

Article

# Stochasticity in the Parasite-Driven Trait Evolution of Competing Species Masks the Distinctive Consequences of Distance Metrics

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**Abstract:** Various distance metrics and their induced norms are employed in the quantitative modeling of evolutionary dynamics. Minimization of these distance metrics when applied to evolutionary optimization are hypothesized to result in different outcomes. Here, we apply the different distance metrics to the evolutionary trait dynamics brought about by the interaction between two competing species infected by parasites (exploiters). We present deterministic cases showing the distinctive selection outcomes under the Manhattan, Euclidean and Chebyshev norms. Specifically, we show how they differ in the time of convergence to the desired optima (e.g., no disease), and in the egalitarian sharing of carrying capacity between the competing species. However, when randomness is introduced to the population dynamics of parasites and to the trait dynamics of the competing species, the distinctive characteristics of the outcomes under the three norms become indistinguishable. Our results provide theoretical cases when evolutionary dynamics using different distance metrics exhibit similar outcomes.

**Keywords:** evolutionary dynamics; quantitative trait; Manhattan norm; Euclidean norm; Chebyshev norm; parasitism; exploitation; egalitarianism

## 1. Introduction

Parasitism-induced coevolution has been one of the interesting topics in evolutionary biology, as parasites can drive biodiversity and balance in communities [1-4]. Specifically, parasite infection greatly influences the population dynamics of species in a competitive environment [5,6]. Species maximize their fitness but resources are limited, leading to the competition for share in the environmental carrying capacity [6,7]. If one species wins, parasites could drive the winner to be loser, giving other species the opportunity to dominate [5-8]. Both competition and parasitism arise as two candidate biotic factors for explaining the evolution of traits in populations [9].

The evolution of traits has been modeled using various mathematical techniques (e.g., game theory, dynamical systems and probability theory). One of which is the selection gradient in differential equation form [10-15]. In this model, if the selection gradient results in a positive change in fitness value, then the trait becomes more favored and further improved. If it is negative, then the trait is reduced. Similarly, we use in this study the idea of selection ascent towards fitness maximization. The trait of a population is represented numerically, and the changes in the trait is modeled using difference equations. The quantitative trait dynamics is governed by the goal of the population (here, termed as evolutionary objective) and by the existent population dynamics of the species modeled using Lotka-Volterra-type equations. We study the population dynamics since the effect of evolution in species are often reflected in their population densities [16-18].

The evolutionary objective is represented by mathematical metrics [19-23]. A metric is a measure of distance between the desired goal and the instantaneous condition of the population. For example, if the evolutionary objective is to reach the maximum population density normalized to 1 and the current population density is  $X$ , then the metric can be represented by  $\|1 - X\|$ . Here, three common distance metrics are studied, namely the Manhattan norm (also known as Taxicab or 1-norm), the Euclidean norm (least squares or 2-norm) and the Chebyshev norm (supremum, uniform or infinity norm) [24,25]. We investigate the differences in the effect of the three metrics to the resulting trait dynamics of competing populations.

The distance metric used in obtaining the desired evolutionary outcome is hypothesized to have significant effect on the trait and population dynamics of species. Predicting the population dynamics of species could be subject to the metric used in data analysis and simulations. This has crucial implications on formulating ecological conclusions. For this reason, it is imperative to determine the advantages and limitations of the metrics. We identify the distinctive characteristics of the resulting trait dynamics under the Manhattan, Euclidean and Chebyshev norms. We also investigate if these characteristics are robust under stochastic noise. Our results provide an answer to the question "Does the choice of measure for adaptation success matter in a stochastic environment?"

The study of evolutionary dynamics encompasses different dimensions. As in the concept of inclusive inheritance, information transfer and changes in traits can happen in genetic, epigenetic, ecological and cultural levels [26]. The changes in traits can be transgenerational (e.g., genetic inheritance from parents to offspring) or intra-generational (e.g., cultural information transfer within the same generation). In this paper, we assume that novel traits of two competing species are selected to adapt or defend against parasites [27-32]. The novel traits may arise in different evolutionary dimensions. As such, our results can be interpreted not only in the perspective of genetics, but also in the perspective of cultural societies where parasites are characterized by exploiters.

## 2. The Mathematical Model

Two competing species ( $X_1$  and  $X_2$ ) maximize their population densities with respect to the environmental carrying capacity. In order to maximize their population, the two competing host species minimize the effect of antagonistic parasites ( $P$ ) by changing the host defense trait. This can be done through minimizing the parasitism exploitation coefficient  $\alpha$  (represented by  $\alpha_1$  and  $\alpha_2$  in our model). However, as the host species compete for available resources in the environment, they cooperatively assure that there is egalitarian (equal) sharing of resources. Our model represents competitive-cooperative interaction of two species that is evolving to defend against the negative influence of parasitism or exploitation [33,34].

We assume that the two competing host species have equal characteristics. This allows our analysis to focus on the effect of the different metrics to the evolutionary objective rather than on the differences between the two species. Without losing generality in our conceptual study, we use a basic Lotka-Volterra-type model [6, 35-38] (with time step  $h \ll 1$ ) for population dynamics with basal growth rate  $r_i$  as follows:

$$X_1(t+h) = X_1(t) + h(r_1 X_1(t) \times (1 - X_1(t) - X_2(t)) - \alpha_1 X_1(t) \times P(t)) \quad (1)$$

$$X_2(t+h) = X_2(t) + h(r_2 X_2(t) \times (1 - X_1(t) - X_2(t)) - \alpha_2 X_2(t) \times P(t)) \quad (2)$$

$$P(t+h) = P(t) + h(P(t) \times (\beta_1 X_1(t) + \beta_2 X_2(t)) - P(t)) + noise_1 \quad (3)$$

where  $\beta_i = \gamma \alpha_i$ ,  $i = 1, 2$ . The parameter  $\gamma$  is the ratio between the parasitism numerical response coefficient ( $\beta_i$ ) and the parasitism exploitation coefficient ( $\alpha_i$ ). When  $\beta_i > \alpha_i$  ( $\beta_i < \alpha_i$ ), the parasites produce more (less) offspring compared to the number of parasitized hosts.

