Appendices

In these appendices, we develop and discuss the tools used to define and solve our model from section 2. The structure is as follows:

A Our model in general terms, with more detail than was possible in section 2. We outline the linear benefit functions used in this paper, and possible generalizations to non-linear benefit functions for future work.

B Proof of a theorem for factoring any replicator dynamics and application of it to the specific case of factoring from $\{x_G, x_V, x_D\} \mapsto \{p, q\}$ (transforming eqs. 4, 5 and 6 to eqs. 7 and 8) presented in this paper.

C Discuss of the generality of replicator dynamics with a focus on populations of constant size (C.1), exponentially growing populations (C.2), and *in vitro* systems (C.3).

D Solution to the gain functions needed to transform the system in equations 7 and 8 into equations 9 and 10. We use this second description of our model to characterize the possible dynamics into the three qualitatively different regimes used in section 3.

E Proof of closed orbits for the heterogeneous regime of section 3.3. To achieve this, we show that – after dynamic rescaling of time – our system is Hamiltonian.

A General model for the double goods game

Following Archetti (2014), we consider the acidity produced by glycolysis, which affects normal cells more than cancer cells, as a public good for cancer cells. Acidity benefits all tumour cells, regardless of whether they have aerobic or anaerobic metabolism. In contrast, the increased oxygen from vascularization benefits only aerobic cells and so within a tumour it is a good that is private to non-glycolytic cells. Among just the aerobic tumour cells, following Archetti (2013), vascularization is a public good since it benefits all aerobic cells in a local population regardless of how much VEGF – or other vascularization increasing factors – a particular individual is producing. Therefore, vascularization is a club good (Buchanan 1965), and in game theoretic terms there are two kinds of defection. All tumour cells benefit from acidity but can defect from contributing to this public good by using aerobic metabolism. Any aerobic cell can benefit from higher vascularization but can defect from contributing to this club good by not producing, or producing less, VEGF. Since being a defector in the public good is required to benefit from the club good, we call the two goods anti-correlated.

If we consider a cell interacting with n other nearby cells and define $A_n(k) = \frac{b_a k}{n}$ as the benefit due to acidity if k cells are producing acid, and $V_n(k) = \frac{b_v k}{n}$ as the benefit (to aerobic cells) due to vascularization if k cells are (over) producing VEGF at a cost c. This results in three pure strategies with the following payoffs:

GLY The glycolytic strategy does not use oxygen and thus produces acid. It does not (over) produce VEGF to call for more blood vessels and thus does not increase vascularization. When interacting with n_G other *GLY* cells, its payoff is: $A_n(n_G + 1)$.

VOP This strategy uses oxygen and thus does not produce acid. It also (over) produces VEGF at a cost c and thus calls for more blood vessels, directly increasing vascularization. When interacting with n_G *GLY* cells and n_V other *VOP* cells, its payoff is: $A_n(n_G) + V_{n-n_G}(n_V + 1) - c$. Note that the oxygen benefit due to increased vasculization is shared only between non-glycolytic cells, hence the club good group size for V is $n - n_G$.

DEF This strategy is the universal defector, it uses oxygen and thus does not produce acid, and it also does not (over) produce VEGF. When interacting with n_G *GLY* cells and n_V *VOP* cells, its payoff is: $A_n(n_G) + V_{n-n_G}(n_V)$.

We do not explicitly consider the case of a strategy that does not use oxygen but produces VEGF; when the cost of (over) producing VEGF $c > 0$, the fitness of this fourth strategy will always be strictly lower than *GLY* and thus always driven to extinction. Across our population of cells, our fitness functions are thus:

$$w_G = \sum_{n_G+n_V+n_D=n} \binom{n}{n_G, n_V, n_D} x_G^{n_G} x_V^{n_V} x_D^{n_D} A_n(n_G + 1) \tag{A.1}$$

$$= \sum_{n_G=0}^{n} \binom{n}{n_G} x_G^{n_G} (1 - x_G)^{n-n_G} A_n(n_G + 1) \tag{A.2}$$

$$= \langle A_n(n_G + 1) \rangle_{n_G \sim \mathbf{B}_n(x_G)} \tag{A.3}$$

$$w_V = \sum_{n_G+n_V+n_D=n} \binom{n}{n_G, n_V, n_D} x_G^{n_G} x_V^{n_V} x_D^{n_D} (A_n(n_G) + V_{n-n_G}(n_V + 1) - c) \tag{A.4}$$

