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The Interaction between Predator Strategy and Prey Competition in a pair of Multi-Predator Multi-Prey Lattices

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Abstract

A computational study of a system of ten prey phenotypes and either one or ten predator phenotypes with a range of foraging behaviours, arranged on two separate one-dimensional lattices, is presented. Mutation between nearest neighbours along the prey lattice occurs at a constant rate, and mutation may or may not be enabled for the predators. The significance of competition amongst the prey is investigated by testing a variety of distributions of the relative intraspecific and interspecific competition. We also study the influence this has on the survival and population size of predator phenotypes with a variety of foraging strategies. Our results indicate that the distribution of competition amongst prey is of little significance, provided that intraspecific is stronger than the interspecific, and that it is typically preferable for a predator to adopt a foraging strategy that scales linearly with prey population sizes if it is alone. In an environment of multiple predator phenotypes, the least or most-focused predators are most likely to persist, dependent on the feeding parameter.

Keywords: Coupled Map Lattice, Predator-Prey System, Predation Strategy, Competition

1. Introduction

Early studies of population dynamics were limited to analytic investigations of low-dimensional dynamical systems. Large scale models of food webs are not generally amenable to yielding analytic results, however their study through numerical simulation has become a viable field in recent years with the proliferation of improved computational resources. Some studies have modelled the coevolution of distinct groups of prey and predator species in the context of evolutionary games and searching for evolutionary stable strategies (ESS) [1, 2], whilst other authors have focused on the coevolution of mutualistic species [3]. One avenue from the ecological literature (with input from network and graph theory) has been the development of eco-evolutionary food web models where all species occupy the same trait space and have the potential to produce mutant offspring that occupy a different trophic niche than the parent. The Webworld model [4, 5], and the Loeuille-Loreau model [6], have been notably successful, but others of interest include the Matching model [7, 8], Bastolla and Lassig's model [9], and models that include mutualistic interactions - for example Yoshida's work [10] and Tokita and Yasutomi's studies [11].

In this study, however, we extend the work of a coupled map lattice (CML) model [12, 13, 14, 15]. In this framework, the species are predefined and separated into two one-dimensional trait spaces: a prey lattice and a predator lattice. Positions on each lattice represent different prey and predator phenotypes, with the prey's reproductive parameter and the predator's degree to which it focuses its feeding efforts on the most populous prey phenotypes dependent on their positions on their respective lattices. All phenotypes are assumed to exist in a single, well-mixed environment. Individuals of a given phenotype have the option to mutate to a neighbouring position along the lattice, but may not jump to the other lattice (i.e. a prey cannot become a predator and vice versa). This approach, unlike the evolutionary food web models cited above, is less suited to exploring the construction and maintenance of ecosystems from a "first species" scenario, but at low mutation rates may provide a suitable model for investigating the coevolution of phenotypes of a given prey and predator in an environment. Previous work on this model demonstrated evidence of dynamic behaviour including chaotic orbits [14], and a variety of predator strategies were compared [13]. Subsequent work was restricted to the most intuitive of these foraging strategies - weighting hunting efforts according to the size of the prey subpopulation. This is the form of predator strategy implemented in this work also, and predator phenotypes are differentiated by the degree to which they adopt this strategy.

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For larger rates of mutation, an alternative interpretation of CML-based approaches is as a spatial model [16, 17, 18]. In this case, there is precisely one prey and one predator phenotype. For the prey, the positions on the lattice represent distinct geographic regions (with differing growth rates between sub-populations representing the degree to which the characteristics of that environment support the prey), between which they can migrate. The “interspecific” competition between neighbouring phenotypes in this scenario represents the inhibiting effects of fellow prey in neighbouring regions. The distinctions in predator strategy along their lattice indicate how that predator subgroup allocate their hunting efforts across the geographic regions - whether they spread evenly across all the areas, or move to and reside only in the subregion which hosts the greatest prey subpopulation. In this way, we represent the degree to which a predator may actively hunt, rather than simply disperse. “Mutation” of the predators in this case indicates the tendency of the predators to alter their foraging strategies by diffusion along the lattice to become slightly more or less focused than before. However, we emphasise that our model is primarily designed to study the mutation of phenotypes in a single environment and that the spatial interpretation is an alternative understanding of the model that can be applied when the rate of “mutation” is too high to represent biological mutation.

This research considers an altered version of the previous model, and investigates two primary aspects: predator strategy, and the distribution of competition between the prey phenotypes. Much effort in behavioural ecology has been devoted to measuring foraging strategies and in particular the development of Optimal Foraging Theory [19]. In the context of dynamic food web models, adaptive foraging has been found to positively impact stability of various types [20, 21, 22].

The study of competition has been a significant topic in mathematical ecology and a number of effects have been observed, depending on the strength of the competition and the precise nature of the model. Some studies have found very strong competition to be destabilising [23, 24], whilst a moderate amount promotes survival and helps to blur trophic levels so that a more complex, realistic network structure can be obtained. For example, in the Loeuille-Loreau model, if interspecific competition is wholly absent this can lead to plain food chains as species evolve towards maximum efficiency at a given body size, as there is no benefit to being anywhere else to avoid competition. In other words, mild interspecific competition provides an incentive for species to occupy new niches/trophic positions that would otherwise be non-optimal. Thus, one principle would seem to be that some moderate degree of competition is necessary for survival and the production of complex food webs that bear the characteristics of real ecosystems, by promoting speciation [6, 25]. Recent studies from a graph-theoretic approach (considering food webs as a transportation network) have suggested that this trade-off between the efficiency of a star-shaped network structure and the avoidance of competition in a chain-shaped network could be the fundamental principle underlying and uniting all food webs. The authors of these works [26, 27] therefore propose a possibly universal property that describes the scaling of transportation cost with the size of subtrees of the spanning tree. Furthermore, a study that considered the effects of intraspecific competition in a selection of empirical soil webs [28] found that whilst patterns of the distribution of the strength of self-regulation across the system (e.g. uniform, biomass-dependent, trophic level-dependent) lacked any strong correlation with its linear stability, it could strongly impact the response of the web to variation in the density-dependence of a given species. Furthermore, for the Webworld model [5], it was found to be necessary for interspecific competition to be weaker than intraspecific competition in order to allow coexistence of multiple species.

In what follows, we use numerical simulations to examine the effects of changing the distribution of competition between neighbouring prey phenotypes, and varying the degree to which predators focus their efforts on the most populated prey phenotypes, in a discrete model that consists of a one-dimensional prey phenotype lattice and a one-dimensional predator phenotype lattice, providing a simple model of coevolution of a pair of species in an ecosystem. We now describe the model and methods in detail.

2. Multiple Species Predator-Prey Model

Consider a system of n prey phenotypes arranged along a one-dimensional lattice, and m predator phenotypes arranged likewise. Prey phenotype j at time-step t is denoted by N_t^j , and predator phenotype i is denoted by P_t^i .

2.1. Scenarios

We study five scenarios separately. In all cases there are precisely ten prey phenotypes (that is, $n = 10$) with mutation enabled between them.

- i) A single, non-mutating predator is introduced to the system.
- ii) A single, mutating predator (the least focused) is introduced to the system.
- iii) The same as (ii), but the predator introduced is the most, rather than the least, focused.
- iv) 10 non-mutating predators are introduced to the system.
- v) 10 mutating predators are introduced to the system.

Therefore, for scenario (i) we have $m = 1$, and in all other scenarios $m = 10$. For each situation, we consider the average total prey and predator populations sizes and numbers of surviving phenotypes, given a variety of initial predator population sizes, distributions of prey competition, and, in the case (i) of a single non-predator, the degree to which it focuses on hunting prey phenotypes that have larger populations. In the cases where 10 predators are introduced, their individual initial populations

will be scaled by 0.1 so that the combined initial population is comparable to scenarios where only one predator initially enters the system.

2.2. Before Mutation

Consider first the prey species. We model a regime whereby each of the prey phenotypes (in competition with itself and its nearest neighbouring phenotype) reproduces by logistic growth, laying eggs and then that generation dies out. Following this, predation on the next generation (that is, the young) then occurs.

2.2.1. Assignment of Control Parameters

The prey phenotypes reproduce according to a logistic map, and they are differentiated according to their reproductive (growth) parameter r_j , which increases linearly with phenotype number according to $r_j = 1 + r_{max}j/n$, where $j \in \{1, \dots, n\}$. In the cases presented here we take $r_{max} = 3$, so that r_j varies uniformly in the range $[1.3, 4]$.

Predator phenotypes are differentiated according to hunting strategy. Each is assigned a value α_i which governs the degree to which they focus on the prey phenotype or local population which is most numerous (the effects of choosing alternative predation strategies in the precursor to this model were investigated in [13]). The effort that predator i expends on prey j at timestep t is then calculated in the following manner:

$$f_t^{i,j} = \frac{(N_t^j)^{\alpha_i}}{\sum_{k=1}^n (N_t^k)^{\alpha_i}} \quad (1)$$

Thus it is ensured that, for each predator i , the natural constraint $\sum_{j=1}^n f_t^{i,j} = 1$ is satisfied. In our model, the effort $f_t^{i,j}$ that predator i devotes to prey j at iteration t can be treated equivalently with the fraction of the population of predator phenotype i that is actively hunting prey phenotype j at that time. For the case of ten predators, the parameter α is simply scaled linearly in $0, 1, \dots, 9$. That is, for predator i , $\alpha_i = i - 1$. However, for the scenario featuring only one predator (with predator mutation switched off), we investigate the cases of $\alpha_1 = \alpha \in \{0, 1, 2, 4, 7, 10, 15, 20, 30, 50, 100, \infty\}$ where $\alpha = \infty$ indicates that at any given time step the predator feeds only upon the most populous prey phenotype. Since the prey are governed by a logistic map, any given prey phenotype has a maximum population determined by the competition parameters. Hence, a maximally-focused predator ($\alpha = \infty$) may be able to eat with more efficiency (in the event of any prey phenotype having a low population), as it does not waste any proportion of its effort on prey phenotypes that are poorly populated, but it is limited in its reproduction as it can only consume a prey population of one phenotype per iteration. A less focused predator is less efficient in this sense, but can potentially consume all ten prey populations simultaneously.

The impact of a predator i on prey j is then largely determined by the control parameter $c^{i,j}$, which controls the number of individuals of prey j killed per individual of predator i that is actively hunting it per unit time, where the encounter rate between the species is determined by $N_t^j f_t^{i,j} P_t^i$. That is, $c^{i,j}$ gives the ratio between the number of kills and the product of the prey population and the predator population actively hunting it. As we shall see later, in order to reduce the number of free parameters in the model, we choose a model such that $c^{i,j}$ equates biologically to both the predator i 's kill rate of prey j and the reproductive efficiency i gains from the kill. We then choose a uniform rate of consumption, so $c^{i,j} = c$ for all predators i and prey j .

2.2.2. Dividing the Prey amongst Predators

Initially, based on our definitions the number of prey j killed by predation at a given time step will be $\sum_{i=1}^m c^{i,j} f_t^{i,j} P_t^i N_t^j$. However, this leads to a problem: because the predator phenotypes choose how to allocate their efforts independently of each other, there could be a situation where this sum is greater than the total population of that prey phenotype. To preclude this, after efforts are determined but before feeding occurs we divide the prey phenotype amongst its potential predators according to the predator's population and the fraction of effort that it is devoting to hunting that particular prey. This ensures that each predator only gains access to a proportionate fraction of the prey. The number of prey killed then becomes:

$$\sum_{i=1}^m c^{i,j} f_t^{i,j} P_t^i \left(N_t^j \frac{f_t^{i,j} P_t^i}{\sum_{k=1}^m f_t^{k,j} P_t^k} \right) = \left(\frac{1}{\phi_t(j)} \sum_{i=1}^m c^{i,j} (f_t^{i,j})^2 (P_t^i)^2 \right) N_t^j, \quad (2)$$

where

$$\phi_t(j) = \sum_{k=1}^m f_t^{k,j} P_t^k \quad (3)$$

represents the total number of predator individuals of all phenotypes hunting prey j . Then,

$$\Phi_t(j) = \begin{cases} 0 & \text{if } \phi_t(j) = 0; \\ \frac{1}{\phi_t(j)} \sum_{i=1}^m c^{i,j} (f_t^{i,j} P_t^i)^2 & \text{otherwise,} \end{cases}$$

so that $\Phi_t(j)$ gives the final impact of predation on prey j , per prey individual, at time t .

2.2.3. The Model without Mutation

Then if the prey reproduce by a logistic model in the order described above (predation follows reproduction and the prey generational life-span is identified with a single iteration), and experience intraspecific competition of strength a and interspecific competition of strength b with nearest neighbours only, we arrive at the following set of equations:

$$N_{t+1}^1 = r_1 N_t^1 (1 - a N_t^1 - b N_t^2) (1 - \Phi_t(1)), \quad (4)$$

$$N_{t+1}^j = r_j N_t^j (1 - b N_t^{j-1} - a N_t^j - b N_t^{j+1}) (1 - \Phi_t(j)) \text{ for } j = 2, \dots, 9, \quad (5)$$

$$N_{t+1}^{10} = r_{10} N_t^{10} (1 - b N_t^9 - a N_t^{10}) (1 - \Phi_t(10)) \quad (6)$$

Note that phenotypes at the ends of the lattice ($j = 1$ or $j = 10$) will in general have a reduced amount of interspecific competition.

For the predator phenotypes, we consider a ‘‘pure predator’’ with no other means of obtaining resources, and so we assume a general form:

$$P_{t+1}^i = \sum_{j=1}^n f_t^{i,j} P_t^i G_t^{i,j} (\beta^{i,j}, c^{i,j}, f_t^{i,j} P_t^i), \quad (7)$$

where $G_t^{i,j}$ is the per capita production and $\beta^{i,j}$ the reproductive parameter of predator i when it consumes prey j . Now, as it is a pure predator, P_t^i must feed with a carrying capacity equivalent to the situation where *every* prey individual is consumed. Since $f_t^{i,j} P_t^i N_t^j$ is the number of encounters between predator i and prey j per iteration, and $c^{i,j}$ gives the fraction of these that result in a successful kill, the carrying capacity of predator i for prey j will be reached when $c^{i,j} f_t^{i,j} P_t^i N_t^j = N_t^j$ and all prey j are killed. Therefore, for the predators to also follow a logistic-like model, we take $G_t^{i,j} = \beta^{i,j} N_t^j (1 - c^{i,j} f_t^{i,j} P_t^i)$. In order to keep the number of free parameters to a minimum, we choose $\beta^{i,j} = c^{i,j} = c$. Therefore, c controls both the killing efficiency and the growth rate of the predator, which seems reasonable as the more efficient it is in slaying its prey, the faster the population will grow. Moreover, if the term $(1 - c f_t^{i,j} P_t^i)$ which governs carrying capacity were the only explicit occurrence of c in the model then an increased kill rate would be detrimental to the predator population. Therefore, by introducing the second dependence on c we minimise the model’s parameters, and determine the following three effects of increasing c : 1) a predator-prey encounter is more likely to result in a successful kill; 2) the reproductive efficiency of predator i when feeding on prey j is increased; 3) predator i requires a greater prey population in order to ensure its own survival.

