

# 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 habitat choice in simple ecosystems under the assumption of a populations or limited choices. Real-life behavioral 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 allow 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, (Křivan, 1997). Linear models are sufficient 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. Instead of assuming a population where all individuals act in lockstep, we assume that each animal acts independently, but that its risk-reward calculus is affected by the population mean 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; Broom and Rychtár, 2013; Parker, 1978), 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 cautious 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 equilibria 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.

## 2 General setting

We envision a setting with  $M$  different types of animals co-existing in a heterogeneous environment. More rigorously, we assume that the environment is a measure space  $(X, \mu)$ . We assume the environment is dynamic, driven by an underlying dynamic and the impact of the animals behavior and population dynamics. We assume the populations  $N_i$ ,  $i \in \{1, \dots, M\}$  are large compared to a single individual, so the  $N_i$  are continuous.

We assume that the migration dynamics are much faster than the population dynamics, as is seen in e.g. marine ecosystems (?). This slow-fast dynamic

allows us to model the migrations as instantaneous (??).

We assume that every animal has an area where it forages at any instant. For an animal of type  $i$  this is a probability distribution  $\sigma_i$  over the environment  $X$ . The distribution  $\sigma_i$  is absolutely continuous with respect to the measure  $\mu$ . By working in this generality, we allow for both continuous and discrete distributions, generalizing the classical model of discrete patch-choice models (Fretwell, 1969; Broom and Rychtár, 2013). By requiring absolute continuity we remove degenerate situations e.g. the emergence of Dirac-type distributions in a continuous setting.

The environment an animal of type  $i$  faces is determined by the ambient environment  $X$  and the foraging choices of all other inhabitants. Modeling this necessitates the introduction of the mean-field-strategy,  $\bar{\sigma}_j$  for type  $j$ . The mean-field strategy  $\bar{\sigma}_j$  is the mean strategy of all individuals of type  $j$ . As a consequence, we can describe the foraging pressure from type  $j$  at a point  $x \in X$  by  $N_j \sigma_j(x)$ .

The choice of optimal foraging strategy  $\sigma_i^*$  for an animal of type  $i$  is a trade-off based on the state of the environment, the presence of competitors, predators or prey. The mean density of competitors, predators or prey at a point  $x$  is described by  $N_j \sigma_j(x)$ . We capture this trade-off in a payoff function  $U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1}^M)$ ,

Phrasing our model in terms of a mean-field game allows determination of the Nash equilibrium. The fundamental assumption is the populations are assumed infinitely large so the choice of a single individual does not change the mean-field strategy (Aumann, 1964). At the Nash equilibrium of a mean-field game every individual of type  $i$  follows the same strategy  $\sigma_i^*$ , (Lasry and Lions, 2007). Heuristically, this is due to interchangeability as if any individual of type  $i$  gains from diverging from  $\sigma_i^*$ , they will all gain. Therefore, if they all follow the optimal strategy, they follow the same strategy.

An advantage of studying games of mean-field type is that they have polymorphic-monomorphic equivalence (?). In a game with polymorphic-monomorphic equivalence an individual is not able to discern whether it is playing against a mixture of populations, weighted with density  $\sigma_j(x)$ , or against a homogeneous population, where all individuals play the strategy  $\sigma_j$ . In short, modeling population games with polymorphic-monomorphic erases the need to consider the difference between having sub-populations with different strategies or a single population with one strategy, which is ecologically advantageous (?).

We can now show that modeling population games as mean-field games is a generalization of the ideal free distribution. Assuming monomorphic populations is the other typical approach to population games for computational tractability (Vincent and Brown, 2005). We show that a monomorphic approach gives a substantially higher payoff at the Nash equilibrium than the ideal free distribution.

**Proposition 1.** *Consider a population of size  $N$  in a discrete habitat with  $L$  patches. We denote the strategy of an individual by  $p$  and the mean-field strategy by  $\bar{p}$ .*

The payoff function  $U(p, \bar{p})$  for an individual playing strategy  $p$  is a bilinear function. The function  $U$  is specified by an  $m \times m$  matrix  $A$  such that  $U(p, \bar{p}) = \langle p, NA\bar{p} \rangle$ .

