EVOLUTIONARY DYNAMICS OF COEXISTING SPECIES

by

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Abstract

Ever since Maynard-Smith and Price first introduced the concept of an *evolutionary stable strategy* (ESS) in 1973, there has been a growing amount of work in and around this field. Many new concepts have been introduced, quite often several times over, with different acronyms by different authors. This led to other authors trying to collect and collate the various terms (for example Lessard, 1990 & Eshel, 1996) in order to promote better understanding of the topic.

It has been noticed that dynamic selection did not always lead to the establishment of an ESS. This led to the development of the concept of a *continuously stable strategy* (CSS), and the claim that dynamic selection leads to the establishment of an ESS if it is a CSS. It has since been proved that this is not always the case, as a CSS may not be able to displace its near neighbours in pairwise ecological competitions. The concept of a *neighbourhood invader strategy* (NIS) was introduced, and when used in conjunction with the concept of an ESS, produced the *evolutionary stable neighbourhood invader strategy* (ESNIS) which is an unbeatable strategy.

This work has tried to extend what has already been done in this field by investigating the dynamics of coexisting species, concentrating on systems whose dynamics are governed by Lotka-Volterra competition models. It is proved that an ESNIS coalition is an optimal strategy which will displace any size and composition of incumbent populations, and which will be immune to invasions by any other mutant populations, because the ESNIS coalition, when it exists, is unique. It has also been shown that an ESNIS coalition cannot exist in an ecologically stable state with any finite number of strategies in its neighbourhood. The equilibrium population when the ESNIS coalition is the only population present is globally stable in a n-dimensional system (for finite n), where the ESNIS coalition interacts with $n-2$ other strategies in its neighbourhood.

The dynamical behaviour of coexisting species was examined when the incumbent species interacted with various invading species. The different behaviour of the incumbent population when invaded by a coalition using either an ESNIS or an NIS phenotype underlines the difference in the various strategies. Similar simulations were intended for invaders who were using an ESS phenotype, but unfortunately the ESS coalition could not be found. If the invading coalition use NIS phenotypes then the outcome is not certain. Some, but not all of the incumbents might become extinct, and the degree to which the invaders flourish is very dependent on the nature of the incumbents. However, if the invading species form an ESNIS coalition, one is certain of the outcome. The invaders will eliminate the incumbents, and stabilise at their equilibrium populations. This will occur regardless of the composition and number of incumbent species, as the ESNIS coalition forms a globally stable equilibrium point when it is at its equilibrium populations, with no other species present. The only unknown fact about the outcome in this case is the number of generations that will pass before the system reaches the globally stable equilibrium consisting of just the ESNIS.

For systems whose dynamics are not given by Lotka-Volterra equations, the existence of a unique, globally stable ESNIS coalition has not been proved. Moreover, simulations of a non Lotka-Volterra system designed to determine the applicability of the proof were inconclusive, due to the ESS coalition not having unique population sizes. Whether or not the proof presented in this work can be extended to non Lotka-Volterra systems remains to be determined.

Preface

The work described in this dissertation was carried out in the School of Mathematics, Statistics and Information Technology at the University of Natal, Pietermaritzburg, from January 1999 to February 2000, under the supervision of Dr J. Apaloo (Department of Mathematics and Applied Mathematics) and Professor J. W. Hearne (Department of Mathematics and Applied Mathematics)

These studies represent original work by the author and have not been submitted in any other form to another university. Where use has been made of the work of others it has been duly acknowledged in the text.

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Chapter 1: Introduction

The interest in ecological modelling has been increasing markedly over the past few years. More and more institutions and people have been getting involved, as man tries to understand the dynamics of his environment, which has resulted in a lot of work on the stability of evolutionary systems being published. In this work, the dynamics of coexisting species as they evolve is considered, with a view to showing that under certain conditions, coevolving species will either work together or against one another. In other words, one or more species may dominate the system to the detriment of the remaining species, who are forced out. Furthermore, under certain conditions one or more species may invade a habitat, and either eliminate the incumbent species, or coexist with them. In this chapter, some of the history of evolutionary game theory, and some of the terminology used in this and other papers are introduced to the reader.

1.1. Evolutionary Game Theory and Stability

Game theory deals with conflicts of interest, and thus evolutionary game theory is ideally suited to model frequency dependent selection. In evolutionary game theory, strategies are assumed to be inheritable (Vincent, Van and Goh, 1996) and maintainable from generation to generation, and it is strategies, not individuals that persist through time (Brown and Vincent, 1987). Evolution is thus defined as changes in strategy frequency over time. In evolutionary game theory, the addition of a second species to a habitat depends on the failure of the first species there to expand fully in its niche (Roughgarden, 1987).

Selection is considered to be density dependent where the selection coefficients or fitnesses of genotypes[1] are a function of the population sizes. Selection is considered to be frequency dependent when the selection coefficients or fitnesses of genotypes are functions of gene frequency (Brown and Vincent, 1987; Roughgarden, 1976). The fitness function is frequency

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[1] genetic or factorial constitution of an individual organism; a group of individuals all of which possess the same genetic constitution - Chambers Twentieth Century Dictionary

independent if it depends on the strategies of other (sub)species only through their population densities and not through their strategies, i.e. $g_i = g_i(v_i, z(u))$ (Apaloo, 1999).

There are two basic assumptions from which the concept of evolutionary stability stems (Eshel, 1983). These are

1. Any phenotypic[2] pattern, strategy or distribution of strategies (i.e. a mixed strategy) is never fully fixed. At best, erratic small deviations are always maintained by forces of second order.
2. There is reason to believe natural selection operates to increase some relatively simple individual payment function, for example viability or fertility (Fisher, 1930; Eshel 1996).

The first assumption means that even if the system in question is globally evolutionary stable there are still small deviations in the strategies, but in the case of an evolutionary stable system, these deviations are negligible. The second assumption is that evolution occurs, and that natural selection operates at an individual level. In other words, the species will evolve to a state which increases its chances of survival, and this is measured by the fitness (or payoff) function. In evolutionary game theory the payoff for a strategy is related to the increase in fitness, and successful strategies will produce more offspring and thus will be able to spread (Nowak, 1990). A strategy is considered *pure* if it consists of a single behaviour which has a probability of 1, and *mixed* if it does not (Lessard, 1990).

1.2. Concepts in Evolutionary Stability

1.2.1. The ESS and δ-Stability

The classical evolutionary game theory concept of an *Evolutionary Stable Strategy* [ESS] was first introduced in 1973 by Maynard Smith and Price. An ESS is a strategy such that, if most members of the population adopt it, there is no 'mutant' strategy that would have a higher reproductive fitness. In other words, a strategy is said to be evolutionary stable if, when

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[2] the observable characteristics of an organism produced by the interaction of genes and environment; a group of individuals having the same characteristics of this kind - Chambers Twentieth Century Dictionary

adopted by a large enough majority in the population it becomes advantageous against any mutant strategy (Eshel, 1983). This means that an ESS is not invadable when it is established. The ESS may be used to predict the outcome of an evolutionary game, but the prediction is not certain, meaning that an ESS may not be the outcome of an evolutionary game through dynamic selection (Apaloo, 1999). It is a common but misleading conclusion that evolution will tend to an ESS (Nowak, 1990). If one does not restrict the number of evolving species, then under a sufficiently rich environment of evolving species, the ESS can usually be obtained

An ESS is not an 'unbeatable' strategy. An 'unbeatable' strategy has a selective advantage over any other strategy at all frequencies of the competing strategy, whereas an ESS only has a selective advantage when the other strategy occurs in low frequency (Nowak, 1990). An ESS provides an idealised state to which individual members of the community tend as a result of some natural selection (Vincent, Van and Goh, 1996). The ESS may be composed of a coalition of more than one strategy. An ESS requires stability with respect to changes in both the population density and to permutations of the coalition strategy frequencies. The concept of *δ-stability* (or *r-stability*) (Taylor, 1989; Lessard, 1990) is locally identical to the concept of an ESS. An ESS has the capability of repelling all mutant strategies once it has been established, but not necessarily of invading an existing community at ecological equilibrium with a strategy close to the ESS. In single species models of evolution in which fitness is negatively density dependent and frequency independent, a phenotype is an ESS if and only if it maximises the equilibrium population density. In the case of positive density dependency a phenotype is an ESS if and only if it minimises the equilibrium population density (Apaloo, 1999). The concept of an ESS has been shown to benefit both individuals and species. Brown and Vincent (1987) generalise the ESS concept to coevolving species and gives definitions for an ESS in terms of the frequencies of the strategies used by the coevolving species.

An evolutionary stable coalition, that is, a coalition which uses an ESS, cannot be invaded by any other population, although in isolation either of the types in the combination can be invaded by others. If, for example, the evolutionary stable coalition is a coalition of two species using two distinct strategies then when both species are present, no other population can invade the coalition. However, should only one of the species be present, then it is possible for another population to invade the system. An ESS, once established, cannot be invaded, but it has the property that it can invade any other nearby type, provided it is in high frequency relative to the other type. There are various factors which could prevent the attainment of an ESS. There is no particular guarantee that a particular formulation will admit an ESS (Ludwig and Levin, 1991).

The *ESS maximum principle* (Vincent, Van and Goh, 1996; Vincent and Vincent, 1996) states that the G-function (fitness generating function) associated with the fitness of every individual in the community must take on a maximum with respect to ESS strategies. ESS's may be determined directly from this principle for a large number of models. The G-function for a group of evolutionary identical individuals (i.e. if they have the same strategy choices and if the ecological consequences of using a given strategy are the same for all individuals in the group) is a function containing all variables and a dummy strategy with the property that the fitness function for any individual is found by replacing the dummy variable with that individual's strategy.

1.2.2. The CSS and m-Stability

A strategy u* is *m-stable* (also called *convergence stable*) (Taylor, 1989; Lessard, 1990) if, whenever the entire population has a strategy which is close enough to it, there will be a selective advantage to some individual strategies which are closer to u*. A m-stable strategy is an "attracting" strategy (Nowak, 1990). A strategy **u** is attracting if there is always a tendency to approach **u**, but it does not necessarily have to be an ESS (Nowak, 1990). The concept of a *Continuously Stable Strategy* [CSS] was first introduced by Eshel and Motro in 1981 and defined for evolution when pure strategies admit a continuum of values (Apaloo, 1998), and is only meaningful in this case. There has since been a lot of work published about the CSS concept, examples of which are Eshel, 1983; Taylor, 1989; Lessard, 1990; Nowak, 1990; Kisdi and Meszéna, 1995. A strategy is continuously stable if, when the majority deviates slightly from it, some reduction of this deviation becomes immediately advantageous (Eshel, 1983). The concept of CSS was defined in terms of ESS.

An ESS is a CSS if, whenever the entire population has a strategy close enough to the CSS, there is a selective advantage to some individual strategies which are closer to the CSS (Eshel and Motro, 1981). In other words, a CSS is an ESS which is m-stable, or m-stability and δ-stability taken jointly define CSS. An ESS is not an automatic outcome of the dynamic process of natural selection. If natural selection is operating to increase the inclusive fitness, it can lead to the establishment of some ESS's, but this is not a certainty. However, CSS as a class represents a possible dynamic selection process which eventually leads to the establishment of a CSS in the population (Eshel and Motro, 1981). A small perturbation of an ESS will be followed by a dynamic selection process which will lead to the restoration of the ESS if it is a CSS. In other words, if a large enough majority of the population select a strategy that is close to the ESS, then only those mutant strategies that are even closer to the ESS will be selectively advantageous. CSS was introduced to deal with the above issue in single species evolutionary models in which strategies admit a continuum of values (Apaloo, 1999). An ESS which is a CSS will be approached through dynamic selection.

In the case of continuous strategies it is possible that a small deviation of the entire population from the ESS makes it advantageous for each individual to move a little further from the ESS. In other cases, any small deviations of the entire population from the ESS will make it advantageous for each individual in the population to move a little closer to the ESS. ESS's of the latter sort are CSS's (Eshel, 1983). If the population had maintained an ESS which was not continuous, following a small displacement in the ESS the population will be in the convergence region of another, continuous stable strategy, and not of the near ESS (Eshel and Motro, 1981).

1.2.3. Finding an Optimal Strategy

An optimal coalition of strategies has the following components (Kisdi and Meszéna, 1993):

a. It can initially increase in the established population of any other strategy.

b. It increases initially, and it spreads until it becomes established excluding the former strategy.

c. It is an ESS, that is its established population cannot be invaded by any other strategy.

d. Having an established strategy u_e in the neighbourhood of the optimal strategy u_o and a rare strategy $u_r = u_e + \delta$ with small δ, u_r can invade u_e if and only if u_r is closer to u_o, i.e. if $|u_r - u_o| < |u_e - u_o|$

Point (a) ensures that there is only one ESS. Point (d) is only valid if there is a continuous strategy set, and it will make the optimal strategy convergence stable.

The concept of ESS remains quite meaningful in fluctuating environments as well. By invasibility analysis we can explore strategies which can't be invaded by any other strategy. Indeed, examples can be given when the ESS emerging in low frequency is excluded from a non-ESS population. Convergence stability is not necessarily satisfied for an ESS in a fluctuating environment. In a specific model Kisdi and Meszéna (1993) found three types of ESS: convergence stable which could invade directly its neighbours, convergence stable which couldn't directly invade, and convergence stable which couldn't ever invade.

When a strategy, sufficiently close to optimum, is established in the population, it can be invaded by another rare strategy, which is sufficiently close to the established one, if and only if the invader is somewhat closer to the optimum than the established strategy. (Kisdi and Meszéna 1995)

1.2.4. Invader Strategies

A *Neighbourhood Invader Strategy* [NIS] is a strategy that is initially able to invade all established communities using strategies that are sufficiently similar to it (Apaloo, 1997a; Apaloo, 1997b; Apaloo, 1998). This concept was first introduced by McKelvey and Apaloo in 1995, where it was initially called an ES II. Similar to the NIS concept is that of an *Evolutionary Compatible Strategy* [ECS], which is a type of strategy that can invade any other type, but it can also be invaded by any other type. There has been an emphasis on the non-invasibility of the ESS, but it is of interest to discover if an ESS can invade other incumbent strategies sufficiently close to the ESS (Apaloo, 1997b). If an ESS is also an NIS, then it is called an *Evolutionary Stable Neighbourhood Invader Strategy* [ESNIS].

The ESNIS concept is not equivalent to the CSS concept. An ESNIS is not invadable by its near neighbours, and it can invade any of its near neighbours. A CSS may not have this capability since it may not be able to displace its near neighbours in pairwise ecological competitions (Apaloo, 1997a; Apaloo, in preparation a). The mathematical conditions for a CSS require only that some phenotypes in a closer neighbourhood of the CSS be able to invade a phenotype that is further away from the CSS. It must be noted that invasion does not mean displacement. A phenotype which is a CSS is not necessarily an ESNIS, but an ESNIS is a CSS (Apaloo 1999). An ESNIS has a better chance of being established over evolutionary time because any strategy that is close enough to the ESNIS can be replaced by the ESNIS (or any strategy closer to the ESNIS). The dynamic process of natural selection leads to the establishment of the ESNIS (Apaloo, 1997b) in a single evolving species if no polymorphisms[3] occur during the evolutionary process, a conclusion which may not hold for a CSS. Even when a CSS is approached dynamically, the CSS itself may not be established as it could also be repelled by an established community using a strategy that is close to the CSS (Apaloo 1997b). Since an ESNIS is a CSS it will be approached dynamically and in addition it can invade any community using a strategy that is close to it (Apaloo, 1999).

It was found in general that the NIS concept is neither equivalent to the ESS nor m-stable concepts (Taylor 1989; Apaloo 1997a) from which we infer the ESNIS and CSS concepts are not equivalent. Thus it can be seen that the ESNIS is an ‘unbeatable’ or ‘optimal’ strategy, meeting all four of the requirements given in the previous section (§1.2.3.).