Finally, we must take into account the division of possible prey amongst the predators by introducing a factor of $f_t^{i,j} P_t^i / \phi_t(j)$ into the sum. This brings us to the following general equation for the predators:

$$P_{t+1}^i = (P_t^i)^2 \sum_{j=1}^n \frac{1}{\phi_t(j)} (f_t^{i,j})^2 c N_t^j (1 - c f_t^{i,j} P_t^i) \quad (8)$$

2.3. Mutation

Throughout, we will employ a Nearest-Neighbour mutation scheme for the prey and for the predators when their mutation is enabled. For either the predators or the prey, let K denote the number of possible phenotype (that is, the number of positions on the lattice), and for a given $1 \leq i, j \leq K$ let $p_{i,j}$ denote the fraction of phenotype i that mutates to phenotype j after reproduction at each time step. Then clearly,

$$\sum_{j=1}^n p_{k,j} = 1, \forall k. \quad (9)$$

As we are using a nearest-neighbour scheme, the probability of mutating to a specified adjacent phenotype is p which is constant throughout a given simulation. There is no possibility of mutating directly to a phenotype more than one position away on the lattice. Thus,

$$p_{k,j} = \begin{cases} p, & |j - k| = 1 \\ 1 - 2p, & j = k \neq 1 \text{ or } K \\ 1 - p, & j = k = 1 \text{ or } K \\ 0, & \text{otherwise.} \end{cases} \quad (10)$$

2.4. Final Model with Mutation

Therefore, incorporating mutation, we have:

$$N_{t+1}^j = \sum_{l=1}^n p_{l,j} r_l N_t^l (1 - bN_t^{l-1} - aN_t^l - bN_t^{l+1})(1 - \Phi_t(l)) \quad (11)$$

$$\begin{aligned} &= pr_{j-1} N_t^{j-1} (1 - bN_t^{j-2} - aN_t^{j-1} - bN_t^j)(1 - \Phi_t(j-1)) \\ &+ (1 - 2p)r_j N_t^j (1 - bN_t^{j-1} - aN_t^j - bN_t^{j+1})(1 - \Phi_t(j)) \\ &+ pr_{j+1} N_t^{j+1} (1 - bN_t^j - aN_t^{j+1} - bN_t^{j+2})(1 - \Phi_t(j+1)), \quad \text{if } j \in \{2, \dots, 9\}. \end{aligned} \quad (12)$$

and

$$P_{t+1}^i = \sum_{l=1}^m p_{l,i} (P_t^l)^2 \sum_{j=1}^n \frac{1}{\phi_t(j)} (f_t^{l,j})^2 c N_t^j (1 - c f_t^{l,j} P_t^l) \quad (13)$$

$$\begin{aligned} &= p(P_t^{i-1})^2 \sum_{j=1}^n \frac{1}{\phi_t(j)} (f_t^{i-1,j})^2 c N_t^j (1 - c f_t^{i-1,j} P_t^{i-1}) \\ &+ (1 - 2p)(P_t^i)^2 \sum_{j=1}^n \frac{1}{\phi_t(j)} (f_t^{i,j})^2 c N_t^j (1 - c f_t^{i,j} P_t^i) \\ &+ p(P_t^{i+1})^2 \sum_{j=1}^n \frac{1}{\phi_t(j)} (f_t^{i+1,j})^2 c N_t^j (1 - c f_t^{i+1,j} P_t^{i+1}), \quad \text{if } i \in \{2, \dots, 9\}. \end{aligned} \quad (14)$$

2.5. Forms of Competition

In this paper, we investigate the significance of the distribution of competition strength between the prey phenotypes, in particular, varying the relative strength of intraspecific competition against interspecific competition with nearest neighbours. We will consider the case where prey phenotypes which are sufficiently biologically similar such that they can mutate to each other, are also sufficiently similar in ecological niche such that they share resources and are in competition. This shall take the general form: $1 - bN_t^{j-1} - aN_t^j - bN_t^{j+1}$ for prey phenotype j , as seen in the model equations in previous sections. Thus, b controls the strength of interspecific competition, and a controls the intraspecific competition. These quantities must always satisfy $a + 2b = 1$, so that the effect observed is of the distribution of competition - that is, the relative strengths of intraspecific to interspecific - rather than being influenced by the total combined strength of competition experienced, which is controlled to be always equal to 1.

The situations studied are as follows:

Competition 0: $a = 1, b = 0$	Competition 4: $a = \frac{22}{30}, b = \frac{4}{30}$	Competition 8: $a = \frac{14}{30}, b = \frac{8}{30}$
Competition 1: $a = \frac{28}{30}, b = \frac{1}{30}$	Competition 5: $a = \frac{20}{30}, b = \frac{5}{30}$	Competition 9: $a = \frac{12}{30}, b = \frac{9}{30}$
Competition 2: $a = \frac{26}{30}, b = \frac{2}{30}$	Competition 6: $a = \frac{18}{30}, b = \frac{6}{30}$	Competition 10: $a = \frac{10}{30}, b = \frac{10}{30}$
Competition 3: $a = \frac{24}{30}, b = \frac{3}{30}$	Competition 7: $a = \frac{16}{30}, b = \frac{7}{30}$	

2.6. Numerical Methods

In all cases, the system is initialised with only the first prey phenotype (with $r = 1.3$) populated, with $N_0^1 = 0.5$, $N_0^j = 0$ for $j \in \{2, 3, \dots, 10\}$, and no predators present. The model is iterated for 10,000 time steps, and predator species with population P_1 are introduced at the beginning of the 10,001st step. The introduction of predators at this step is governed by which of the five scenarios described in Section 3.1 is being investigated, and for each case and set of parameters (e.g. competition type) we test each of $P_1 \in \{0.1, 0.2, 0.3, 0.4, 0.5\}$.

Therefore, for scenarios one and two $P_{10001}^1 = P_1$, $P_{10001}^j = 0$ for $j \neq 1$. For scenario three, $P_{10001}^{10} = P_1$, $P_{10001}^j = 0$ for $j \neq 10$. And for scenarios four and five, where all ten predators are initially introduced, $P_{10001}^j = P_1/10$ for $j = 1, \dots, 10$.

There are a maximum of ten possible prey and predator phenotype positions on their respective one-dimensional lattices. Following the introduction of the predator(s), we run the simulation for a further 90,000 iterations and then the data is collected by averaging the number of surviving prey and predator species over iterations 100,001-110,000. All phenotypes are considered to have a minimum population size of 10^{-6} , and if a phenotype falls below this size at any time-step, it is set to zero.

The initial data is generated by performing this procedure over the (c, p) parameter space, for 240 values of c in $(0, 6]$ and 200 values of p across the range $(0, 0.5]$. If predator mutation is switched on, it is given the same value of p as for the prey lattice. For each scenario (one or ten initial predators, mutation amongst predators enabled or disabled, initial predator population P_1) we examine a number of properties of both the prey and predators. The most important of which are the following:

- i) Phenotype Survival: the average number (between 0 and 10) of prey/predator phenotypes that are alive (population greater than 10^{-6}) over the final 10,000 iterations.
- ii) Total Population Size: the average sum of the populations of all ten phenotypes over the final 10,000 iterations.

A number of other derived quantities are calculated, but for the constraints of time and space, they are presented only in the supplementary material, and are described there. The only one we shall refer to within the main text is Expectation. That is, the expected value of the prey and predators, averaged over the final 10,000 iterations. At a given iteration, the expected value of phenotype $i = 1, \dots, 10$ with populations $\{x_1, \dots, x_{10}\}$ is given by:

$$E = \frac{\sum_{i=1}^{10} ix_i}{\sum_{j=1}^{10} x_j}. \quad (15)$$

We also consider plots of averaged species survival and population size against competition type. To produce these images, the data for average species survival S and population size P over iterations 100,001-110,000 are averaged across the (c, p) parameter space. For a given scenario and species, we then plot the maximum, minimum and average of this data across the five-possible predator initial conditions as a function of competition type. As per the ordering of the competition types described above, the x -axis is therefore a measure of the degree of diffusion of competition strength across nearest neighbours, being fully concentrated on intraspecific competition at Type 0 and spread equally between a phenotype and each of its neighbours at Type 10.

Therefore, we are plotting the maximum, minimum and average of the following quantities separately for predators and prey with respect to P_1 as a function of competition type:

$$S' = \frac{1}{p_{num}c_{num}t_{ave}} \sum_{r=1}^{p_{num}} \sum_{s=1}^{c_{num}} \sum_{t=1+t_{max}-t_{ave}}^{t_{max}} S|_{n=t, c=\frac{s}{40}, p=\frac{r}{400}}, \quad (16)$$

$$P' = \frac{1}{p_{num}c_{num}t_{ave}} \sum_{r=1}^{p_{num}} \sum_{s=1}^{c_{num}} \sum_{t=1+t_{max}-t_{ave}}^{t_{max}} P|_{n=t, c=\frac{s}{40}, p=\frac{r}{400}}, \quad (17)$$

where S denotes phenotype survival and P denotes the total population across all phenotypes of the species. $c_{num} = 240$ and $p_{num} = 200$ are the number of gradations of the (c, p) parameter space as above. $t_{max} = 110,000$ is the maximum number of iterations, and $t_{ave} = 10,000$ is the number of iterations over which the average properties are calculated.

All numerical simulations are performed with double precision variables using the Fortran 90 programming language. Each individual run (240x200 values of c, p for a given predator scenario, Competition Type and P_1) took 2.5-3 hours on a single core of a Skylake i7 6700k processor, using the Intel Fortran compiler (ifort). The main body of data, that is excluding at least 400 hours of processor time producing the material of the appendices, is the product of 880 such runs and therefore at least 2200 hours of processor time (in actual fact much more, as often less capable processors had to be employed).

2.7. Outline of Contents

We begin in Section 3 with a broad illustration of the role of competition in the system, given by the averaging plots described above.

In Section 4, we present a selection of Feigenbaum diagrams gathered by variation of a single parameter (both p and c are tested). This begins with an investigation of the effects of varying p in a scenario where no predators are ever introduced.

Next in Section 5 we discuss the main body of work, where the primary results of variation across the parameter space of

c and p are presented for the cases of $P_1 = 0.1$ (as final results do not appear to depend strongly on this choice).

The Discussion and Conclusions follow in Sections 6 and 7.

2.7.1. Contents of Supplementary Material

Properties (i)-(ii), together with a number of other properties, for $P_1 = 0.1$, all scenarios, all values of α (where relevant) and a selection of Competition Types (0,1,2,4,6,8,9,10) are all collected and presented in the supplementary material that accompanies this manuscript. Selected plots are reproduced in the main text below. Furthermore, the supplementary document features an appendix containing additional data that was produced in response to some observations from the initial material. These include some results for $P_1 = 0.3$, and for the scenario of Ten Non-Mutating Predators with a variety of different initial conditions of both predators and prey, in order to illustrate the aspects of the survival plots that are sensitive to such variation and those that are robust.

A further appendix shows a selection of material showing the full range of $0 < p \leq 1$ and $0 < c \leq 10$. The takeaway from these results is the discontinuity of the plot at $p = 0.5$, and that the area of predator survival tends to be reflected in this line and then compressed - regions of particularly high c and p are suppressed compared to an exact symmetry - however, predator populations are always substantially larger for $0.5 < p$. Unsurprisingly, therefore, for all competition types there exists a threshold of p above which prey populations are substantially reduced. However, the average number of surviving prey phenotypes is also reduced beyond this threshold, and we observe that this threshold in p decreases monotonically with increasing competition type until it reaches $p < 0.5$ for Competition Type 10. This trend occurs in all the scenarios tested: One Non-Mutating Predator with $\alpha = \infty$; One Mutating Predator with $\alpha = 0$; One Mutating Predator with $\alpha = 9$; Ten Non-Mutating Predators; and Ten Mutating Predators. Prey survival is inhibited for these impossibly high rates of mutation even when the predators are extinct, but as can be seen in the case of Ten Non-Mutating Predators, when the predators are present and $p > 0.5$ the effect on prey survival is even more pronounced, matching the region of predator survival, and disappearing as soon as the p -threshold is reached.

Finally, Appendix 4 of the supplement contains plots relating to the scenario of One Mutating Predator, but where it is instead predator #2, 3, ... or 9 that is initially populated with size P_1 at the 10,001st time step. This choice, surprisingly, has significant and persistent effects on the system and on predator survival at intermediate p in particular.

3. Results - Integral of Species Survival and Population against Competition Type

3.1. One Non-Mutating Predator

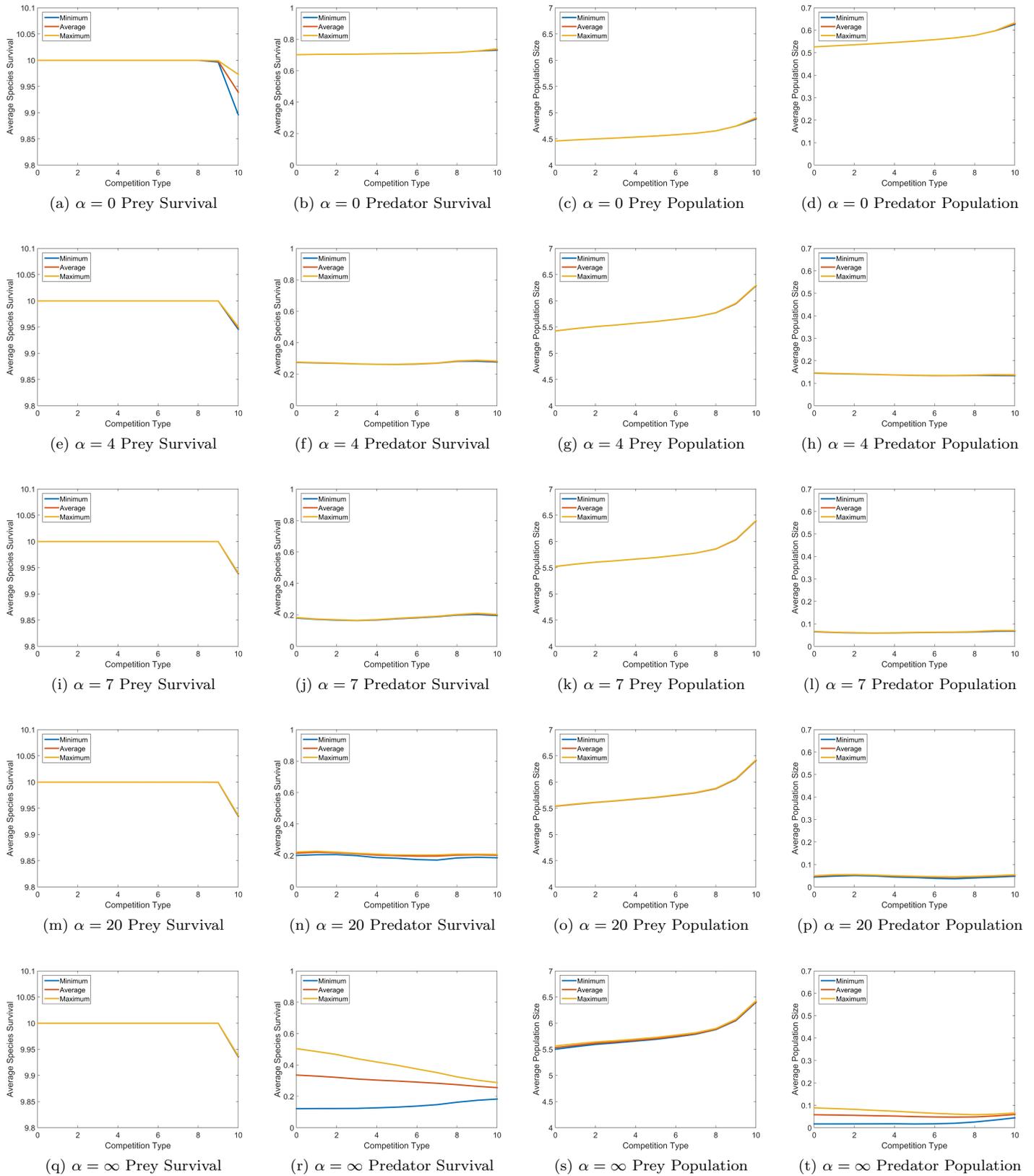


Figure 1: One Non-Mutating Predator

Fig. 1 shows the prey and predator phenotype survival and total population, averaged across the (c, p) -space and then again over $P_1 \in \{0.1, 0.2, 0.3, 0.4, 0.5\}$, as a function of Competition Type for a selection of values of α . In all cases, the total prey populations (summed across all 10 phenotypes) always benefit from increasing the spread of competition within the range considered, with the greatest increases between Competition Types 9 and 10. The average survival of the prey is almost total for all competition types except Types 9 and 10. This is potentially in line with the results for the Webworld model [5], that intraspecific effects should be stronger, however the axes scales on the plots must be emphasised - the decrease in average prey survival at this point is an extremely weak effect. In fact, overall, the nature of the competition distribution appears to have very little impact on the number of surviving prey phenotypes. Between Types 8 and 9 the decrease is negligible, and between Types 9 and 10 the decrease is much greater in each case (such that the new maximum is less than the previous minimum) but still relatively minor overall. Indeed, the average falls by just 0.6% between Types 8 and 10. The prey behaviours do not change much as α increases, indicating that predation is (in this model) a less important consideration than the prey’s own internal dynamics. The only significant change is that the prey population plot shifts upward by 20% between $\alpha = 0$ and $\alpha = 4$, in correspondence with the drop in predator populations. Thereafter, prey populations show minor uniform increases as α increases further.