$$= \langle A_n(n_G) \rangle_{n_G \sim \mathbf{B}_n(x_G)} + \langle V_{n-n_G}(n_V + 1) \rangle_{(n_G,n_V) \sim \mathbf{M}_n(x_G,x_V)} - c \tag{A.5}$$

$$w_D = \sum_{n_G+n_V+n_D=n} \binom{n}{n_G, n_V, n_D} x_G^{n_G} x_V^{n_V} x_D^{n_D} (A_n(n_G) + V_{n-n_G}(n_V)) \tag{A.6}$$

$$= \langle A_n(n_G) \rangle_{n_G \sim \mathbf{B}_n(x_G)} + \langle V_{n-n_G}(n_V) \rangle_{(n_G,n_V) \sim \mathbf{M}_n(x_G,x_V)} \tag{A.7}$$

where $\mathbf{B}_n(x_G)$ is the binomial distribution with n samples and x_G is the probability of success; $\mathbf{M}_n(x_G, x_V)$ is the multinomial distribution with n samples and x_G is the probability of the first outcome, x_V of the second; and $\langle f(k) \rangle_{k \sim \mathbf{K}}$ means the expected value of $f(k)$ over k sampled from the distribution $\mathbf{K}$.

If we define the proportion of glycolytic cells as $p := x_G$ and the proportion of VEGF producers among the aerobic cells as $q := \frac{x_V}{x_V + x_D}$, then we can express the replicator dynamics in the factored form (see appendix B):

$$\dot{p} = p(1-p)(w_G - \langle w \rangle_{V,D}) \tag{A.8}$$

$$\dot{q} = q(1-q)(w_V - w_D) \tag{A.9}$$

where $\langle w \rangle_{V,D} = qw_V + (1-q)w_D$.

We discuss the generality and applicability of replicator dynamics in appendix C. In appendix D, we show how the gain functions of these dynamics are simplified significantly in the linear case that we consider in this paper. Our focus on the linear case allows us to borrow many tools of analysis from the optional public goods game (Hauert et al. 2002; Vander Velde 2016). More complicated functional forms of A_n and V_n could be considered, and yield a fascinating family of possible dynamics, but this is beyond the scope of the current paper. For an initial treatment of the non-linear case, see Kaznatcheev (2015). In the case of $p = 0$ the non-linear case reduces to Archetti (2013), and in the case of $q = 0$ or $q = 1$ the non-linear case reduces to Archetti (2014).

Mathematica notebooks code for visualizing and interacting with the model are available at `https://github.com/kaznatcheev/MathOnco` as dgLinB.nb, dgLinB_Simplexes.nb, and dgLinB_TreatPlayer.nb.

A.1 Extinction of glycolytic VEGF (over)-producers

In the body of the paper, we do not explicitly consider the case of a strategy that does not use oxygen but produces VEGF. This is because when the cost of (over) producing VEGF $c > 0$ the fitness of this fourth strategy will always be strictly lower than *GLY* and thus always driven to extinction. To see this explicitly, let us define the fitness function for glycolytic VEGF (over)-producers:

$$w_{GV} = \langle A_n(n_G + 1) \rangle_{n_G \sim \mathbf{B}_n(x_G)} - c \tag{A.10}$$

$$= w_G - c \tag{A.11}$$

Let r be the proportion of VEGF (over)-producers among the glycolytic cells then the factored replicator dynamics (see eq. A.8, A.9, and appendix B) become:

$$\dot{p} = p(1-p)(\langle w \rangle_{GV,G} - \langle w \rangle_{V,D}) \tag{A.12}$$

$$\dot{q} = q(1-q)(w_V - w_D) \tag{A.13}$$

$$\dot{r} = r(1-r)(w_{GV} - w_G) \tag{A.14}$$

where $\langle w \rangle_{GV,G} = rw_{GV} + (1-r)w_G$ is the average fitness of glycolytic cells. But notice that by plugging eq. A.11 into eq. A.12 and A.14, we get:

$$\dot{p} = p(1-p)(w_G - \langle w \rangle_{V,D} \underbrace{- rc}_{\text{perturbation to general model}}) \tag{A.15}$$

$$\dot{r} = -r(1-r)c \tag{A.16}$$

In words: the proportion r of VEGF (over)-producers among glycolytic cells goes logistically towards zero with rate c and with it its peruturbation to our model goes to zero. Thus, we can safely disregard glycolytic VEGF (over)-producers if we are looking at the long term dynamics of our system, either in terms of stable points or cycles.