The evolutionary trait dynamics using Manhattan 1-norm,  $|1 - X_1(t)| + |1 - X_2(t)|$ , is modeled by:

$$\alpha_1(t+h) = \alpha_1(t) - h \left( \varepsilon \frac{|1 - X_1(t)| + |1 - X_2(t)|}{\max\{X_1(t), 10^{-6}\}} \right) + noise_2 \quad (4)$$

$$\alpha_2(t+h) = \alpha_2(t) - h \left( \varepsilon \frac{|1 - X_1(t)| + |1 - X_2(t)|}{\max\{X_2(t), 10^{-6}\}} \right) + noise_3. \quad (5)$$

88 Using Euclidean 2-norm,  $\sqrt{(1 - X_1(t))^2 + (1 - X_2(t))^2}$ , the evolutionary trait dynamics is  
 89 represented as:

$$\alpha_1(t+h) = \alpha_1(t) - h \left( \varepsilon \frac{\sqrt{(1 - X_1(t))^2 + (1 - X_2(t))^2}}{\max\{X_1(t), 10^{-6}\}} \right) + noise_2 \quad (6)$$

$$\alpha_2(t+h) = \alpha_2(t) - h \left( \varepsilon \frac{\sqrt{(1 - X_1(t))^2 + (1 - X_2(t))^2}}{\max\{X_2(t), 10^{-6}\}} \right) + noise_3. \quad (7)$$

90 For the Chebyshev infinity-norm,  $\max\{|1 - X_1(t)|, |1 - X_2(t)|\}$ , the model is:

$$\alpha_1(t+h) = \alpha_1(t) - h \left( \varepsilon \frac{\max\{|1 - X_1(t)|, |1 - X_2(t)|\}}{\max\{X_1(t), 10^{-6}\}} \right) + noise_2 \quad (8)$$

$$\alpha_2(t+h) = \alpha_2(t) - h \left( \varepsilon \frac{\max\{|1 - X_1(t)|, |1 - X_2(t)|\}}{\max\{X_2(t), 10^{-6}\}} \right) + noise_3. \quad (9)$$

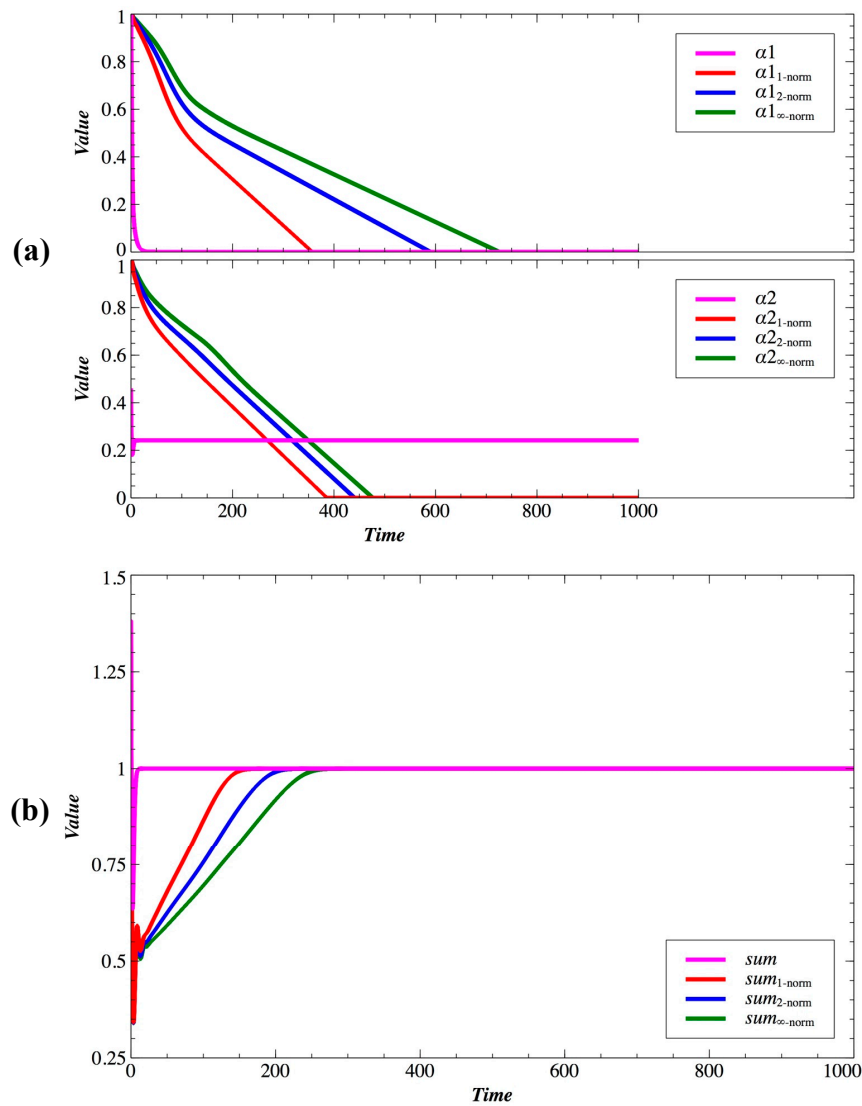
91 For comparison, we also consider a model where the competing species evolve independently of each  
 92 other. We use a model that follows a non-cooperative optimization with no assured egalitarian  
 93 sharing of resources (refer to Equation A5 and A6 in Appendix A: Methods).

