

Article

# An equilibrium theorem of strategies in non-linear population matrix models

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Version April 28, 2023 submitted to Journal Not Specified

**Abstract:** Real world evolutionary games have significant complexity that is seldom directly modeled. In endeavouring to model such complexity we consider organisms with state dependant strategic actions which affecting vital rates in the context of arbitrary non-linear population matrix models. We discuss the extreme complexity of such systems and the flexibility of phenomena which can be modeled using them. We treat such systems mathematically, demonstrating that any equilibrium between mixed strategies can be represented as finite combination of pure strategies, which can then imply an effective population mixed strategy. This reduction allows us to consider the evolutionary dynamics of such a population mixed strategy, under replicator dynamics and towards evolutionary stability, where we outlay a software package implementing a matrix perturbation method for simulating such dynamics. We demonstrate the complexity of these systems and the power of our modelling approach by presenting a model of the sexual selection of a deleterious mutation with heterozygous advantage, in the context of a variable sexual dimorphism and between resource states. This model of sexual selection encompasses 24 states 54 strategic dimensions yielding  $2^{54}$  unique and pure strategies, and we use our software package to interrogate the equilibrium and disequilibrium dynamics of such a game across a range of 5 different parameters.

**Keywords:** Evolutionary Stable Strategies; Evolutionary Game Theory; Evolutionary Dynamics; Population Dynamics

## 1. Introduction

Biological species are well recognised as being engaged in a fight-for-survival and Evolutionary Game Theory has been used to analyse the strategies in such a fight. Evolutionary Game Theory encompasses games of different forms, but one of the most standard forms concerns the continuous growth/decay of organism types where the organism types are defined by the strategy they play as they are continuously randomly paired to participate in a simultaneous symmetric two-player game where the expected payoff determines the growth-rate of their strategy.[? ? ?]

Whereas the sets of actions that actual organisms employ can depend-upon and influence the lifecycles of organisms within an ecosystem, which in turn determines their growth-rate. These details, such as the stages of the lifecycles of organisms and the web of mutual influences between them, are seldom directly modelled in evolutionary game theory. Lifecycles are most directly described by matrix models of population dynamics, where the growth-rate of an organism type is naturally given by its population matrix, and where the influences between lifecycle stages are recognised as a potential source of non-linear dynamics and chaotic behaviour [? ? ?].

Within this paper we consider game-theoretic strategies in the context of lifecycles, and make a contribution by providing a proof that in such games that any search for equilibrium points need only consider pure strategies, and can ignore stochastic combinations of actions - or 'mixed' strategies. In this way, dynamic points of interest in these complicated games can be discovered and characterised much more directly.

## 1.1. Structure

- In section 3 we introduce some of the concepts in population matrix models, particularly the concept of *vital rates* and we illustrate how equilibrium population distributions are given by eigenvectors of the population matrix.
- In section 4 we give the elements of the game, showing how game-theoretic strategies and vital rates can be brought together to create population matrices for each strategy.
- In section 5 we give a verbal description of our main result about how equilibrium can be described by pure strategies alone.
- In section 6 we give the mathematical demonstration of our primary result.
- And section 7 gives some concluding comments.

## 2. Related Work

The formal theory of state has been introduced and considered in the context of population ecology by multiple authors, such as by Boling [?] Caswell et.al [?] and Metz [?]. Particularly Metz & Diekmann[?] considered the state of an individual organism (or the ‘i-state’) as the information necessary to make the response of an organism to its environment determinate, and contrasts this against the population state variable (or ‘p-state’) characterising the number of individuals in each i-state. Where it is possible to consider the population dynamics determined by the p-state, population matrix models have been increasingly employed in ecological studies to model the lifecycles and dynamics of various organisms between states.[?] Example models include modelling growth-rate by fecundity across age brackets [?], the dynamics of sexual reproduction and sex ratios [?] as well as the dynamics of genetic spread and population control measures [?] etc. In these matrix models, the ratio of population numbers moving between states are called *vital rates*, which directly model the increase or decrease in organism numbers between states.