Predator phenotype “survival” (in this scenario, more accurately described as the probability of the single predator species surviving across the parameter space) and population size both follow much more interesting trends that are dependent on the degree of adaptive foraging utilised. When there is no adaptive foraging ($\alpha = 0$), the shape of both the predator survival and population graphs are almost identical to each other and that of the total prey populations. Both increase monotonically with competition type and the increase is greatest at the final step where competition spread is greatest. However, for low levels of adaptive foraging ($\alpha \in \{1, 2\}$, shown in the supplementary material: Fig. 1), the increase is still typically monotonic until Competition Type 8 where it rapidly begins to drop. For larger α , there is relatively little correlation between predator properties and prey competition distribution. For all finite α , these properties also show little variation with P_1 . However at $\alpha = \infty$, where the predator only consumes the prey that is most populous at that time step, there is significant variation with initial condition - the greatest range of values being obtained when competition is solely within the phenotype (Competition Type 0). Overall the relationship between both predator properties and the degree of prey competition dispersal changes from positive at $\alpha = 0$ to negative at $\alpha = \infty$, with regard to the shape of the graph. Considering the values themselves, the predator properties display the following trends: both probability of survival and population size increase slightly between $\alpha = 0$ and $\alpha = 1$, and then decrease monotonically in maximum, minimum and average as α increases from 1 to 10. For predator survival, between $\alpha = 10$ and $\alpha = 15$ the pattern reverses for the maximum trendline, which increases thereafter. The minimum values fluctuate, showing no clear pattern, however the disparity between values (that is, the influence of initial predator population size) increases with further increasing α . For the predator population, the decrease across competition types slows between $\alpha = 15$ and $\alpha = 20$, and similarly the discrepancy between minimum and maximum values grows from there.

Next we take the average values (the red middle lines) and superimpose them at $\alpha = 0, 4, 7, 20, \infty$. This is shown in Fig. 2.

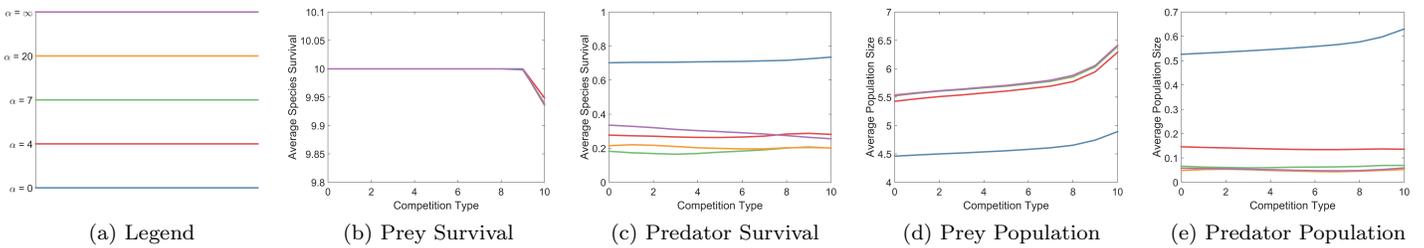


Figure 2: Variation of properties for $\alpha = 0, 4, 7, 20, \infty$ with Competition Type

From Fig. 2, it appears that out of $\alpha \in \{0, 4, 7, 20, \infty\}$, choosing $\alpha = 0$ is by far the best predator strategy no matter what kind of competition the prey phenotypes are experiencing. When put in perspective, variation in competition type has relatively little effect when averaged across the (c, p) -space and initial conditions, with the exception of Types 9 and 10 impacting prey survival negatively and prey population positively, both to a very small degree. Therefore, for each value of α we can justifiably average these averages again - this time across all 11 Competition Types - and then plot them as a function of increasing α . The results of this procedure are displayed in Fig. 3.

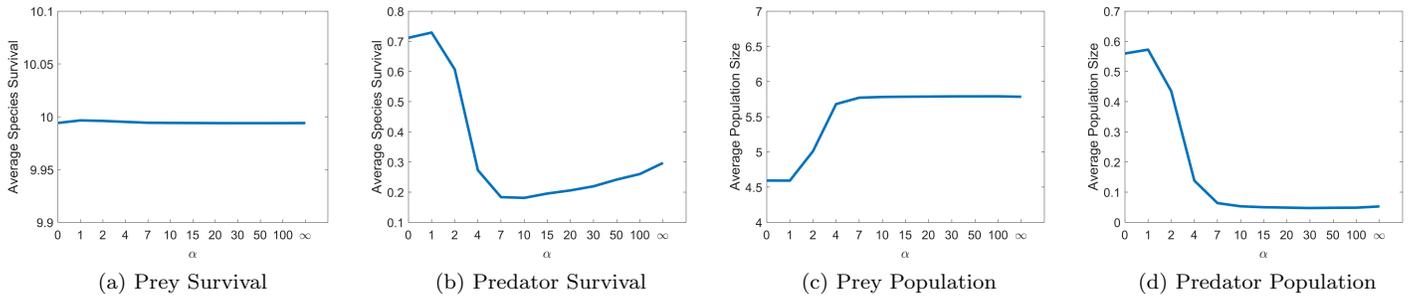


Figure 3: Variation of average properties (across Competition Types) with α for One Non-Mutating Predator

From these plots we can see the following effects of α : as α increases prey species survival is barely affected, however the prey population moderately increases (by approximately 25%) and quickly plateaus, in correspondence to the inverse trend suffered by the probability of predator survival which greatly and swiftly decreases from approximately 0.7 to 0.2. The predator population also mirrors the prey population's increase in its significant decline between $\alpha = 1$ and $\alpha = 7$. The main outcome of increasing α beyond 10 is to slightly improve the predator's survival chance, but this does not appear to influence the predator's population. Although $\alpha = 0$ is still a very good strategy, it is $\alpha = 1$ (a linear degree of adaptive foraging) that permits both the greatest average population and probability of survival out of the full range considered ($\{0, 1, 2, 4, 7, 10, 15, 20, 30, 50, 100, \infty\}$) when it is the only predator phenotype present in the environment.

3.2. One Mutating Predator: $\alpha = 0$

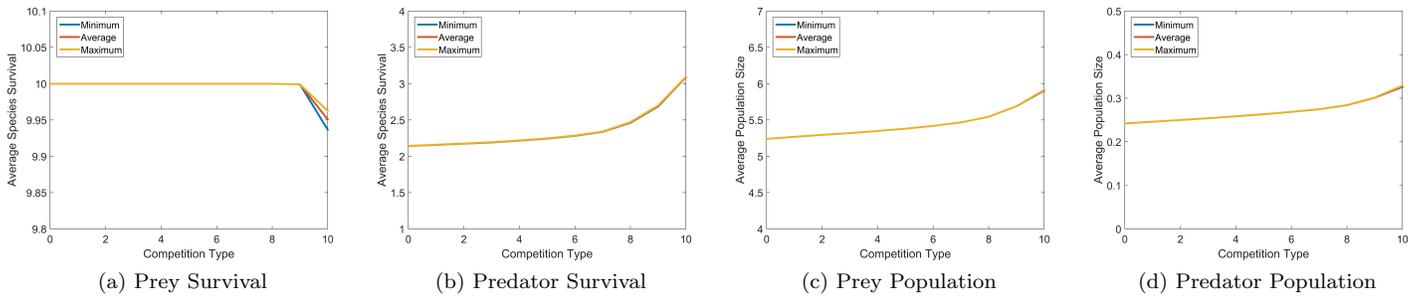


Figure 4: One Mutating Predator, $\alpha = 0$

Consider now the scenarios introducing one mutating predator with $\alpha = 0$. In this case, total prey and predator populations are monotonically increasing functions of the degree to which prey competition intensity is spread amongst neighbouring phenotypes. The same is true of the average number of surviving predator phenotypes. Similar to all of the previous cases, the average prey survival follows a very different trend, remaining near constant (and maximal) throughout until close to the point at which intraspecific competition is equal in strength with interspecific competition between nearest neighbours, at which point there is a drop.

3.3. One Mutating Predator: $\alpha = 9$

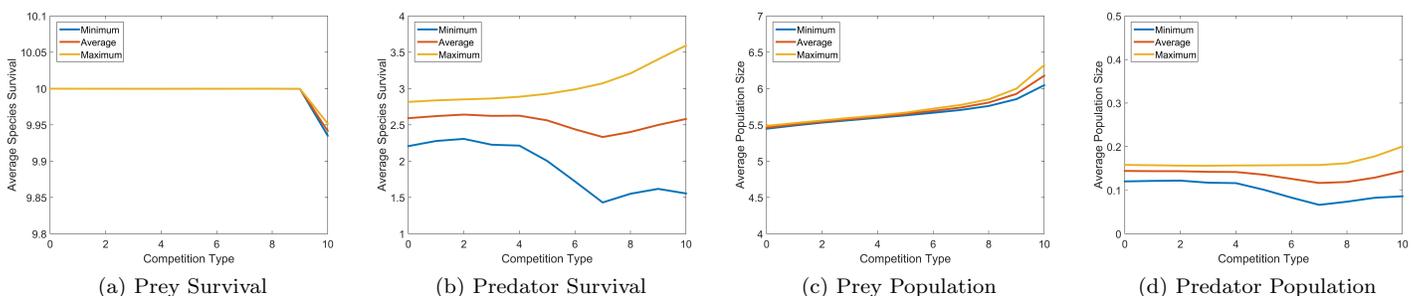


Figure 5: One Mutating Predator, $\alpha = 9$

If instead it is the tenth predator that is initially introduced at the 10,001st time step, there are unexpected consequences. Although the maximum trendlines for predator survival and population are similar in shape to those where it is the first predator ($\alpha = 0$) that is introduced (Fig. 4), the survival line has been translated to higher values whilst the population line has significantly reduced values. Furthermore, the average trendlines are no longer monotonic and diverge significantly from the maximum. The minimum trendlines for both properties reach a minimum at Competition Type 7, showing very different patterns to the monotonic increase seen for the previous scenario. Simulation results for different initial populations show that when the first predator is the one initially introduced, the population size with which it is introduced is relatively inconsequential. However, when the tenth predator is instead the invader, the simulation's final state is in fact very sensitive to its initial population size - and this dependence appears to generally increase with competition type (the trendlines diverge). We also note that the total predator population is reduced by approximately 30% for every competition type, compared to introducing the first predator.

3.4. Ten Non-Mutating Predators

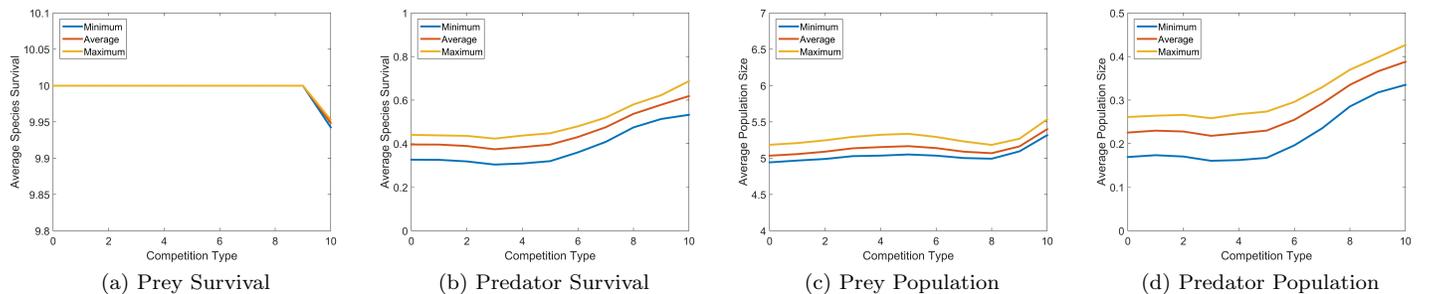


Figure 6: Ten Non-Mutating Predators

The results for Ten Non-Mutating Predators (Fig. 6) follow broadly similar trends, with the average number of surviving predator phenotypes, total prey population and total predator population all generally increasing as the prey competition strength becomes more evenly distributed. However there is now substantially greater variation resulting from the initial predator population sizes - at least, there is greater variation than the case of Ten Mutating Predators (not shown) or of starting with only predator #1 (Fig. 4). This is to be expected, as the inability of the predators to mutate will prevent the system from recovering from the effects of major perturbations that cause extinctions which, if the predators could mutate, would be merely transient phenomena. This constrains the overall predator populations and their preferred final distributions, which then affects final prey populations. Similarly, although the predator survival graph is of similar shape to that of previous scenarios, it is shifted down to substantially lower values. Intuitively, we would expect enabling mutation to improve the possibility of survival, for the reasoning outlined above, and this appears to be validated on average.

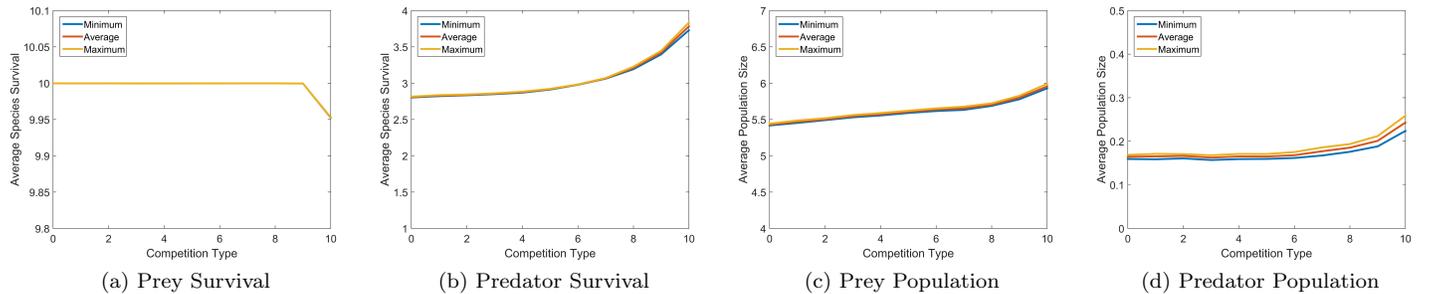


Figure 7: Ten Mutating Predators

Finally, let us consider the case of Ten Mutating Predators (Fig. 7). As we can see, the shape of the plots are similar to those given by previous scenarios, and we note that out of the other scenarios considered, the values assumed by these plots match closest to the maximal lines for One Mutating Predator (#10). The dependence on P_1 that existed in that case (i.e. the divergence of the three plot lines in Fig. 5) is not strongly present here.