1.3. Coevolution

The fitness of each individual may be affected by the strategies of all the other individuals, in which case we are dealing with coevolution. Coevolution is a game where the fitness maximising strategy for an individual of one species is dependent on the strategies used by individuals of its own species and/or other species (Brown and Vincent, 1987). That is, “coevolution” is a term applied to the simultaneous evolution of interacting populations

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[3] any one of several forms in which the same thing may occur: an organism occurring in several forms - Chambers Twentieth Century Dictionary

(Roughgarden, 1979). Coevolution may be defined as evolution where the fitness of each phenotype depends on the population size of that species and on both the population sizes and gene frequencies of the other species (Roughgarden 1976). In coevolution, there is occasionally the formation of a physically close and relatively permanent relationship between two or more individuals of different species, which is called a symbiotic relationship. There are three kinds of symbiotic relationships (Roughgarden 1977; Roughgarden 1979):

1. A parasitic relationship, where one party benefits at the clear expense of the other.
2. A commensal relationship, where one party, the guest, benefits from the other, the host, with negligible harm to the host.
3. A mutualistic relationship where both parties clearly benefit from each other.

A coalition vector is a combination of strategies where all species have a positive stable equilibrium density. An evolutionary stable coalition vector is one in which the same stable ecological equilibrium density is obtained under the population dynamics, no matter what strategies are used for the other components in the strategy vector. A coalition with these properties is called an ESS.

1.4. A Brief Summary of the Main Concepts Used in the Following Chapters

The main concepts used are the ESS, the NIS and the ESNIS. By definition, the ESS cannot be invaded once it has been established by any small, ‘mutant’ population, whereas a NIS is able to invade any of its near neighbours, and an ESNIS is an ESS which can invade any of its near neighbours, and as such is an optimal (unbeatable) strategy.

1.5. Thesis Structure

In chapter 2, the necessary and sufficient conditions for the establishment of the ESS, NIS and ESNIS concepts are looked at, and defined mathematically. The terminology used and assumptions made in setting up the dynamical system, and the mathematics underlying both m-stability and δ-stability are presented.

In chapter 3 it is proved that an ESNIS coalition will be attained by dynamic selection under coevolution, and that this coalition will be globally stable. In chapter 4 the consequences of the proof are looked at using a Lotka-Volterra competition model. In chapter 5, a non Lotka-Volterra dynamical model for coexistence was found, in order to see if the proof could extend to a non Lotka-Volterra model. The simulations performed on a modified version of the model, and the reasons for having to make the modification, are given in chapter 5. Finally in chapter 6 some concluding remarks are made.

Chapter 2: Background Mathematics

The previous chapter introduced several terms which are used in evolutionary stability, such as ESS, NIS and CSS. There is a need to have a mathematical understanding of these terms, and this will be addressed in this chapter. In the first section, the assumptions underlying and some of the terminology used to describe the ecological system are given, especially that of the ESS and NIS conditions. Then in the second section (§2.2) the principles and mathematics of m-stability and δ-stability are presented in detail. Finally, in §2.3, the sufficient conditions for the ESS, NIS and strong-NIS stability concepts are given.

2.1. Terminology and Assumptions

If there are n distinct ecologically interacting species, then the system is termed n-dimensional. It is assumed that the population density dynamics of the n-dimensional system may be described by differential equations. Thus if the population size of species i at time t is given by $z_i(t)$, the population densities at time t for the whole community are denoted by

$$\mathbf{z}(t) = [z_1(t), z_2(t), \ldots, z_n(t)].$$

The population densities are from this point forward written as

$$\mathbf{z} = [z_1, z_2, \ldots, z_n],$$

that is the dependence on time is suppressed for simplicity, but it should not be forgotten. The evolutionary phenotype which is of dimension m, for species i is denoted by the vector $\mathbf{u}_i$, and the phenotypes for the community are denoted by

$$\mathbf{u} = [\mathbf{u}_1, \mathbf{u}_2, \ldots, \mathbf{u}_n].$$

It is assumed that the evolutionary phenotype $\mathbf{u}_i \in U_i$, where U_i is a m-dimensional phenotype space for the i^{th} species. It is also assumed that the dynamics of the species forming the community is given by the n-dimensional system of differential equations

$$\frac{1}{z_i}\frac{dz_i}{dt} = G_i(\mathbf{u}, \mathbf{z})$$

where i = 1, 2, ... n.

$G_i(\mathbf{u}, \mathbf{z})$ is the per-capita fitness function for an individual of species i with phenotype $\mathbf{u}_i$ in the community with phenotype $\mathbf{u}$ at time t. This is not the same as the G-function introduced on page 4. That is a fitness generation function, whereas $G_i(\mathbf{u}, \mathbf{z})$ is the fitness function for species i. At ecological equilibrium, the per-capita fitness functions are zero simultaneously, i.e.

$$G_i(\mathbf{u}, \mathbf{z}) = 0,$$

for $i = 1, 2, \ldots, n$.

Thus the equilibrium population densities $\check{\mathbf{z}}$ depend on the incumbent community phenotype $\mathbf{u}$ (i.e. $\check{\mathbf{z}}(\mathbf{u}) = [\check{\mathbf{z}}_1(\mathbf{u}), \check{\mathbf{z}}_2(\mathbf{u}), \ldots, \check{\mathbf{z}}_n(\mathbf{u})]$). An ecological equilibrium will be locally stable if the eigenvalues of the community matrix of the above system are all negative.

A fixed community phenotype $\breve{\mathbf{u}}$ is now looked at. The fitness of an individual invader with phenotype $\mathbf{u}_i$ of an incumbent community with phenotype $\breve{\mathbf{u}}$ and corresponding equilibrium population densities $\check{\mathbf{z}} = \check{\mathbf{z}}(\breve{\mathbf{u}})$ is denoted by $g_i(\mathbf{u}_i, \breve{\mathbf{u}}, \check{\mathbf{z}})$. It is important to note that $g_i(\mathbf{u}_i, \mathbf{u}, \mathbf{z}) = G_i(\mathbf{u}, \mathbf{z})$. Thus the convention has been adopted that the first argument ($\mathbf{u}_i$) of g_i is the phenotype of the invader, that the second argument ($\mathbf{u}$) is the incumbent community phenotype and that the third argument ($\mathbf{z}$) is the incumbent community equilibrium population density. The last two arguments of g_i are the arguments of G_i.

It has been assumed that the above system of differential equations has ecological stable equilibrium solutions for any $\mathbf{u}$ in an arbitrarily close neighbourhood of $\breve{\mathbf{u}}$. This assumption has been referred to as the *ecological stability* assumption (Apaloo, 1997b). The consequence of this assumption is that $g_i(\mathbf{u}_i, \mathbf{u}, \mathbf{z}) = G_i(\mathbf{u}, \mathbf{z}) \equiv 0$ for all $\mathbf{u}$ in a close neighbourhood of $\breve{\mathbf{u}}$ which implies that the derivatives of $g_i(\mathbf{u}_i, \mathbf{u}, \mathbf{z})$ with respect to components of $\mathbf{u}$ are identically zero for each i. These conditions are used to simplify the conditions for ESS, NIS and strong NIS below. The community equilibrium densities will sometimes be suppressed and the community phenotype will be written explicitly as arguments of g_i.

Now let $\breve{u}^j = [\breve{u}_1, \breve{u}_2, \ldots, \breve{u}_{j-1}, \mathbf{u}_j, \breve{u}_{j+1}, \ldots, \breve{u}_n]$. With this notation, the following definitions can be given (Apaloo, 1997b).

Definition 2.1: The community phenotype $\breve{u}$ with corresponding ecological equilibrium population densities $\check{\mathbf{z}}$ is an **evolutionary stable strategy (ESS)** if it cannot be invaded by any mutant that is arbitrarily close to any of its members for each $i = 1, \ldots., n$ (i.e. $g_i(\mathbf{u}_i, \breve{u}, \check{\mathbf{z}}) < 0$ for any $\mathbf{u}_i \in U_i$ in a close neighbourhood of and distinct from $\breve{u}_i$).

$\square$

Definition 2.2: The community phenotype $\breve{u}$ is a **neighbourhood invader strategy (NIS)** if its i^{th} member can successfully achieve invasion of any arbitrarily close community phenotype $\breve{u}^i$ at its corresponding ecological equilibrium densities $\mathbf{z}$ for each $i = 1, \ldots., n$ (i.e. $g_i(\breve{u}_i, \breve{u}^i, \mathbf{z}(\breve{u}^i)) > 0$ for any $\mathbf{u}_i \in U_i$ in a close neighbourhood of and distinct from $\breve{u}_i$).

$\square$

Definition 2.3: A community phenotype $\breve{u}$ is a **strong neighbourhood invader strategy (Strong NIS)** if its ith member can successfully achieve invasion of any arbitrarily close community phenotype $\mathbf{u}$ at its corresponding ecological equilibrium densities $\mathbf{z}$ for each $i = 1, \ldots., n$ (i.e. $g_i(\breve{u}_i, \mathbf{u}, \mathbf{z}(\mathbf{u})) > 0$ for any $\mathbf{u} \in U$ in a close neighbourhood of and distinct from $\breve{u}$).

$\square$

Definition 2.1 and definition 2.2 are the definitions that are going to be used most in this paper. Taken together they give the definition for an ESNIS. Definition 2.3 has only been included for interest, but it will not be used in the simulations of the Lotka-Volterra competition models in chapter four.

In examining the above definitions, it can be seen that algebraic conditions for the various strategies can be stated in terms of conditions for extreme values of the fitness functions. A community phenotype $\breve{u}$ that is an ESS maximises $g_i(\mathbf{u}_i, \breve{u}, \check{\mathbf{z}})$ at $\mathbf{u}_i = \breve{u}_i$ for each $i = 1, 2, \ldots, n$, where the maximum value is actually 0. Similarly $\breve{u}$ is a NIS if $g_i(\breve{u}_i, \breve{u}^i, \mathbf{z})$ is minimised at $\mathbf{u}_i = \breve{u}_i$ for each $i = 1, 2, \ldots, n$. Also $\breve{u}$ is a strong NIS if $g_i(\breve{u}_i, \mathbf{u}, \mathbf{z})$ is minimised at $\mathbf{u} = \breve{u}$ for each $i = 1, 2, \ldots, n$.

2.2. m-Stability and δ-Stability (Taylor, 1989)

Taylor defined the terms m-stability and δ-stability in terms of a fitness function W(m, δ), where m is the normal population strategy and δ is the mutant population strategy, as opposed to $g_i(\mathbf{u}_i, \breve{u})$ as given in the previous section, where the community equilibrium densities have been suppressed. Note that the form of the two fitness functions is different. If there was only one species, then the fitness function defined in the previous section would be $g_1(\mathbf{u}_1, \breve{u})$, where $\mathbf{u}_1$ is the is strategy of the invader, and $\breve{u}$ is the strategy of the incumbent. With this in mind it is possible to look at m-stability and δ-stability (Taylor, 1989).

m-stability (first order) and δ-stability (second order) are both local stability conditions in terms of the fitness function W(m, δ). For m* to be locally stable, it is necessary to consider a population which has a slight alteration from a pure m*-population, and require that the action of selection moves the population back towards m*. In general it is not easy to formulate. The number of types of alterations is often large and it is not easy to perceive long term effects.

For a system where W(m, δ) is the fitness function with variables m (normal population strategy) and δ (mutant population strategy), the following statements are true.

Definition 2.4: m* is m-stable if for m near m* and δ near 0,

whenever $m < m^*$, W(m, δ) has the same sign as δ, and

whenever $m > m^*$, W(m, δ) has the opposite sign to δ.

m* is δ-stable if for δ near to but different from 0, $W(m^*, \delta) < 0$

□

If W is differentiable and m* an interior point then each condition implies the equilibrium condition

$$\frac{\partial W}{\partial \delta}(m^*, 0) = 0.$$ Note that W(m, 0) = 0 for all m.

Theorem 2.5: Suppose $W(m, \delta) = \delta a(m) + \tfrac{1}{2}\delta^2 b(m) + O(\delta^2)$ where

$$a = \frac{\partial W}{\partial \delta} \text{ and } b = \frac{\partial^2 W}{\partial \delta^2}, \qquad \text{evaluated at } \delta = 0.$$

2.5.1. If $a(m) \neq 0$, then for δ near 0, selection favours mutants with $\delta a(m) > 0$ and disfavours mutants with $\delta a(m) < 0$.

2.5.2. If $a(m^*) = 0$, m^* is an equilibrium point and is m-stable if $\frac{da}{dm} < 0$ at $m = m^*$, that is

$$\frac{\partial^2 W(m^*, 0)}{\partial \delta \partial m} < 0 \qquad (1)$$

and δ-stable if $b(m^*) < 0$, that is

$$\frac{\partial^2 W(m^*, 0)}{\partial \delta^2} < 0 \qquad (2)$$

☐

Eshel & Motro (1981) call condition (2) from theorem 2.5.2. the ESS condition, and when both conditions (1) and (2) hold the ESS is a CSS because (1) from theorem 2.5.2. only makes sense when m is a continuous variable. Practically, m-stability is a lot easier to verify than δ-stability.

Classic ESS assumes that the fitnesses are linear. The fitness of any strategy is a linear function of the population strategy mix. So, as far as fitnesses are concerned, many different kinds of alterations are equivalent, and the simple condition that requires m* to be more fit than average in the altered population works well, at least locally (i.e. for small alterations).

If the fitnesses are non-linear there is a natural order structure on the parameter set. We suppose that the possible m values lie along a line segment (eg m is probability or proportion of resources). The two natural conditions for the stability of m* are

1 δ-stability, where in an m*-population all local mutants are less fit, and

2 m-stability, where, if we take m near m*, and in an m*-population, local mutants on the m*-side of m are more fit than those on the other side.

Under m-stability, if $m < m^*$ then selection should favour mutants with $\delta > 0$, and if $m > m^*$ then selection should favour mutants with $\delta < 0$. Under δ-stability, at $m = m^*$, all mutants should be less fit than the normal.

For equilibria which are δ-stable but not m-stable:- The overall population m value should drift sideways and then mutants which take it further away will be favoured, although at the exact equilibrium point all rare local mutants are penalised. The end result is the establishment of a stable equilibrium at another point, or a polymorphic equilibrium which might straddle the original point.

For equilibria which are m-stable but not δ-stable:- Selection pressure will keep m from drifting but will allow the spread of mutants with $\delta > 0$ or $\delta < 0$ or both, this results in a polymorphic population not described by the function $W(m, \delta)$.

By the definition of ESS, if $\breve{u}$ is an ESS then $g_i(\mathbf{u}_i, \breve{u}) < 0$ for any $\mathbf{u}_i \; \varepsilon \; U_i$ in a close neighbourhood of and distinct from $\breve{u}_i$ for each $i = 1, ..., n$. Alternatively, m* is δ-stable if, for δ near to but different from 0, $W(m^*, \delta) < 0$. By comparing these two statements, it is easily seen that the ESS and the δ-stable strategies are equivalent, as stated in chapter 1.

2.3. Sufficient Conditions

The sufficient conditions for the evolutionary stabilities defined in §2.1 are given by the following theorems. The derivatives below are taken with respect to the components of $\mathbf{u}_i$ in Theorems 2.6 and 2.7, and with respect to all components of $\mathbf{u}$ in Theorem 2.8. Also, ∇g_i and $\nabla^2 g_i$ denote the gradient vector and the Hessian matrix of g_i respectively (Apaloo, 1997b).