### 94 3. Simulation Results and Discussion

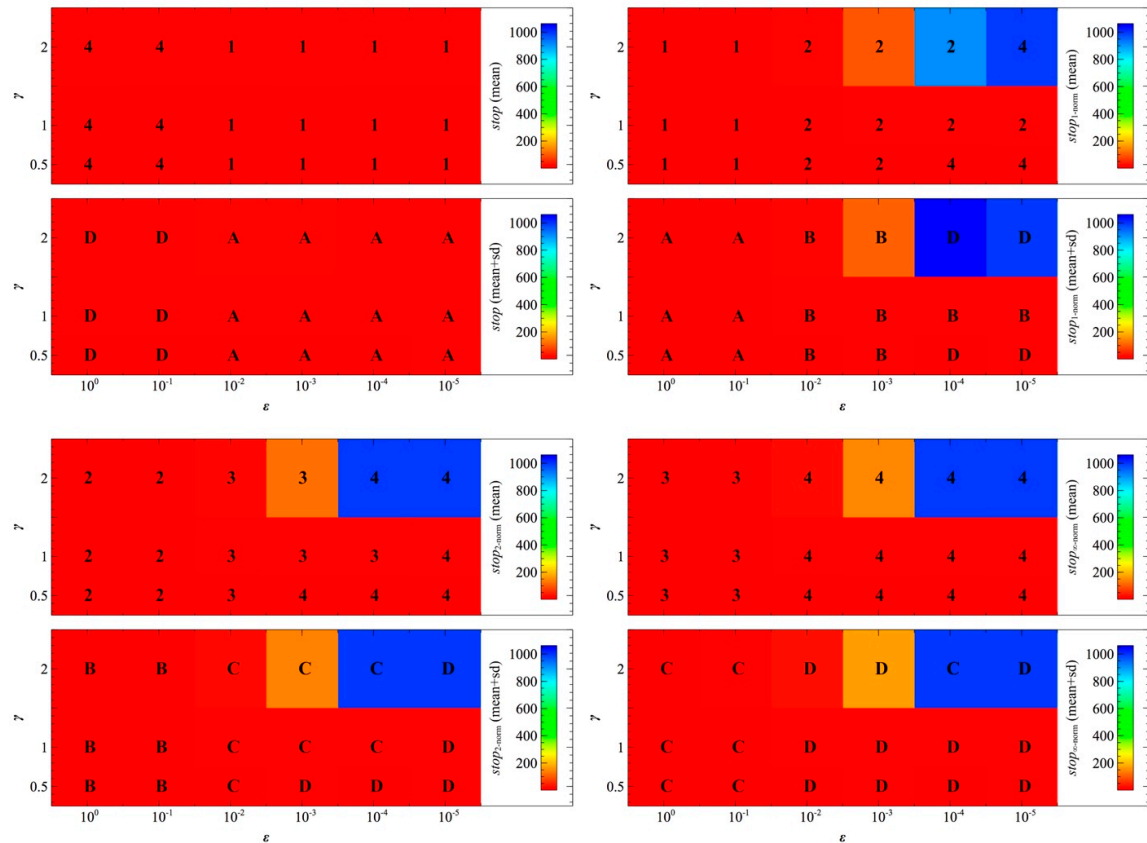
95 *Deterministic Case.* Without stochastic noise, the population densities of the evolving competing  
 96 host species converge to a stable equilibrium point (Figure 1). The evolutionary objective is to drive  
 97 the parasitism exploitation coefficient  $\alpha$  to zero as well as to reach the maximum population density  
 98 (Figures 1a and 1b). We expect that the convergence to the desired evolutionary outcome is faster  
 99 when using Manhattan, then Euclidean and lastly, the Chebyshev norm (Figures 1a, 1b and 2). This

100 is because  $|1 - X_1(t)| + |1 - X_2(t)| \geq \sqrt{(1 - X_1(t))^2 + (1 - X_2(t))^2} \geq \max\{|1 - X_1(t)|, |1 - X_2(t)|\}$ .  
 101 In a biological or social context, this behavior implies that we may consider the Manhattan or  
 102 Euclidean norm as the metric when time of convergence is essential in evolutionary optimization  
 103 (e.g., during crisis and catastrophes).

104 To understand the extent of the regularity of the trait dynamics convergence, we investigate the  
 105 pattern of convergence under different parameter values of  $\varepsilon$  and  $\gamma$  (Figures 2). The parameter  $\varepsilon$  is  
 106 the speed of evolutionary adaptation, which reflects the effect of the distance metric to the trait  
 107 dynamics in one generation. In Figure 2, the speed of convergence of the trait dynamics following  
 108 non-cooperative optimization is slowest in the cases when  $\varepsilon = 10^0$  to  $10^{-1}$  compared to the trait  
 109 dynamics that utilize the Manhattan, Euclidean and Chebyshev norms. In the cases  $\varepsilon = 10^{-2}$  to  
 110  $10^{-5}$ , the trait dynamics following non-cooperative optimization is fastest. In most cases, when  $\varepsilon$   
 111 and  $\gamma$  are varied, the convergence of the trait dynamics with Manhattan norm is faster than the  
 112 Euclidean norm, and the convergence of the trait dynamics with Euclidean norm is faster than the  
 113 Chebyshev norm.

