0} - \frac{\langle \sigma_p, u \rangle \langle \sigma_p, h \rangle}{F_p + \langle \sigma_p, x \rangle} \tag{29}$$

then $H(x, u) > 0$ since $\langle \sigma_p, u \rangle = 0$, so S is strictly pseudomonotone.

To show that there exists a solution, start by noting that for all $h \in H^2$, the mapping $S \mapsto \langle dU(S), w \rangle$ is continuous in S, hence lower semi-continuous, hence also lower-semicontinuous on line segments. For the technical criterion of ?? pick $u_0 = [1, 1]$ and consider $R = 1 + \varepsilon$, $\varepsilon > 0$. Then we wish to show that there exists ε such that

$$\langle -dU(\sigma_c, \sigma_p), (1 - \sigma_c, 1 - \sigma_p) \rangle \geq 0$$
$$\langle dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle \geq 0 \tag{30}$$

for $\|(\sigma_c, \sigma_p)\| = 1 + \varepsilon$. It is sufficient to show that there exists ε such that each term in the inner product is positive. We start with the consumer term, where we utilize that $\langle \sigma_c, 1 \rangle = 1$

$$1 - \langle \sigma_c, \sigma_c - 1 \rangle \frac{C\beta_c}{K\varphi + K_0} - \frac{\langle \sigma_p, \sigma_c - 1 \rangle}{F_p + \langle \sigma_p, \sigma_c \rangle}$$
$$= 1 - (1 - \|\sigma_c\|^2) \frac{C\beta_c}{K\varphi + K_0} + (1 - \langle \sigma_p, \sigma_c \rangle) \frac{1}{F_p + \langle \sigma_p, \sigma_c \rangle} \tag{31}$$

The terms $1 - \|\sigma_c\|^2$ and $1 - \langle \sigma_p, \sigma_c \rangle$ are uniformly bounded above by $\varepsilon_1^2 + 2\varepsilon_1$. 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_1 can be determined by solving the inequality

$$(\varepsilon_1^2 + 2\varepsilon_1)(\xi + \eta) \leq 1 \tag{32}$$

Proceeding in the same fashion with the second term, we arrive at a pair of constants $\varepsilon_1, \varepsilon_2$. 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 (20), we are also interested in showing that the fixed-point of the dynamics exists and is unique. Here we can directly use the theory we have developed. The functions f_1/C and f_2/P are strictly monotone, and the set of fixed-points is uniformly bounded due to the metabolic terms and logistic terms, respectively. Therefore, by Theorem 2 there is a unique equilibrium for the population game.

4.2 Numerical approach and implementation

In order to find Nash equilibria and fix-points of the behaviorally modified Rosenzweig-MacArthur system, we use the formulation of Equation (13). 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. The equations Equation (20) and the derivatives of the

monomorphic payoffs Equation (25) are formulated via. the symbolic language CasADi (Andersson et al., 2019), where we then solve the complementarity problem as a feasibility problem using IPOPT (Wächter and Biegler, 2006) using the HSL subroutines for linear algebra (HSL, 2007)

The numerical approach is extremely fast, and should scale to much larger problems. It allows for determination of fixed-points of the dynamics in less than 1 second.

5   Numerical results

5.0.1   Population dynamics

We study the population impact of varying the environmental and ecosystem variables of carrying capacity, intraspecific predator competition and carrying capacity on the behaviorially modified Rosenzweig-MacArthur model introduced in Section 4. 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$<$