State also has a history as part of Game Theory literature, particularly the concept of state and actions are most directly modelled in Markov Decision Processes (MDPs) which can bear direct extension to many players in Lloyd Shapley’s Stochastic-Games (SG) [?]. Stochastic Games are games where the game itself has a set of possible states or ‘positions’ (which might be the combination of the states of all players). Within this context each of the individual players have actions which they can execute which jointly determine the likely transitions between the states of the game and the immediate payoffs to each of them.

State has some history in the context of Evolutionary Game Theory, which can be seen in the context of various ‘evolutionary games on graphs’ where the players have the state of belonging to nodes on a grid or graph structure. In these games the players at a node play actions against their nearest neighbours and it can be seen that the structure in these games capture a general sense of position as a state for the players, and this introduces unique and dynamic behaviours.[?]

Another approach of integrating state into Evolutionary Game Theory extends from the works of Eitan Altman et.al [?] who introduce the Markov-Decision-Evolutionary-Game (MDEG) and variants thereof. In MDEG games each organism can occupy one of a finite set of states and has actions available to it depending on what state it is in. The organisms are paired randomly and each of the participants chooses one of their available actions (as determined by their strategy) to execute. The actions that the organisms execute determine their immediate payoffs and the probable transitions in state that they will make. The expected sum of payoffs determine the growth-rate of the presence of the strategy in the population, and this then changes the composition of the population in which the random pairings occur.

Our work contrasts against other games, primarily as we model the growth-rate of strategies not in relation to the expected summation of payoffs, but in relation to the equilibrium between states defined by vital rates. This attitude is also reflected in the works of J. M. Cushing [?] who analyses evolutionary dynamics in population matrix models particularly focusing on bifurcation.

### 3. Vital Rates and Population Matrix Models

The demographic flow of individuals of a population between states of a lifecycle is sometimes described in ecological-studies by a matrix that is not necessarily Markov. The simplest example of such matrices are Leslie Matrices used for studying the structure of populations of individuals transitioning between evenly spaced age-states. Leslie Matrices are square, and they have form [? ]:

$$\mathbf{M} = \begin{bmatrix} F_0 & F_1 & F_2 & \dots & F_{m-1} & F_m \\ P_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & P_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & P_2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & P_{m-1} & 0 \end{bmatrix}$$

Where  $P_i$  represents the probability of an individual in the  $i$ th age bracket successfully living into the  $(i + 1)$ th age bracket, and  $F_i$  is average number of offspring for an individual in  $i$ th age bracket within the duration of the age bracket. The positive elements of these matrices identify the ‘flow’ of individuals from one state to another and are called *vital rates*. For a column vector  $\mathbf{n}(t)$  representing the number of individuals in each age-bracket at time  $t$ ,  $\mathbf{Mn}(t)$  gives the number of individuals in the population after the duration of one age bracket of time, and  $\mathbf{M}^2\mathbf{n}(t)$  the number of individuals after two age brackets, and so on.

$$\mathbf{n}(t + 1) = \mathbf{Mn}(t)$$

Successive applications eventually yield a steady population profile and a constant exponential growth rate  $\lambda$  given by the Euler–Lotka equation, where  $\lambda$  is the dominant and only real-positive eigenvalue of the matrix, with the steady population profile  $\mathbf{n}$  as its corresponding eigenvector, that is  $\mathbf{Mn} = \lambda\mathbf{n}$ .

A Leslie matrix is a specific example of a population/projection matrix which projects the growth/decline of a population whose vital rates remain constant. However, more complicated scenarios exist where the vital rates vary depending on the distribution of the population itself. For instance, the number of offspring and survival probability to a successive age-state may depend on the density of predators, mates and/or competitors for resources. In this context the elements of  $\mathbf{M}$  may depend on  $\mathbf{n}(t)$  in some arbitrary way, which we denote as  $\mathbf{M}_{\mathbf{n}(t)}$  and:

$$\mathbf{n}(t + 1) = \mathbf{M}_{\mathbf{n}(t)}\mathbf{n}(t)$$

This is the form of a non-linear population matrix model; such models have been shown to yield dynamic behaviours such as non-linear growth, unstable cyclic behaviour and chaos. Additionally as the matrix  $\mathbf{M}$  is non-negative it has a maximum non-negative real eigenvalue  $\lambda$  (which might be 1) and corresponding population vector  $\mathbf{n}$

$$\mathbf{M}_{\mathbf{n}}\mathbf{n} = \lambda\mathbf{n}$$

We consider then that the vector  $\mathbf{n}$  characterises a potential equilibrium of the population with  $\lambda$  its equilibrium growth rate. We now consider how to represent different strategies within the population.