A.2 Representing explicit costs of glycolysis

Glycolysis leads to the production of much less ATP than aerobic metabolism, and it is tempting to represent this by introducing an explicit fitness cost k into eq. A.3. It is important to resist this temptation, since introducing k would not change the dynamics. It would only introduce an extra parameter that should be absorbed into either V_n or A_n. This follows from the fact that EGT and replicator dynamics focus on relative fitness. In particular, if one considered the following alternative model:

$$w_G = \langle \tilde{A}_n(n_G + 1) \rangle_{n_G \sim \mathbf{B}_n(x_G)} - k \tag{A.17}$$

$$w_V = \langle \tilde{A}_n(n_G) \rangle_{n_G \sim \mathbf{B}_n(x_G)} + \langle \tilde{V}_{n-n_G}(n_V + 1) \rangle_{(n_G, n_V) \sim \mathbf{M}_n(x_G, x_V)} - c \tag{A.18}$$

$$w_D = \langle \tilde{A}_n(n_G) \rangle_{n_G \sim \mathbf{B}_n(x_G)} + \langle \tilde{V}_{n-n_G}(n_V) \rangle_{(n_G, n_V) \sim \mathbf{M}_n(x_G, x_V)} \tag{A.19}$$

where we introduced a cost k and $\tilde{\cdot}$ over V_n and A_n to differentiate from the original model. Then this model is mathematically equivalent to our original model with either: (1) $A_n = \tilde{A}_n$ and $V_n(\cdot) = \tilde{V}_n(\cdot) + k$, (2) $V_n = \tilde{V}_n$ and $A_n(n_G + 1) - A_n(n_G) = \tilde{A}_n(n_G + 1) - \tilde{A}_n(n_G) - k$ for all $n_G \in (0, n)$, or (3) any convex combination of the above two cases.
because it leaves unchanged the gain functions that determine the game (and that we derive in appendix D).

For the linear case that we consider in the body of the paper (i.e. eq. 1, 2, and 3), it is easier to take the second option and have $b_A = \tilde{b}_A - (n + 1)k$.

B Factoring the replicator equation

In this section, we are going to present a general trick for factoring replicator dynamics into a nested form. We will then apply that trick to transform $\{x_G, x_V, x_D\} \mapsto \{p, q\}$. An early form of the account in this appendix first appeared in Kaznatcheev (2014), and Hauert et al. (2002) previously considered the special case of optional public goods game.

Definition. *A compound strategy (Y_j, W_j, c_j) of a set of strategies $\{x_i, w_i\}_{i=1}^n$ is defined by:*

- *a component function c_j with $\sum_{i=1}^n c_j(i) = 1$,*
- *a weight $Y_j := \sum_i^n c_j(i) x_i$*
- *a profile $y_{ij} = \frac{c_j(i) x_i}{Y_j}$, and*

- *a fitness* $W_j = \sum_{i=1}^{n} y_{ij} w_i$.

Definition. *A set of compound strategies* $\{(Y_j, W_j, c_j)\}_{j=1}^{m}$ *factors a set of strategies* $\{(x_i, w_i)\}_{i=1}^{n}$ *with* $x_i = \sum_{j:c_j(i)\neq 0} \frac{y_{ij} Y_j}{c_j(i)}$ *if for all* $1 \leq i \leq n$, $\sum_{j=1}^{m} c_j(i) = 1$.

Theorem. *If* $\{(Y_j, W_j, c_j)\}_{j=1}^{m}$ *factors* $\{(x_i, w_i)\}_{i=1}^{n}$ *then the system*

$$\dot{x_i} = x_i(w_i - \langle w \rangle) \tag{B.1}$$

where $\langle w \rangle = \sum_{k=1}^{n} x_k w_k$, *and the system*

$$\dot{Y_j} = Y_J(W_j - \langle W \rangle) \tag{B.2}$$
$$\dot{y_{ij}} = y_{ij}(w_i - \langle w \rangle_j) \tag{B.3}$$

where $\langle W \rangle = \sum_{k=1}^{m} Y_k W_k$ *and* $\langle w \rangle_j = \sum_{k=1}^{n} y_{kj} w_k$ *describe the same dynamics.*