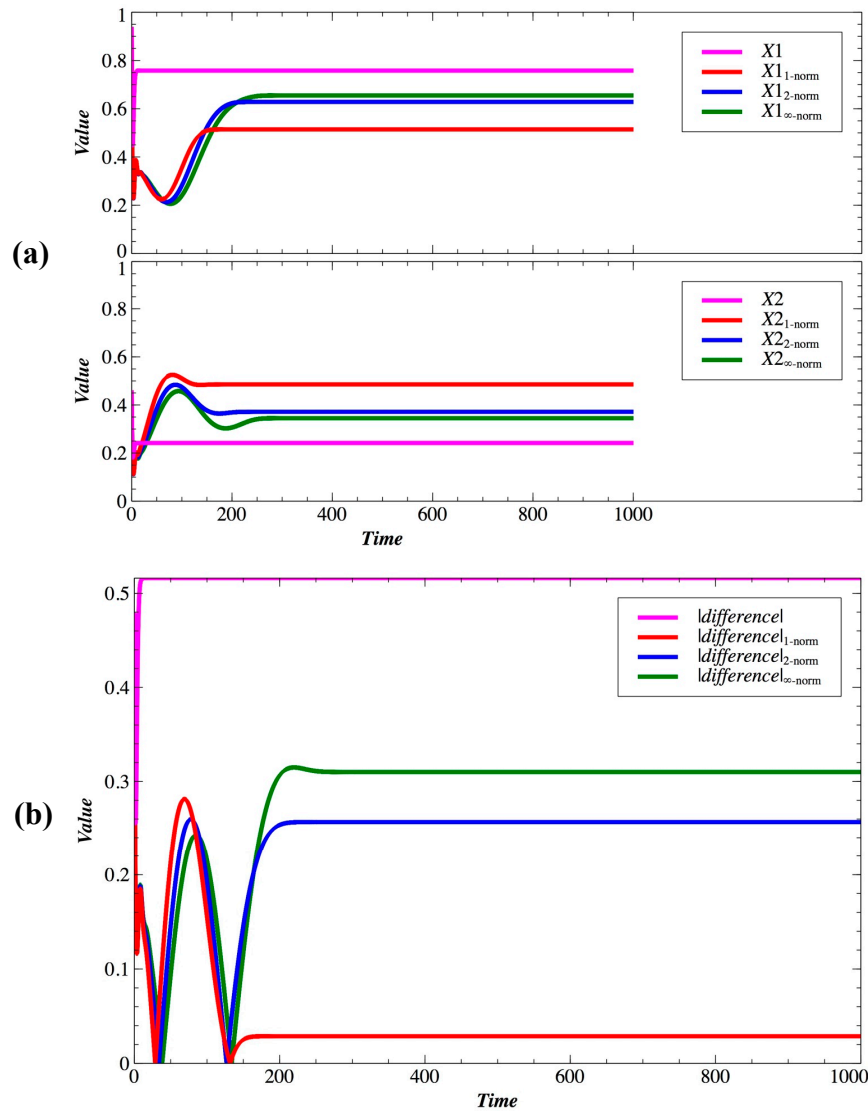


**Figure 1.** Effect of using different norms in the evolutionary objective under deterministic case. (a) Effect on lowering the parasitism exploitation coefficient ( $\alpha$ ). The parameter  $\alpha_1$  and  $\alpha_2$  in the figure are the parasitism exploitation coefficients using non-cooperative optimization for the competing species 1 and 2, respectively. The parameters  $\alpha_{1-norm}$ ,  $\alpha_{2-norm}$  and  $\alpha_{\infty-norm}$  ( $\alpha_{1-norm}$ ,  $\alpha_{2-norm}$  and  $\alpha_{\infty-norm}$ ) are the parasitism exploitation coefficients for species 1 (species 2) using Manhattan, Euclidean and Chebyshev norms, respectively. The figure shows which method converges faster to the desired value  $\alpha = 0$  (no disease). (b) In the figure,  $sum = X_1 + X_2$  (for non-cooperative optimization),  $sum_{1-norm} = X_{1-norm} + X_{2-norm}$ ,  $sum_{2-norm} = X_{1-norm} + X_{2-norm}$  and  $sum_{\infty-norm} = X_{1-norm} + X_{2-norm}$ . The sums represent the carrying capacity of the environment where species 1 and 2 compete for the available resources. The desired goal is to maximize the utilization of the resources (sum equals 1). Note that the variables  $X_1$  and  $X_2$  are the population densities of species 1 and 2 using non-cooperative optimization, respectively. The variables  $X_{1-norm}$ ,  $X_{2-norm}$  and  $X_{\infty-norm}$  ( $X_{1-norm}$ ,  $X_{2-norm}$  and  $X_{\infty-norm}$ ) are the population densities for species 1 (species 2) using Manhattan, Euclidean and Chebyshev norms, respectively.



**Figure 2.** Convergence time to the evolutionary objective under deterministic case. In this figure, ‘stop’ means time of convergence towards the evolutionary objective for non-cooperative optimization, and ‘stop’ with index means time of convergence towards the evolutionary objective using the corresponding mathematical norm. The parameter  $\gamma$  denotes the ratio between the numerical response coefficient ( $\beta_i$ ) and parasitism exploitation coefficient ( $\alpha_i$ ), and  $\varepsilon$  is the speed of evolutionary adaptation. The larger the  $\varepsilon$ , the larger the effect of the distance metric to the trait dynamics in one generation. Here, we consider  $\gamma = 0.5$  which means  $\beta_i$  as half of  $\alpha_i$ ,  $\gamma = 1$  which means  $\beta_i$  equals  $\alpha_i$ , and  $\gamma = 2$  which means  $\beta_i$  as double of  $\alpha_i$ . The numerals 1 to 4 and letters A to D represent the ranking of convergence, where 1 and A denote fastest convergence while 4 and D denote slowest convergence. We took the mean and the mean plus standard deviation (sd) of 1000 numerical simulations with random population initial conditions.

In terms of egalitarian sharing of resources, each of the distance metric provides opportunity for the competing species to maintain nearly equal sharing of available resources even though the species maximize their population densities in a zero-sum game. If the difference between the population densities of the competing species is near zero then it means that the competition system is egalitarian. The effect of the trait dynamics can be observed from the population densities of the competing species (Figure 3a). The population densities of the competing species following the trait dynamics with non-cooperative optimization can converge faster to the evolutionary objective. However, the outcome may not be egalitarian, that is, there is large difference between the population densities of the competing species (Figure 3b).