If we assume that the population is monomorphic  $p = \bar{p}$ , the payoff is  $U(p, p)$ .

Denote the Nash equilibria for the mean-field and monomorphic games respectively by  $p_{MFG}^*$  and  $p_{mon}^*$ . Then:

The Nash equilibrium for the mean-field game  $p_{MFG}^*$  is the ideal free distribution.

The value of the payoff-function at the Nash equilibrium is twice as high in the monomorphic game compared to the mean-field game  $U(p_{mon}^*, p_{mon}^*) = 2U(p_{MFG}^*, p_{MFG}^*)$ .

*Proof.* Consider the payoff in the mean-field situation  $U(p, \bar{p})$ .

$$U(p, \bar{p}) = \langle p, AN\bar{p} \rangle \quad (1)$$

Using the KKT conditions, we can write up the requirements for an extremum.

$$\begin{aligned} AN\bar{p} + \mu &= \lambda_1 \\ \langle p_{MFG}^*, \mu \rangle &= 0 \\ \mu &\geq 0, \quad p_{MFG}^* \geq 0 \\ \sum_{j=1}^L p_{MFG,j}^* &= 1 \end{aligned} \quad (2)$$

As we are in the mean-field case, at the Nash equilibrium  $p^* = \bar{p}^*$ , ie.

$$p_{MFG}^* = \operatorname{argmax}_p U(p, p_{MFG}^*) \quad (3)$$

so we can insert  $p = \bar{p}$  in the KKT conditions, to get:

$$\begin{aligned} ANp_{MFG}^* + \mu &= \lambda_1 \\ \langle p_{MFG}^*, \mu \rangle &= 0 \\ \mu &\geq 0, \quad p_{MFG}^* \geq 0 \\ \sum_{j=1}^L p_{MFG,j}^* &= 1 \end{aligned} \quad (4)$$

The first equation ensures that  $ANp + \mu$  is constant. At the same time,  $p = 0$  whenever  $\mu \geq 0$  due to the second equation. Hence  $ANp$  is constant, and equals  $\lambda_1$ . For any  $j$  where  $(ANp)_j$  would be less than  $\lambda_1$ , the value of  $p$  is zero. These are exactly the criteria for the ideal free distribution, showing the ideal free distribution as a special case of a mean-field game. Analogously, consider the

(KKT) conditions at the Nash equilibrium for the monomorphic game

$$\begin{aligned}
2ANp_{mon}^* + \mu &= \lambda_2 \\
\langle p_{mon}^*, \mu \rangle &= 0 \\
\mu &\geq 0, \quad p_{mon}^* \geq 0 \\
\sum_{j=1}^L p_{mon,j}^* &= 1
\end{aligned} \tag{5}$$

At every point with a non-zero concentration, the payoff for the monomorphic population is  $\lambda_2$ . The only difference between the two sets of KKT conditions is the factor of 2 in the first line. Hence the pointwise payoff in monomorphic case is  $\lambda_2 = 2\lambda_1$ , as desired.  $\square$

As Proposition 1 shows, assuming a monomorphic population has a drastic effect on the expected payoff. In Proposition 1 the classical ideal free distribution emerges as the mean-field equilibrium. The emergence of the ideal-free distribution is a compelling argument for the mean-field model.

### 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 (Karamardian, 1969; Nabetani et al., 2011). 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. Since the basic object of consideration in our setup is that of habitat selection games, we need to be able to consider the overlap of two habitats. In the setting with a finite number of habitats, this is the inner product of the vectors describing their habitat distributions. Therefore, the natural setting for the continuous habitat selection game is a Hilbert space, to allow the calculation of habitat overlaps.

We build up the theory for monomorphic games, and then show how the the mean-field case can be incorporated.

**Definition 1.** 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 2.** 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  $T : K \rightarrow H$ .