Proof. First, notice that $\langle w \rangle_j := \sum_i y_{ij} w_i = W_j$, and

$$\langle W \rangle = \sum_j Y_j W_j = \sum_j Y_j \sum_i y_{ij} w_i \tag{B.4}$$
$$= \sum_{i,j} c_j(i) x_i w_i = \sum_i x_i w_i \tag{B.5}$$
$$= \langle w \rangle. \tag{B.6}$$

Now check that the dynamics are equal:

$$\dot{x_i} = \frac{d}{dt}(\sum_{j:} c_j(i) x_i = \frac{d}{dt}(\sum_{j:c_j(i)\neq 0} c_j(i) \frac{y_{ij} Y_j}{c_j(i)}) \tag{B.7}$$
$$= \sum_j \frac{d}{dt}(y_{ij} Y_j) = \sum_j (\dot{y_{ij}} Y_j + y_{ij} \dot{Y_j}) \tag{B.8}$$
$$= (\sum_j y_{ij}(w_i - \langle w \rangle_j) Y_j + y_{ij} Y_j (W_j - \langle W \rangle)) \tag{B.9}$$
$$= \sum_j y_{ij} Y_j (w_i - \langle w \rangle) = (\sum_j c_j(i) x_i)(w_i - \langle w \rangle) \tag{B.10}$$
$$= x_i(w_i - \langle w \rangle) \tag{B.11}$$

□

We can apply the above theorem to the particular game in section 2 and appendix A.

Corollary. *The dynamics given in section 2 for GLY-VOP-DEF competition:*

$$\dot{x_G} = x_G(w_G - \langle w \rangle) \tag{B.12}$$
$$\dot{x_V} = x_V(w_V - \langle w \rangle) \tag{B.13}$$
$$\dot{x_D} = x_D(w_D - \langle w \rangle) \tag{B.14}$$

are equivalent to their factored form for glycolysis and angiogenesis competition:

$$\dot{p} = p(1-p)(w_G - \langle w \rangle_{V,D}) \tag{B.15}$$
$$\dot{q} = q(1-q)(w_V - w_D) \tag{B.16}$$

where $\langle w \rangle_{V,D} = qw_V + (1-q)w_D$.

Proof. Use the component functions $c_A(G) = 1, c_A(V) = 0, c_A(D) = 0$ and $c_B(G) = 0, c_B(V) = 1, c_B(D) = 1$ and name $p := Y_A = x_G$ and $q := y_{B,V} = \frac{x_V}{x_V + x_D}$. Notice that $W_A = w_G$ and $W_B (= \langle w \rangle_B) = \langle w \rangle_{V,D}$, giving us the equations:

$$\begin{aligned}
\dot{p} &= p(w_G - \langle w \rangle) && \text{(B.17)}\\
&= p(w_G - pw_G - (1-p)\langle w \rangle_{V,D}) && \text{(B.18)}\\
&= p(1-p)(w_G - \langle w \rangle_{V,D}) && \text{(B.19)}\\
\dot{q} &= q(w_V - \langle w \rangle_{V,D}) && \text{(B.20)}\\
&= q(w_V - qw_V - (1-q)w_D) && \text{(B.21)}\\
&= q(1-q)(w_V - w_D) && \text{(B.22)}
\end{aligned}$$

□

C Replicator dynamics for constant and exponentially growing populations

In the late 1970s, replicator dynamics were introduced into theoretical biology and ecology literature by a number of authors (Hofbauer, Schuster, and Sigmund 1979; Maynard Smith 1982; Taylor and Jonker 1978; Zeeman 1980). As we discussed in the introduction, they have been used extensively since then, coming into mathematical oncology near the turn of the millennium (Tomlinson 1997; Tomlinson and Bodmer 1997). However, confusion still exists about the range of applicability of replicator dynamics. In this section, we will describe three different ways to get the replicator equation from micro-dynamical or experimental considerations:

C.1 We discuss the Traulsen, Claussen, and Hauert (2006) treatment of constant size populations.

C.2 We build up from an exponential growth model.

C.3 We will start from an experimental system with arbitrary *in vitro* growth.

None of these micro-dynamical foundations perfectly capture the *in vivo* conditions of a cancer patient. But the robustness of the replicator equations to changes in founding assumptions should convince us that they are a good starting point for the heuristic model in this paper. This appendix closely follows Kaznatcheev (2016c).