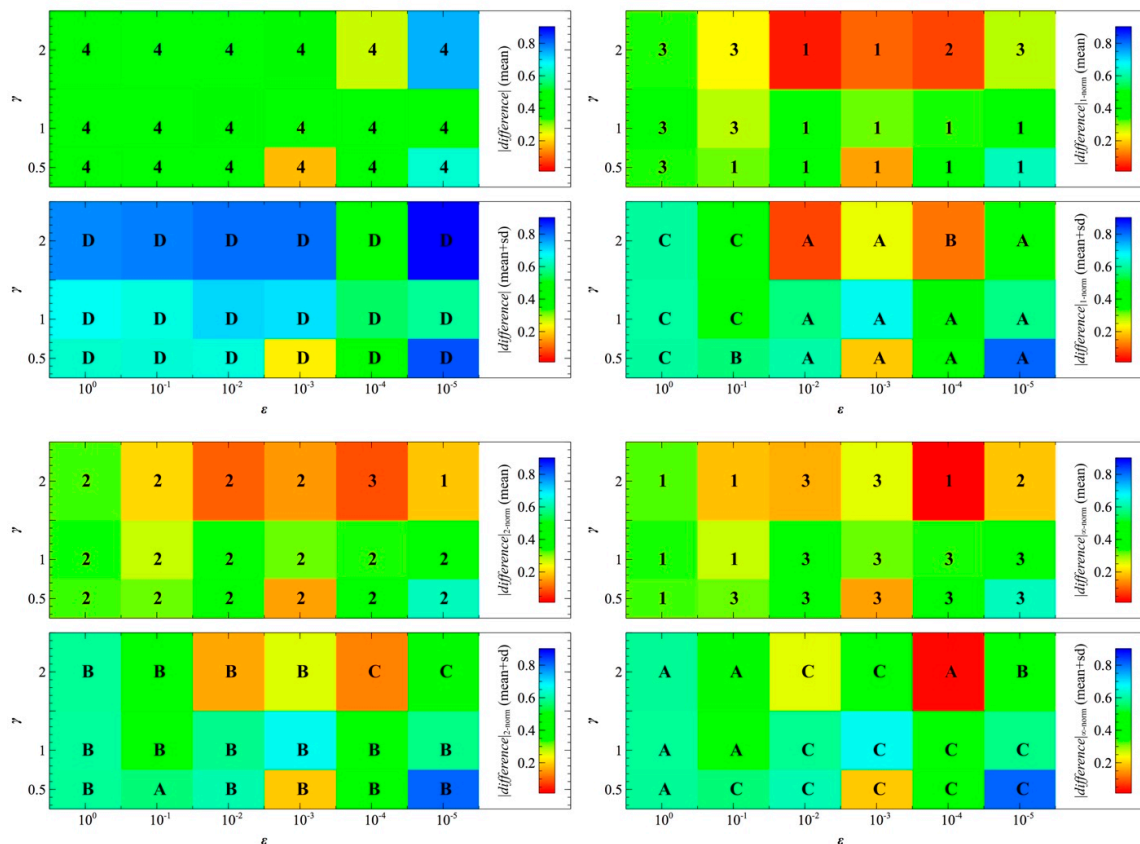


**Figure 3.** Effect of using different norms in the population dynamics of the host species under deterministic case. (a) Effect on the population densities ( $X_1$  and  $X_2$ ). The variables  $X_1$  and  $X_2$  in the figure are the population densities of species 1 and 2 using non-cooperative optimization, respectively. The variables  $X_{1-1-norm}$ ,  $X_{1-2-norm}$  and  $X_{1-\infty-norm}$  ( $X_{2-1-norm}$ ,  $X_{2-2-norm}$  and  $X_{2-\infty-norm}$ ) are the population densities for species 1 (species 2) using Manhattan, Euclidean and Chebyshev norms, respectively. (b) In the figure,  $|difference| = |X_1 - X_2|$ ,  $|difference|_{1-norm} = |X_{1-1-norm} - X_{2-1-norm}|$ ,  $|difference|_{2-norm} = |X_{1-2-norm} - X_{2-2-norm}|$  and  $|difference|_{\infty-norm} = |X_{1-\infty-norm} - X_{2-\infty-norm}|$ . Here, we can see what method provides opportunity for the competing species to maximize each of their population densities while maintaining equal sharing of the available resources. If the difference is near zero then it means that the competition system is egalitarian.

When varying the parameter values of  $\varepsilon$  and  $\gamma$ , the trait dynamics with non-cooperative optimization is ranked with very low egalitarian sharing of resources (Figure 4). In most cases in Figure 4, the degree of being egalitarian of the population dynamics with Euclidean norm falls between that with Manhattan and Chebyshev norms. The dynamics with Chebyshev norm shows very high degree of egalitarianism (rank 1 in most cases in Figure 4) when  $\varepsilon = 10^0$  to  $10^{-1}$ . This means that when speed of adaptation is fast (e.g., trait evolution significantly affects current or 1st generation of offspring), the dynamics with Chebyshev norm may result in almost equal population densities. In most cases, when  $\varepsilon = 10^{-2}$  to  $10^{-5}$ , the dynamics with Manhattan norm is the first in rank (Figure 4). That is, when the consequence of evolution is exhibited mostly in 2nd or later



generations, the dynamics with Manhattan norm results in higher degree of egalitarianism. However, when  $\gamma = 2$ , this pattern may not be always the case. A parameter  $\gamma > 1$  indicates that infection of host leads to high reproduction rate of parasites.