Theorem 2.6: Let $\breve{u}$ be an interior point of the community strategies space. Then sufficient conditions for $\breve{u}$ to be an ESS are

$$\nabla g_i(\mathbf{u}_i, \breve{u}, \check{\mathbf{z}}) = \mathbf{0}, \text{ evaluated at } \mathbf{u}_i = \breve{u}_i, \text{ for } i = 1, 2, ..., n$$

$$g_i(\mathbf{u}_i, \breve{u}, \check{\mathbf{z}}) = 0, \text{ evaluated at } \mathbf{u}_i = \breve{u}_i, \text{ for } i = 1, 2, ..., n$$

and

$$\nabla^2 g_i(\mathbf{u}_i, \breve{u}, \check{\mathbf{z}}), \text{ evaluated at } \mathbf{u}_i = \breve{u}_i, \text{ is negative definite for each } i,\ i = 1, 2, ..., n.$$

□

Theorem 2.7: Let $\breve{\mathbf{u}}$ be an interior point of the community strategies space. Then sufficient conditions for $\breve{\mathbf{u}}$ to be an NIS are

$$\nabla g_i(\breve{\mathbf{u}}_i, \breve{\mathbf{u}}^i, \mathbf{z}) = \mathbf{0}, \text{ evaluated at } \mathbf{u}_i = \breve{\mathbf{u}}_i, \text{ for } i = 1, 2, \ldots, n$$

$$\nabla^2 g_i(\breve{\mathbf{u}}_i, \breve{\mathbf{u}}^i, \mathbf{z}) = 0, \text{ evaluated at } \mathbf{u}_i = \breve{\mathbf{u}}_i, \text{ for } i = 1, 2, \ldots, n$$

and

$$\nabla^2 g_i(\breve{\mathbf{u}}_i, \breve{\mathbf{u}}^i, \mathbf{z}), \text{ evaluated at } \mathbf{u}_i = \breve{\mathbf{u}}_i, \text{ is positive definite for each } i,\ i = 1, 2, \ldots, n.$$

□

Theorem 2.8: Let $\breve{\mathbf{u}}$ be an interior point of the community strategies space. Then sufficient conditions for $\breve{\mathbf{u}}$ to be a strong NIS are

$$\nabla g_i(\breve{\mathbf{u}}_i, \mathbf{u}, \mathbf{z}) = \mathbf{0}, \text{ evaluated at } \mathbf{u} = \breve{\mathbf{u}}, \text{ for } i = 1, 2, \ldots, n$$

$$\nabla^2 g_i(\breve{\mathbf{u}}_i, \mathbf{u}, \mathbf{z}) = 0, \text{ evaluated at } \mathbf{u} = \breve{\mathbf{u}}, \text{ for } i = 1, 2, \ldots, n$$

and

$$\nabla^2 g_i(\breve{\mathbf{u}}_i, \mathbf{u}, \mathbf{z}), \text{ evaluated at } \mathbf{u} = \breve{\mathbf{u}}, \text{ is positive definite for each } i,\ i = 1, 2, \ldots, n.$$

□

The sufficient conditions for the two dimensional case are given in Appendix 1.

In the following chapters, only the ESS and the NIS concepts are going to be used. The other concepts are presented here for interest and for the sake of comparison, but they will not be referred to again.

Chapter 3: The Proof

The ecological system used in this, and the following chapter, is given by the Lotka-Volterra competition model. The *n*-dimensional system of equations is given by

$$\frac{dz_i}{dt} = \frac{r\,z_i}{k(u_i)}\left[k(u_i) - \sum_{j=1}^{n}\alpha(u_i - u_j)\,z_j\right], \quad i = 1, 2, \ldots n, \tag{I}$$

This system will be referred to from now on as the system of equations (I). In (I), $k(u_i)$ is the carrying capacity as a function of the species phenotype and $\alpha(u_i - u_j)$ is the competitive interaction function. The carrying capacity and competitive interaction functions used for the various simulations are defined in Chapter 4. For simplicity, the carrying capacity and the competitive interaction functions are abbreviated as follows: $k(u_i) = k_i$ and $\alpha(u_i - u_j) = \alpha_{ij}$. Also note that competitive interaction function is defined such that $\alpha(u_i - u_i) = \alpha_{ii} = 1$.

3.1 Introduction

This chapter contains the proof that there is only one stable equilibrium point for the *n*-dimensional system (I), and that equilibrium is globally stable. To be able to show this using the Index Theorem (Hofbauer and Sigmund, 1988), certain statements about the nature of the equilibrium points of the *n*-dimensional system (I) had to be made. These statements concerned the existence of interior points (∮ 3.2), the local stability of the boundary equilibrium point relating to the ESNIS coalition (∮ 3.3), and the regularity of the equilibrium points (∮ 3.4). Finally, the Index Theorem (see Appendix 2) was used to show that for the *n*-dimensional system (I), with $n > 2$, there is only one stable equilibrium point, which is globally stable.

3.2 The Existence of Interior Points

Claim 3.1: The system of equations (I) has no interior equilibrium point when $n > 2$.

Proof 3.1: Consider the following n-dimensional system of equations

$$\frac{dz_1}{dt} = \frac{r_1 z_1}{k_1}(k_1 - z_1 - \alpha_{12} z_2 - \alpha_{13} z_3 - \cdots - \alpha_{1n} z_n)$$

$$\frac{dz_2}{dt} = \frac{r_2 z_2}{k_2}(k_2 - \alpha_{21} z_1 - z_2 - \alpha_{23} z_3 - \cdots - \alpha_{2n} z_n)$$

$$\vdots$$

$$\frac{dz_n}{dt} = \frac{r_n z_n}{k_n}(k_n - \alpha_{n1} z_1 - \alpha_{n2} z_2 - \alpha_{n3} z_3 - \cdots - z_n)$$

From Strobeck 1973 the necessary and sufficient conditions for the above system of equations to have a locally stable interior equilibrium $(\check{z}_1, \check{z}_2, \cdots, \check{z}_n)$ are

$$\Delta_1 = \begin{vmatrix} k_1 & \alpha_{12} & \cdot & \alpha_{1n} \\ k_2 & 1 & \cdot & \alpha_{2n} \\ \cdot & \cdot & \cdot & \cdot \\ k_n & \alpha_{n2} & \cdot & 1 \end{vmatrix} = k_1 - \sum \alpha_{1j} \check{z}_j^{(1)} > 0$$

$$\Delta_2 = \begin{vmatrix} 1 & k_1 & \cdot & \alpha_{1n} \\ \alpha_{21} & k_2 & \cdot & \alpha_{2n} \\ \cdot & \cdot & \cdot & \cdot \\ \alpha_{n1} & k_n & \cdot & 1 \end{vmatrix} = k_2 - \sum \alpha_{2j} \check{z}_j^{(2)} > 0$$

$$\vdots$$

$$\Delta_n = \begin{vmatrix} 1 & \alpha_{12} & \cdot & k_1 \\ \alpha_{21} & 1 & \cdot & k_2 \\ \cdot & \cdot & \cdot & \cdot \\ \alpha_{n1} & \alpha_{n2} & \cdot & k_n \end{vmatrix} = k_n - \sum \alpha_{nj} \check{z}_j^{(n)} > 0$$

and for $n > 2$

$$\begin{vmatrix} a_1 & a_3 \\ 1 & a_2 \end{vmatrix} > 0, \qquad \begin{vmatrix} a_1 & a_3 & a_5 \\ 1 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{vmatrix} > 0, \cdots,$$

where

$$a_1 = \sum_{i=1}^{n} \frac{r_i \check{z}_i}{k_i}$$

$$a_2 = \sum_{i=1}^{n} \sum_{j=1}^{i-1} \frac{r_i r_j \check{z}_i \check{z}_j}{k_i k_j} \begin{vmatrix} 1 & \alpha_{ij} \\ \alpha_{ji} & 1 \end{vmatrix}$$

$$a_3 = \sum_{i=1}^{n} \sum_{j=1}^{i-1} \sum_{k=1}^{j-1} \frac{r_i r_j r_k \check{z}_i \check{z}_j \check{z}_k}{k_i k_j k_k} \begin{vmatrix} 1 & \alpha_{ij} & \alpha_{ik} \\ \alpha_{ji} & 1 & \alpha_{jk} \\ \alpha_{ki} & \alpha_{kj} & 1 \end{vmatrix}$$

$$\vdots$$

$$a_n = \frac{r_1 r_2 \cdots r_n \check{z}_1 \check{z}_2 \cdots \check{z}_n}{k_1 k_2 \cdots k_n} \Delta$$

where

$$\Delta = \begin{vmatrix} 1 & \alpha_{12} & \alpha_{13} & \cdot & \alpha_{1n} \\ \alpha_{21} & 1 & \alpha_{23} & \cdot & \alpha_{2n} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \alpha_{n1} & \alpha_{n2} & \alpha_{n3} & \cdot & 1 \end{vmatrix}$$

$$\check{z} = \frac{\Delta_i}{\Delta}$$

When n = 3:

We have three strategies, namely $\breve{u}_1$, $\breve{u}_2$ and u_3 where $\breve{u}_1$ and $\breve{u}_2$ form an ESNIS. As u_3 is not part of the ESNIS, it will not be able to invade $\breve{u}_1$ or $\breve{u}_2$ in the system of equations

$$\frac{dz_i}{dt} = \frac{r\, z_i}{k_i}(k_i - \alpha_{i1}\check{z}_1 - \alpha_{i2}\check{z}_2 - \alpha_{i3}z_3), \quad \text{for } i = 1, 2, 3,$$

so $k_3 < \sum_{j=1}^{2} \alpha_{3j}\check{z}_j^{(3)}$

and therefore $k_3 - \sum_{j=1}^{2} \alpha_{3j}\check{z}_j^{(3)} < 0$

and therefore there is no interior equilibrium point.

Inductively it can be seen that there will never be an interior equilibrium point for $n \geq 3$. For example, when $n = 4$ if u_4 can invade the coalition of (u_1, u_2, u_3) in equilibrium then it is possible to have an interior equilibrium point consisting of (u_1, u_2, u_3, u_4). But by the above argument it has been shown that the coalition of (u_1, u_2, u_3) does not exist in equilibrium. Thus for $n = 4$ there are no interior equilibrium points. Similar arguments hold for $n > 4$, and thus there are no interior points for $n \geq 3$.

The following result also holds. There are no interior equilibrium points if and only if there are no limit cycles. Thus all equilibrium points are on the boundary (Hofbauer and Sigmund, 1988).

$\square$

3.3 The Local Stability of the Boundary Equilibrium Point

Claim 3.2: $(\check{z}_1, \check{z}_2, 0, \ldots, 0)$ is a locally stable equilibrium point of the system equations (I) when $\check{u}_1, \check{u}_2$ is an ESNIS with equilibrium populations of $\check{z}_1$ and $\check{z}_2$.

Proof 3.2:

For **n = 2:**

As $\check{u}_1, \check{u}_2$ is an ESNIS the following results hold:

$$k_1 - \check{z}_1 - \alpha_{12}\check{z}_2 = 0 \tag{1a}$$

$$k_2 - \alpha_{21}\check{z}_1 - \check{z}_2 = 0. \tag{1b}$$

Also $\check{z}_1^{(2)} = k_1$ and $\check{z}_2^{(1)} = k_2$, and

$$\Delta_1 = k_1 - \alpha_{12}k_2 > 0 \tag{2a}$$

$$\Delta_2 = k_2 - \alpha_{21}k_1 > 0 \tag{2b}$$

as each population can invade the other, thus $(\check{z}_1, \check{z}_2)$ is a locally stable equilibrium point located on the boundary of the two dimensional system.

For **n = 3:**

When n=3, the system of equations (I) is:

$$\frac{dz_1}{dt} = \frac{r\,z_1}{k_1}[k_1 - z_1 - \alpha_{12}\,z_2 - \alpha_{13}\,z_3],$$

$$\frac{dz_2}{dt} = \frac{r\,z_2}{k_2}[k_2 - \alpha_{21}\,z_1 - z_2 - \alpha_{23}\,z_3],$$

$$\frac{dz_3}{dt} = \frac{r\,z_3}{k_3}[k_3 - \alpha_{31}\,z_1 - \alpha_{32}\,z_2 - z_3],$$

For there to be an equilibrium point the right hand side of each of the three equations above must be equal to zero. Thus

$z_1 = 0$ or $k_1 - z_1 - \alpha_{12}\,z_2 - \alpha_{13}\,z_3 = 0$, and
$z_2 = 0$ or $k_2 - \alpha_{21}\,z_1 - z_2 - \alpha_{23}\,z_3 = 0$, and
$z_3 = 0$ or $k_3 - \alpha_{31}\,z_1 - \alpha_{32}\,z_2 - z_3 = 0$.

The fact that $\breve{u}_1$, $\breve{u}_2$ form an ESNIS coalition means that

$k_1 - \check{z}_1 - \alpha_{12}\,\check{z}_2 = 0$, and
$k_2 - \alpha_{21}\,\check{z}_1 - \check{z}_2 = 0$,

so if $\check{z}_3 = 0$, the following three statements are all true:

$k_1 - \check{z}_1 - \alpha_{12}\,\check{z}_2 - \alpha_{13}\,\check{z}_3 = 0$, and
$k_2 - \alpha_{21}\,\check{z}_1 - \check{z}_2 - \alpha_{23}\,\check{z}_3 = 0$, and
$\check{z}_3 = 0$.

Thus $(\check{z}_1, \check{z}_2, 0)$ is an equilibrium point, where $(\check{z}_1, \check{z}_2)$ are the equilibrium populations corresponding to the ESNIS coalition $(\breve{u}_1, \breve{u}_2)$

At the equilibrium point $(\check{z}_1, \check{z}_2, 0)$, the three differential equations are all equal to zero. If this point is now perturbed to $(\check{z}_1 + \varepsilon_1, \check{z}_2 + \varepsilon_2, \varepsilon_3)$, where ε_i is small, the system of equations becomes

$$\frac{d\varepsilon_1}{dt} = \frac{r\,(\check{z}_1 + \varepsilon_1)}{k_1}[k_1 - (\check{z}_1 + \varepsilon_1) - \alpha_{12}\,(\check{z}_2 + \varepsilon_2) - \alpha_{13}\,\varepsilon_3], \qquad (3a)$$

$$\frac{d\varepsilon_2}{dt} = \frac{r\,(\check{z}_2 + \varepsilon_2)}{k_2}[k_2 - \alpha_{21}\,(\check{z}_1 + \varepsilon_1) - (\check{z}_2 + \varepsilon_2) - \alpha_{23}\,\varepsilon_3], \qquad (3b)$$

$$\frac{d\varepsilon_3}{dt} = \frac{r\,\varepsilon_3}{k_3}[k_3 - \alpha_{31}\,(\check{z}_1 + \varepsilon_1) - \alpha_{32}\,(\check{z}_2 + \varepsilon_2) - \varepsilon_3], \qquad (3c)$$

Using a Taylor Series expansion of the above equations at the equilibrium point $(\check{z}_1, \check{z}_2, 0)$ yields

$$\acute{\varepsilon}_1 = \frac{r\,(k_1 - 2\,\check{z}_1 - \alpha_{12}\,\check{z}_2)}{k_1}\,\varepsilon_1 - \frac{r\,\alpha_{12}\,\check{z}_1}{k_1}\,\varepsilon_2 - \frac{r\,\alpha_{13}\,\check{z}_1}{k_1}\,\varepsilon_3 + O(\varepsilon_i^2)$$

$$\acute{\varepsilon}_2 = \frac{-\,r\,\alpha_{21}\,\check{z}_2}{k_2}\,\varepsilon_1 + \frac{r\,(k_2 - \alpha_{21}\,\check{z}_1 - 2\,\check{z}_2)}{k_2}\,\varepsilon_2 - \frac{r\,\alpha_{23}\,\check{z}_1}{k_2}\,\varepsilon_3 + O(\varepsilon_i^2)$$

$$\acute{\varepsilon}_3 = \frac{r\,(k_3 - \alpha_{31}\,\check{z}_1 - \alpha_{32}\,\check{z}_2)}{k_3}\,\varepsilon_3 + O(\varepsilon_i^2)$$

where $\acute{\varepsilon}$ is shorthand for $(d\varepsilon / dt)$.