C.1 Fitness as probability to reproduce in populations of constant size

A focus on individual agents pushes the theorist to look for definitions of fitness on the individual – rather than population – level. We find such a definition in the Moran process (Moran 1958; Taylor et al. 2004), and with it comes the realization of replicator dynamics as a process on well-mixed and large but fixed sized populations.

In a Moran process, we imagine that a population is made up of a fixed number N of individuals. An agent is selected to reproduce in proportion to their game payoff, and their offspring replaces another agent in the population, chosen uniformly at random. This gives us a very clear individual account of fitness as a measure of the probability to place a replicate into the population.

Traulsen, Claussen, and Hauert (2006) wrote down the Fokker-Planck equation for the above Moran process, and then use Ito-calculus to derive a Langevin equation for the evolution of the proportions of each strategy x_k. The fluctuations in this stochastic equation scale with $1/\sqrt{N}$ and so vanish in the limit of large N. This reduces them to a deterministic limit of the replicator equation in Maynard Smith form (Maynard Smith 1982), with the fitness functions as the payoff functions:

$$\dot{x}_k = x_k \frac{w_k - \langle w \rangle}{\langle w \rangle} \tag{C.1}$$

where the extra condition of $\langle w \rangle > 0$ is introduced. In the limit of weak-selection, this form is equivalent to the Taylor form (Taylor and Jonker 1978) used in the body of the paper:

$$\dot{x}_k = x_k(w_k - \langle w \rangle) \tag{C.2}$$

Even without weak-selection, the two systems of equations differ only by dynamic time rescaling and thus have the same fixed points, orbits, and paths. Since these are often the things we care most about during our analyses, we can use the equations interchangeably.

C.2 Exponentially growing populations

Suppose that for some theoretical reasons, we think that the microdynamics of our population is well represented by an exponential growth model. Consider m types of cells with $N_1, ..., N_m$ individuals each, growing with growth rates $w_1, ..., w_m$, which could be functions of various other parameters. The population dynamics are then described by the set of m differential equations: $\dot{N}_k = w_k N_k$ for $1 \leq k \leq m$.

Let $N = N_1 + ... + N_m$, and look at the dynamics of $x_k = N_k/N$:

$$\dot{x}_k = \frac{\dot{N}_k}{N} - \frac{N_k \dot{N}}{N^2} \tag{C.3}$$

$$= \frac{w_k N_k}{N} - \frac{N_k}{N} \frac{\sum_{i=1}^{m} w_i N_i}{N} \tag{C.4}$$

$$= \frac{N_k}{N}(w_k - \sum_{i=1}^{m} w_i \frac{N_i}{N}) \tag{C.5}$$

$$= x_k(w_k - \langle w \rangle) \tag{C.6}$$

which is just the replicator dynamics. Thus, replicator dynamics perfectly describe an exponentially growing population.

C.3 Fitness as experimental growth rate

Alternatively, we can start from measurement. In particular, measurements of growth rates as would be done for *in vitro* experiments. We will recover replicator dynamics from purely experimental outputs or their limits.

If we are running an experiment with some tagged cells of m many types: $1, ..., m$ then our most basic primitives are (estimates of) the sizes of the seeding populations $N_1^I, ..., N_m^I$ and the size of the final populations $N_1^F, ..., N_m^F$. Given these values and a time difference Δt between when the experiment was started and when it ended, the experimental population growth rates are:

$$w_k := \frac{N_k^F - N_k^I}{N_k^I \Delta t} \tag{C.7}$$

this can be rotated to give us a mapping $N_I \mapsto N_F$:

$$N_k^F = N_k^I(1 + w_k \Delta t) \tag{C.8}$$

From defining the initial and final population sizes $N^{\{I,F\}} = \sum_{k=1}^{m} N_k^{\{I,F\}}$, we can compare the initial and final proportions of each cell type:

$$x_k^I = \frac{N_k^I}{N^I} \tag{C.9}$$

$$x_k^F = \frac{N_k^F}{N^F} \tag{C.10}$$

$$= x_k^I \frac{1 + w_k \Delta t}{1 + \langle w \rangle \Delta t} \tag{C.11}$$

where $\langle w \rangle = \sum_{k=1}^{m} x_k^I w_k$.