The complementarity problem  $CP(T, K)$  is the problem of finding an element  $x^*$  such that

$$\begin{aligned} \langle x^*, Tx^* \rangle &= 0 \\ Tx &\in K^*, \quad x \in K \end{aligned} \quad (6)$$

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

**Definition 3.** Let  $H$  be a real Hilbert space and  $K \subset H$  be a non-empty subset of  $H$ . Let  $T : K \rightarrow H$ . The variational inequality  $VI(T, K)$  is the following system

$$x \in K, \langle y - x, Tx \rangle \geq 0, \quad \forall y \in K \quad (7)$$

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  $\sigma_i$ . At the Nash equilibrium, each payoff function  $U_i$  must satisfy the Karush-Kuhn-Tucker (KKT) conditions with respect to  $\sigma_i$ .

$$\nabla_{\sigma_i} U_i((\sigma_j)_{j=1}^N) + \mu_i - \lambda \cdot 1 = 0 \quad \langle \sigma_i, \mu_i \rangle = 0 \quad \mu_i \geq 0 \quad \sigma_i \geq 0 \quad \int_X \sigma_i - 1 = 0 \quad (8)$$

The Nash equilibrium of the game specified by the family  $(U_i)$  corresponds to finding a system  $\sigma_i^*$  satisfying the KKT conditions simultaneously for every pair  $U_i$ , (Deimling, 2010). Thus the condition for a Nash equilibrium is:

$$\begin{aligned} \begin{pmatrix} \nabla_{\sigma_1} U_1 \\ \vdots \\ \nabla_{\sigma_N} U_N \end{pmatrix} + \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_N \end{pmatrix} + \begin{pmatrix} \lambda_1 \cdot 1_k \\ \vdots \\ \lambda_N \cdot 1_k \end{pmatrix} &= 0 \\ \left\langle \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_N \end{pmatrix}, \begin{pmatrix} \sigma_1 \\ \vdots \\ \sigma_N \end{pmatrix} \right\rangle &= 0 \\ \mu_i &\geq 0 \\ \sigma_i &\geq 0 \\ \int \sigma_i dx &= 1 \end{aligned} \quad (9)$$

To simplify Equation (9), 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

$$\langle dU(S) + \lambda, S \rangle = 0 \quad \langle S_i - 1, 1 \rangle \lambda = 0 \quad -dU(S) - \lambda \geq 0 \quad \langle S_i - 1, 1 \rangle \in \{0\} \quad S \geq 0 \quad \lambda \in \mathbb{R} \quad (10)$$

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

$$T(S, \lambda) = \begin{pmatrix} dU(S) + \lambda \\ (\langle \sigma_i, 1 \rangle - 1)_{i=1}^M \end{pmatrix} \quad (11)$$

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

$$\langle dU(S), S - T \rangle \geq 0 \forall T \in K^n \quad (12)$$

i.e. solves a variational inequality. Searching for a solution to a variational inequality is more tractable for theoretical considerations, while the complementarity formulation is preferable for solving the problem numerically.

In case the payoff-functions  $\sigma_i$  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.** *Consider a game with  $N$  players with strictly pseudoconvex payoff functions  $U_i$  and strategies  $\sigma_i$  in  $H$ . The game has a unique Nash equilibrium if*

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

*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 bi-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 ?.  $\square$

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  $\sigma_i$  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  $\sigma$ .*

*Proof.* The game specified by  $\sigma_i$  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  $G : K^N \rightarrow \mathbb{R}^N$ , (Barbagallo and Cojocaru, 2009, Theorem 4.2). Likewise, due to the assumptions on  $f_i$  the complementarity problem  $\langle (f_i)_{i=1}^N(x), x \rangle$  has a unique solution for every  $\sigma$ . 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  $F \circ H : \mathbb{R}_+^N \rightarrow \mathbb{R}_+^N$ . 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  $\sigma$ , the variational inequality

$$x \in \mathbb{R}_+^n, \langle (f_i/x_i)_{i=1}^N(x), y - x \rangle \geq 0 \quad y \in \mathbb{R}_+^n \quad (14)$$

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

$$\begin{aligned} S \in K^n, \langle dU(S), S' - S \rangle &\geq 0, \quad S' \in K^n \\ x \in \mathbb{R}_+^n, \langle (f_i/x_i)_{i=1}^N(x), y - x \rangle &\geq 0 \quad y \in \mathbb{R}_+^n \end{aligned} \quad (15)$$

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

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.