The higher order terms are negligible, and then because of the ESNIS coalition, the following are true:

$k_1 - \check{z}_1 - \alpha_{12}\,\check{z}_2 = 0,$ (4)
$k_2 - \alpha_{21}\,\check{z}_1 - \check{z}_2 = 0,$ (5)
$k_3 - \alpha_{31}\,\check{z}_1 - \alpha_{32}\,\check{z}_2 < 0,$ (6)
$k_1 - \alpha_{12}\,k_2 > 0,$ and (7)
$k_2 - \alpha_{21}\,k_1 > 0.$ (8)

It is also true that

$$\check{z}_1 = \frac{k_1 - \alpha_{12}\, k_2}{1 - \alpha_{12}\, \alpha_{21}} \qquad (9a) \qquad \text{and} \qquad \check{z}_2 = \frac{k_2 - \alpha_{21}\, k_1}{1 - \alpha_{12}\, \alpha_{21}} \qquad (9b)$$

Using these facts, and putting the equations into vector form, the result is

$$\underline{\acute{\varepsilon}} = A\, \underline{\varepsilon}$$

where $\underline{\acute{\varepsilon}}$ and $\underline{\varepsilon}$ are vectors and A is the 3x3 matrix,

$$A = \begin{bmatrix} - r\, \check{z}_1 / k_1 & -r\, \alpha_{12}\, \check{z}_1 / k_1 & - r\, \alpha_{13}\, \check{z}_1 / k_1 \\ - r\, \alpha_{21}\, \check{z}_2 / k_2 & -r\, \check{z}_2 / k_2 & - r\, \alpha_{23}\, \check{z}_1 / k_2 \\ 0 & 0 & r\,(k_3 - \alpha_{31}\, \check{z}_1 - \alpha_{32}\, \check{z}_2) / k_3 \end{bmatrix}$$

Solving the equation $|A - \lambda I| = 0$ for the eigenvalues λ resulted in three possible eigenvalues, namely

$$\lambda_1 = -r, \qquad (10a)$$

$$\lambda_2 = \frac{-r}{k_1\, k_2} \left[\frac{(k_1 - \alpha_{12}\, k_2)(k_2 - \alpha_{21}\, k_1)}{(1 - \alpha_{12}\, \alpha_{21})} \right], \text{ and} \qquad (10b)$$

$$\lambda_3 = \frac{-r}{k_3} \left[\frac{[\alpha_{31}(k_1 - \alpha_{12}\, k_2) + \alpha_{32}(k_2 - \alpha_{21}\, k_1) - k_3\,(1 - \alpha_{12}\, \alpha_{21})}{(1 - \alpha_{12}\, \alpha_{21})} \right]. \qquad (10c)$$

If the terms in square brackets from (10b) and (10c) are both positive, then all the eigenvalues will be negative, and the equilibrium point will be locally stable.

Looking first at λ_2, there are three terms in the large square brackets. From (7) and (8) the two terms in the numerator are both positive, and it follows from (9) that the denominator is also positive. Thus the term in the square brackets is positive, and therefore $\lambda_2 < 0$.

Now taking the square bracket in λ_3, and using (9) to simplify it, it becomes $[\alpha_{31}\, \check{z}_1 + \alpha_{32}\, \check{z}_2 - k_3]$. Thus, from (6), the term in the square brackets is positive. Therefore $\lambda_3 < 0$.

As $\lambda_i < 0$ for i = 1, 2, 3, the equilibrium point $(\check{z}_1, \check{z}_2, 0)$ is locally stable.

Inductively, it can be shown that $(\check{z}_1, \check{z}_2, 0, \cdots, 0)$ is a locally stable equilibrium point for $n \geq 2$. Firstly every n-dimensional system of equations will have $(\check{z}_1, \check{z}_2, 0, \cdots, 0)$ as a stable equilibrium point, because $(\breve{u}_1, \breve{u}_2)$ is an ESNIS coalition. Secondly, following an argument similar to that used above, the equilibrium point $(\check{z}_1, \check{z}_2, 0, \cdots, 0)$ will be locally stable, largely due to the ESNIS conditions. Thus a slight perturbation from the equilibrium point will result in the equilibrium point being reestablished and so the equilibrium point $(\check{z}_1, \check{z}_2, 0, \cdots, 0)$ is locally stable.

□

Definition 3.3: A rest point $\check{z}$ of the *n*-dimensional system of equations (I) is said to be saturated if $f_i(\check{z}) \leq 0$ when $\check{z}_i = 0$ and $f_i(\check{z}) = 0$ when $\check{z}_i > 0$ (Hofbauer and Sigmund, 1988).

□

From this definition it is possible to see that the stable equilibrium point $(\check{z}_1, \check{z}_2, 0, \cdots, 0)$ is saturated for all dimensions $n \geq 2$. For $n = 2$, $\check{z}_i > 0$ for $i = 1$ and 2, and $f_i(\check{z}) = 0$. Similarly for $n = 3$, $f_i(\check{z}) = 0$ for $i = 1, 2$, and $f_3(\check{z}) \leq 0$ where $\check{z}_i > 0$ for $i = 1, 2$, and $\check{z}_3 = 0$.

Definition 3.4: Let U be a bounded open subset of $\mathbb{R}^n$ and **f** a vector field defined on a neighbourhood of its closure $\underline{U}$. A point $\mathbf{z} \in U$ is said to be regular if $\det D_z\mathbf{f} \neq 0$ where $D_z\mathbf{f}$ is the Jacobian matrix of **f** evaluated at $\mathbf{z} \in \mathbb{R}^n$.

□

3.4 The Regularity of the Equilibrium Points

It was assumed that all equilibrium points are regular.

3.5 The Existence of Only One Stable Equilibrium Point

To prove that there is only one stable and saturated equilibrium point in all cases with three or more different strategies, one first looks at the three and then the four dimensional cases. Then by following an intuitive argument, it is possible to show that there is only one stable and saturated equilibrium point for any dimension greater than two.

3.5.1 The Case When $n = 3$

In the three dimensional case (i.e. three different populations with three different strategies), where there is an ESNIS consisting of $\breve{u}_1$ and $\breve{u}_2$ and a third strategy u_3 which is not part of the ESNIS. Then there are eight possible equilibrium points, namely:

$(0, 0, 0)$;
$(\check{z}_1, 0, 0)$;
$(0, \check{z}_2, 0)$;
$(0, 0, z_3)$;
$(\check{z}_1, \check{z}_2, 0)$;
$(\check{z}_1, 0, z_3)$;
$(0, \check{z}_2, z_3)$;
$(\check{z}_1, \check{z}_2, z_3)$.

It has already been shown that there are no interior points, thus $(\check{z}_1, \check{z}_2, z_3)$ does not exist. Also, a slight perturbation in $(0, 0, 0)$ will result in $z'_i > 0$ for $i = 1, 2, 3$ and thus the populations will grow, so $(0, 0, 0)$ is unstable. Because $\breve{u}_1$ and $\breve{u}_2$ form an ESNIS, they can invade each other, as well as any other incumbent population. Thus $(\check{z}_1, 0, 0)$ and $(0, \check{z}_2, 0)$ and $(0, 0, z_3)$ are all unstable as $(\check{z}_1, 0, 0)$ can be invaded by $\breve{u}_2$, $(0, \check{z}_2, 0)$ can be invaded by $\breve{u}_1$, and $(0, 0, z_3)$ can be invaded by both or one of $\breve{u}_1$ and $\breve{u}_2$.

This leaves three possible equilibrium points that could be stable, namely $(\check{z}_1, \check{z}_2, 0)$ $(\check{z}_1, 0, z_3)$, and $(0, \check{z}_2, z_3)$. Now we have shown that $(\check{z}_1, \check{z}_2, 0)$ is a stable equilibrium point as it corresponds to the equilibrium population of the ESNIS population. Thus $(\check{z}_1, \check{z}_2, 0)$ is saturated, and will have an index of $(-1)^3 = -1$.

Claim 3.5: Neither $(\check{z}_1, 0, z_3)$ nor $(0, \check{z}_2, z_3)$ is saturated.

Proof 3.5: All equilibrium points are regular and the equilibrium point $(\check{z}_1, \check{z}_2, 0)$ is saturated and has an index of -1.

Case 1: Suppose $(\check{z}_1, 0, z_3)$ is saturated and $(0, \check{z}_2, z_3)$ is not saturated. Thus $(\check{z}_1, 0, z_3)$ has an index of -1 as it will have three negative eigenvalues. Then there are two saturated and regular equilibria with indices of -1, and the sum of their indices is -2. But by the index theorem (Hofbauer and Sigmund, 1988; Appendix 2) the sum must be -1 which is a contradiction, thus $(\check{z}_1, 0, z_3)$ is not saturated.

Case 2: Suppose $(0, \check{z}_2, z_3)$ is saturated and $(\check{z}_1, 0, z_3)$ is not saturated. Thus $(0, \check{z}_2, z_3)$ has an index of -1 as it will have three negative eigenvalues. Then there are two saturated and regular equilibria with indices of -1, and the sum of their indices is -2. By the index theorem the sum must be -1 which is a contradiction, thus $(0, \check{z}_2, z_3)$ is not saturated.

Case 3: Suppose both $(\check{z}_1, 0, z_3)$ and $(0, \check{z}_2, z_3)$ are not saturated. Thus both $(\check{z}_1, 0, z_3)$ and $(0, \check{z}_2, z_3)$ have an index of -1 as they each have three negative eigenvalues. Then there are three saturated and regular equilibria with indices of -1, and the sum of their indices is -3. But by the index theorem the sum must be -1 which is a contradiction, thus $(\check{z}_1, 0, z_3)$ and $(0, \check{z}_2, z_3)$ are not saturated.

Thus by cases one to three neither of the equilibrium points $(\check{z}_1, 0, z_3)$ or $(0, \check{z}_2, z_3)$ is saturated therefore $(\check{z}_1, \check{z}_2, 0)$ is the only saturated point. Thus it is also the only locally stable point, therefore it is also globally stable.

☐

3.5.2 The Case When $n = 4$

We now look at the four dimensional case (i.e. four different populations with four different strategies), where there is an ESNIS consisting of $\check{u}_1$ and $\check{u}_2$ and a two other strategies u_3 and u_4 that are not part of the ESNIS. There are then sixteen possible equilibrium points, namely:

$(0, 0, 0, 0)$;
$(\check{z}_1, 0, 0, 0)$;
$(0, \check{z}_2, 0, 0)$;
$(0, 0, z_3, 0)$;
$(0, 0, 0, z_4)$;
$(\check{z}_1, \check{z}_2, 0, 0)$;
$(\check{z}_1, 0, z_3, 0)$;

$(\check{z}_1, 0, 0, z_4)$;
$(0, \check{z}_2, z_3, 0)$;
$(0, \check{z}_2, 0, z_4)$;
$(0, 0, z_3, z_4)$;
$(\check{z}_1, \check{z}_2, z_3, 0)$;
$(\check{z}_1, \check{z}_2, 0, z_4)$;
$(\check{z}_1, 0, z_3, z_4)$;
$(0, \check{z}_2, z_3, z_4)$;
$(\check{z}_1, \check{z}_2, z_3, z_4)$.

It has already been shown that there are no interior points, thus $(\check{z}_1, \check{z}_2, z_3, z_4)$ does not exist. A slight perturbation in $(0, 0, 0, 0)$ will result in $z'_i > 0$ for $i = 1, 2, 3, 4$ and thus the populations will grow, so $(0, 0, 0, 0)$ is unstable. Because $\breve{u}_1$ and $\breve{u}_2$ form an ESNIS, they can invade each other, and any other incumbent population. Thus $(\check{z}_1, 0, 0, 0)$, $(0, \check{z}_2, 0, 0)$, $(0, 0, z_3, 0)$ and $(0, 0, 0, z_4)$ are all unstable as $(\check{z}_1, 0, 0, 0)$ can be invaded by $\breve{u}_2$, $(0, \check{z}_2, 0, 0)$ can be invaded by $\breve{u}_1$, and $(0, 0, z_3, 0)$ and $(0, 0, 0, z_4)$ can each be invaded by both or one of $\breve{u}_1$ and $\breve{u}_2$.

This leaves ten possible equilibrium points which could be stable, namely $(\check{z}_1, \check{z}_2, 0, 0)$, $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3, 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$. Now we have shown that $(\check{z}_1, \check{z}_2, 0, 0)$ is a stable equilibrium point as it corresponds to the equilibrium population of the ESNIS population. Thus $(\check{z}_1, \check{z}_2, 0, 0)$ is saturated, and will have an index of $(-1)^4 = 1$.

Claim 3.6: None of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, or $(0, \check{z}_2, z_3, z_4)$ is saturated.

Proof 3.6: All equilibrium points are regular and the equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ is saturated and has an index of 1. Each locally stable point will have four negative eigenvalues and will therefore have an index of 1.

Case 1: Only one of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$ or $(0, \check{z}_2, z_3, z_4)$ is saturated and all others are unstable. The one saturated point is locally stable and therefore has an index of 1. Also the stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is 2. But by the index theorem, the sum must be 1, which is a contradiction.

Case 2: Assume only two of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ are saturated, and the others are all unstable equilibrium points. The two saturated points are both locally stable, each with an index of 1, and together with point $(\check{z}_1, \check{z}_2, 0, 0)$, the sum of the indices of the regular and saturated equilibria is 3. By the index theorem the sum must be 1, which is a contradiction.

Case 3: Assume three of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ are saturated and the others are all unstable. The three saturated points are locally stable and thus each have an index of 1. The stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ also has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is 4. But by the index theorem the sum must be 1, which is a contradiction.

Case 4: Assume four of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ are saturated and the others are all unstable. The four saturated points are locally stable and thus each has an index of 1. The stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ also has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is 5. But by the index theorem the sum must be 1, which is a contradiction.

Case 5: Assume five of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ are saturated and the others are all unstable. The five saturated points are locally stable and thus each has an index of 1. The stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ also has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is $(\check{z}_1, \check{z}_2, 0, 0)$. By the index theorem the sum must be 1, which is a contradiction.

Case 6: Assume six of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ are saturated and the others are all unstable. The six saturated points are locally stable and thus each has an index of 1. The stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ also has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is 7. But by the index theorem the sum must be 1, which is a contradiction.

Case 7: Assume seven of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ are saturated and the others are all unstable. The seven saturated points are locally stable and thus each have an index of 1. The stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ also has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is 8. The index theorem says that the sum must be 1, which is a contradiction.

Case 8: Assume eight of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ are saturated and the others are all unstable. The eight saturated points are locally stable and thus each has an index of 1. The stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ also has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is 9. But by the index theorem the sum must be 1, which is a contradiction.

Case 9: Assume each of $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, and $(0, \check{z}_2, z_3, z_4)$ is saturated. The saturated points are locally stable and thus each has an index of 1. The stable equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ also has an index of 1. Thus the sum of the indices of the regular and saturated equilibria is 10. But by the index theorem the sum must be 1, which is a contradiction.

By cases one to nine none of the points $(\check{z}_1, 0, z_3, 0)$, $(\check{z}_1, 0, 0, z_4)$, $(0, \check{z}_2, z_3, 0)$, $(0, \check{z}_2, 0, z_4)$, $(0, 0, z_3, z_4)$, $(\check{z}_1, \check{z}_2, z_3\ 0)$, $(\check{z}_1, \check{z}_2, 0, z_4)$, $(\check{z}_1, 0, z_3, z_4)$, or $(0, \check{z}_2, z_3, z_4)$, or any combination of them, are saturated therefore point $(\check{z}_1, \check{z}_2, 0, 0)$ is the only saturated point and the only locally stable equilibrium point. Thus equilibrium point $(\check{z}_1, \check{z}_2, 0, 0)$ is globally stable

□

3.5.3. Conclusion of Proof

From claims 3.5 and 3.6, for the three and four dimensional cases, we can postulate that for any dimensional system, there will be only one saturated equilibrium point, and thus, only one stable equilibrium point, which will be globally stable. For any dimension, there will be the equilibrium point of the form $(\check{z}_1, \check{z}_2, 0, 0, \ldots, 0)$ which will be saturated and have an index of $(-1)^n$. Any other equilibrium point which is saturated, and thus locally stable, will also have an index of $(-1)^n$. But by the index theorem the sum of the indices of all regular and saturated equilibria must be equal to $(-1)^n$. Thus there can be only one regular and saturated equilibrium point, which will be globally stable, and have the form $(\check{z}_1, \check{z}_2, 0, 0, \ldots, 0)$.