4. Results - Feigenbaum Diagrams

We present Feigenbaum diagrams from a selection of eight different competition types: 0, 1, 2, 4, 6, 8, 9, 10. These are produced by considering 10,000 increments of p in $(0, 0.5]$ or c in $(0, 6]$. For each value, the simulation is run for 1,200,000 iterations,

with predators introduced at the 10,001st time step when applicable, and the bifurcation diagrams show the final 100 iterations - that is, time steps 1,190,901-1,200,000. Furthermore, in the case of 10-prey and no predators, we calculate the characteristic Lyapunov exponent of the system. This is determined over 1,000,000 iterations following 100,000 transients, using a version of the Householder QR-decomposition method [29].

First, the legends (Fig. 8). These are divided according to (a) the case of only prey being considered, and (b) all other cases, where predators are also featured:

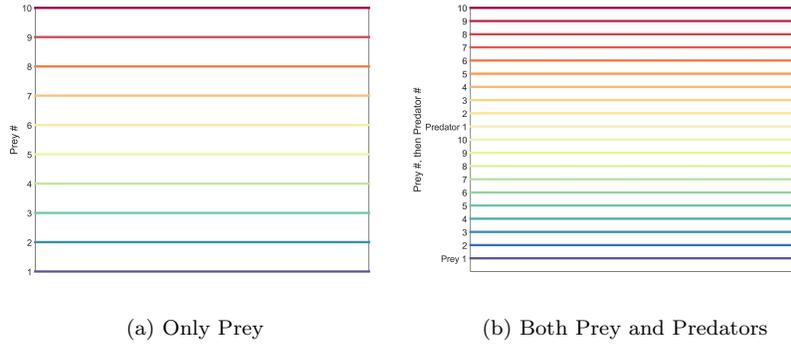


Figure 8: Feigenbaum Diagram Legend

4.1. Varying p , fix $c = 2.0$

4.1.1. No Predators

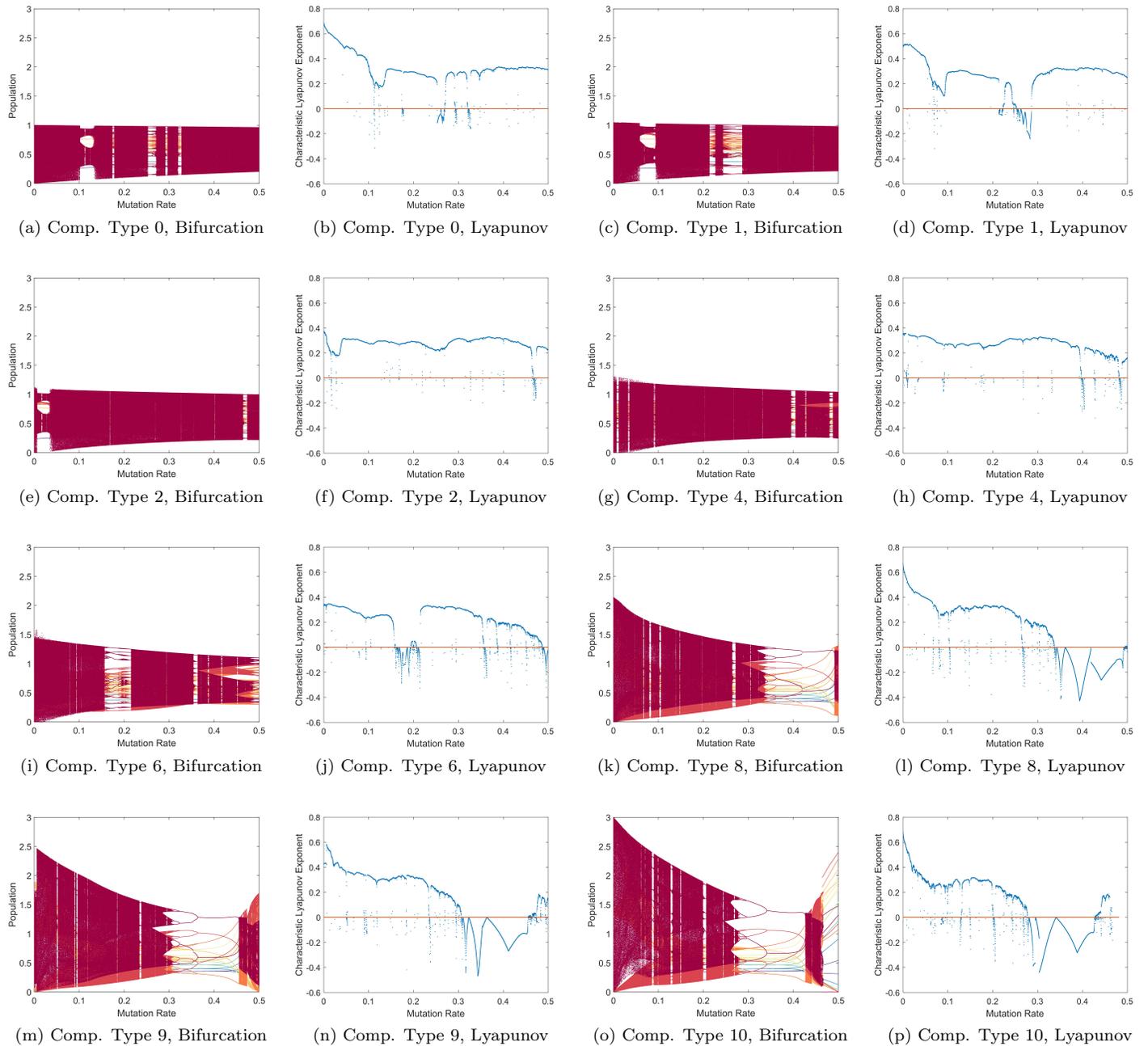


Figure 9: No Predators, varying p .

As competition type increases, the range of population sizes achieved (most notably at $p = 0$) increases monotonically (Fig. 9). This makes sense, as intraspecific competition is monotonically decreasing - allowing larger populations to be reached when neighbours are not present. Phenotypes #8 and #10 reach the highest population sizes, suppressing phenotype #9 between them, achieving these values for $p < 0.1$. In this range of p , this suppression of alternate phenotypes occurs more generally - for example, at Competition Type 10 there is a clear separation of behaviours in this region, with phenotypes 2, 4, 6, 8 and 10 tending to higher values than the oddly-numbered species whose populations tend to zero as $p \rightarrow 0$. Within these groups, the maximum values are ordered by r -value. However, note that there could theoretically be situations of neighbouring phenotypes both achieving very large values on a bifurcation diagram provided they were alternating each iteration.

In the range considered, inverse period doubling is observed as p increases, until a critical value is reached where forward period doubling begins again. This critical value of p is beyond the observed range for Competition Type 0-6, becoming visible and with value decreasing with Competition Type for Competition Type 8-10. For Competition Type 1, in the two bifurcation

windows in close proximity to $p = 0.25$, there is an example of bifurcation phenomena for prey phenotype #10. Namely, period doubling in one window followed immediately by inverse period doubling in the subsequent window - together, this is known as period-bubbling. It is clear from a closer inspection that at least phenotypes #8 and #9 are also doing this in the same space. This is also well-demonstrated in Competition Type 6 (Fig. 9(i)).

These Feigenbaum diagrams show that changing the Competition Type in the range 0-6 is having a substantial effect on the prey dynamics, despite the survival and total population plots showing relatively little change in global behaviour. Note that it appears as though increasing Competition Type is pulling the diagram to the left in a sense - as Competition Type increases, regions of behaviour enter from high c and move to progressively lower values. We also clearly observe that the ten phenotypes experience chaotic synchronisation, despite each possessing a unique r -value, due to their coupling interactions.

4.1.2. Ten Non-Mutating Predators

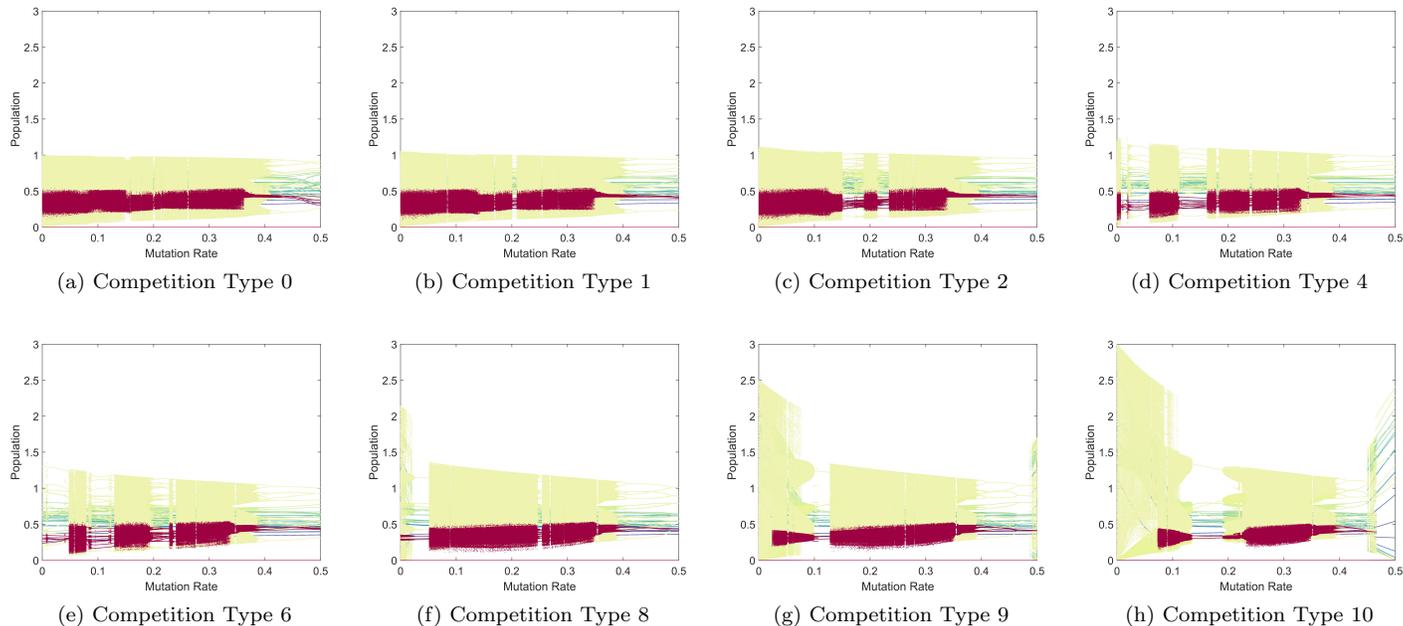


Figure 10: Ten Non-Mutating Predators, varying p , $c = 2.0$ fixed.

The introduction of predators induces a number of changes to the bifurcations structure (Fig.10). At $c = 2$, only the most focused predator (#10) is surviving, but it is enough to alter the prey dynamics from chaotic (and covering a wide range) to periodic and within a much narrower range for some values of p - for example, $p < 0.05$ for Competition Type 6 and $0.13 < p < 0.19$ for Competition Type 10. This predator also synchronises with the prey phenotypes - its bifurcation structure seems to mirror that of the multiple prey phenotypes - despite being only indirectly governed by the logistic map and being coupled in a qualitatively distinct manner to the rest of the maps.

4.1.3. Ten Mutating Predators

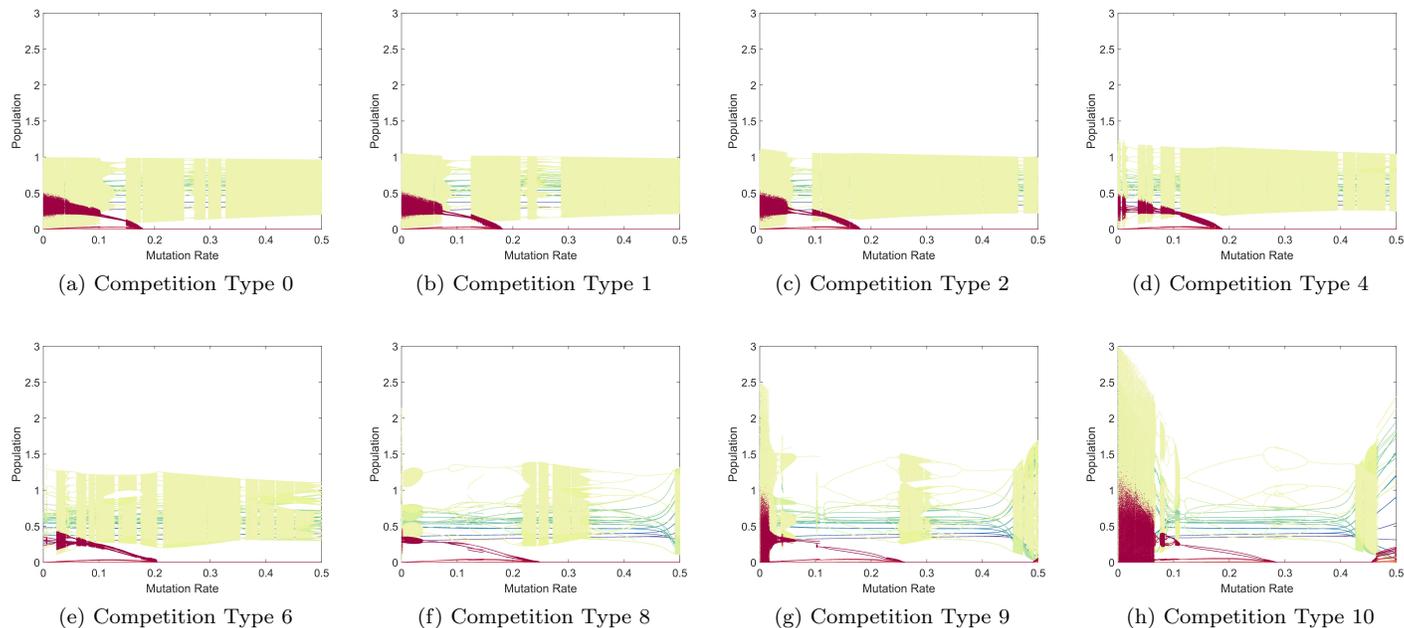


Figure 11: Ten Mutating Predators, varying p , $c = 2.0$ fixed.

Enabling mutation between predators (using the same scheme as the prey) causes further changes (Fig. 11). At $c = 2$, only the top three predators are surviving, and even then only when the rate of mutation is sufficiently low (or, in the case of Competition Type 10, sufficiently high) and #8 has an extremely low population. When there was only one possible predator, it flourished most when it had $\alpha = 0$, so it is interesting that for this choice of c (and thus, one suspects, for all of the transition regions from no predator survival) in a competitive environment with multiple predators it is the phenotypes of highest α that are most successful. Again, for some ranges of p the dynamics have changed from chaotic to periodic and vice versa, compared to the case of Ten Non-Mutating Predators.