Figure 1: Dynamics
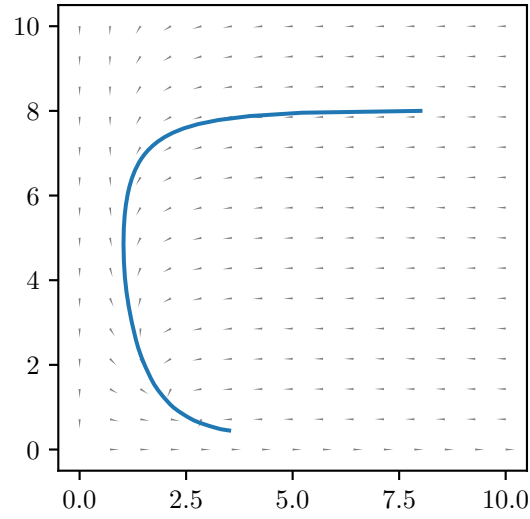
The plot Figure 1 shows the general phase-portrait and the trajectories of the population dynamics for three different starting points. The dynamics have been stabilized in contrast to the Hopf bifurcation in the Rosenzweig-MacArthur model under the paradox of enrichment, but the direction of the flow is consistent with the usual Rosenzweig-MacArthur model.
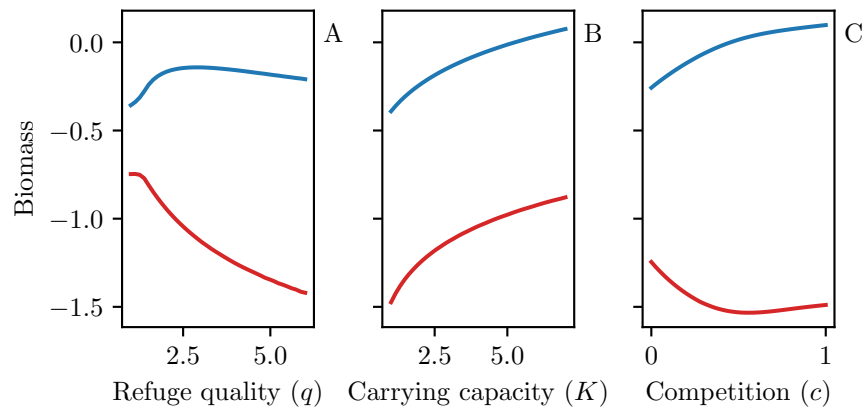
Figure 2: Pop levels c

Figure 2 reveals how the population levels of consumers and predators change

at equilibrium with varying refuge quality (Figure 2(A)), carrying capacity (Figure 2(B)) and intraspecific predator competition (Figure 2(C)). Increasing the quality of the refuge (Figure 2)(A) initially causes an increase in consumer populations (Figure 2(A, blue)) and a decrease in predator populations. The refuge quality reaches a point (Figure 2)($q \approx 2.2$)) 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 (Figure 2). 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 (Figure 2(C, red)) until a point where the population stabilizes (Figure 2($c \approx 1/3$)), while the population of consumers continues to increase (Figure 2(C, blue)). The increasing quantity of consumers available must compensate for the intraspecific losses.

5.0.2 Spatial distribution

Figure 3: Increasing carrying

Carrying capacity (K) Consumer Carrying capacity (K) Predator
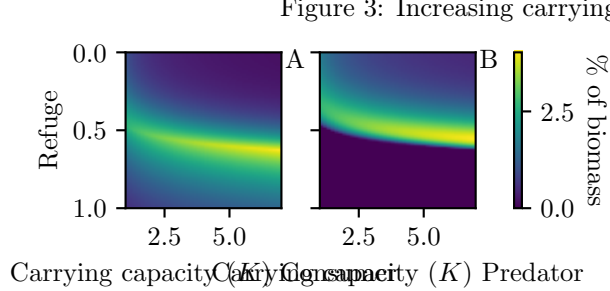
The plots in (Figure 3) illustrate the strategies of the consumers (Figure 3(A)) and predators (Figure 3) at equilibrium when carrying capacity varies. At low carrying capacities, both consumers and predators are relatively spread out, with the peak concentration about halfway to the refuge. As the carrying capacity increases, the distribution becomes more cocentrated 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.

Figure 4: Increasing competition

Competition (c) Consumer   Competition (c) Predator
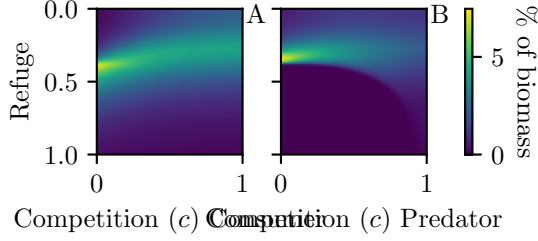
In Figure 4 the intraspecific predator competition is varied and we see the emergent equilibrium strategy of the consumers (Figure 4(A)) and predators (Figure 4(B)). When there is no intraspecific predator competition, both consumers and predators are highly concentrated at about 0.4. The equilibrium 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 incentivicizing predator-spread. When the consumer population spreads out, the distribution trends towards the more productive layers. Summarizing, highly competitive predators leads to dispersed populations.

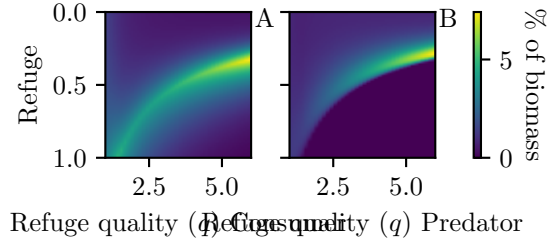Figure 5: Consumer (A) and predator (B) concentration at equilibrium as a function of changing refuge quality

Refuge quality (q) Consumer   Refuge quality (q) Predator

Figure 5 shows the strategy of consumers (Figure 5(A)) and predators (Figure 5(B)) at equilibrium with varying refuge quality.