### 4. Description of the Game

Consider an ecosystem of different organisms, where the organisms a set of states and each state has a set of actions which they will execute depending on their strategy. let:

- $S$  be indexed finite set of states
- $A_s$  be set of actions available organisms in state  $s \in S$
- $W$  be the set of possible strategies such that for any strategy  $w \in W$  that  $w_{a,s}$  denotes the probability that an organism with strategy  $w$  will execute action  $a$  if it is in state  $s$ .
- $P_{s,w}$  is the number of organisms in a state  $s \in S$  with strategy  $w \in W$ ;

- 103 •  $P_{s,a}^* = \sum_{w \in W} P_{s,w} w_{a,s}$  is the number of organisms in a state  $s \in S$  which are going to take action  $a$ .
- 104 •  $T_{s,a}(P^*)$  are vital rates depending<sup>1</sup> on  $P^*$ , giving the rate of the organism to a state  $s \in S$  when it
- 105 executes an action  $a \in A_s$ .

Thus every strategy  $w$  has its own population matrix  $\mathbf{M}_{P^*}^w$  with components  $M_{i,j}^w$ .

$$\mathbf{M}_{P^*}^w = M_{i,j}^w = \sum_{a \in A_i} T_{j,a}(P^*) w_{a,i} \quad (1)$$

And thus the matrix of a strategy  $\mathbf{M}_{P^*}^w$  is composed of columns which are weighted by its probability terms  $w_{a,s}$ , and it is possible to consider probabilistic mixes of strategies, for instance if strategies  $w^1$  and  $w^2$  are mixed by a factor  $0 \leq \alpha \leq 1$  to form a new strategy  $w^\alpha$  whose matrix is then:

$$\mathbf{M}_{P^*}^{w^\alpha} = \sum_{a \in A_i} T_{j,a}(P^*) (\alpha w_{a,i}^1 + (1 - \alpha) w_{a,i}^2) = \alpha \mathbf{M}_{P^*}^{w^1} + (1 - \alpha) \mathbf{M}_{P^*}^{w^2} \quad (2)$$

106 In this way one strategy can be considered as a linear combination of other strategies.

## 107 5. Searching for Stable Equilibria

108 In direct correspondence with common game theory language, it is possible to define basic  
 109 relationships between the strategies. Each organism's strategy  $w$  encodes the probabilities of what  
 110 actions it will take across its states. A strategy is 'pure' if these probabilities encode certainty of taking  
 111 a single action per state otherwise it is 'mixed'. Any mixed strategy can be decomposed into a linear  
 112 combination of pure strategies. And any set of pure strategies defines a span of mixed strategies which  
 113 can be linearly composed of them.

114 If we define an 'equilibrium' as being the condition where all the  $\mathbf{M}_{P^*}^w$  population matrices remain  
 115 constant - and an 'equilibrium point' being defined by those matrices. Then it is necessarily the case  
 116 that an equilibrium leads to a condition where all the strategies that are significantly present in the  
 117 population are steadily growing by the same growth-rate in steady-state. For if any organisms of a  
 118 strategy existed in the population with a lesser steady-state growth-rate then it would proportionally  
 119 die out, or if any organisms of a strategy existed with a greater steady-state growth-rate then it would  
 120 lead the others to proportionately die out.

121 We further define the equilibrium as being 'stable' in a similar way to Maynard Smith [? ? ? ],  
 122 specifically if it cannot be disturbed from equilibrium by the presence of a small incorporation-of (or  
 123 'invaded by') any possible 'mutant' strategy. We note that this is at-least the case where no 'mutant'  
 124 strategy has a greater steady-state growth-rate in the context of the population.