Up till now, our theory only handles monomorphic games.

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 4.** Consider a mean-field game with populations  $N_1, \dots, N_M$  with individual payoffs specified by  $U_i(\sigma_i, (\bar{\sigma}_j)_{j=1}^M, (N_j)_{j=1}^M)$ . Assume  $\nabla_{\sigma_i} U_i|_{\sigma_i=\bar{\sigma}_i}$  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  $U_{mon}^i$  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 4 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.

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  $\beta_l$  varies locally and  $\beta_0$  is the minimal clearance rate. The function  $\beta_p$  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  $c \langle \bar{\sigma}_p, \beta_p \bar{\sigma}_p \rangle$  where  $c$  describes the level of competition. The carrying capacity is given by  $K\varphi + K_0$ , where  $K$  varies,  $\varphi$  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  $\beta_c$ , the dynamics are given by:

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

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

Introducing the quality ( $q$ ) of the habitat as a parameter, the functions  $\beta_p$  and  $\varphi$  are given by

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

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

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 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  $\sigma_c$  and  $\sigma_p$  respectively, the instantaneous fitness  $U_c$  of a consumer and a predator  $U_p$  are:

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

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

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

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

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

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*

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

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  $\sigma_p$  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, 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  $\varepsilon$  such that

$$\begin{aligned} \langle -dU(\sigma_c, \sigma_p), (1 - \sigma_c, 1 - \sigma_p) \rangle &\geq 0 \\ \langle dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle &\geq 0 \end{aligned} \quad (27)$$

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

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

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  $\eta = \frac{1}{F_p + \langle \sigma_p, \sigma_c \rangle}$ ,  $\varepsilon_1$  can be determined by solving the inequality

$$(\varepsilon_1^2 + 2\varepsilon_1)(\xi + \eta) \leq 1 \quad (29)$$

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 (17), 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.

## 5 Numerical approach and results

### 5.1 Numerical implementation

In order to find Nash equilibria and fix-points of the behaviorally modified Rosenzweig-MacArthur system Section 4, we use the formulation of Equation (10). 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 (17) and the derivatives of the monomorphic payoffs Equation (22) 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 for finding Nash equilibria and fixed points 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 with several hundred grid points. Simulating the population dynamics is, in contrast, a comparatively slow affair since we simulate the population dynamics using a forward Euler method.

## 5.2 Population dynamics and levels

With a numerical approach in place, we can study the population dynamics and the sensitivity of Section 4 to parameters. We vary the carrying capacity ( $K$ ) and the intraspecific predator competition ( $c$ ). We are interested in both the population levels at equilibrium, and the associated spatial distributions. The parameters for the model are:

Name	Value	Meaning
$q$	3	Refuge quality
$K_0$	$10^{-4}$	Minimal carrying capacity
$\beta_{p,0}$	$10^{-4}$	Minimal predator clearance rate
$\beta_c$	1	Consumer clearance rate
$\mu_p$	0.15	Predator metabolic rate
$F_p$	100	Predator maximum growth rate
$\varepsilon$	0.1	Trophic efficiency

Figure 1: Phase portrait of the population dynamics of the behaviorally modified Rosenzweig-MacArthur system at carrying capacity of  $K = 40$ . The blue line illustrates a system trajectory with initial conditions  $C(0) = 8$ ,  $P(0) = 8$ .

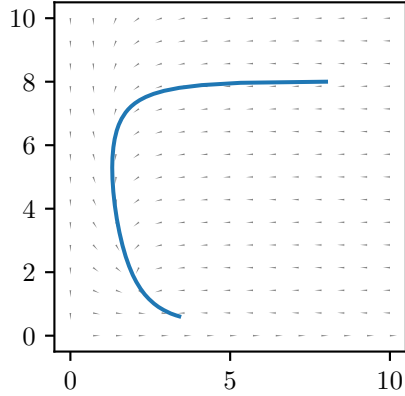


Figure 1 illustrates the phase portrait for the behaviorally modified Rosenzweig-MacArthur model, along with a sample trajectory. The direction of the flow is consistent with the usual Rosenzweig-MacArthur model. The phase portrait reveals that the system dynamics have been stabilized. Looking at the sample trajectory, this stabilization is quite substantial with not even a full oscillation. The stable dynamics stand in contrast to the Rosenzweig-MacArthur model with constant behavior ( $\sigma_p = \sigma_c = 1$ ) where the point of the Hopf bifurcation has been passed, leading to limit cycles. Adding optimal individual behavior appears to eliminate the paradox of enrichment (Rosenzweig, 1971).