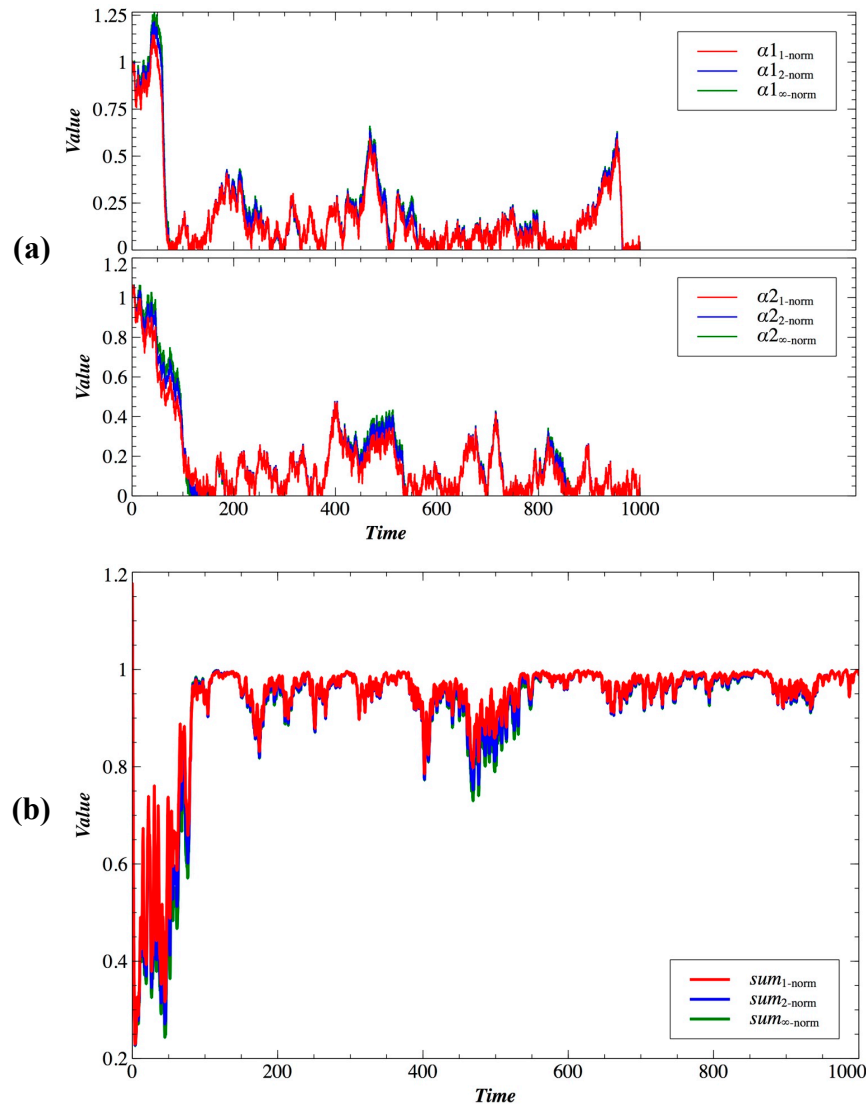


**Figure 4.** Absolute difference between the population densities of host species 1 and 2. In this figure,  $|difference| = |X_1 - X_2|$  (for non-cooperative optimization),  $|difference|_{1-norm} = |X_{1-1-norm} - X_{2-1-norm}|$ ,  $|difference|_{2-norm} = |X_{1-2-norm} - X_{2-2-norm}|$  and  $|difference|_{\infty-norm} = |X_{1-\infty-norm} - X_{2-\infty-norm}|$ . If the difference is near zero then it means that the competition system is egalitarian. The parameter  $\gamma$  denotes the ratio between the numerical response coefficient ( $\beta_i$ ) and parasitism exploitation coefficient ( $\alpha_i$ ), and  $\varepsilon$  is the speed of evolutionary adaptation. The larger the  $\varepsilon$ , the larger the effect of the distance metric to the trait dynamics in one generation. Here, we consider  $\gamma = 0.5$  which means  $\beta_i$  as half of  $\alpha_i$ ,  $\gamma = 1$  which means  $\beta_i$  equals  $\alpha_i$ , and  $\gamma = 2$  which means  $\beta_i$  as double of  $\alpha_i$ . The numerals 1 to 4 and letters A to D represent the ranking of the degree of egalitarianism, where 1 and A denote most egalitarian while 4 and D denote least egalitarian. We took the mean and the mean plus standard deviation (sd) of 1000 numerical simulations with random population initial conditions.

The trait dynamics using Manhattan and Euclidean norms have advantages over the Chebyshev norm. Nevertheless, the speed of convergence entails evolutionary trade-off. The trait dynamics with Manhattan norm requires higher energy cost compared to that with Euclidean norm. Also, the trait dynamics with Euclidean norm requires more energy cost than that with Chebyshev norm. More so in the stochastic case, the distinctive advantages of the three metrics become indistinguishable.

*Stochastic Case.* Random perturbations, such as uncertain environmental noise, are frequent in biological and social systems [39,40]. The presence of randomness can be disadvantageous in predicting future events when perturbations do not follow the regularity posted by known probability distributions. However, randomness can also pose benefits to populations, and drive diversity in biological and social systems. A dominant species can lose its competitive advantage over its competitor because of environmental noise, resulting in the switching of winners [6,39].

We have introduced a degree of stochastic noise to the population dynamics of parasites (Equation 3) and to the trait dynamics of the competing species (Equations 4-9). It is observable that the distinctive characteristics of the outcomes under the Manhattan, Euclidean and Chebyshev norms become indistinguishable (Figure 5a). The patterns of convergence to the desired evolutionary outcomes which is to drive the parasitism exploitation coefficient  $\alpha$  to zero (Figure 5a) and to reach the maximum population density (Figure 5b) become almost similar for the trait dynamics under the three norms.