125 In the next section 6 there is a demonstration that for any stable equilibrium established with a  
 126 population of mixed strategies that it is possible to establish the same equilibrium point without the  
 127 mixed strategies at all. Informally the reasoning is that: because any mixed strategy is a stochastic mix  
 128 of pure strategies then it can only perform as well as the best of them. And when it performs equal  
 129 to the best then they must all perform equally. And in this case there is a combination of the pure  
 130 strategies which have the same state-action profile  $P^*$  as the mixed strategy; the same profile which  
 131 defines the population matrices and thus the equilibrium point itself. From these considerations it is  
 132 thus unnecessary to consider mixed strategies in the search for stable equilibria because every stable  
 133 equilibria can be established by combinations of pure strategies alone (although there may be zero or  
 134 multiple such stable equilibria between them).

135 In our mathematics we assume that all population vectors grow exponentially under stable  
 136 equilibrium with a common growth-rate equal to a maximum real non-negative eigenvalue (which  
 137 may be one), and in proportions to a corresponding population matrix eigenvector. This is a simplifying

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<sup>1</sup> where  $P^*$  is shorthand for the set of all the numbers across  $s$  and  $a$ ,  $P^* = \{P_{s,a}^* \mid s \in S, a \in A_s\}$

assumption and there exist possible population matrices where this assumption would be violated (specifically in the context of defective matrices), and in this context, other mathematics would need to be used to assert our conclusions.

## 6. That any stable equilibrium point can always be rendered among pure strategies

We consider a strategy's being *replaceable* by other strategies if there exists a possible replacement of one's organisms for the others' in a population such as would not disturb the stable equilibrium point. The equilibrium point is defined by constant matrices  $\mathbf{M}_{P^*}^w$ , which is preserved at least when  $P^*$  remains unchanged. If there is a stable equilibrium, each strategy  $w$  has population in proportion to an eigenvector  $\mathbf{n}^w$  with components  $n_s^w$ , thus its contribution to  $P^*$  (per its definition) is:

$$P_{s,a}w_{a,s} \propto n_s^w w_{a,s}$$

The strategy is replaceable if there is a combination of other strategy's organisms to give this same contribution.

**Definition 1.** A strategy  $\bar{w}$  is **replaceable at stable equilibrium** by a set of other strategies  $W$ , if all strategies  $w \in W$  are in equilibrium and thus have population matrices with the same maximal real eigenvalue and there exists non-negative corresponding eigenvectors  $n_s^w$  and non-negative coefficients  $d^w$  such that:

$$\forall a, s \quad n_s^{\bar{w}} \bar{w}_{a,s} = \sum_{w \in W} d^w n_s^w w_{a,s}$$

Thus replaceability is a specific relationship between the eigenvectors of different strategy matrices and the weights of the strategies themselves (which in turn determine those matrices). Replaceability has an intuitive transitive property:

**Definition 2** (Transitive Property of replaceability). If organisms of strategy  $A$  are replaceable by organisms of a set of strategies  $B$ , and if each of the organisms in the set of strategies in  $B$  are replaceable by those of a set of strategies  $C$ , then organisms of strategy  $A$  are also replaceable by those of set of strategies  $C$ .

In light of this we demonstrate that all mixed strategies are replaceable by pure strategies, by showing that every mixed strategy can be iteratively replaced by other strategies that are more 'extreme':

**Definition 3.** A strategy  $w$  is **extreme** with respect to an action  $a \in A_s$ , if  $w_{a,s}$  equals zero or one. A strategy  $w$  is more **extreme** than another strategy  $\bar{w}$  if  $w$  is extreme with regards to more actions than  $\bar{w}$  is.

To make our demonstration we first show that any specific mixed strategy can be decomposed into a linear combination of two strategies more extreme than it, and then we show that the mixed strategy is also replaceable by those two more extreme strategies.