For Competition Type 9 (Fig. 11(g)), it appears from the bifurcation diagram that at $p = 0.25$ the number of predators surviving falls from three to zero. However, the survival images indicate that there is some survival beyond that point during the last 10,000 iterations. Inspecting the data reveals that at Competition Type 9, the top predator survives throughout to $p = 0.353$ - where the situation alternates every iteration between predators #9 and #10, and #10 only, being alive - albeit with extremely low populations. At $p = 0.354$ the top predator is struggling so much that it cannot succeed in generating the #9 predator every iteration, and by $p = 0.355$ all predators are extinct by the final 100 iterations, and do not survive again until $p = 0.449$.

The bifurcation diagrams of varying c indicate that for larger c the top three predators (#8-10) survive permanently to settled periodic orbits. In this particular instance, phenotypic population sizes in the periodic orbits increase with α . Combined with these observations, it seems that at least in the case of mutation, for all varieties of competition amongst the prey, having a larger α is preferable to ensure survival of the predator.

4.2. Varying c , fix $p = 0.25$

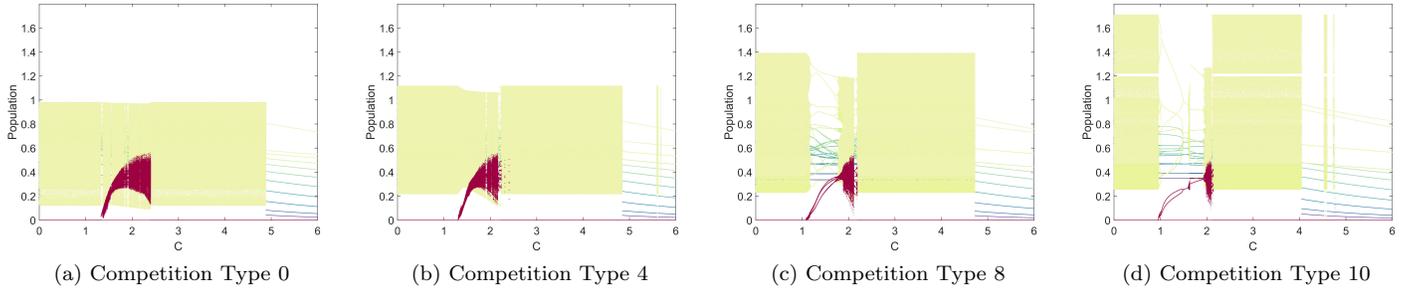


Figure 12: Ten Non-Mutating Predators, varying c , $p = 0.25$ fixed.

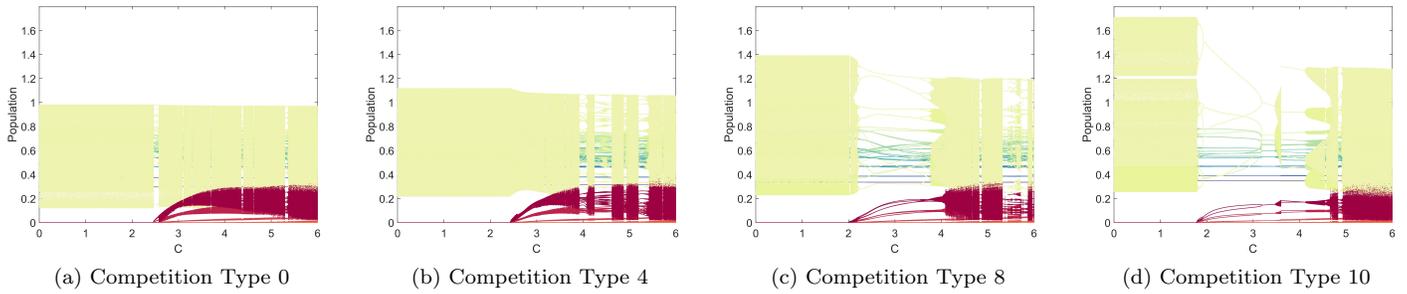


Figure 13: Ten Mutating Predators, varying c , $p = 0.25$ fixed.

Fixing $p = 0.25$ and varying c as the bifurcation parameter, we see that again with mutation enabled we have the possibility of predator phenotype #9 surviving in addition to #10. The synchronisation of the predators with the preys' bifurcation structure in c , just as it was previously with variation of p , is apparent. Comparing Fig. 12 and 13, we see something of the impact of enabling mutation amongst the predators: the range of values attained by the two surviving predators is constrained to lower populations, but the possibility of mutation also enables them to persist in much greater ranges of the parameter than when mutation is disabled. In particular, the predators are able to survive for much larger values of c in this range, and the minimum c that permits survival is also increased. This suggests the following effects of predator mutation: increased number of surviving phenotypes, increased parameter range permitting survival, and decreased individual phenotype subpopulations (likely due to resource competition). This is consistent with the expected effects of mutation described in Section 3. The prey bifurcation structure is also altered, primarily due to how mutation is changing the range of c where the predators are surviving.

5. Results - (c, p) -space of Individual Scenarios, $P_1 = 0.1$

5.1. One Non-Mutating Predator

For Competition Types 0-9, we find that for all values of α all ten prey phenotypes are surviving on average, throughout the (c, p) -space. These results are therefore not shown.

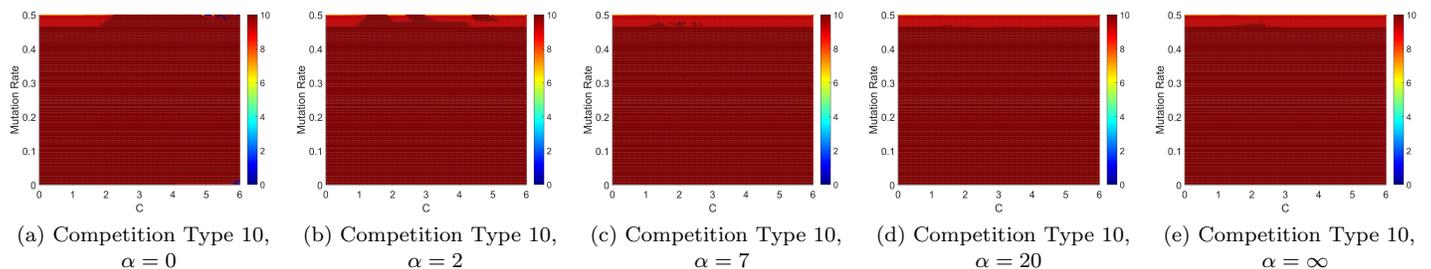


Figure 14: One Non-Mutating Predator: Prey Survival

Considering Competition Type 10 then, these results are given in Fig. 14. For regions within the range $0.47 < p < 0.50$ on average one of the ten prey phenotypes is not surviving, although a closer inspection reveals that within these ranges three of the phenotypes are typically extinct at the edge of the space ($0.495 < p$), and there is the possibility of total extinction at high c for $\alpha = 0$. In the corresponding prey-only bifurcation diagram (Fig. 9(o)), it can be observed that some of the periodic points in the orbits of the prey phenotypes are approaching small population sizes at large p , and at least one phenotype is visiting 0 during its orbit. Indeed, at $p = 0.5$, prey 5-10 are all observed from the data to visit 0, alternating such that prey 5, 7, 9 and 10 are extinct in one iteration, with 6, 8 and 10 extinct in the following iteration, and then they are repopulated whilst prey 7 and 9 instead go extinct in the next after that. Therefore the average extinction of one phenotype in this range of p is not necessarily related to the introduction of predation (indeed, c has relatively minor effect on the structure of this region), and it appears to be simply a consequence of the structure of the coupled logistic map's Feigenbaum diagrams extending to regions of very high and very small values. The choice of α does affect the exact boundary of the region of suppressed survival, but the dependency is minimal. The only other occurrence of incomplete prey survival is for Competition Type 10, $\alpha = 0$, where on average one extinction occurs for $4 < c < 5.8$ and very low p , and complete prey extinction is possible in $5.8 < c < 6$, $p < 0.01$, where feeding rates are very high and mutation may be too weak to quickly repopulate an extinct prey phenotype.

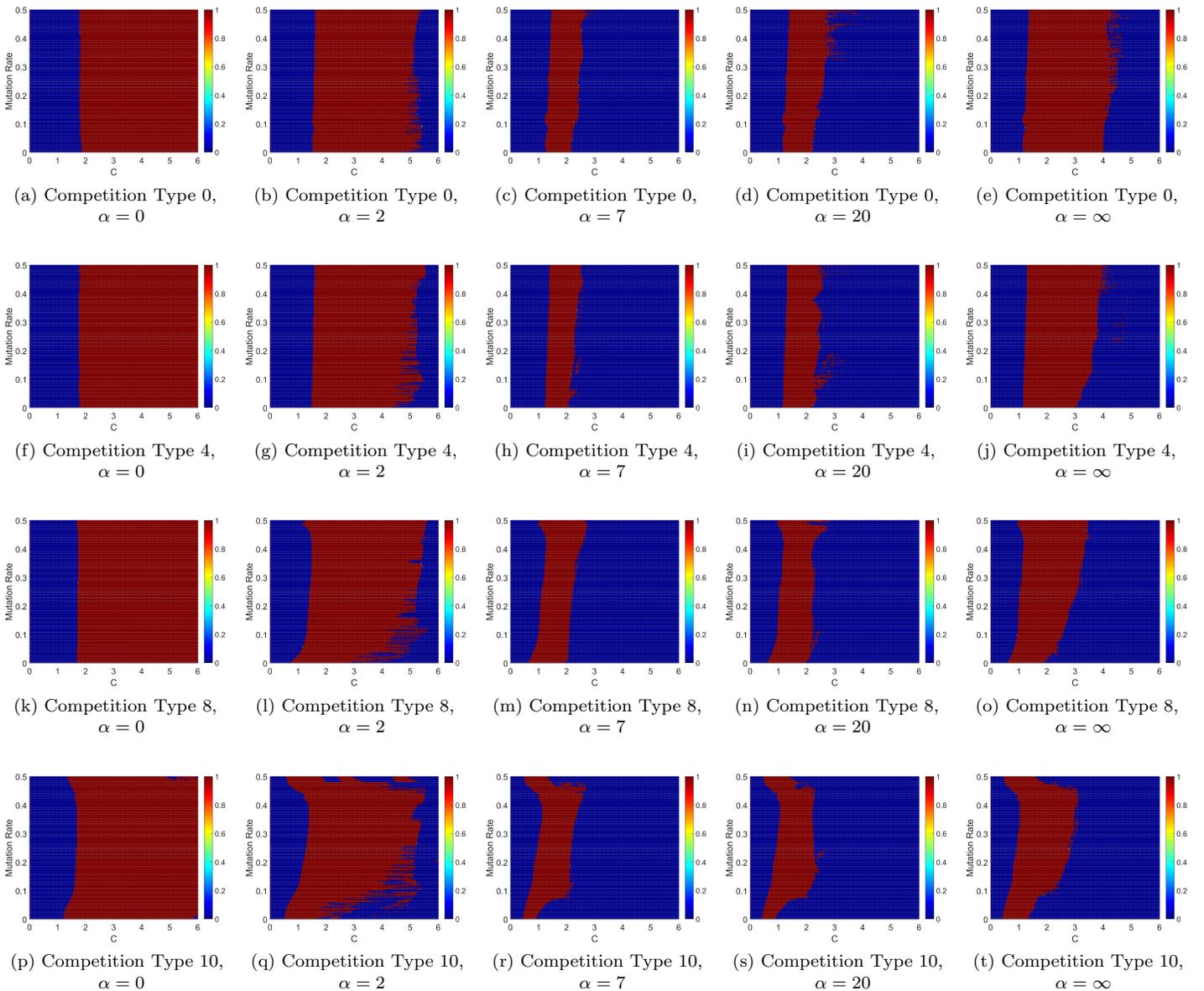


Figure 15: One Non-Mutating Predator: Predator Survival

For predator survival (Fig. 15), let us first consider Competition Type 0. For $\alpha \in \{0, 1\}$, once the predator exists (in terms of minimum c) it exists for all greater c in the considered range. However, for $\alpha = 2$ and higher there is an upper limit less than 6 on the value of c that permits the existence of the predator. This upper limit decreases for $\alpha = 4$, and again for $\alpha = 7$. There appears to be no further compression of the column of predator survival between $\alpha = 7$ and 10, and indeed by 10 a new

trend is beginning to emerge: at the top of the column (high p) the column begins to “streak” into higher c . As α increases further, this streaking extends to higher values of c and fills downward to lower p , so that by $\alpha = 100$ it exists for $p > 0.17$ and reaches $c = 4.5$ but with a very non-smooth boundary. We expect that this process continues to fill down to the right of the column as α increases further, as by $\alpha = \infty$ the whole p -range is filled again for $1.3 < c < 4.1$. We also observe (for all Competition Types) that the column of predator survival shifts slightly to the left, beginning at lower values of c , as α increases.

This streaking pattern in α is not so clear for larger Competition Types, but it still appears from the curvature of the regions of survival that when the trend reverses, it does so primarily from the larger values of p . Inspecting Competition Type 6 suggests it happens simultaneously at particularly high and low p -values in that instance. The boundary of maximum c for survival is often non-smooth, particularly at low values of α . Furthermore, as Competition Type increases, the curvature in the boundaries of the predator survival region increases. For all α shown, the lower bound in c becomes increasingly concave, as does a large intermediate section of the upper bound in c for the range $4 < \alpha < 30$. In addition, for all $\alpha > 0$ it is visible that the upper bound in c notably decreases at the extremes of high and low p .