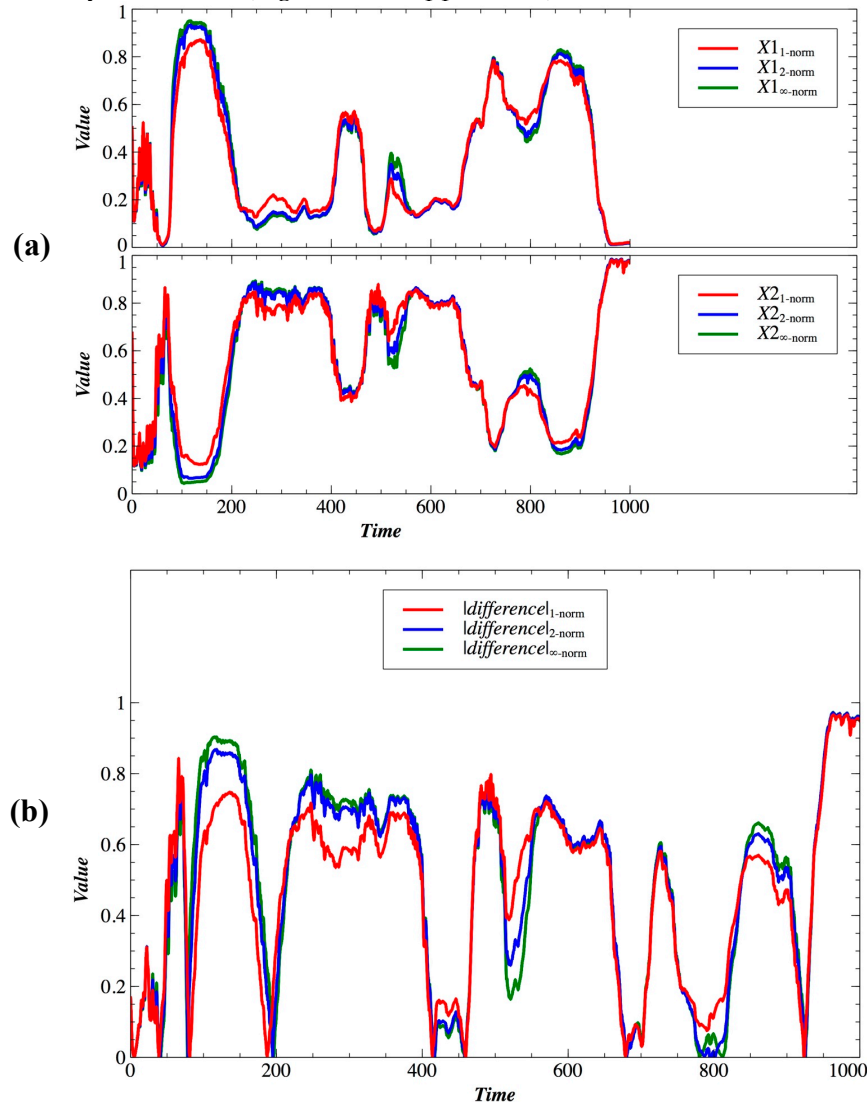


**Figure 5.** Effect of using different norms in the evolutionary objective under stochastic case. The distinctive characteristics of the outcomes under the Manhattan, Euclidean and Chebyshev norms become homogenous. (a) Effect on lowering the parasitism exploitation coefficient ( $\alpha$ ). The parameters  $\alpha_{1-norm}$ ,  $\alpha_{2-norm}$  and  $\alpha_{\infty-norm}$  ( $\alpha_{2-norm}$ ,  $\alpha_{2-norm}$  and  $\alpha_{\infty-norm}$ ) are the parasitism exploitation coefficients for species 1 (species 2) using Manhattan, Euclidean and Chebyshev norms, respectively. (b) In the figure,  $sum_{1-norm} = X_{1-norm} + X_{2-norm}$ ,  $sum_{2-norm} = X_{1-norm} + X_{2-norm}$  and  $sum_{\infty-norm} = X_{1-norm} + X_{2-norm}$ . The sums represent the carrying capacity of the environment where species 1 and 2 compete for the available resources. The desired goal is to maximize the utilization of the resources (sum equals 1).

The patterns of egalitarian sharing of resources becomes indistinguishable when randomness is introduced (Figure 6). That is, the stochastic population dynamics with trait dynamics using Manhattan, Euclidean and Chebyshev norms are similar in many cases (Figure 6a). We cannot determine what norm could result in an observable higher degree of egalitarianism (Figure 6b).



Moreover, randomness can result in negative frequency-dependent selection as shown by the population fluctuations in Figure 6a. This reveals that randomness can drive switching of winners (dominant populations). We have also simulated a case where  $r_1$  and  $r_2$  are the evolving traits, and the result shows that there are only minute differences in the population densities using Manhattan, Euclidean and Chebyshev norms (Figure B1 in Appendix B).



**Figure 6.** Effect of using different norms in the population dynamics of the host species under stochastic case. Oscillations arise due to stochasticity, and the temporal patterns of egalitarian sharing of resources becomes indistinguishable. (a) Effect on the population densities ( $X_1$  and  $X_2$ ). The variables  $X_{1-1-norm}$ ,  $X_{1-2-norm}$  and  $X_{1-\infty-norm}$  ( $X_{2-1-norm}$ ,  $X_{2-2-norm}$  and  $X_{2-\infty-norm}$ ) are the population densities for species 1 (species 2) using Manhattan, Euclidean and Chebyshev norms, respectively. (b) In the figure,  $|difference|_{1-norm} = |X_{1-1-norm} - X_{2-1-norm}|$ ,  $|difference|_{2-norm} = |X_{1-2-norm} - X_{2-2-norm}|$  and  $|difference|_{\infty-norm} = |X_{1-\infty-norm} - X_{2-\infty-norm}|$ . If the difference is near zero then it means that the competition system is egalitarian.

#### 4. Conclusions

Our results provide theoretical cases when evolutionary dynamics using different distance metrics exhibit distinguishable outcomes. However, random perturbations could mask the effect of using different evolutionary measures. This has two important implications. First, the use of different metrics entails employing different strategies but whatever metric is used, the outcomes may be indistinguishable in a stochastic environment. Consequently, a simpler metric can be used rather than using a metric that is too costly to implement in evolutionary dynamics. Second, when data are

available, the intrinsic and extrinsic noise may lead to difficulty in tracking the evolutionary measure that was utilized during evolutionary events. In investigating evolutionary strategies of populations, it is advisable to clear the data of randomness such as by compressing the data to reflect only the deterministic trends.