Chapter 4: Lotka-Volterra Example

In this chapter, examples are given to validate the proof of the previous chapter. Firstly, an ESNIS coalition is found for the system of equations (I) in §4.1.1, using the conditions given in Appendix 1. This coalition is then studied in detail (§4.1.2), after which its dynamical interaction with varying incumbent species is observed in §4.2. Then in §4.3. examples of other ESNIS coalitions are given, as well as their interaction with varying numbers of incumbent species, when the incumbents are in equilibrium, and the ESNIS coalition populations are small. In each of these cases, it is expected that the ESNIS coalition will eliminate the incumbent populations and form a new equilibrium population consisting of only the ESNIS coalition populations. Once the behaviour of ESNIS coalitions has been simulated, a similar process is carried out for various NIS coalitions which are <u>not</u> also ESS coalitions. This is §4.4. Finally in §4.5. the results of trying to find an ESS coalition which was not also an NIS are given.

4.1. The ESNIS Coalition for the System of Equations (I)

4.1.1. Finding the ESNIS Coalition

For the system of equations (I), the following carrying capacity and competitive interaction functions were chosen (Vincent & Brown, 1988):

$$k(u) = k_m \exp\left[-\frac{u^2}{2(\sigma_k)^2}\right]$$

$$\alpha(u_i - u_j) = 1 + \exp\left[-\frac{(u_i - u_j + \beta)^2}{2(\sigma_\alpha)^2}\right] - \exp\left[-\frac{\beta^2}{2(\sigma_\alpha)^2}\right]$$

where k_m, σ_k, σ_α, and β are parameters. Note that α is symmetric if $\beta = 0$ and non symmetric otherwise. Also, $\alpha(0) \equiv 1$. The parameter values were initially set as follows: $r = 0.25$, $k_m = 100$, $\sigma_\alpha^2 = \beta^2 = 4$, $\sigma_k^2 = 12.5$.

Solving the necessary conditions for the evolutionary stable strategies using Mathematica, an ESNIS coalition of $\breve{u}_1 = 3.12943$ and $\breve{u}_2 = -0.23973$ with equilibrium populations $\check{z}_1 = 51.0618$ and $\check{z}_2 = 39.2839$ was obtained. These are the same values obtained by Apaloo, 1997b. The second order conditions could be checked numerically to determine whether this point possesses any of the evolutionary stabilities. However these computations are of an extremely time-consuming nature when dealing with coevolution, and so the second order conditions were checked graphically.

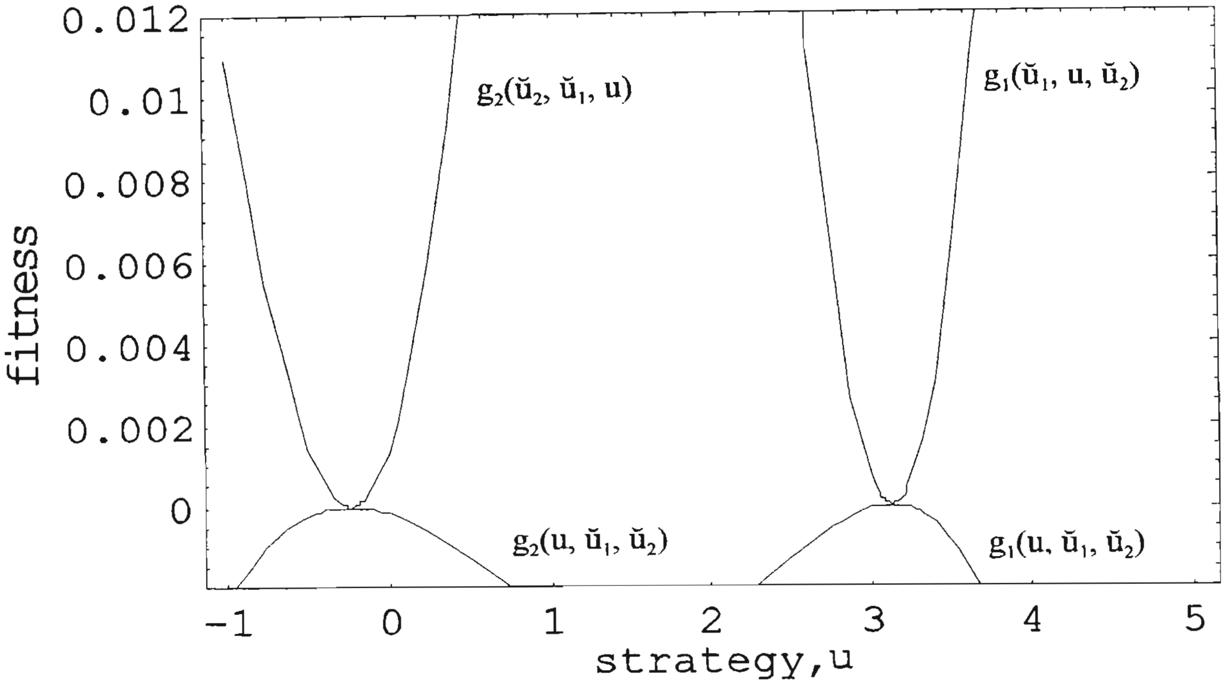

Figure 1. Graphs of fitnesses $g_1(\breve{u}_1, u, \breve{u}_2, z_1(u, \breve{u}_2), z_2(u, \breve{u}_2))$, $g_2(\breve{u}_2, \breve{u}_1, u, z_1(\breve{u}_1, u), z_2(\breve{u}_1, u))$, $g_1(u, \breve{u}_1, \breve{u}_2, \check{z}_1, \check{z}_2)$ and $g_2(u, \breve{u}_1, \breve{u}_2, \check{z}_1, \check{z}_2)$ as functions of u when $\breve{u}_1 = 3.12943$ and $\breve{u}_2 = -0.23973$. The figure shows that $(\breve{u}_1, \breve{u}_2)$ is an ESS since it cannot be invaded by any close neighbour, that is any close neighbour has negative fitness in the environment established by $(\breve{u}_1, \breve{u}_2)$. Also $\breve{u}_1$ and $\breve{u}_2$ can independently invade community phenotypes of the form $(u_1, \breve{u}_2)$ and $(\breve{u}_1, u_2)$ respectively and $(\breve{u}_1, \breve{u}_2)$ is therefore an NIS. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is thus an ESNIS.

The graphs of $g_1(\breve{u}_1, u, \breve{u}_2, z_1(u, \breve{u}_2), z_2(u, \breve{u}_2))$, $g_2(\breve{u}_2, \breve{u}_1, u, z_1(\breve{u}_1, u), z_2(\breve{u}_1, u))$, $g_1(u, \breve{u}_1, \breve{u}_2, \check{z}_1, \check{z}_2)$, $g_2(u, \breve{u}_1, \breve{u}_2, \check{z}_1, \check{z}_2)$ as functions of u are shown in Figure 1. Observe that $(\breve{u}_1, \breve{u}_2)$ satisfies the conditions for ESS and NIS since $g_1(\breve{u}_1, u, \breve{u}_2, z_1(u, \breve{u}_2), z_2(u, \breve{u}_2))$ and $g_2(\breve{u}_2, \breve{u}_1, u, z_1(\breve{u}_1, u), z_2(\breve{u}_1, u))$ have minimum values of 0 at $u = \breve{u}_1$ and $u = \breve{u}_2$ respectively, while $g_1(u, \breve{u}_1, \breve{u}_2, \check{z}_1, \check{z}_2)$ and $g_2(u, \breve{u}_1, \breve{u}_2, \check{z}_1, \check{z}_2)$ have maximum values of 0 at $u = \breve{u}_1$ and $u = \breve{u}_2$ respectively.

4.1.2. Characteristics of the ESNIS Coalition

The characteristics of the ESNIS coalition were studied by observing the effects of the coalition, and the individual members of the coalition, when they were introduced into various incumbent populations (Apaloo, 1997b).

The above ESNIS coalition was introduced at low densities ($z_1 = z_2 = 10$) into a community at ecological equilibrium ($z_3 = 38.0368$, $z_4 = 37.3404$) established by the community phenotype $u_3 = 4$ and $u_4 = -4$. Ecological dynamic interaction of the augmented community over 800 generations was simulated. The result, shown in Figure 2a, was that the ESNIS phenotypes exclude the phenotypes that do not form an ESNIS coalition, and form a new ecologically stable and evolutionary non-invadable community. Each of $\breve{u}_1$ and $\breve{u}_2$ can invade the community formed by (u_3, u_4), and the community ($\breve{u}_1$, $\breve{u}_2$) cannot be invaded by any of u_3 or u_4 since it is an ESNIS coalition.

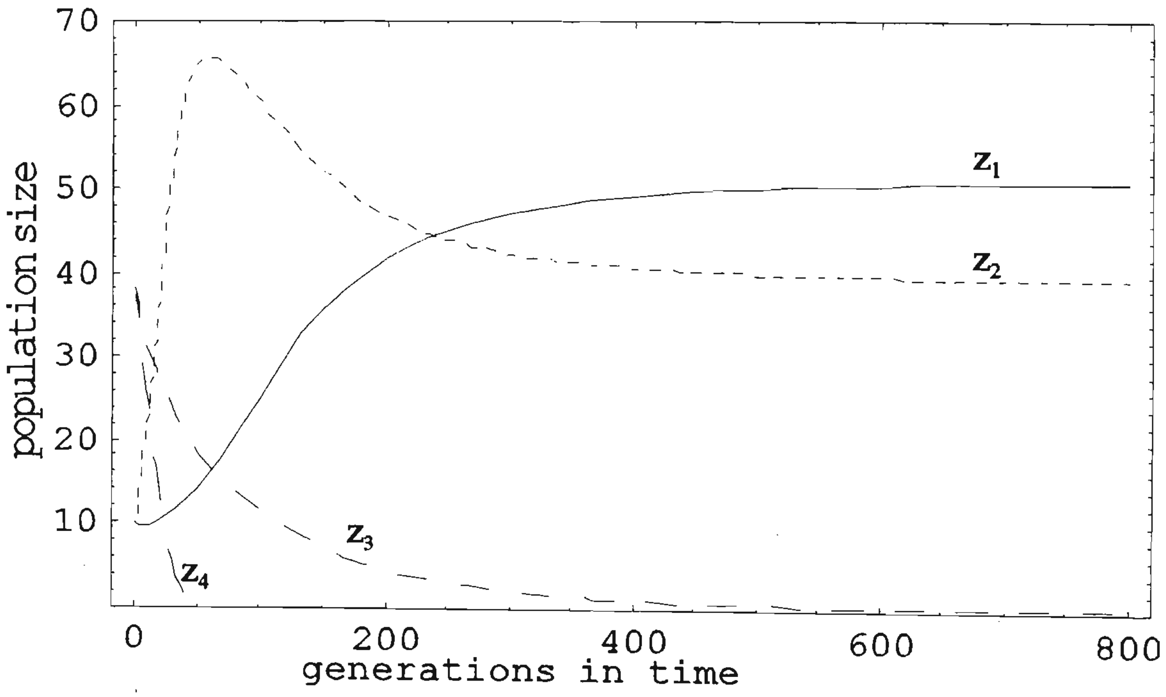

Figure 2a. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.12943, -0.23973, 4, -4). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition any of $\breve{u}_1$ and $\breve{u}_2$ can invade (u_3, u_4). The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

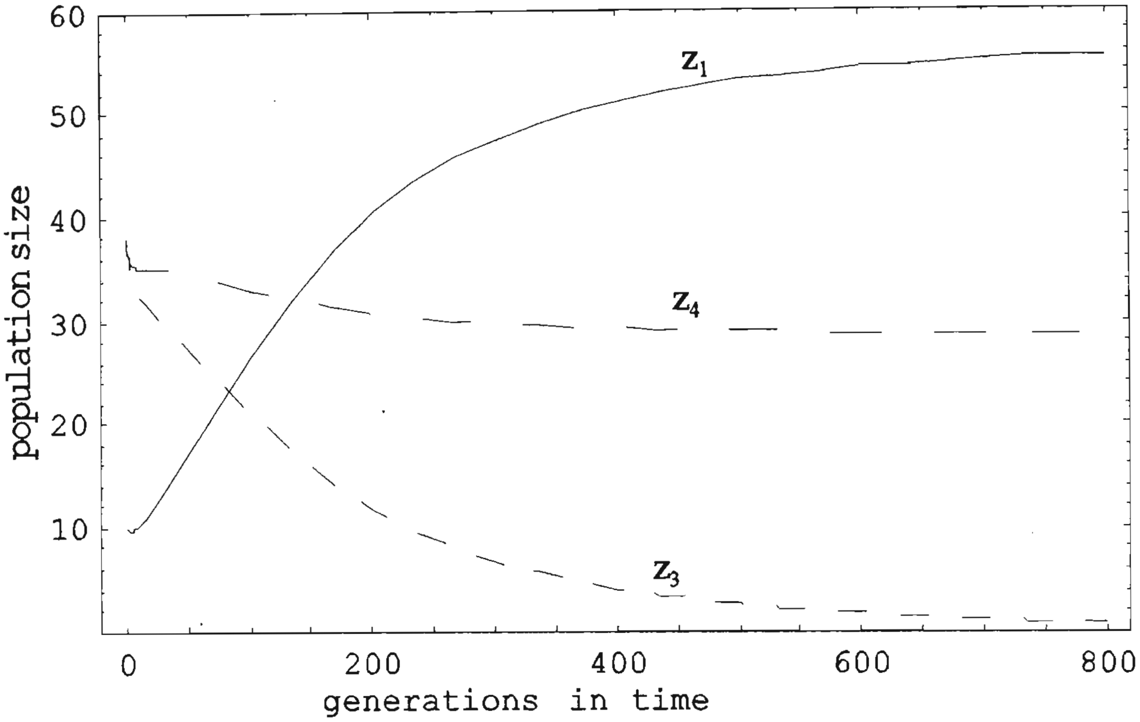

Figure 2b. Ecological dynamics of a community with phenotype $(\breve{u}_1, u_3, u_4) = (3.12943, 4, -4)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition any of $\breve{u}_1$ and $\breve{u}_2$ can invade (u_3, u_4). The invader species 1, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, u_3 and u_4 respectively. The respective population densities are z_1, z_3, and z_4.