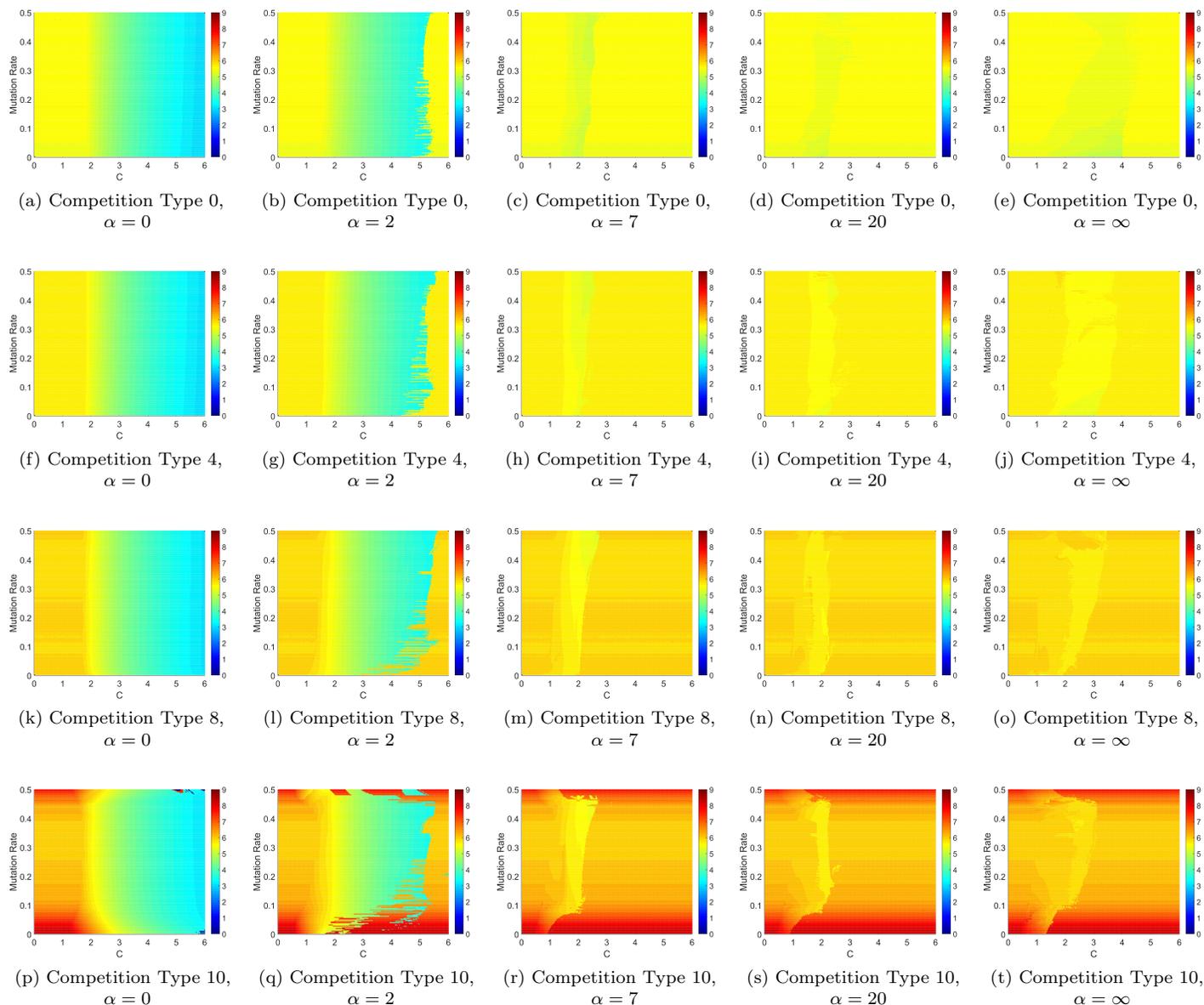


Figure 16: One Non-Mutating Predator: Prey Population

We next consider the effect of α and prey competition on the summed populations of the prey and predator phenotypes. Although average prey phenotype survival is completely indifferent to predation, with the minor exceptions noted above, the total prey population size (Fig. 16) does mirror the region of predator survival. When c has increased to the necessary threshold, the total prey population monotonically decreases as c increases further within this region of predator survival. Uniquely for Competition Type 10, in regions where the predators die out, the total prey populations are maximised at the extremes of p .

A note here regarding the influence of predation on the distribution of the prey. We observe that when α is low, prey expectation increases in the regions of predator survival, indicating that on average the lower r -valued phenotypes are particularly affected. This even occurs for the full range of p in the case of only intraspecific competition and when only the non-mutating predator with $\alpha = 0$ is present (Supplementary material, Fig. 15(e)) - ruling out the explanation of mutation and interspecific competition causing an alternating ordering of prey subpopulations (as discussed in Section 2). Rather, the prey with higher r values do indeed have higher populations when no predators are present (the expectation is still greater than 6 the predators are absent), and thus when a low- α predator is introduced it affects all of the prey populations equally, causing the low- r , low-population prey phenotypes to suffer a proportionally greater decrease in absolute population size. Conversely, when a more focused predator is introduced, they consume prey with high r and thus higher subpopulations, causing the prey expectation to decrease in regions of predator survival - which we observe, for example, in the case of Competition Type 0, $\alpha = \infty$ (Supplementary material, Fig. 37(e)) although the effect is much less pronounced due to the lower populations of high- α predators (Fig. 3(d)).

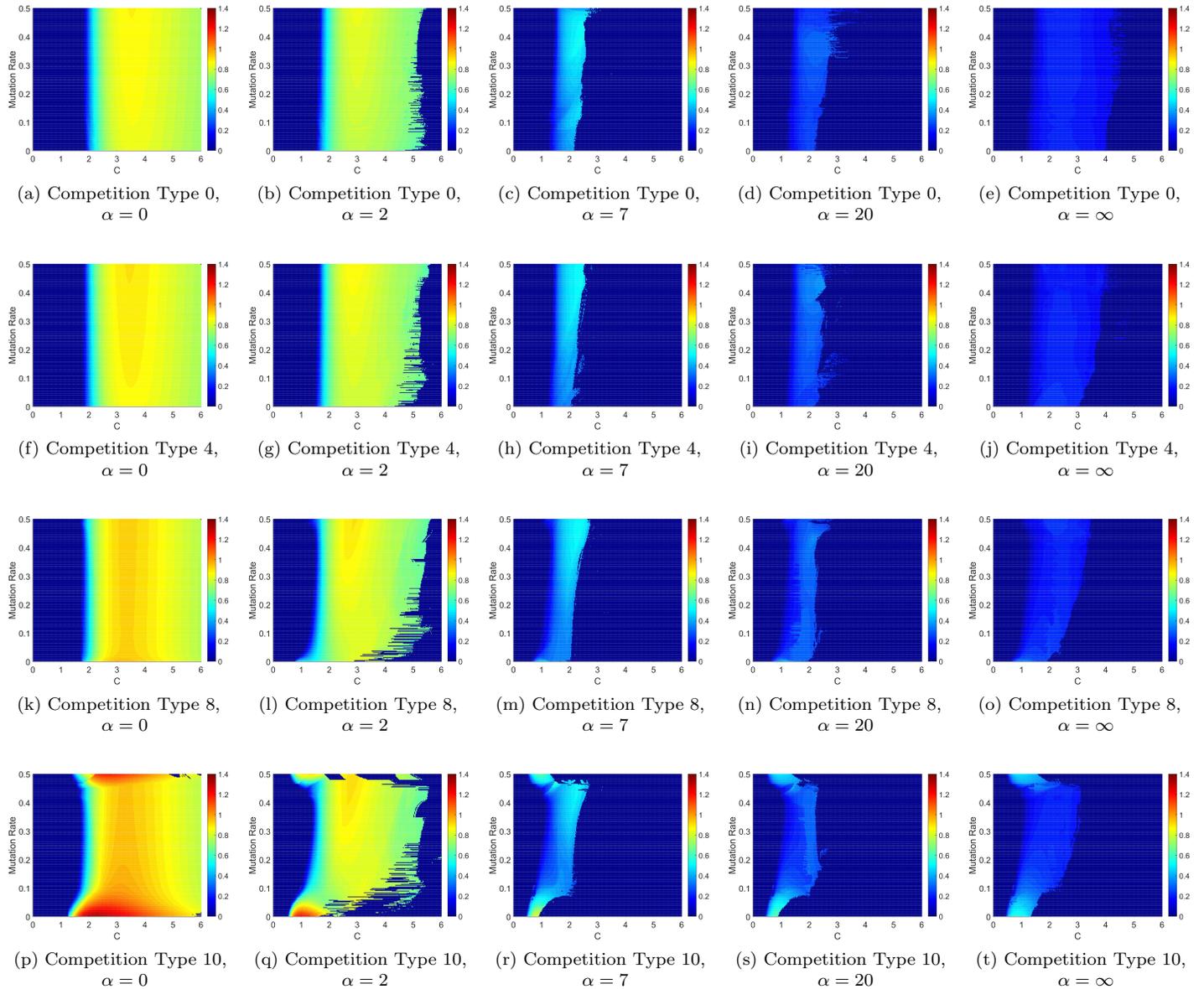


Figure 17: One Non-Mutating Predator: Predator Population

Again, first consider Competition Type 0. As c increases, the predator population (Fig. 17) increases to a maximum for c approximately 3-4, then decreases slightly and stabilises. This does not fully match the pattern of the prey population, which decreases monotonically with increasing c . Instead the sole predator phenotype finds an optimal intermediate value of c within the survival region. This is not surprising as although increased c benefits the predator by allowing it to reproduce faster, it also causes each individual to kill more prey and thus lower populations can be sustained. As α increases past 2, this maximum value

of the predator population decreases monotonically with α .

In general, as with species survival, the behaviour and trends for total predator populations are qualitatively similar across most Competition Types 0-8. In all cases, an upper limit of c for predator survival enters the considered range at $\alpha = 2$, and the population is maximised at an intermediate value of c . However, some changes are beginning to occur at Competition Type 9, and are fully realised at the point of changing to Competition Type 10 (where intraspecific competition is no longer stronger). The population is still reduced if c is too low or too high within the survival region for most α . However, there is now a significant dependence on p , with the population greatest at the extremes of high and low p where the predator is not extinct. These peaks can also be seen entering the considered parameter space for Competition Type 8 with larger values of α .

5.2. One Mutating Predator with $\alpha = 0$ (#1)

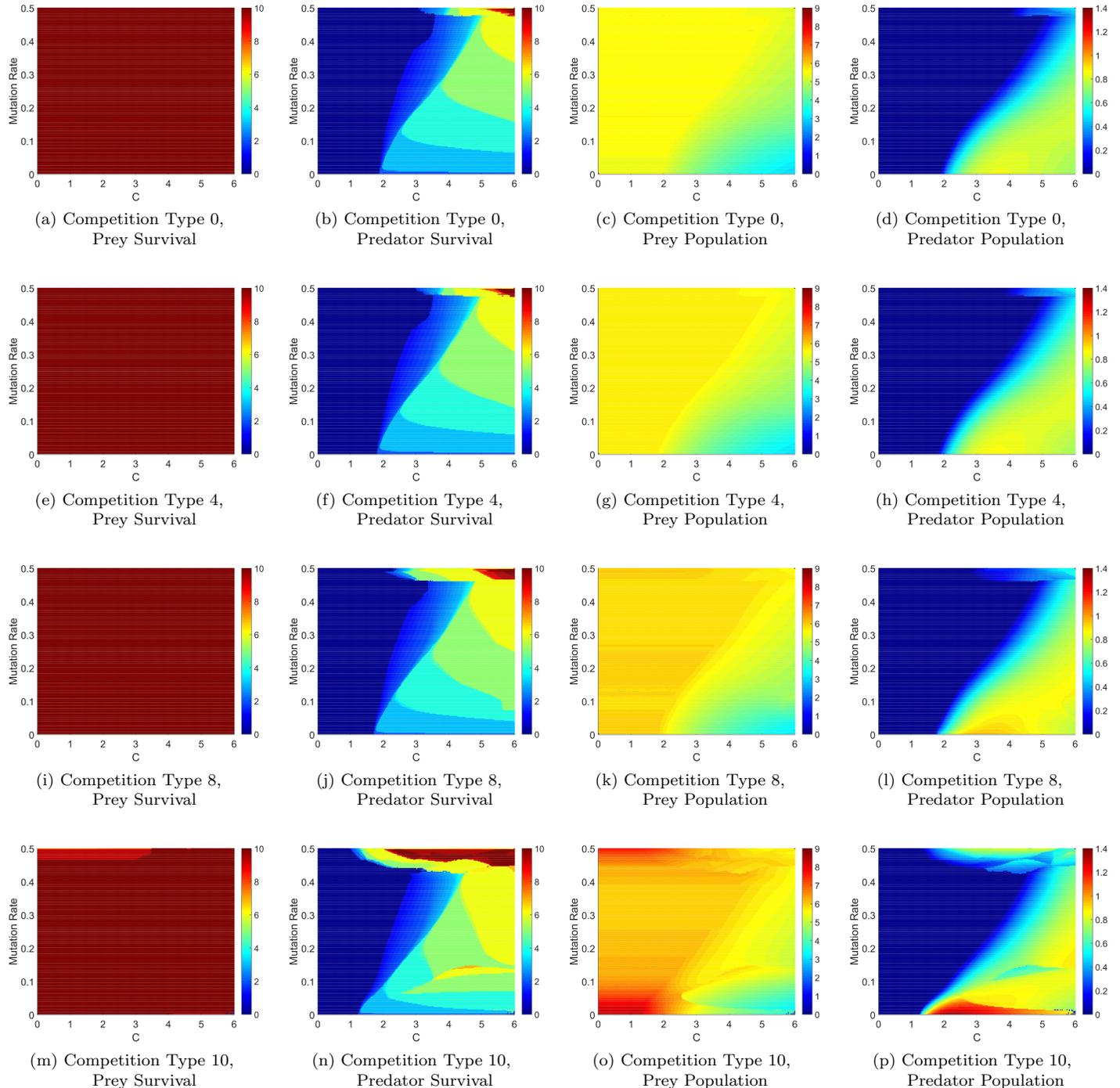


Figure 18: One Mutating Predator ($\alpha = 0$)

Now we return to the scenario where the predator with $\alpha = 0$ is introduced, but mutation along the predator lattice is enabled (with the same p), thus allowing the presence of multiple predator phenotypes. Once again, all ten prey phenotypes always survive except for Competition Type 10 where in a subset of $0.47 < p < 0.5$, $0 < c < 4.5$ on average only nine phenotypes persist, and similarly for high c and extremely low values of p ($0 < p < 0.01$). Total extinction is also possible in the latter region, but the occurrence of this is negligible. For all other Competition Types, the total prey population decreases monotonically with increasing c and decreasing p within the region of predator survival. This means that, just as before, the prey populations do not mirror the fact that predator populations are maximised at a lower value of c than this, and the reasoning is the same as in the previous scenario. For Competition Type 10, as we would expect, in the regions where the predator has died out the space displays the same trends that occurred in the previous scenario when the single non-mutating predator went extinct, with prey populations now separated along the p -axis and maximised at the extremes of high and low p . In this scenario, prey expectation tends to increase (from 6 towards 7) as c increases and p decreases, coinciding with the survival of predators and their increasing populations. By considering the predator expectation (Supplementary material, Fig. 207(f)), we see that within the main region of predator survival (i.e. discounting the distinct region that occurs for $p > 0.46$) the predator population is overwhelmingly weighted towards low- α . Thus, there is consistency with the results of Section 5.1, where we saw that low- α predation increases the prey expectation, whilst high- α predation lowers it. Here, the full range of effects are occurring simultaneously, but the former trend dominates due to the proportion of low- α predator phenotypes.

As before, for all values of p , there is a minimum threshold of c where predator survival begins, and we infer from the Feigenbaum diagrams of other scenarios (Ten Non-Mutating Predators and Ten Mutating Predators) in the previous section that it is the highest α predators which exist first in these transition regions where 1-2 phenotypes survive. This threshold increases smoothly with p , although it decreases again at very high p as the boundary curves back on itself at a non-differentiable point, due to an intersection with a distinct region of survival that exists at high p (approximately $0.45 < p < 0.50$). We note that allowing mutation still allows predator survival at least as far as $c = 6$, likely because predator #1 is present (which, as we saw in Fig. 15, was the only phenotype that on its own could survive for such large c). However the lower bound of predator survival has increased, particularly for high p , compared to the scenario of introducing the same predator without the possibility of mutation. In this case, indirect competition between predator phenotypes is sufficiently strong to drive the whole species to extinction, without consuming all of the prey who are therefore able to fully recover by the 100,000th iteration. Thus, the possibility of mutation and changing hunting strategy is not necessarily beneficial to the predator for all parameter choices.