6 Discussion and conclusion

We redefine the notion of a population game, based on choices optimizing individual growth, modifying the definition of (Vincent and Brown, 2005). This is done through the introduction of mean-field games. We establish the necessity of the mean-field approach, showing that it generalizes the classical ideal free distribution. In addition, we show that the individual optimization is much less efficient when assuming a population playing a mean-field game compared to a monomorphic population. We demonstrate a procedure to reformulate a large class of mean-field games into normal-form games, allowing analysis as classical games. Having reduced our problem to that of finding Nash equilibria for classical games, we establish existence and uniqueness of Nash equilibria for a large class of games using variational inequalities. A major advance is that we are inherently able to handle continuous strategy spaces. Having determined existence and uniqueness of Nash equilibrium the instantaneous game, we turn to the existence and uniqueness of fixed-points for population games. We show that a large class of population games as we define them have a unique equilibrium. Using the framework CasADi, we are able to efficiently solve these population games numerically, and analyze the sensitivity of population levels and strategy distributions. We illustrate this with a behaviorially modified Rosenzweig-MacArthur system.

We show the framework of mean-field games is applicable in ecology through multi-species population games with optimal individual behavior. We establish theoretical results for existence and uniqueness of Nash equilibria with continuous strategy spaces.

The payoff for an individual in a large population of indistinguishable individuals is shown much higher when all individuals are a-priori assumed to follow the same strategy.

Though a population of animals may all be indistinguishable, and appear to follow the same strategy, it is important to consider how this monomorphism emerges. The per capita utility from each individual optimizing is much higher for a population which is assumed monomorphic in comparison to one where the monomorphism emerges as a mean-field nash equilibriums.

We showed that the Nash equilibrium exists is and is unique for a large class of games, even with continuous strategy spaces, and the results can be applied to mean-field games through the notion of equivalent monomorphic games. Our results on the existence and the uniqueness of the Nash equilibrium allowed us to show that there exists a unique equilibrium for a wide class of biologically relevant population games. The approach based on fixed-point theory used to show the existence and uniquenss of this simultanous problem appears generalizble to a wider class of population games, allowing for populations where the problem of finding a fixed point cannot be interpreted as a variational inequality.

We found that increasing carrying capacity causes an all-round population increase, and more dispersed populations, in agreement with empirical evidence. When increasing intrapredator competition, we found that predators were more dispersed at the population fixed-point. In accordance with the ideal free dis-

tribution, the population of consumers was also increasingly dispersed due to intraspecific competition from the increasing population caused by lower predation loss. Adding behavior to a relatively simple model drastically expands the scope of phenonenoma that can be modeled, and allows us to make complex predictions from simple models that correspond to empirical findings on population distributions in ecosystems.

By bringing the results from variational inequalities into mathematical ecology, we introduce relatively simple criteria for when a game has a unique Nash equilibrium, allowing for a much less ad-hoc approach to population games and instead providing general tools for the working mathematical biologist. In this way, incorporating behavior in a wide array of models becomes feasible for non-experts, and in particular behavior can be easily incorporated in population models. Our results highlight the need to take care of whether considering individual or group-level optimization, and directly illustrate the strength of group-level optimization. This shows the benefit of hive-mentalities, where individuals might optimize for themselves, but with the knowledge of what the rest of the population is doing.

Our numerical approach for finding Nash equilbria is simple, and can readily be applied in general models. Since our approach is inherently built for continuous habitats, we allow the simulation of realistic ecosystems, and models incorporating behavior in this fashion could e.g. include diffusion terms for resources in continuous ecosystems. The general applicability also allows for modeling complex habitats in hihgher dimensions.

We provide a large step forward from previous approaches based on linear models, where specialized software for solving the linear complementarity was used (**?**). By using a general-purpose optimization package, we are unable to leverage the structure inherent in the variational inequality. If the approach is used in large-scale ecosystem modeling for concrete applications, it is probably advantageous to solve the complementarity problem with dedicated software such as PATH or Siconos.

We have not touched on the topic of differential games, instead focusing on myopic optimization. By using Pontryagins princiople, the approach we introduce can also be applied setting by considering the players' Hamiltonians through differential variational inequalities (**?**).

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