Figure 2: Panel (A) shows population levels of consumers (blue) and predators (red) at equilibrium with changing carrying capacity ( $K$ ). Panel (B) again shows the population levels, but with varying intraspecific predator competition ( $C$ ).

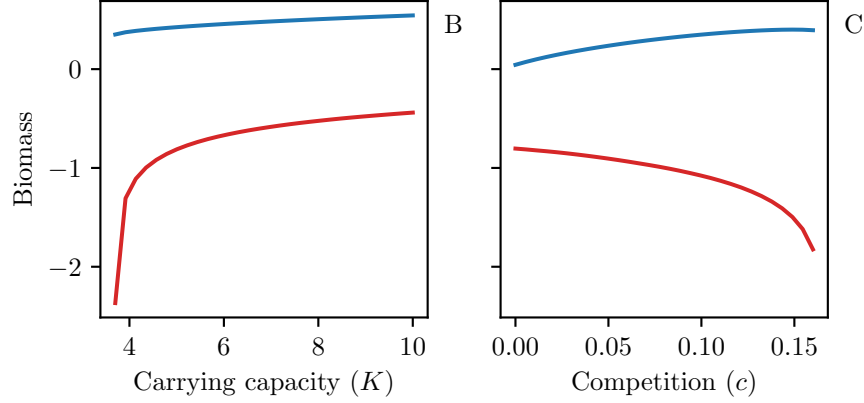


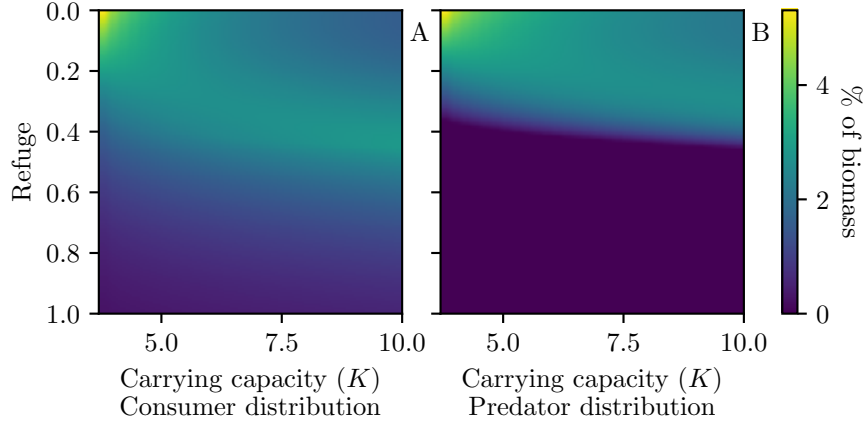
Figure 2 reveals how the population levels of consumers and predators change at equilibrium with varying refuge quality (Figure 2(A)), carrying capacity (Figure 2(B)) and intraspecific predator competition (Figure 2(C)). Increasing the quality of the refuge (Figure 2(A)) initially causes an increase in consumer populations (Figure 2(A, blue)) and a decrease in predator populations.

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.