**Lemma 1.** Any mixed strategy  $\bar{w}$  in stable equilibrium is replaceable by strategies which are more extreme.

**Proof.** A mixed strategy  $\bar{w}$  is (by definition of mixed) not extreme with regards to some action  $\bar{a} \in A_{\bar{s}}$ , then we consider two other similar strategies  $w^1$  and  $w^2$  that are otherwise the same except with re-weighted actions about the  $\bar{s}$  state, such as to make them extreme in regards to action  $\bar{a}$ , ie. that  $w_{\bar{a},\bar{s}}^1 = 1$  and  $w_{\bar{a},\bar{s}}^2 = 0$ .

$$\mathbf{M}_{P^*}^{\bar{w}} = \bar{w}_{\bar{a},\bar{s}} \mathbf{M}_{P^*}^{w^1} + \left( \sum_{a \in A_{\bar{s}} \setminus \{\bar{a}\}} \bar{w}_{a,\bar{s}} \right) \mathbf{M}_{P^*}^{w^2}$$

$$\text{where } \forall a \in A_{\bar{s}} \setminus \{\bar{a}\}, \quad w_{a,\bar{s}}^1 = 0 \quad \text{and} \quad w_{a,\bar{s}}^2 = \frac{\bar{w}_{a,\bar{s}}}{\sum_{\hat{a} \in A_{\bar{s}} \setminus \{\bar{a}\}} \bar{w}_{\hat{a},\bar{s}}}$$

We note that if  $\bar{w}$  is extreme with regards to any other action  $a^*$  then the two other strategies  $w^1$  and  $w^2$  also extreme with regards to action  $a^*$ . Thus any mixed strategy can be considered as a linear combination of two other strategies more extreme than it, all that remains to do is to show that this linear combination is also a replaceable combination as well.

If we consider  $\alpha = \bar{w}_{\bar{a},\bar{s}}$  then  $\mathbf{M}_{p^*}^{\bar{w}} = \alpha \mathbf{M}_{p^*}^{w^1} + (1 - \alpha) \mathbf{M}_{p^*}^{w^2} = \mathbf{M}(\alpha)$  and Theorems A1 and A2 apply. Theorem A1 informs us that the equilibrium growth rate (the spectral radius of the matrices) of strategies  $w^1$  to  $\bar{w}$  to  $w^2$  is either monotonically increasing or decreasing or otherwise constant. If it is monotonically increasing/decreasing then either  $w^1$  or  $w^2$  will have a greater equilibrium growth rate than  $\bar{w}$ , thus  $\bar{w}$  is not part of stable equilibrium creating contradiction; thus  $w^1, w^2$  and  $\bar{w}$  must have the same growth rate.

Consequently Theorem A2 informs us that the change in eigenvectors are linear, hence  $\mathbf{n}^{\bar{w}} = \alpha \mathbf{n}^{w^1} + (1 - \alpha) \mathbf{n}^{w^2}$  and that  $n_s^{\bar{w}} = n_s^{w^1} = n_s^{w^2}$  and selecting  $d^{w^1} = \alpha$  and  $d^{w^2} = 1 - \alpha$  consequently satisfies definition 1.  $\square$

**Theorem 1.** *Every mixed strategy in stable equilibrium is replaceable by a set of pure strategies*

**Proof.** By Lemma 1 any mixed strategy can be replaced by other strategies that are more extreme than it, and those strategies (if they are mixed) can then be replaced by strategies which are even more extreme, and so on. Thus by the transitive property (definition 2), every mixed strategy can be replaced by ever increasing sets of strategies which are more extreme, and thus replaced by strategies which are most extreme - ie. pure strategies.  $\square$

## 7. Conclusion

In this paper we have described a game in the context of non-linear population models, and we have given an equilibrium theorem 1 proving that all equilibria in such games can be found and described by proportions of pure strategies. This theorem's primary utility is that it eliminates the complexity of needing to consider the space of mixed strategies in searching-for and characterising such points of interest.

The elements of the game are simply that there be organisms which move between states in response to the actions and interactions with others, and the only implicit limitation on such a game is that organisms be sufficiently numerous for their population and their dynamics to be modelled continuously. Because of this flexibility, it is difficult to understate the potential span of things that could be represented, and therefore the potential applicability of our theorem. The primary limitation of our theorem is the assumption that equilibrium growth-rates are given by population matrix eigenvalues/vectors (ie. no defective matrices) and thus it is interesting to consider what (if any) populations of things might naturally be described by defective matrices in which our theorem might also fail to hold.