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**Author Contributions:** J.F.R. conceived the study and built the model; C.A.H.B. and D.A.SJ.T. ran the simulations and produced the results; A.L.C. summarized the simulation results and created the figures; A.L.B., G.A.C. and J.F.R. analyzed, interpreted and discussed the results; A.L.B., J.F.R., D.A.SJ.T. and M.K.A.G. wrote the paper; all authors reviewed the manuscript.

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

## Appendix A: Methods

The deterministic evolutionary trait dynamics using a mathematical norm  $\|1 - X\|$  is modeled by:

$$\alpha(t + h) = \alpha(t) - h \left( \varepsilon \frac{\|1 - X\|}{\max\{X, 10^{-6}\}} \right). \quad (\text{A1})$$

The parameter  $\varepsilon$  is the speed of evolutionary adaptation. The quantitative trait  $\alpha$  will increase when the expression  $\frac{\|1 - X\|}{\max\{X, 10^{-6}\}} < 0$ . On the other hand, the quantitative trait  $\alpha$  will decrease when the expression  $\frac{\|1 - X\|}{\max\{X, 10^{-6}\}} > 0$ . The evolutionary effect of  $\|1 - X\|$  is regulated by the density of the population ( $\max\{X, 10^{-6}\}$ ), where the number  $10^{-6}$  is introduced to avoid division by zero during numerical simulations. Here, low population size facilitates trait evolution.

The stochasticity in the model are represented by the following:

$$\text{noise}_1 = \sigma_1 e^{-P} \sqrt{h} N(0,1) \quad (\text{A2})$$

$$\text{noise}_2 = \sigma_2 \sqrt{h} N(0,1) \quad (\text{A3})$$

$$\text{noise}_3 = \sigma_2 \sqrt{h} N(0,1) \quad (\text{A4})$$

where  $\sigma_i$  is the amplitude of the noise, and  $N(0,1)$  is a normally distributed random number. The expression  $e^{-P}$  characterizes density-dependent noise in parasite population, where a large parasite population leads to homogeneity. In the numerical simulations, it is assured that all state variables ( $X$ ) and the quantitative trait ( $\alpha$ ) are nonnegative.

The non-cooperative optimization model that we have considered is:

$$\alpha_1(t + h) = \alpha_1(t) - h(\alpha_1(t) \times \max(|X_1(t) - X_1(t - 100)|, 10^{-6})) \quad (\text{A5})$$

$$\alpha_2(t + h) = \alpha_2(t) - h(\alpha_2(t) \times \max(|X_2(t) - X_2(t - 100)|, 10^{-6})). \quad (\text{A6})$$

In this model,  $\alpha_1$  is directly independent of  $X_2$ . Also,  $\alpha_2$  is directly independent of  $X_1$ .

In the figures, we have used the following values:  $\alpha_1(0) = \alpha_2(0) = 1$ ,  $h = 0.01$ ,  $\sigma_1 = 10^{-0.5}$ , and  $\sigma_2 = 10^{-2}$ . Lower values of  $\sigma_1$  and  $\sigma_2$  may result in approximately deterministic case. The initial values for the 1000 simulation runs are uniformly distributed random numbers between 0 and 1 per host and parasite population state variables.

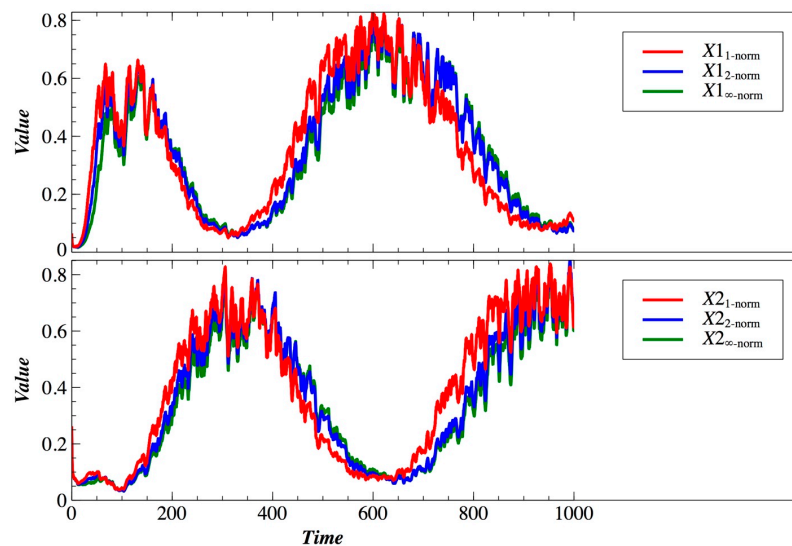
## Appendix B

We have also simulated a case where  $r_1$  and  $r_2$  are the evolving traits with  $\alpha_1 = \alpha_2 = 1$ . The quantitative trait evolution equations are

$$r_1(t+h) = r_1(t) - h \left( \varepsilon \frac{\|1-X\|}{\max\{X_1(t), 10^{-6}\}} \right) + noise_2 \quad (B1)$$

$$r_2(t+h) = r_2(t) - h \left( \varepsilon \frac{\|1-X\|}{\max\{X_2(t), 10^{-6}\}} \right) + noise_3 \quad (B2)$$

where  $\|1-X\|$  represents the corresponding mathematical norm. Figure B1 shows sample paths of the population dynamics with  $\sigma_1 = 10^{-1}$  and  $\sigma_2 = 0$ .



**Figure B1.** Effect of using different norms in the population dynamics of the host species under stochastic case with  $r_1$  and  $r_2$  as the evolving traits. The variables  $X1_{1\text{-norm}}$ ,  $X1_{2\text{-norm}}$  and  $X1_{\infty\text{-norm}}$  ( $X2_{1\text{-norm}}$ ,  $X2_{2\text{-norm}}$  and  $X2_{\infty\text{-norm}}$ ) are the population densities for species 1 (species 2) using Manhattan, Euclidean and Chebyshev norms, respectively.

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