So far we were looking at a discrete process. But we can approximate it with a continuous one. In that case, we can define $x_k(t) = x_k^I$, $x_k(t + \Delta t) = x_k^F$ and look at the limit as Δt gets very small:

$$\dot{x} = \lim_{\Delta t \to 0} \frac{x_k(t + \Delta t) - x_k(t)}{\Delta t} \tag{C.12}$$

$$= \lim_{\Delta t \to 0} \frac{x_k^I}{\Delta t}\left(\frac{1 + w_k \Delta t}{1 + \langle w \rangle \Delta t} - 1\right) \tag{C.13}$$

$$= \lim_{\Delta t \to 0} x_k \frac{w_k - \langle w \rangle}{1 + \langle w \rangle \Delta t} \tag{C.14}$$

$$= x_k(w_k - \langle w \rangle) \tag{C.15}$$

Therefore, we recover replicator dynamics and give an explicit experimental interpretation for all of our theoretical terms.

D Gain functions to characterize dynamics

This section closely follows Hauert et al. (2002) and Kaznatcheev (2016a).

In the linear public goods that we consider in this paper, each contributor increases the public (or club) good by a constant amount and the whole good is divided evenly among the whole public (or club) regardless of if they contributed. In symbols: $A_n(k) = \frac{b_a k}{n+1}$ and $V_n(k) = \frac{b_v k}{n+1}$.

This gives us the gain functions for q:

$$w_V - w_D = \sum_{n_G + n_V + n_D = n} \binom{n}{n_G, n_V, n_D} x_G^{n_G} x_V^{n_V} x_D^{n_D} \left(\frac{b_v}{n - n_G + 1} - c\right) \tag{D.1}$$

$$= \sum_{m=0}^{n} \binom{n}{m} p^{n-m} (1-p)^m \frac{b_v}{m+1} - c \tag{D.2}$$

where we relabeled by defining $m := n_V + n_D (= n - n_G)$ as the number of participants in the club good. The issue now is to eliminate the $m + 1$ in the denominator which can be done by observing that $\binom{n}{m} = \frac{m+1}{n+1}\binom{n+1}{m+1}$. Resuming:

$$w_V - w_D = \sum_{m=0}^{n} \binom{n+1}{m+1} p^{n-m}(1-p)^m \frac{b_v}{n+1} - c \tag{D.3}$$

$$= \frac{b_v}{(1-p)(n+1)}([\sum_{m'=0}^{n'} \binom{n'}{m'} p^{n'-m'}(1-p)^{m'}] - \binom{n'}{0} p^{n'}) - c \tag{D.4}$$

$$= \frac{b_v}{(1-p)(n+1)}(1-p^{n+1}) - c, \tag{D.5}$$

$$= \frac{b_v}{n+1}[\sum_{k=0}^{n} p^k] - c \tag{D.6}$$

where in the first to second step, we relabel with $n' = n+1$ and $m' = m+1$ to get the binomial distribution. The final step follows from polynomial division.

Continuing on to the edge between *GLY* and *DEF*:

$$w_G - w_D = \sum_{n_G+n_V+n_D=n} \binom{n}{n_G, n_V, n_D} x_G^{n_G} x_V^{n_V} x_D^{n_D} (\frac{b_a}{n+1} - \frac{b_v n_V}{n-n_G+1}) \tag{D.7}$$

$$= \frac{b_a}{n+1} - \Big(\sum_{m=0}^{n} \binom{n}{m} p^{n-m}(1-p)^m \Big(\sum_{k=0}^{m} \binom{m}{k} q^k (1-q)^{m-k} \frac{b_v k}{m+1}\Big)\Big) \tag{D.8}$$

$$= \frac{b_a}{n+1} - \sum_{m=0}^{n} \binom{n}{m} p^{n-m}(1-p)^m b_v q (1 - \frac{1}{m+1}) \tag{D.9}$$

$$= \frac{b_a}{n+1} - b_v q + \frac{b_v q}{(1-p)(n+1)}(1-p^{n+1}). \tag{D.10}$$

Which means that the gain function for p is:

$$w_G - \langle w \rangle_{V,D} = w_G - (q w_V + (1-q) w_D) \tag{D.11}$$

$$= w_G - w_D - q(w_V - w_D) \tag{D.12}$$

$$= \frac{b_a}{n+1} - b_v q + \frac{b_v q}{(1-p)(n+1)}(1-p^{n+1}) - q(\frac{b_v}{(1-p)(n+1)}(1-p^{n+1}) - c) \tag{D.13}$$

$$= \frac{b_a}{n+1} - q(b_v - c). \tag{D.14}$$

Thus, our replicator dynamics are given by:

$$\dot{p} = p(1-p)(\overbrace{\frac{b_a}{n+1} - q(b_v - c)}^{\text{gain function for } p}) \tag{D.15}$$

$$\dot{q} = q(1-q)(\underbrace{\frac{b_v}{n+1}[\sum_{k=0}^{n} p^k] - c}_{\text{gain function for } q}) \tag{D.16}$$