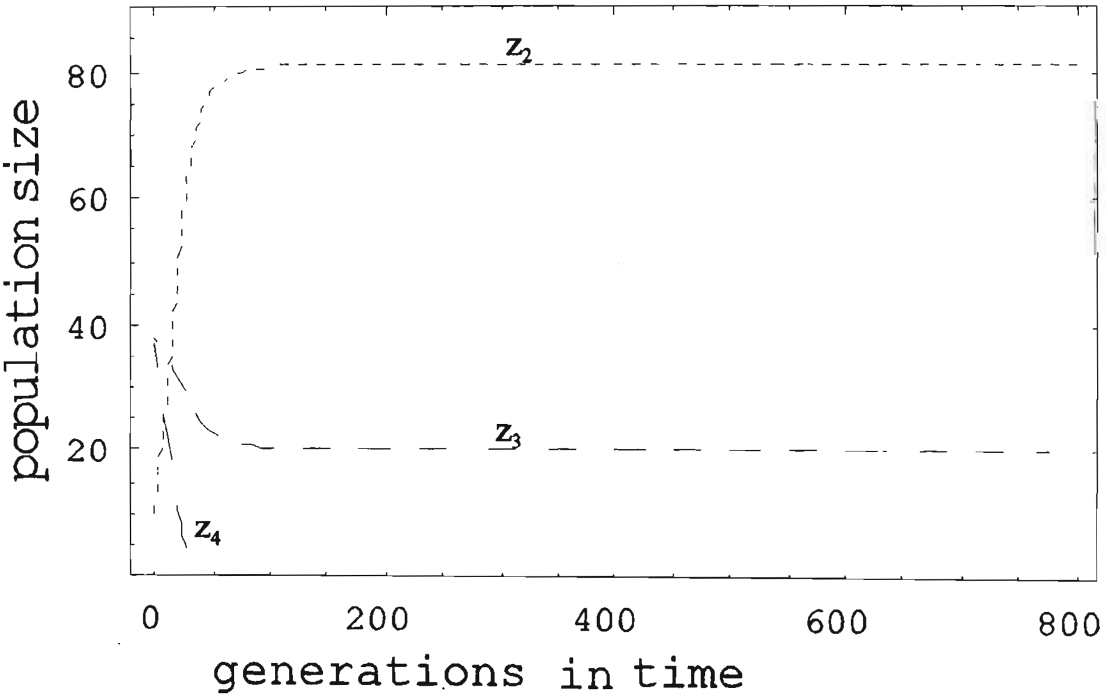

Figure 2c. Ecological dynamics of a community with phenotype $(\breve{u}_2, u_3, u_4) = (-0.23973, 4, -4)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition any of $\breve{u}_1$ and $\breve{u}_2$ can invade (u_3, u_4). The invader species 1, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_2, z_3, and z_4.

Figures 2b and 2c show the resulting ecological dynamics when the community (u_3, u_4) is invaded by $\breve{u}_1$ and $\breve{u}_2$ respectively. In Figure 2b $\breve{u}_1$ replaces the phenotype u_3 and in Figure 2c $\breve{u}_2$ replaces u_4. However, as will now be shown, these are not general outcomes of ecological competition between ESS coalition and non-ESS coalitions. It is however interesting to note, that if the initial populations of z_1 and z_2 are reduced radically in size, that the same end result occurs, just over a longer time period.

Two other incumbent community phenotypes are now looked at (Apaloo, 1997b). (2.8, −0.6) can be invaded by $\breve{u}_1$ and it repels $\breve{u}_2$, while (3.1, −0.7) repels $\breve{u}_1$ and can be invaded by $\breve{u}_2$. The ecological dynamics for these two communities are shown in Figures 3a-c and 4a-c respectively.

In Figure 3a, $\breve{u}_1$ successfully invades the incumbent population, but it neither replaces nor excludes the incumbent phenotypes. The three phenotypes maintain an ecologically stable community. Figure 3b shows $\breve{u}_2$ being repelled by the community with phenotype (2.8, −0.6). Figure 3c shows the dynamics involving $\breve{u}_1$, $\breve{u}_2$, 2.8, −0.6 where the phenotypes 2.8 and −0.6 are excluded. The results from Figure 3c are qualitatively the same as those from Figure 2a. That is, the population sizes will end up being the same in Figure 3c as they end up in Figure 2a.

Similar conclusions can be inferred from the dynamics shown in Figures 4a-c. In Figure 4a, $\breve{u}_1$ is repelled by the incumbent phenotypes (2.8, −0.6), while in Figure 4b, $\breve{u}_2$ invades the incumbent phenotypes, and the three phenotypes form an ecological stable community. Finally, in Figure 4c, the ESNIS coalition invades and displaces the incumbent phenotypes, with the final ESNIS coalition populations being the same as found in Figures 2a and 3c. Note that the system in Figure 4c only stabilizes after a very large generation time.

It is also of interest to note that in the interactions between $\breve{u}_1$ (or $\breve{u}_2$) with the community (u_3, u_4), $\breve{u}_1$ (or $\breve{u}_2$) does not necessarily invade the incumbent phenotypes, and if it does invade it does not necessarily replace one of the incumbents, as happened in Figure 2b and Figure 2c. Thus only if the whole ESNIS coalition ($\breve{u}_1$, $\breve{u}_2$) invades the incumbent community, as opposed to one of the members of the coalition, can one be certain of the incumbent population being displaced.

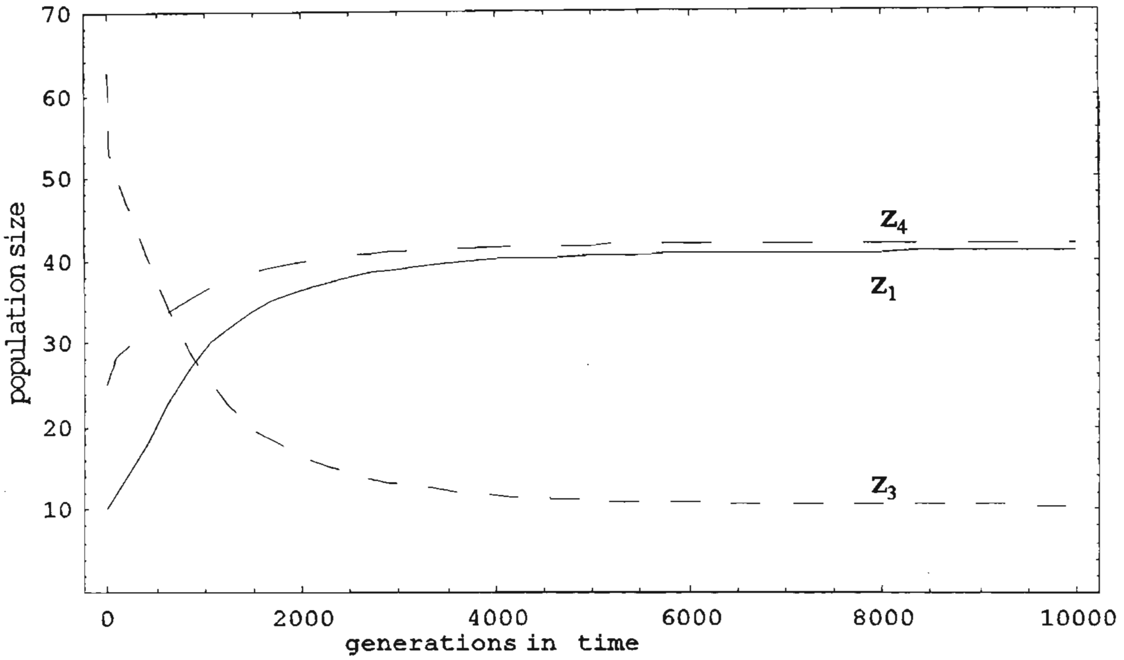

Figure 3a. Ecological dynamics of a community with phenotype ($\breve{u}_1$, u_3, u_4) = (3.12943, 2.8, −0.6). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition $\breve{u}_1$ can (and $\breve{u}_2$ cannot) invade (u_3, u_4). The invader species 1, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $_3$ and u_4 respectively. The respective population densities are z_1, z_3, and z_4.

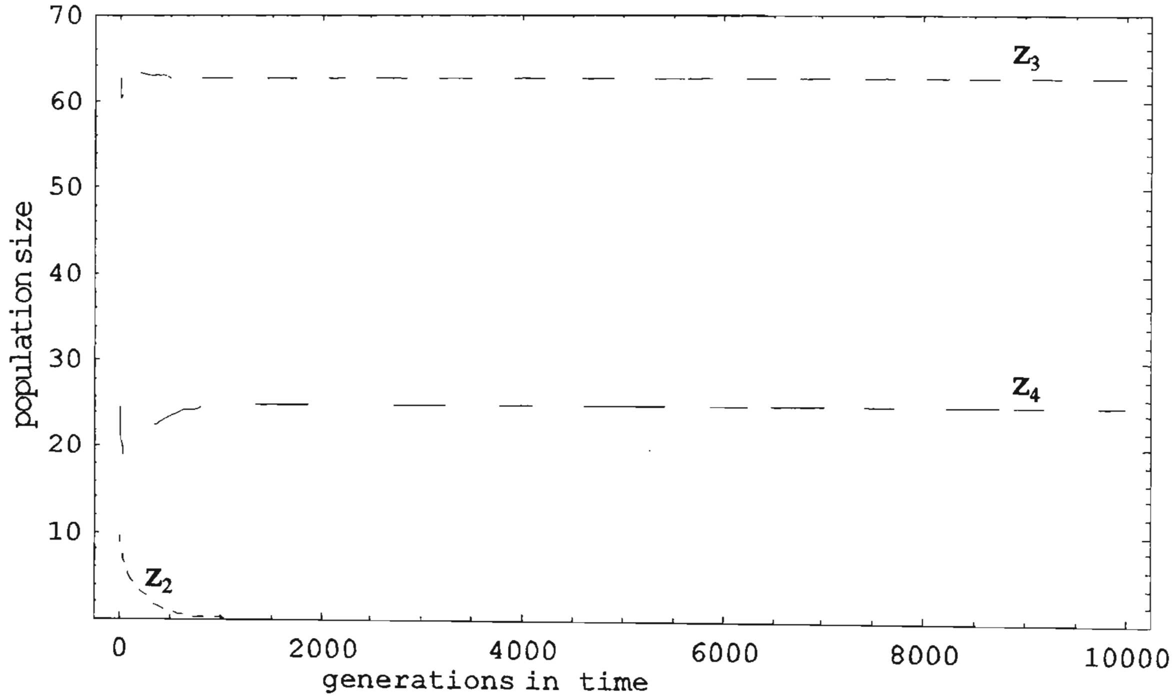

Figure 3b. Ecological dynamics of a community with phenotype ($\breve{u}_2$, u_3, u_4) = (−0.23973, 2.8, −0.6). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition $\breve{u}_2$ cannot (and $\breve{u}_1$ can) invade (u_3, u_4). The invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_2, z_3, and z_4.

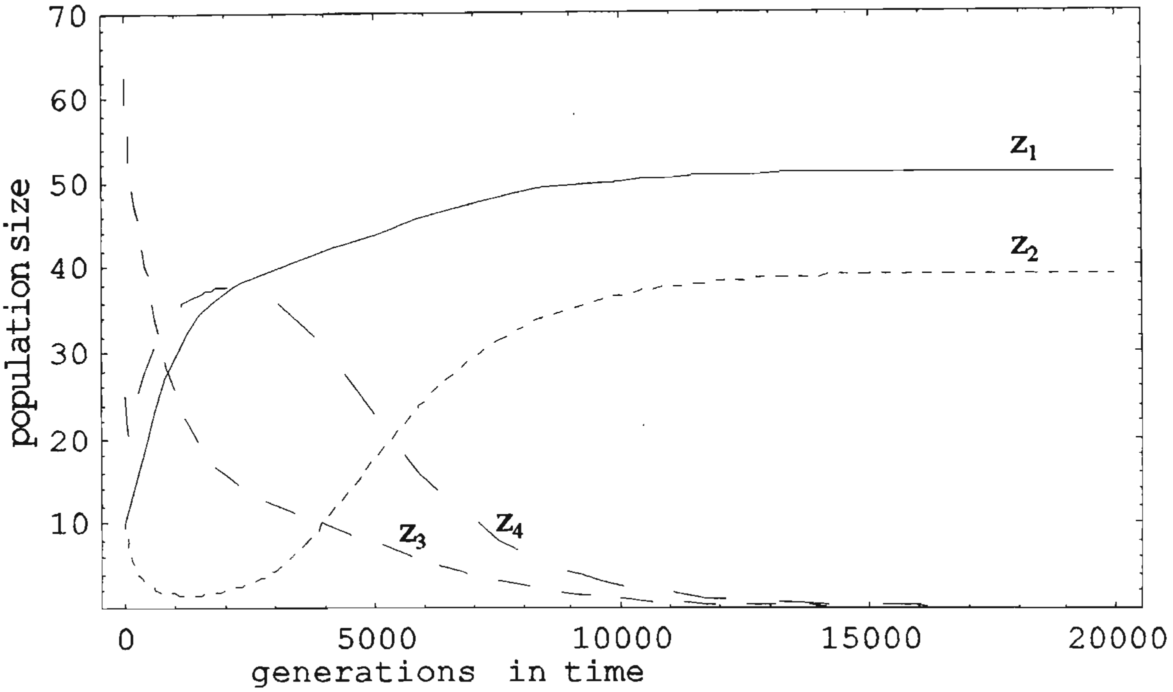

Figure 3c. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4) = (3.12943, -0.23973, 2.8, -0.6)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition $\breve{u}_1$ can and $\breve{u}_2$ cannot invade (u_3, u_4). The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

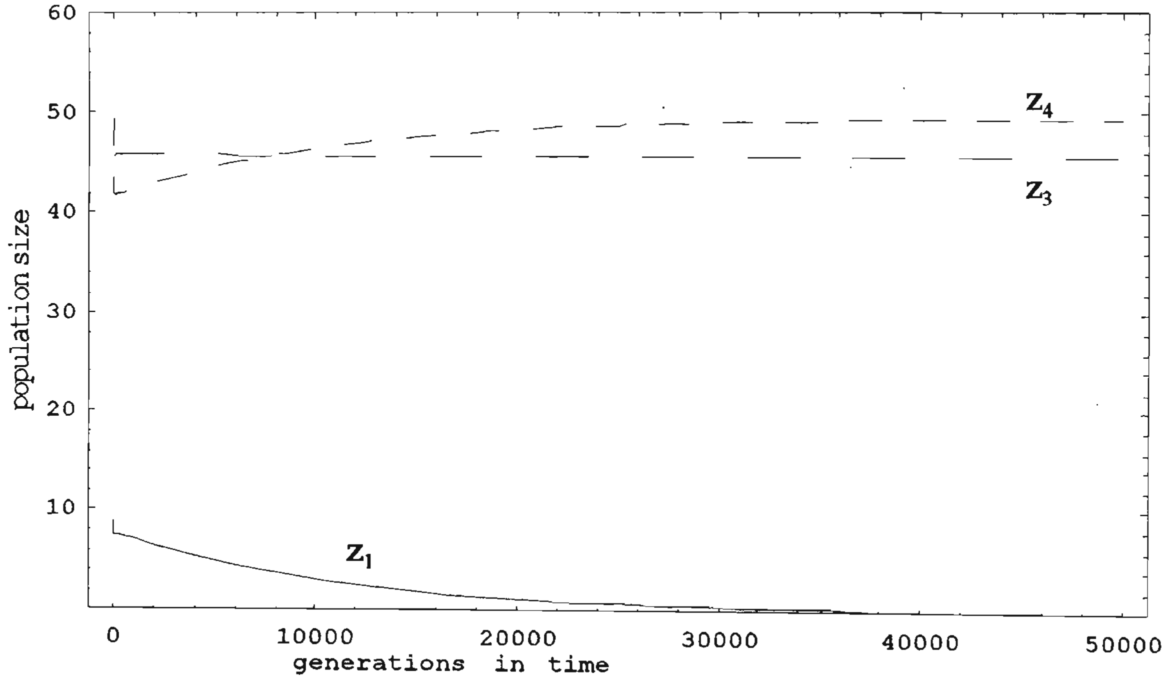

Figure 4a. Ecological dynamics of a community with phenotype $(\breve{u}_1, u_3, u_4) = (3.12943, 3.1, -0.7)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition $\breve{u}_1$ cannot (and $\breve{u}_2$ can) invade (u_3, u_4). The invader species 1, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, u_3 and u_4 respectively. The respective population densities are z_1, z_3, and z_4.