Within the region of survival (excluding the distinct region at high p), the total predator population typically increases with increasing c and decreasing p (although it is maximised at minimum p and intermediate c), but the average number of surviving predator phenotypes increases with increasing c and p . As previously stated, by examining expectation, we see that the predators are very strongly weighted towards the lower end (phenotype #1, the least focused hunter, in particular) in the entire primary region of survival. It is only in the distinct upper region of large p where the expectation becomes much more varied. At Competition Type 10, changes in total population are much more extreme, with the total predator population rising steeply at very low values of p .

Finally, we note that as interspecific prey competition grows, the smoothness of the trends in both prey and predator population is hampered by a new artefact: as Competition Type increases to 8 and beyond a region of suppressed prey and predator populations for approx $0.05 < p < 0.1$ enters the visible range from high c , and by Competition Type 10 it has become a significant feature that begins at $c \approx 2.6$. It appears that predator phenotype #2 totally dominates in this region, which is not clearly visible in any other scenario. However, there are disturbances in the region of high- c low- p in the One Mutating Predator (#10) (Fig. 19) and Ten Mutating Predators (Fig. 22) scenarios, but it is far from obvious that they evidence the same trend.

5.3. One Mutating Predator with $\alpha = 9$ (#10)

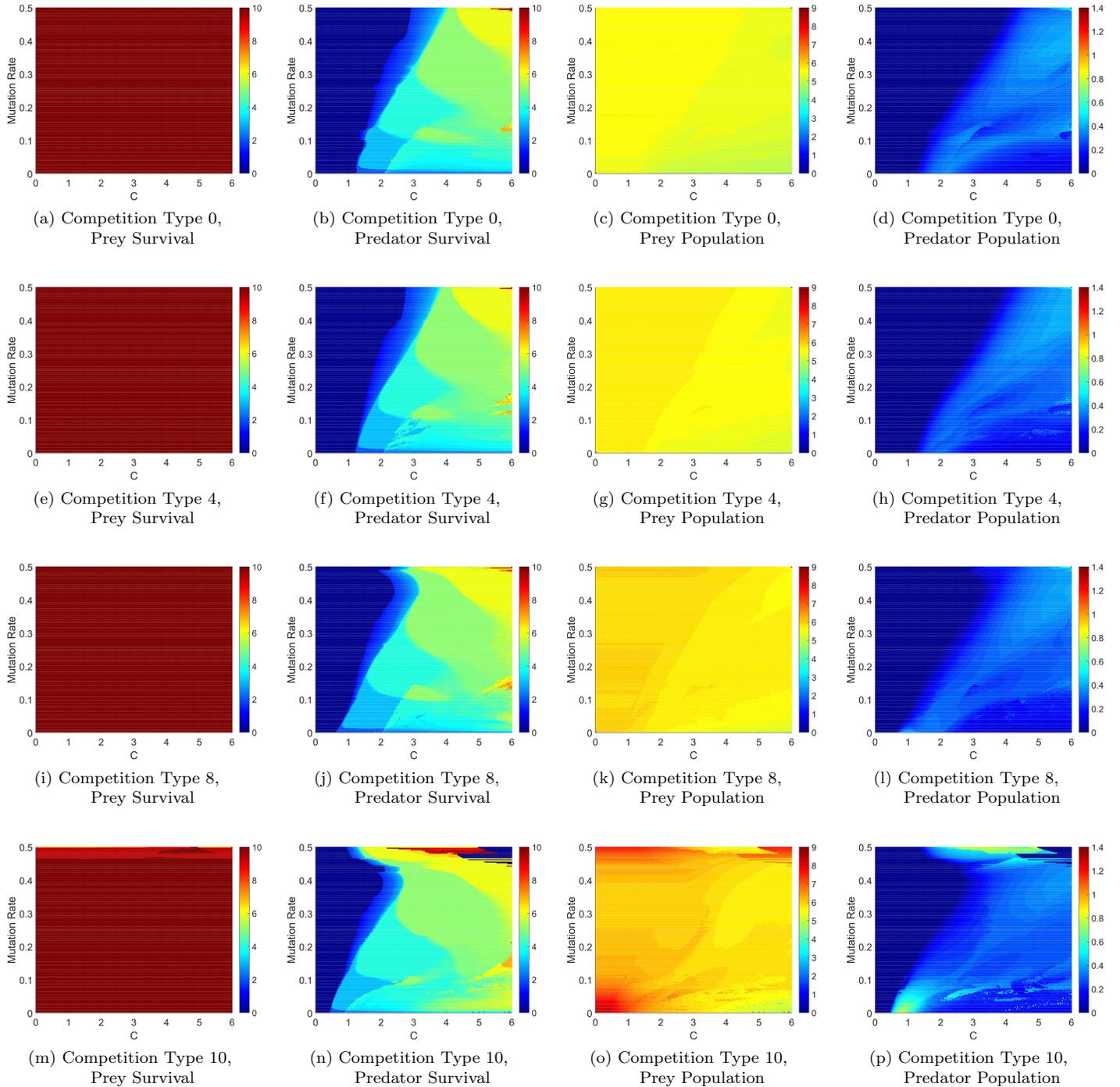


Figure 19: One Mutating Predator ($\alpha = 9$)

These results are broadly similar to the previous scenario, with the exception of the total predator population which is more complicated than before. For Competition Type less than 10 it is maximised at the extremity of high- c high- p , and overall the main area of “large” population is medium to high- c and high to very high- p (but separated from the maximum at the extreme which appears to be the edge of a distinct overlapped region). There is a distinct “central” region of survival at intermediate p where the predator population decreases, but not as much as for medium to high- c and low- p where the total predator population decreases with p and becomes very small. This coincides with a curved overlapping region of increased average survival which is the only significant change to the predator survival plots. The artefact that appeared for high Competition Types in the previous scenario does not obviously occur here. Instead, as Competition Type increases to 8 and above we observe increased curvature (the boundary begins to bend back on itself) of the boundary of minimum c for predator survival, and furthermore regions of very high predator population enter the image (beginning at Competition Type 8 and becoming clearly visible by Competition

Type 9) both at low- c low- p , and high- c , high- p of of the region of predator survival. These are the regions of maximum predator population, similar to what was observed for various values of α at high Competition Type in the scenario of One Non-Mutating predator. However, even the greatest predator populations for this scenario are a significant reduction ($\sim 60\%$) from those achieved in the case of predator #1 being introduced first. This accounts for the other major difference between these scenarios, which is that the total prey population is more robust, decreasing much less than before as c increases and p decreases.

This scenario was investigated solely to determine if the choice of starting predator has any significant effect, by comparing with the previous case of One Mutating Predator #1 and also the later case of Ten Mutating Predators. The results, primarily relating to the patterns of predator population, are closer to that of Ten Mutating Predators than to One Mutating Predator (#1). The conclusion to draw here is that the existence of constant mutation amongst both prey and predators is *not* some sort of equalising mixer that smooths everything out. Indeed, even when predator mutation is present, and after 100,000 iterations, there are clear differences present in the averages of this fully-deterministic system resulting from variation of initial conditions in the predator introduction - that is, introducing the tenth instead of the first predator - and distinctions are visible even for very high rates of mutation ($0.4 < p$). In particular, compare Competition Type 10 for One Mutating Predator(#1) (Fig. 18 (m)-(p)), One Mutating Predator(#10) (Fig. 19 (m)-(p)) and Ten Mutating Predators (Fig. 22 (m)-(p)). The latter two are very clearly similar whilst the first is distinct. This may imply that it is easier to propagate down that lattice than up. That is, starting at #10 will more easily result in predator phenotype #1 being populated than vice versa. This scenario nonetheless retains some differences from Ten Mutating Predators - for example, in that scenario when c is large and p is low, artefacts can occur where predator populations are large but prey populations relatively small, whilst that does not happen in this case.

We therefore examined data for initialising predator #2, 3, \dots , 9 (with $\alpha = 1, 2, \dots, 8$ respectively). The full results are contained in Appendix 4 of the supplementary document. Most trends persist across the full range of initial predators - for example, in all cases the lower bound in c for predator survival at the edges of the range of p (i.e. p close to 0 and close to 0.5) decreases as Competition Type increases. However, the fact that discrepancies persist between the final averaged results, dependent on which predator was first introduced, is far clearer when these intermediate values of α are considered. As we might expect, the images are generally similar across α for sufficiently large p , but even for a highly non-trivial rate of mutation - for example, $p = 0.3$ in the case of Competition Type 2 - strong distinctions remain after many iterations. In particular, two regions of variation should be highlighted. First, in the range between approximately $0.2 < p < 0.38$. Across all competition types, as α changes from 1 to 2 the region of low predator survival vanishes, leaving a transition (at a higher boundary in c) directly from zero to moderate predator survival. This remains the case until the change from $\alpha = 6$ to $\alpha = 7$, where the missing transition region is mostly filled in from above, leaving a smaller gap in $0.2 < p < 0.3$ that does not extend to such high values of c . This is mostly addressed in the change to $\alpha = 8$, leaving only a small discontinuity that is smoothed over by the final scenario of $\alpha = 9$. The second feature is the region which lies beneath the previous one, mainly within the range $0.1 < p < 0.2$, which for $\alpha = 0, 9$ was visible as little more than an discontinuity primarily noticeable in Competition Type 10. We see from the additional images that when introducing a predator of intermediate α this expands in p to create a new region of high (but not maximal) predator survival, reaching a maximal area at $\alpha = 5$ and then reducing again so that it is barely visible (and has large predator survival only at the upper bound of the region in c) by $\alpha = 9$. Both of these trends are represented in the selection, taken at Competition Type 8, shown in Fig. 20.

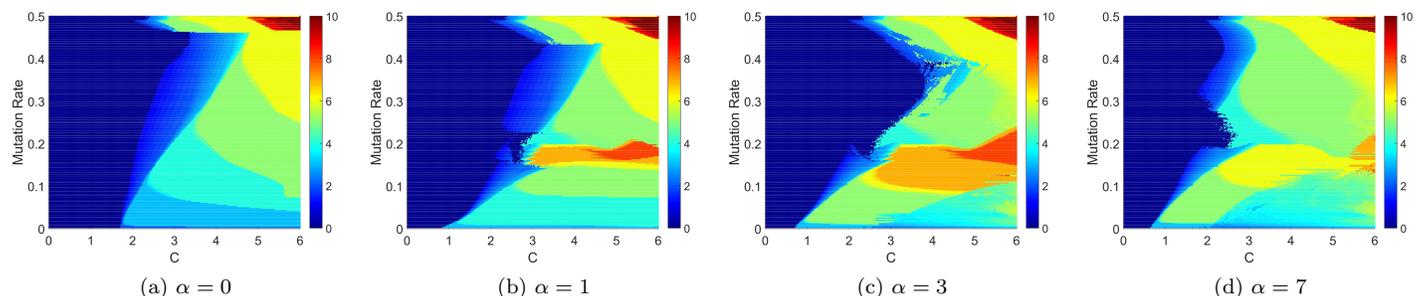


Figure 20: Effect of Initial Predator Phenotype on Predator Survival; One Mutating Predator, Competition Type 8

5.4. Ten Non-Mutating Predators

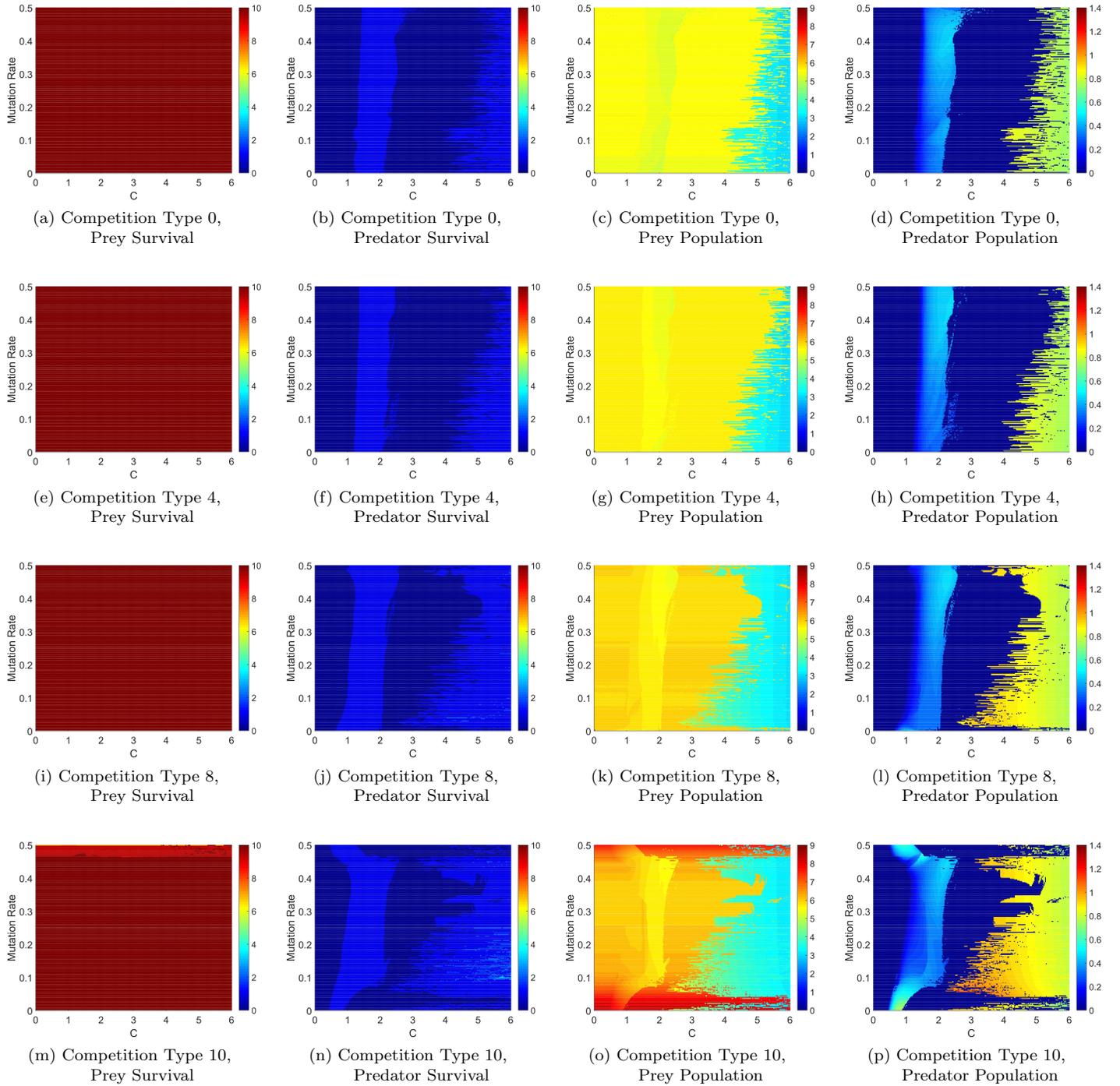


Figure 21: Ten Non-Mutating Predators

In this scenario (Fig. 21), we introduce all ten predators simultaneously (but with a total population equal to that of a single predator introduced in the previous cases) but with predator mutation now disabled. Note the first effect of this - just as in the case of One Non-Mutating predator, p has relatively little effect on the behaviour of the system except at the extremes of p when the Competition Type is 9 or 10, and when we consider the non-smooth boundary of the right-hand region predator survival (which, when we consider the additional tests shown in the supplementary material, is highly dependent on initial conditions including P_1). At most, only one predator phenotype survives, and it survives for two separated columns of p : one of approx $1.2 < c < 2.1$ and a second of roughly $5 < c$. The first column is smooth and better defined in terms of c , and consists entirely of the most focused predator phenotype #10, whereas the second is much more shattered and indistinct but permits a much larger (x2) population throughout. This indistinct region is composed entirely of the least focused predator (#1), which we determine by examining the predator expectation plots in the supplementary material. Note, therefore, that there is an intermediate region

where now no predator species survive, but where if the low- α predators (#1,2) were introduced *alone* (albeit with a larger phenotype-specific population) they would survive. This suggests that predator phenotypes may have inhibiting effects on each other, with indirect competition for resources playing a strong role in determining which phenotypes persist, even though the effect is not due to overpredation simply wiping out the prey, as the prey survive enough to repopulate fully after the predator extinctions. This clearly illustrates the often counter-intuitive and unpredictable responses of nonlinear dynamical systems to perturbations - namely, more is not always better for the predators.