To find the boundaries between the dynamics, we then have to solve for when the gain functions in eqs. D.5 and D.14 are equal to zero. From these gain functions, we can see that the the linear goods can have three possible dynamics. First, consider when the gain function for p crosses 0:

- If $b_a > (b_v - c)(n+1)$ then the gain function for p is positive regardless of q, and the population converges towards all *GLY* (green in figure 1), else
- if $b_a < (b_v - c)(n+1)$ then we have consider when the gain function for q crosses 0. One of two cases is possible:
  - If $b_v > c(n+1)$ then regardless of the value of p, the gain function for q is positive, so $q \to 1$ making the gain function for p negative and the population converges towards all *VOP* (red in figure 1), else
  - if $b_v < c(n+1)$ then the population will orbit around an internal fixed-point at $q^* = \frac{b_a}{(b_v - c)(n+1)}$ (i.e. the zero of the gain function for p) and p^* as the unique positive root of $\sum_{k=0}^{n} p^k = \frac{c(n+1)}{b_v}$ (i.e. the zero of the gain function for q). Thus, $1 - \frac{b_v}{c(n+1)} \leq p^* \leq \frac{c(n+1)}{b_v} - 1$. This is the yellow region in figure 1.

For a proof of closed orbits, see appendix E.

E Orbits in a Hamiltonian System

Let us rigorously establish the existence of closed orbits around the internal fixed point in the third dynamic region (yellow in figure 1). For this, we will follow closely the analysis of the optional public good by Hauert et al. (2002) as specified to this model in Kaznatcheev (2016b).

Consider the equations governing the dynamics of the linear goods as given in eqs. D.15 and D.16. Since $pq(1-p)(1-q)$ is strictly positive for $p, q \in (0,1)$, dividing the right hand side of the system in eqs. D.15 and D.16 by $pq(1-p)(1-q)$ results only in a change of rate (dynamic rescaling of time). Thus, the resulting system preserves the orbits of our replicator dynamics. This new system is given by:

$$\dot{p} = \frac{b_a}{(n+1)q(1-q)} - \frac{b_v - c}{1-q} \tag{E.1}$$

$$\dot{q} = \frac{b_v}{(n+1)p(1-p)}[\sum_{k=0}^{n} p^k] - \frac{c}{p(1-p)} \tag{E.2}$$

$$= \frac{b_v}{n+1}\Big(\frac{1}{p(1-p)} + \frac{n}{1-p} - \sum_{k=0}^{n-2}(n-1-k)p^k\Big) - \frac{c}{p(1-p)} \tag{E.3}$$

where eq. E.3 follows from eq. E.2 by dividing $\sum_{k=0}^{n} p^k$ by $p(1-p)$.
Define the following primitives:

$$R(p) := \frac{b_v - c(n+1)}{n+1}\ln\frac{p}{1-p} - \frac{b_v}{n+1}(n\ln(1-p) + \sum_{k=0}^{n-2}\frac{n-1-k}{k+1}p^{k+1}) \tag{E.4}$$

$$S(q) := \frac{b_a}{n+1}\ln\frac{q}{1-q} + (b_v - c)\ln(1-q) \tag{E.5}$$

and the Hamiltonian $H = R - S$.

Notice that eq. E.1 and E.3 can be rewritten as $\dot{p} = -\frac{\partial H}{\partial q}, \dot{q} = \frac{\partial H}{\partial p}$. Thus, we have a 1-dimensional Hamiltonian system. When our conditions $b_a < (b_v - c)(n+1)$ and $b_v < c(n+1)$ are met then (p^*, q^*) from appendix D is a unique strict global minimum of H in $(0,1)^2$. Thus (p^*, q^*) is a center of the dynamics with orbits of constant H. Finally, as p or q go to 0 or 1, $H(p,q)$ goes to ∞ if our conditions are met; thus the orbits are internal to $(0,1)^2$ and closed. Since our transformations preserved orbits, this means that the replicator dynamics of linear public and club goods have the same closed orbits.

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