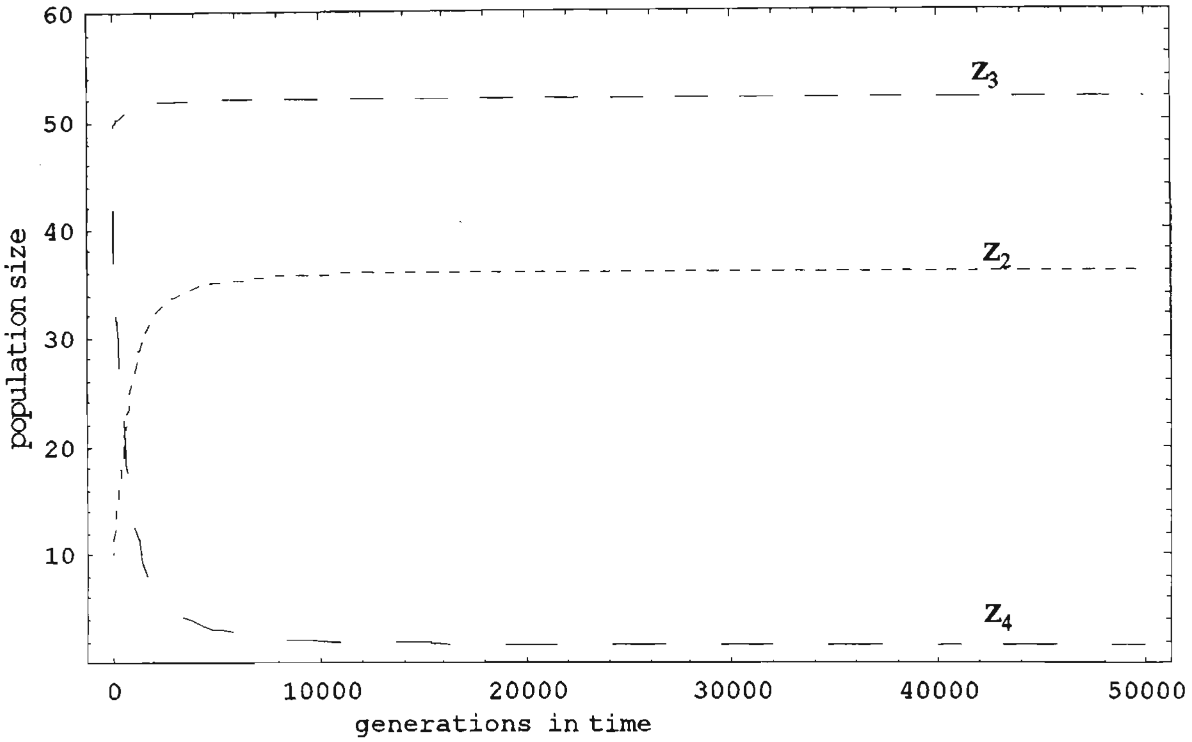

Figure 4b. Ecological dynamics of a community with phenotype ($\breve{u}_2$, u_3, u_4) = (−0.23973, 3.1, −0.7). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition $\breve{u}_2$ can (and $\breve{u}_1$ cannot) invade (u_3, u_4). The invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_2, z_3, and z_4.

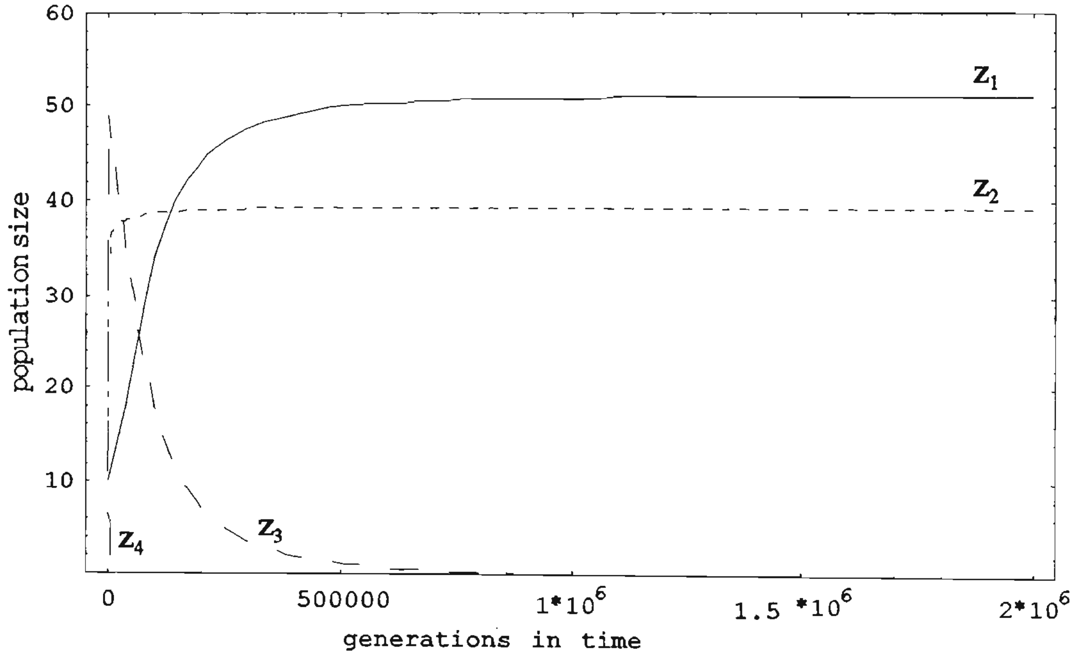

Figure 4c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.12943, −0.23973, 3.1, −0.7). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. In addition $\breve{u}_1$ cannot and $\breve{u}_2$ can invade (u_3, u_4). The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

4.2 Dynamics of the ESNIS Coalition with Phenotypes (3.12943, −0.23973)

The dynamics of the ESNIS coalition with phenotypes (3.12943, −0.23973) when there are one, two, three and four incumbent populations all at equilibrium, with the ESNIS populations being introduced at low frequency are now looked at. According to the theory presented in the previous chapter, the ESNIS should displace all incumbent populations, regardless of their phenotypes. In Figures 5a-d, the situation where there is one incumbent phenotype at equilibrium was being simulated, and the ESNIS was introduced at low frequency.

In Figure 5a the incumbent phenotype was $u_3 = 3.1$ and the equilibrium incumbent population was $z_3 = 68.09$. In this case, a long time (800 000 generations) was needed before the ESNIS totally eliminated the incumbent population, but as expected, the incumbent population was eliminated. In Figure 5b, where $u_3 = -0.2$ and the corresponding equilibrium population density was $z_3 = 99.84$, and it took 600 000 generations before the incumbent population became extinct. In both these cases the incumbent population was using a phenotype which was close to that of one of the ESNIS coalition's phenotypes.

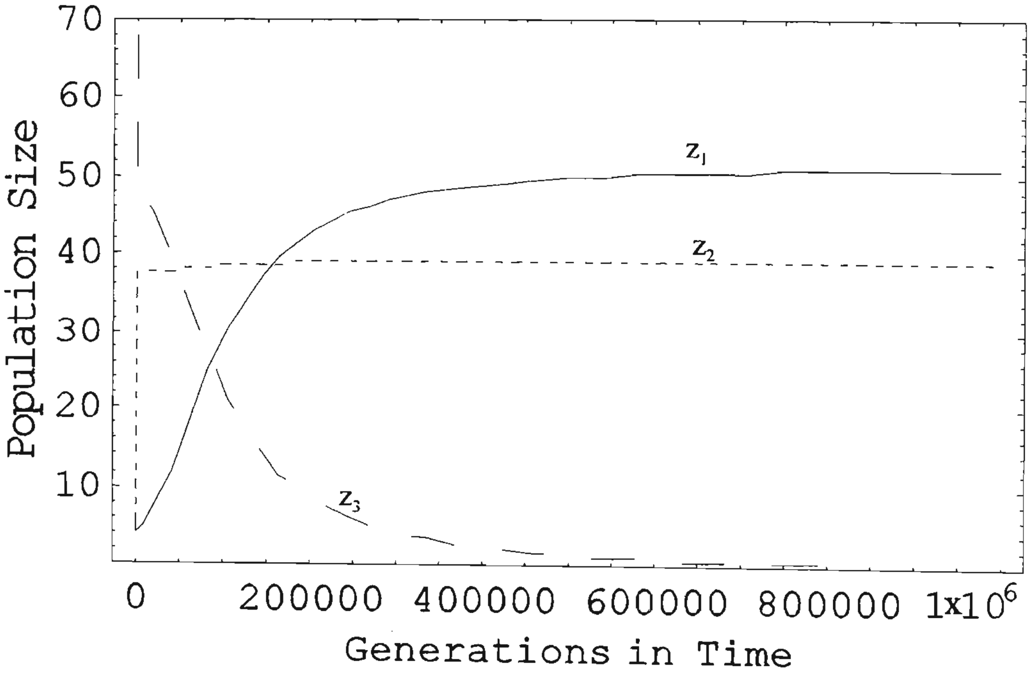

Figure 5a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (3.12943, -0.23973, 3.1)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3) is neither an ESS nor an NIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

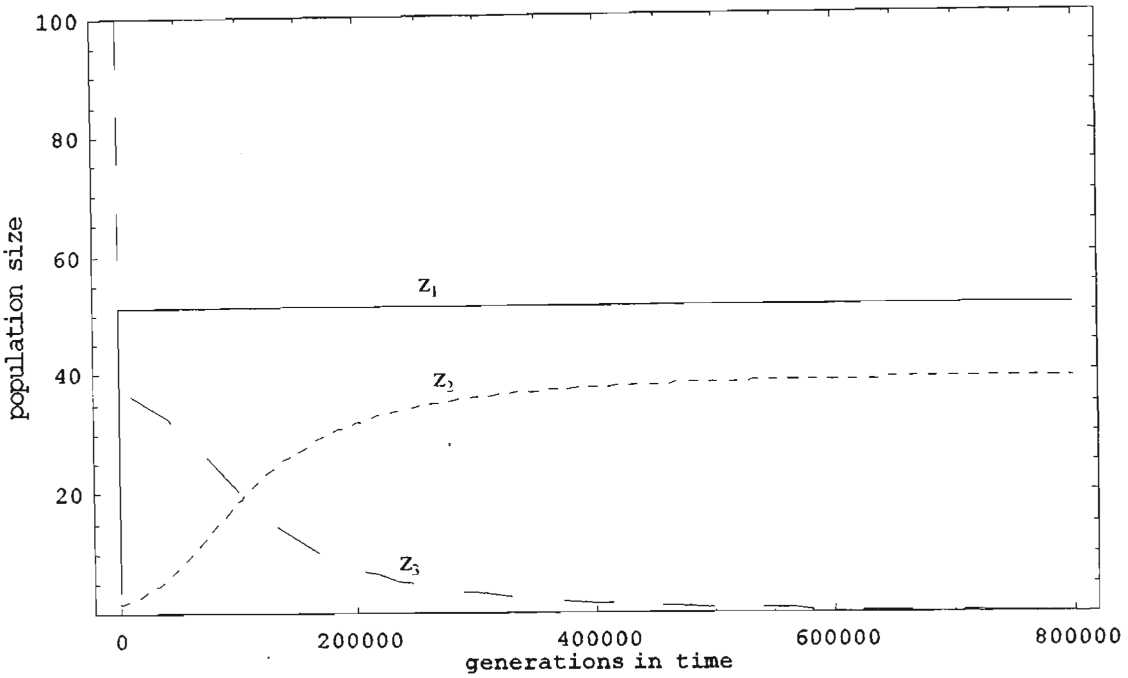

Figure 5b. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (3.12943, -0.23973, -0.2)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3) is neither an ESS nor an NIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

In Figure 5c, the incumbent phenotype was the average of the two ESNIS phenotypes taken to two decimal places, namely $u_3 = 1.44$ and its corresponding equilibrium population was $z_3 = 91.99$, but in this case it only took 1000 generations for the ESNIS coalition to displace the incumbent population completely. Lastly, in Figure 5d, the incumbent phenotype was chosen as $u_3 = 2.8$, as it was for the simulations shown in Figures 3a-c. The incumbent equilibrium population was $z_3 = 73.08$, and it took 10 000 generations for it to be displaced. Note that in all the cases, the ESNIS coalition displaces the incumbent population, although in some cases it takes a large number of generations to do so. This is in keeping with what we would have predicted based on our work in the previous chapter.

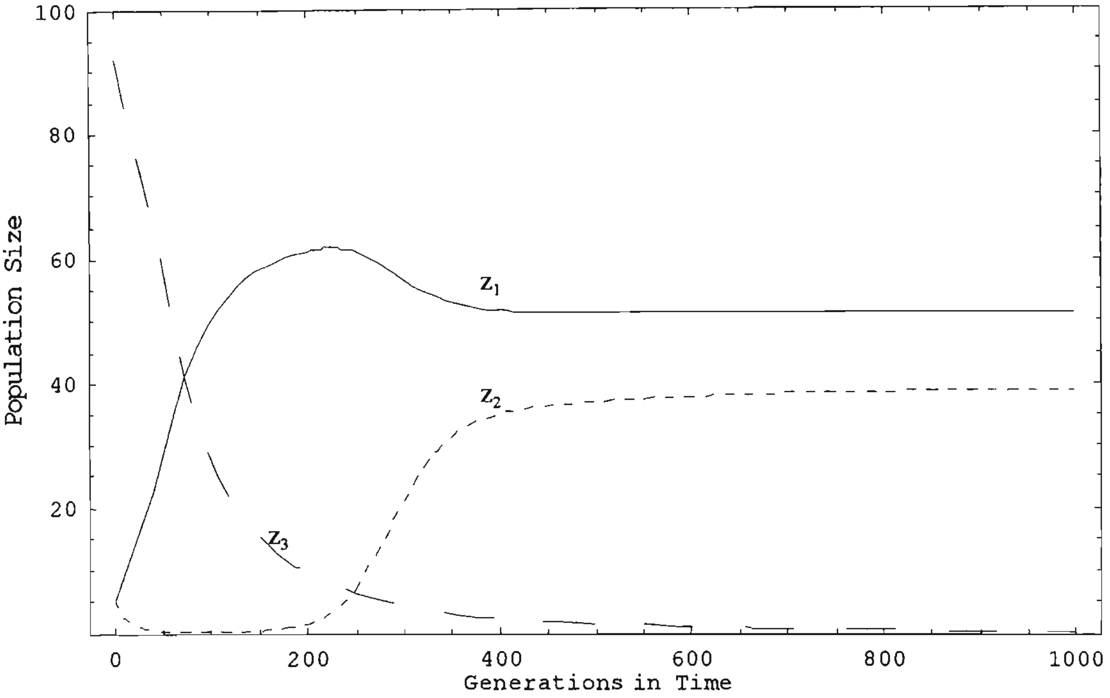

Figure 5c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3) = (3.12943, -0.23973, 1.44). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3) is neither an ESS nor a NIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