All prey phenotypes survive throughout, except for $0.47 < p$ with Competition Type 10 as usual (Fig. 21(m)), and total prey populations are decreased in correspondence with the total predator populations, with the exception that in the high- c region of predator survival the prey populations decrease more as c increases whilst the predator population is also decreasing - although this effect is very minor. As Competition Type increases, this trend becomes slightly clearer.

Furthermore, as competition type increases, the right-hand (large c) area of predator survival generally solidifies and moves left to begin at lower c . Simultaneously, the lower- c column shifts (both lower and upper bounds) very slightly to the left (toward lower c) as competition type increases. The constituent phenotypes of both regions remain the same throughout, and we discuss this in further detail in Section 6. Similar to previous scenarios, at Types 9-10 the shape of the left column becomes more complex with the sections of lowest and higher p shifting to lower c and with both prey and predators having larger populations at these extremes within the column. Again, however, the predator total populations are qualitatively larger in the right-hand section (more broken and beginning at lower c than ever) than in the left-hand column. Also once again, the prey adopt the new trend of maximum populations occurring at the extremes of p in regions where the predators have gone extinct.

5.5. Ten Mutating Predators

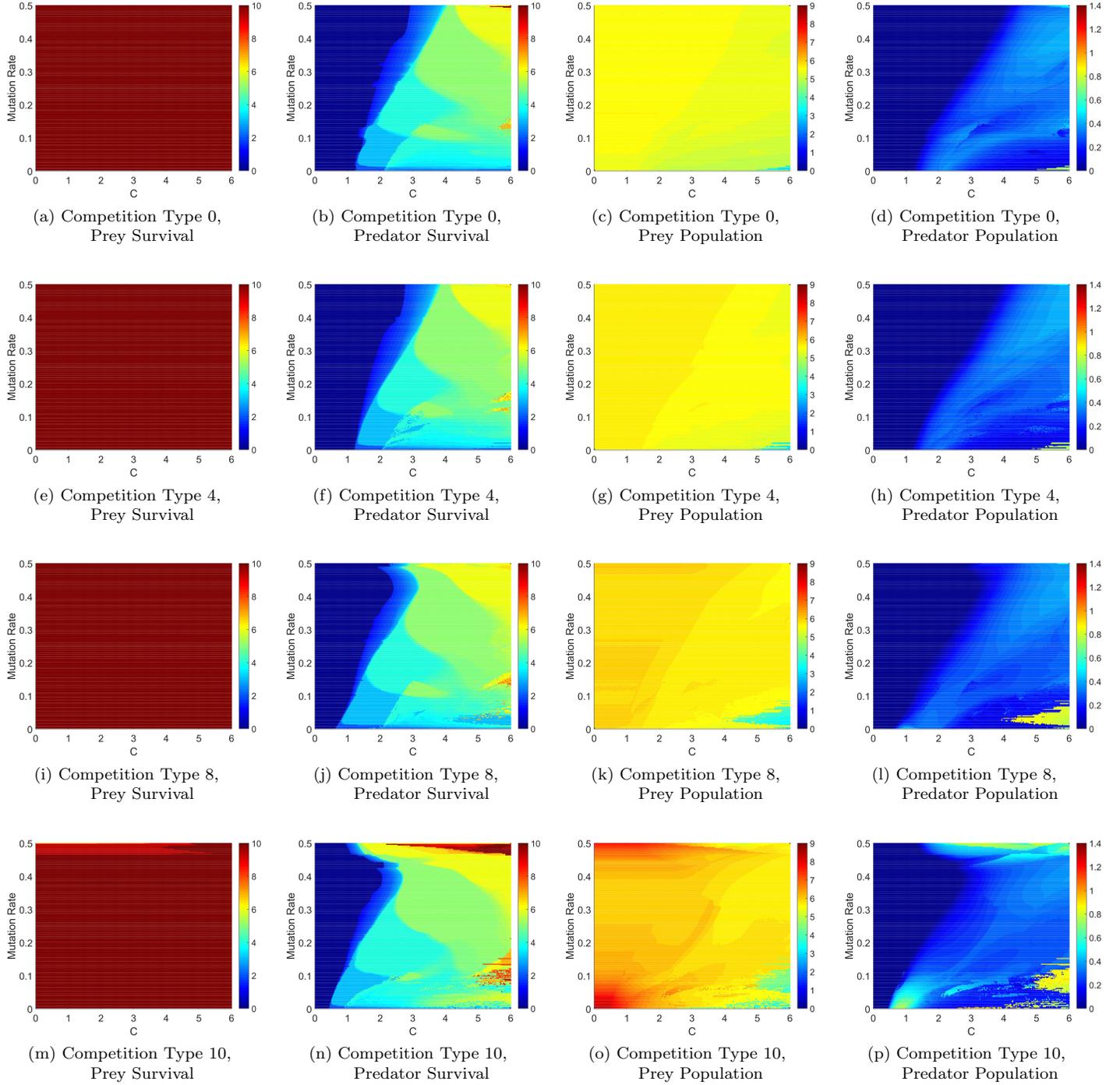


Figure 22: Ten Mutating Predators

As previously stated, the case of introducing Ten Mutating Predators (Fig. 22) is highly similar to that of the single highest- α mutating predator being introduced (Fig. 19). The only major difference is that an artefact of very high predator population (and moderately high predator survival, resulting in the minimal total prey population in the region) has appeared at high c and low p , moving further into the visible parameter space as Competition Type increases. Its highly non-smooth boundary suggests that it too is highly dependent on initial conditions.

6. Discussion

Our results demonstrate that this complex system can in general be very robust for a large range of parameters, but when the cases of Competition Type 10 and $\alpha = \infty$ are considered, the system exhibits rapid changes to pathological cases once

thresholds that exist at the edges of the α -Competition Type parameter space are crossed.

Looking first at the dependence on Competition Type, in all cases, the averaging plots (Fig. 1-7) show that the prey populations increase by between 10 and 20% as the competition varies from fully-intraspecific (Competition Type 0) to evenly-distributed (Competition Type 10). Other changes to survival and population patterns generally begin to show in Types 8 and 9, revealing a gradual change that is complete at Type 10. The bifurcation diagrams with p as the varying parameter (Fig. 9-11) demonstrate the clear, major effects that can occur as a consequence of changes in competition type, and in particular show that certain changes begin between Types 6 and 8. We also note that by comparing the averaging plots for One Non-Mutating Predator that superimpose a selection of predator behaviours as a function of Competition Type (Fig. 2), neither their survivability nor their population (averaged over five choices of P_1) showed a large degree of variation or a consistent trend. The most significant effect on a predator is the approximately 20% monotonic increase in population, accompanying a 5% increase in probability of survival, between Competition Type 0 and Competition Type 10 for a predator with $\alpha = 0$.

In all cases, for Competition Type 10 only, beyond $p = 0.47$ we enter a region where there may be one extinct prey phenotype on average. The exact values of c for which this occurs within the region varies according to the scenario and Competition Type. From the prey-only bifurcation diagrams (Fig. 9), it appears that some prey phenotypes (in particular, including #10) temporarily visit zero in their orbits throughout $0.465 < p < 0.5$. This is the only significant region in the (c, p) -parameter space, aside from extremely low values of p , where not all prey phenotypes are surviving on average.

The survival and population plots with $P_1 = 0.1$ show a significantly greater degree of similarity between Ten Mutating Predators (Fig. 22) and One Mutating Predator (#10) (Fig. 19) than between Ten Mutating Predators and One Mutating Predator (#1) (Fig. 18). This is also true for the averaging diagrams over the whole space and the five choices of P_1 , but only when we restrict our considerations to the ‘‘maximum’’ line of the averaging diagrams for One Mutating Predator (#10). Examining the survival and population images for a different initial condition, $P_1 = 0.3$, at Competition Type 10 (Supplementary material, Section 5), it is clear that in this case as well the general structure in parameter space is much closer between Ten Mutating Predators and One Mutating Predator (#10) than One Mutating Predator (#1), which differs primarily in that the total predator population is much larger on average and tends to increase at low p . However, One Mutating Predator (#10) suffers many additional extinctions for $c > 3.5$ which visibly appear to be artefacts rather than part of the attractor. These extinctions may explain why the averaging diagrams for One Mutating Predator (#10) (Fig. 5) vary much more with initial predator population size than the other scenarios, and that there is greater similarity in the *average* trendlines for predator survival between One Mutating Predator (#1) and Ten Mutating Predators (despite the attractors of these systems being a relatively poorer fit to each other) than the *average* trendlines for predator survival between One Mutating Predator (#10) and Ten Mutating Predators. As we have noted, the system as a whole does maintain a surprising dependence on the initial conditions - in particular, precisely which predator is introduced - even when mutation is enabled and at a relatively high rate.

Considering the averaging diagrams for One Non-Mutating Predator (in particular, Fig. 2 and 3), the best foraging strategy for a solo predator is the linear weighting $\alpha = 1$. Overall, $\alpha = 1$ optimises both the survival and population size of a lone predator, but if it must have a more focused strategy then an exclusive hunting strategy ($\alpha = \infty$) is better than any finite $\alpha > 4$ for ensuring survival. However, its population will be limited to less than the values achieved at $\alpha = 1, 2, 4, 7$ and, unlike survival, predator population sizes do not show significant growth again as α continues to increase. This is likely due to the logistic map’s limitation on the population size of any given prey phenotype, which in turn particularly constrains the population size of a focused predator in the subsequent iteration.

In contrast, when looking at the predator survival plots for Ten Non-Mutating Predators (Fig. 21), in a mixed environment initially featuring predators of all kinds it is the two extremes of predator foraging strategy that are optimal. Throughout the (c, p) -space for this scenario (regardless of competition type) it is never preferable to have a value of $\alpha \in \mathbb{R}^+ \setminus \{0\}$. In particular, only one optimal phenotype will survive and it is always either that with the lowest or highest α . For a region of low c , it is best to have the highest α in a mixed environment as this is preferable when a single prey phenotype’s population is sufficient to sustain a predator, whereas in the region of high c (separated by a region of total extinction for an intermediate range of c) only the least focused phenotype will survive. At high c , the predators must kill more to survive - that is, they are dependent on a greater prey population (see Section 2.2.3, effect (3) of increasing parameter c). At this point, the most focused predator will feel the limitation of being restricted to a single, limited population - preventing it from flourishing any further at high c - whereas the low- α predator can effectively continue to increase to potentially ten times this limit (by feeding on all ten prey phenotypes) as increased c continues to improve its reproductive efficiency. Thus, it is not surprising that the phenotype with lowest α should be the most competitive phenotype at high c , given that the number of surviving prey phenotypes are undiminished by predation. This is reinforced by the predator survival plots for a single Non-Mutating Predator (Fig. 15): at $\alpha = 0, 1$ there is no upper limit in c within $0 < c < 6$, but this does enter and become limiting for all larger values of α . Similarly for the scenarios of One Mutating Predator (Fig. 18, 19) they either start with or can produce predator phenotype #1, hence if there is an upper limit of predator survival it is beyond $c > 6$. Such evidence supports this explanation of the Ten Non-Mutating Predators case breaking down into #10 at low c and #1 at high c .

6.1. Interpretation as a Spatial Model

When p is too large to represent biological mutation, let us recall the spatial interpretation of our model (see Section 1). In this case we take the prey lattice as subpopulations of a single phenotype in geographical subregions, whilst the predator lattice continues to represent a range of predator strategies (*not* geographical subpopulations). The higher the position on the lattice, the larger the value of α for the predator group - and the more they focus their efforts on feeding in a single region rather than distributing their efforts throughout the regions. In effect, the predator lattice here defines the mobility of a subpopulation of the predator phenotype, and the “mutation” they undergo is a small change in strategy.

As discussed above, our results indicate that for a single non-mutating predator, $\alpha = 1$ (closely followed by $\alpha = 0$) is preferable. In a mixed competitive (i.e. multiple predator phenotypes) environment, $\alpha = 0$ is best when c is high and $\alpha = \infty$ is best when c is low. In the spatial interpretation, this means that a solo predator can sustain the greatest population if it feeds from prey in all subregions at every turn, but weighs its preference in a linear relationship with the prey subpopulation sizes. However, in an environment where the predator is divided into subgroups according to their current degree of adaptive foraging, when demand is low a highly adaptive predator may succeed, and if the success rate of attacks (c) is high then a clear advantage is given to those predators which split their hunting effort completely evenly across all ten regions, regardless of the current distribution of prey population.

7. Conclusion

Our primary finding in this article concerns the choice of foraging behaviours that maximise a predator’s population and chances of survival across a variety of initial conditions and parameter choices. For a non-mutating single predator phenotype (only one behaviour is permissible) adaptive foraging linearly proportional to the prey phenotype population size ($\alpha = 1$) is optimal. If individuals can incrementally vary their behaviour over time, no adaptive foraging is best when the kill rate (c) is high, and exclusive adaptive foraging may be the best chance of survival when the rate is low.

For a predator with a given degree of adaptive foraging, its properties are relatively robust against variation in the distribution of competition amongst its prey over a large range (Competition Type 0-6). This is reassuring with regard to constructing population models where the relative weights of competitive effects are not known, that so long as intraspecific is stronger than interspecific competition the system is not highly sensitive to variations in this distribution. The main effect observed is that (in all cases, regardless of predation’s presence or absence) total prey populations increase with a greater degree of interspecific competition - supporting the hypothesis that it is a necessary factor to promote survival. The case where intraspecific and interspecific competition are equal in strength is unlikely to occur in nature, and the system typically exhibits qualitative changes as this case is approached - such as a minor but consistent decrease in average prey survival and populations at high mutation rates.

With regard to shortcomings in the model, c is somewhat loosely defined in terms of biological processes. It would also be useful to uncouple the predator and prey mutation rates, as they do not represent the same idea in the spatial interpretation of the model, and even when representing mutation they should only necessarily coincide for different species at extremely large scales - i.e. ensuring that mutation for both species occurs on the same scale of e.g. millenia, rather than decades for one and millenia for the other. A change to the model with a more intuitive spatial interpretation in mind would be to define the predator lattice as the amount of the species in a given subregion - coinciding with the prey lattice. Thus, predator #5 would be restricted to feeding on prey #5. The predator strategy would then be defined as its tendency to expend effort migrating between regions rather than hunting in its current domain. Strategies of predator-avoidance, instead of just random diffusion between neighbouring regions, could also be implemented. In the future, we intend to study these principles in a two-dimensional grid using a variety of more realistic and sophisticated multi-species eco-evolutionary models.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at [10.1016/j.cnsns.2017.06.012](https://doi.org/10.1016/j.cnsns.2017.06.012).

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