### 5.2.1 Spatial distribution

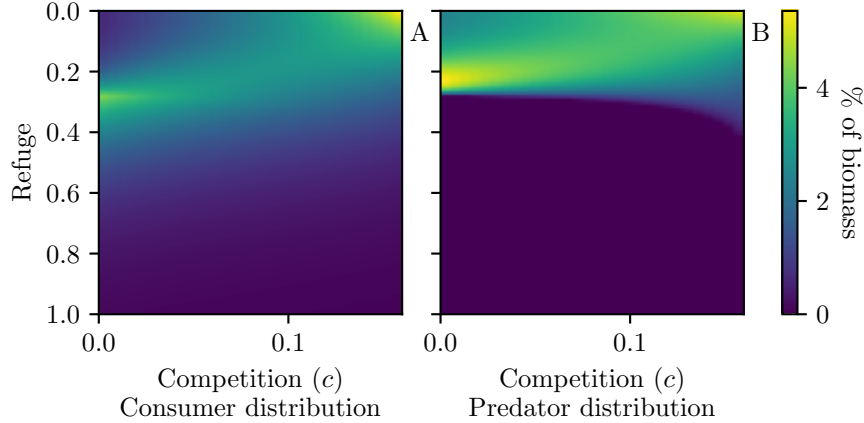
Figure 3: Spatial distribution of consumers ( $A$ ) and predators ( $B$ ) at the equilibrium with increasing carrying capacity ( $K$ ).



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 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.

Figure 4: Distribution of consumers (A) and predators (B) at equilibrium under changing predator competition ( $c$ ).



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 incentivizing predator-spread. The spreading out of the consumer population can be interpreted in terms of the ideal free distribution. An increase in consumer population Figure 2 causes an increase in concentration on the less productive spots. When the consumer population spreads out, the distribution trends towards the more productive layers. Summarizing, highly competitive predators leads to dispersed populations.

## 6 Discussion and conclusion

We redefined the notion of a population game, based on optimizing individual growth, modifying the definition of (Vincent and Brown, 2005). This is done through the introduction of mean-field games to handle a population which is not assumed a-priori monomorphic. We establish the necessity of the mean-field approach, showing that it generalizes the classical ideal free distribution (Fretwell, 1969). 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. 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 individ-

ual optimizing is much higher for a population which is assumed monomorphic in comparison to one where the monomorphism emerges as a mean-field Nash equilibrium.

This expands on qualitative work for instantaneous migrations (Křivan et al., 2008; Collet, 2019), and is in accord with the results from Abrams. We provide yet another reason why the the monomorphic approach should be used with caution.

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.

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. In particular, we are inherently able to handle continuous strategy spaces. Having determined existence and uniqueness of Nash equilibrium for the instantaneous game, we show the corresponding results for fixed-points for population games. By going this general route, we provide a more efficient way of showing existence and uniqueness and uniqueness than the usual tailor-made methodes (Cressman and Křivan, 2010; Křivan and Cressman, 2009). The general nature of the payoff functions that can be handled by our method provides a large step forward from previous approaches, which only allowed bilinear payoffs (Mariani et al., 2016; Pinti et al., 2021). We can simulate population dynamics with behavior in realistic ecosystems, since we inherently handle a mixture of discrete and continuous habitats. Using a general-purpose optimization package, we are unable to leverage the structure inherent in the variational inequality. If the method we advance 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 (Dirkse and Ferris, 1995; Acary et al., 2019).

Analyzing a Rosenzweig-MacArthur model with behavior, revealed a powerful stabilization of the population dynamics. This stabilization agrees with results on population games in models with finite strategy spaces (Křivan, 2007; Valdovinos et al., 2010). We have been unable to show mathematically why this stability emerges, but a fruitful avenue of attack could be drawing on the theory of complementarity-constrained dynamical systems (Adly, 2018; Brogliato and Tanwani, 2020). In the sensitivity analysis, 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 distribution, 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 phenomena that can be modeled, and allows us to make complex predictions from simple models that correspond to empirical findings on population distributions in ecosystems.



The 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 uniqueness of this simultaneous problem appears to generalize 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. By bringing the results from variational inequalities into mathematical ecology, we introduce criteria to establish when a game has a unique Nash equilibrium. This gives us a general approach to population games, where previously only a few specific types could be handled. (Sandholm, 2010). Our focus has been on population games, but our results on existence and uniqueness are generally applicable to games in ecology.

We have not touched on the topic of differential games, instead focusing on myopic optimization. By using Pontryagin's principle, the approach we introduce can also be applied setting by considering the players' Hamiltonians through differential variational inequalities (Pang and Stewart, 2008).

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