**Conflicts of Interest:** The authors declare no conflict of interest; The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results

## Appendix A Matrix Proofs

**Lemma A1.** *for a  $n \times n$  matrix  $A$ , and  $n$  column vector  $b$ , with  $A^{b,k}$  denoting the matrix with its  $k$ th column as  $b$ . If  $\lambda$  is an eigenvalue for both  $A$  and  $A^{b,k}$  then it is also an eigenvalue for  $\alpha A + (1 - \alpha) A^{b,k}$  for any  $\alpha \in \mathbb{R}$*

**Proof.** Consider the characteristic polynomials of  $\lambda$  for  $A$  and  $A^{b,k}$ :

$$\det(A - \lambda I) = \det(A^{b,k} - \lambda I) = 0$$

If we let  $C(\cdot)_{i,j}$  denote the  $i,j$ th cofactor of a matrix, then these determinants can be expanded along

the  $k$ th column to give:

$$(\sum_i A_{i,k}C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k} = (\sum_i b_i C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k} = 0$$

Therefore:

$$\begin{aligned} & \alpha ((\sum_i A_{i,k}C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k}) + (1 - \alpha) ((\sum_i b_i C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k}) = 0 \\ & = (\sum_i (\alpha A_{i,k} + (1 - \alpha)b_i)C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k} = \det(\alpha A + (1 - \alpha)A^{b,k} - \lambda I) = 0 \end{aligned}$$

Thus it is demonstrated that  $\lambda$  is also an eigenvalue for  $\alpha A + (1 - \alpha)A^{b,k}$ .  $\square$

**Theorem A1.** For a real  $n \times n$  non-negative matrix  $A$ , and real non-negative column vector  $b$ , with  $A^{b,k}$  denoting the matrix with its  $k$ th column as  $b$ . For the matrix mapping  $B(\alpha) = \alpha A + (1 - \alpha)A^{b,k}$  defined on a range  $0 \leq \alpha \leq 1$ . If  $\rho(B(\alpha))$  denotes the spectral radius of  $B(\alpha)$ .

Then  $\rho(B(\alpha))$  is continuous, and either constant or strictly monotonic with  $\alpha$ .

**Proof.** Because  $B(\alpha) = \alpha A + (1 - \alpha)A^{b,k}$  is a matrix continuous in all its elements it will have  $n$  continuous eigenvalues (counting multiplicities).<sup>2</sup> Thus  $\rho(B(\alpha))$  is also continuous with  $\alpha$  for all  $\alpha$ .

Furthermore the value  $\rho(B(\alpha))$  is itself an eigenvalue of  $B(\alpha)$  for all  $\alpha$  via the Perron-Frobenius theorem for non-negative matrices. Suppose for a contradiction that  $\rho(B(\alpha))$  is not monotone, in this case there must exist at least three values of alpha,  $\alpha_1 < \alpha_2 < \alpha_3$  such that  $\rho(B(\alpha_2)) > \max(\rho(B(\alpha_0)), \rho(B(\alpha_3)))$  or  $\rho(B(\alpha_2)) < \min(\rho(B(\alpha_0)), \rho(B(\alpha_3)))$ .

- suppose that  $\rho(B(\alpha_2)) > \max(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$ : let  $\beta$  be a value between  $\rho(B(\alpha_2))$  and  $\max(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$ . Thus via the intermediate value theorem there exists  $\gamma_1$  ( $\alpha_1 < \gamma_1 < \alpha_2$ ) and  $\gamma_2$  ( $\alpha_2 < \gamma_2 < \alpha_3$ ) such that  $\rho(B(\gamma_1)) = \rho(B(\gamma_2)) = \beta$ . Thus  $\beta$  is an eigenvalue of  $B(\alpha_1)$  (via Lemma A1), and  $\beta > \rho(B(\alpha_1))$  which contradicts the construction of  $\rho(B(\alpha_1))$ .
- suppose that  $\rho(B(\alpha_2)) < \min(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$ : let  $\beta$  be a value between  $\rho(B(\alpha_2))$  and  $\min(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$ . Thus via the intermediate value theorem there exists  $\gamma_1$  ( $\alpha_1 < \gamma_1 < \alpha_2$ ) and  $\gamma_2$  ( $\alpha_2 < \gamma_2 < \alpha_3$ ) such that  $\rho(B(\gamma_1)) = \rho(B(\gamma_2)) = \beta$ . Thus  $\beta$  is an eigenvalue of  $B(\alpha_2)$  (via Lemma A1), and  $\beta > \rho(B(\alpha_2))$  which contradicts the construction of  $\rho(B(\alpha_2))$ .

Therefore  $\rho(B(\alpha))$  is monotonic.

If there does not exist any  $\alpha_1, \alpha_2 \in [0, 1]$  such that  $\rho(B(\alpha_1)) = \rho(B(\alpha_2))$

then  $\rho(B(\alpha))$  is strictly monotonic.

If there does exist an  $\alpha_1, \alpha_2 \in [0, 1]$  such that  $\rho(B(\alpha_1)) = \rho(B(\alpha_2))$

then  $\rho(B(\alpha))$  is constant via lemma A1.

Which completes the proof.  $\square$

**Theorem A2.** For a real  $n \times n$  non-negative matrix  $A_{i,j}$ , and non-negative column vectors  $b$  and  $c$ , with  $A^{b,k}$  and  $A^{c,k}$  denoting the matrix with its  $k$ th column as  $b$  and  $c$  respectively. For the non-defective matrix mapping  $B(\alpha) = \alpha A^{b,k} + (1 - \alpha)A^{c,k}$  let  $\rho(B(\alpha))$  be the spectral radius of  $B(\alpha)$ . If  $\rho(B(\alpha))$  is a constant  $\lambda$  then there is a corresponding eigenvector  $v(\alpha)$  that changes linearly with  $\alpha$ , with its  $k$ th value  $v(\alpha)_k$  being constant.

**Proof.** By the Perron-Frobenius theorem for non-negative matrices for any  $\alpha$  there exists a non-negative  $v(\alpha)$  which is an eigenvector for eigenvalue  $\rho(B(\alpha))$ , thus for any  $\alpha$ :

$$(\alpha A^{b,k} + (1 - \alpha)A^{c,k})v(\alpha) = \lambda v(\alpha)$$

The derivative of non-defective matrix eigenvectors exist [? ? ], and so it is possible to differentiate with respect to  $\alpha$  giving:

$$(\alpha A^{b,k} + (1 - \alpha)A^{c,k} - \lambda I) \frac{\partial v(\alpha)}{\partial \alpha} + (b - c)v(\alpha)_k = 0$$

<sup>2</sup> An informal outline of the proof is that: 1. If the elements of a matrix are continuous 2. Then the coefficients of the characteristic polynomial are continuous (as they are additions and multiplications of them) 3. Then the  $n$  roots (via fundamental theorem of algebra) of the characteristic polynomial are continuous (see [? ]) 4. Hence the eigenvalues are continuous

There are two cases: if there is an  $\bar{\alpha}$  such that  $v(\bar{\alpha})_k = 0$  then:

$$\left( \bar{\alpha} A^{b,k} + (1 - \bar{\alpha}) A^{c,k} - \lambda I \right) \frac{\partial v(\bar{\alpha})}{\partial \alpha} = 0$$

Setting  $\frac{\partial v(\alpha)}{\partial \alpha} = 0$  is permissible, thus constant  $v(\alpha) = v(\bar{\alpha})$  is a solution.

Otherwise:

It is possible do scaling, thus setting  $v(\alpha)_k = d$  to be a non-zero constant, thus

$$\left( \alpha A^{b,k} + (1 - \alpha) A^{c,k} - \lambda I \right) \frac{\partial v(\alpha)}{\partial \alpha} + d(b - c) = 0$$

$$\left( \sum_{j,j \neq k} (A_{i,j} - \lambda I_{i,j}) \frac{\partial v(\alpha)_j}{\partial \alpha} \right) + d(b_i - c_i) = 0$$

therefore  $\frac{\partial v(\alpha)}{\partial \alpha}$  can be constant, thus  $v(\alpha)$  changes linearly.  $\square$

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