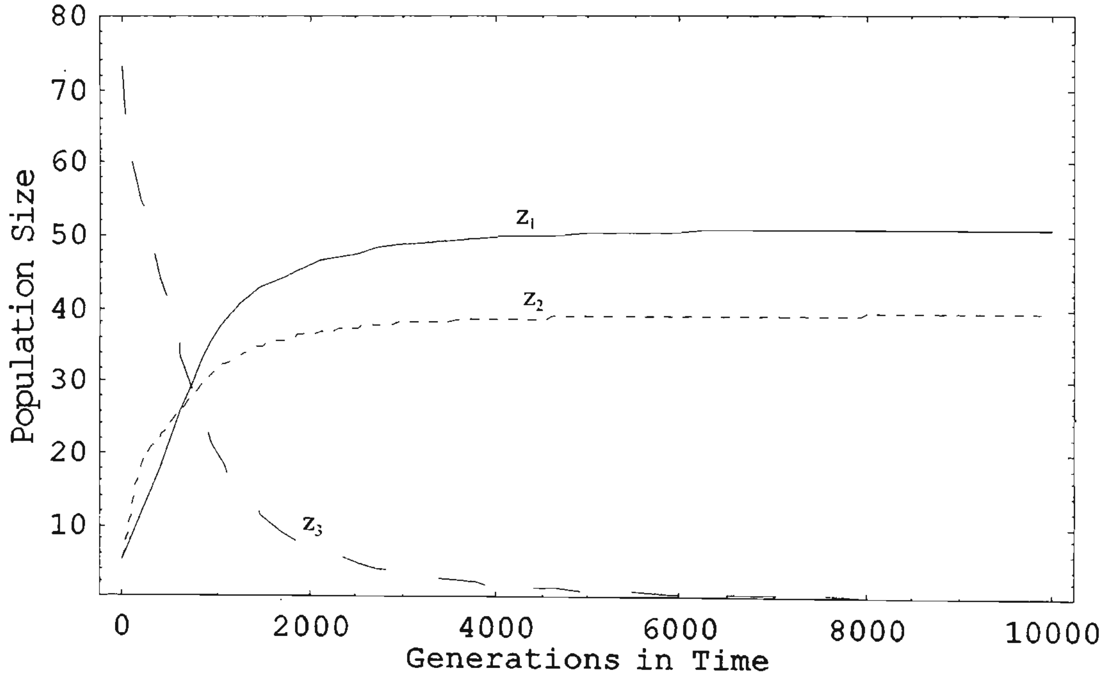

Figure 5d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3) = (3.12943, -0.23973, 2.8). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3) is neither an ESS nor a NIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

In Figures 6a-c we have the ESNIS coalition entering at low frequency into two incumbent populations which are in equilibrium, and again displacing them. These are similar to the simulations run in figures 2a to 4c, except that different phenotypes for the incumbent populations have been chosen. In Figure 6a, the equilibrium populations of $z_3 = 52.62$ and $z_4 = 36.54$ with phenotypes $u_3 = 3.1$ and $u_4 = -0.2$ respectively are incumbent. Again these phenotypes are close the phenotypes of the ESNIS coalition, but the ESNIS coalition still displaces the incumbents, albeit that it takes almost 10^6 generations. In Figure 6b the ESNIS coalition only takes 10 000 generations to displace the phenotypes $u_3 = 4$ and $u_4 = -0.6$ whose equilibrium populations densities are $z_3 = 20.10$ and $z_4 = 82.03$ respectively. In Figure 6c, the incumbent community phenotype is $u_3 = 6$ and $u_4 = -5.6$ with population sizes of $z_3 = 14.75$ and $z_4 = 22.72$ at equilibrium respectively. In this case the ESNIS coalition only took 300 generations to displace the incumbents.

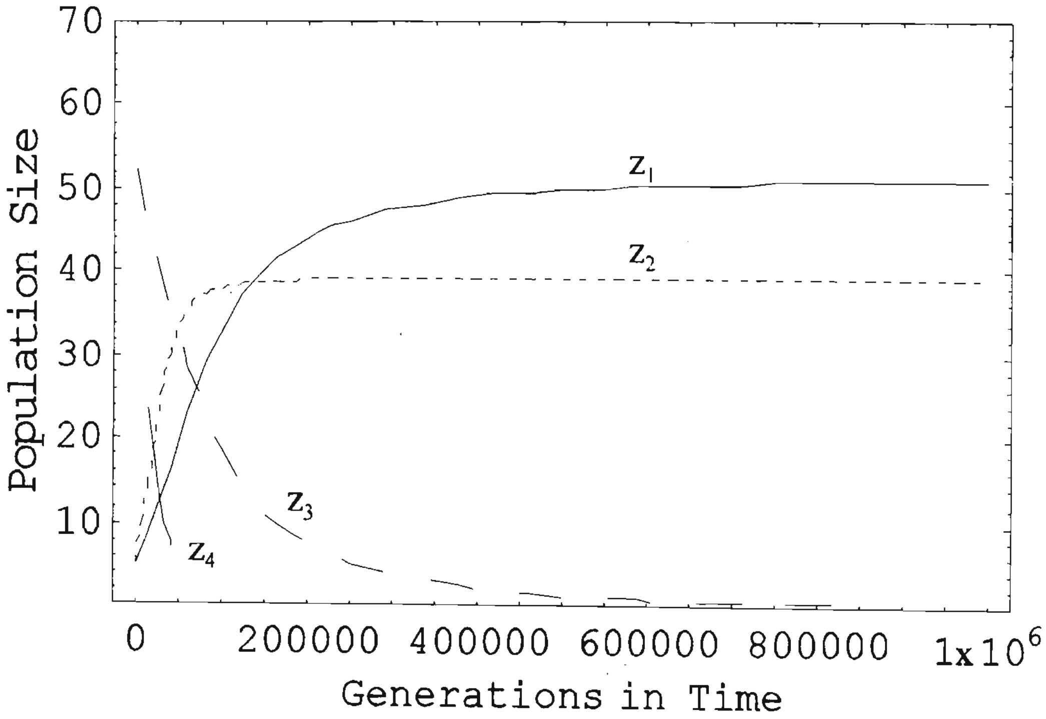

Figure 6a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4) = (3.12943, -0.23973, 3.1, -0.2)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

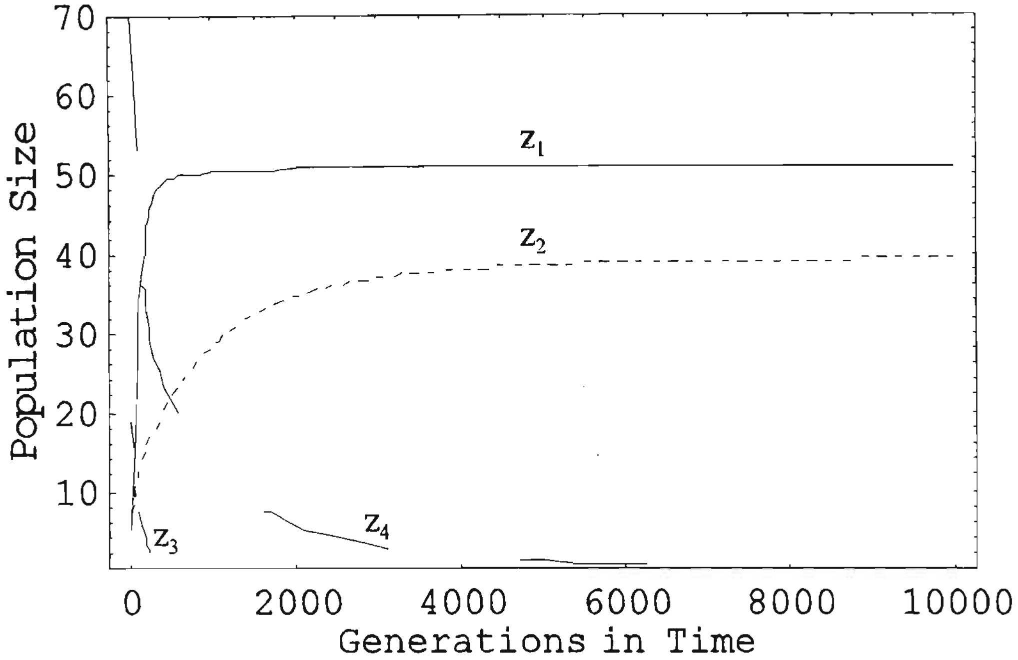

Figure 6b. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.12943, −0.23973, 4, −0.6). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

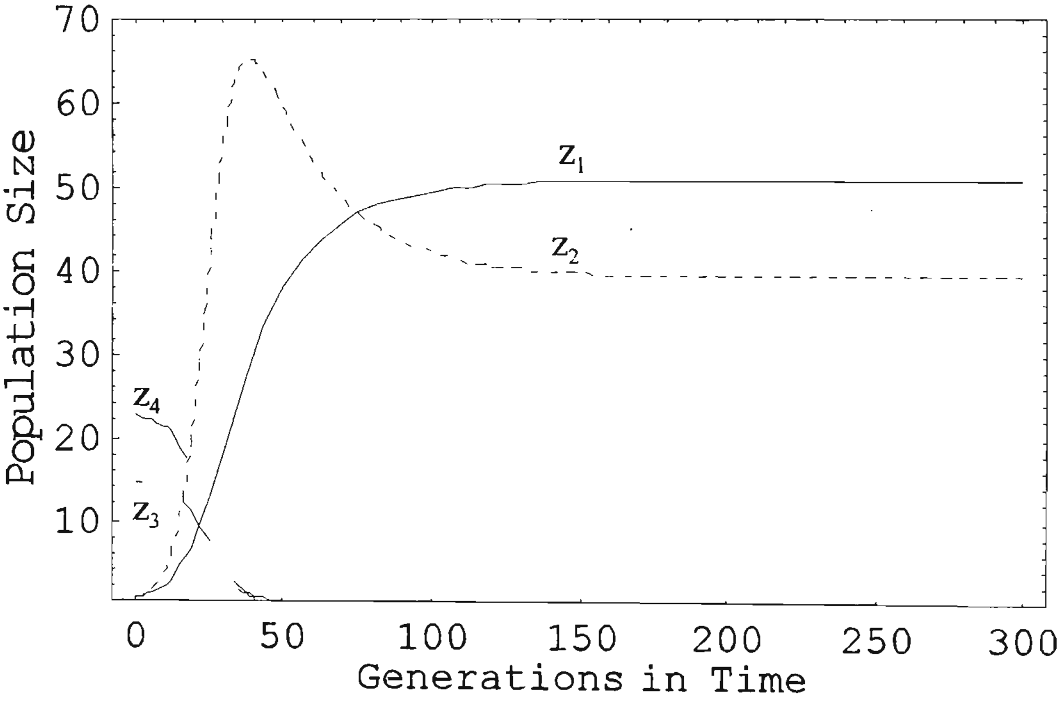

Figure 6c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.12943, −0.23973, 6, −5.6). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

In Figure 7 and Figure 8 there are three and four incumbent populations respectively. In Figure 7 the ESNIS coalition was introduced into an incumbent population using the three different phenotypes $u_3 = 3.1$, $u_4 = 2.1$ and $u_5 = -1.2$ whose respective equilibrium population densities are $z_3 = 44.30$, $z_4 = 8.96$ and $z_5 = 43.32$. As the one incumbent population density (z_4) was so low, the ESNIS coalition was allowed to enter with population sizes of 0.5 for both phenotypes in the ESNIS coalition. In Figure 8, a fourth incumbent phenotype $u_6 = -4$ was added to the three incumbent phenotypes used in Figure 7. The incumbent equilibrium population densities became $z_3 = 45.10$, $z_4 = 31.54$, $z_5 = 2.74$ and $z_6 = 20.11$. Again the ESNIS coalition entered with population sizes well below 1. In both cases it took almost one million generations for the ESNIS coalition to displace the incumbents, but the incumbents were displaced by the ESNIS coalition, as was expected.

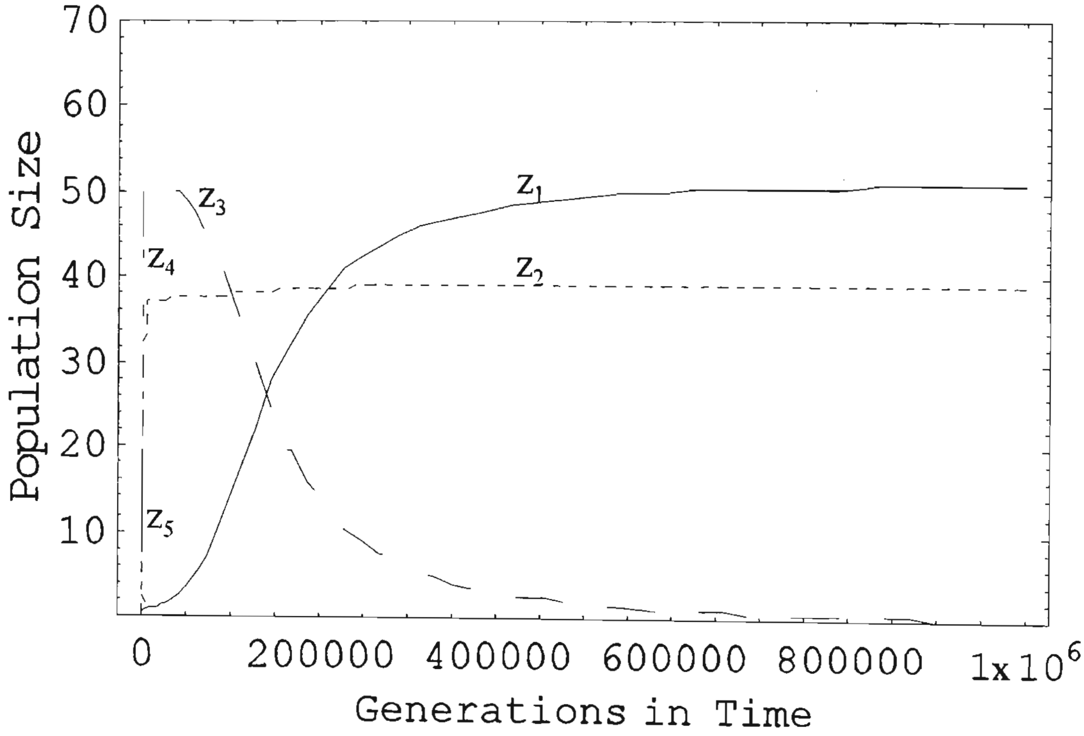

Figure 7. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4, u_5) = (3.12943, -0.23973, 3.1, 2.1, -1.2)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4, u_5) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4 and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4, and z_5.

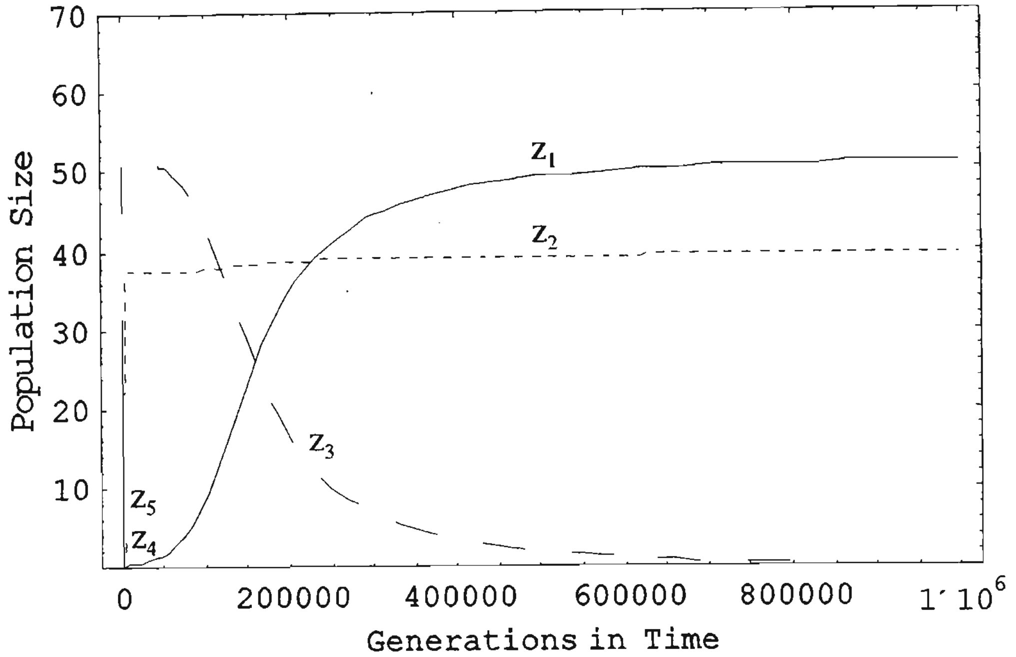

Figure 8. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4, u_5, u_6) = (3.12943, -0.23973, 3.1, 2.1, -1.2, -4)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4, u_5, u_6) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 , incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6.

4.3 Dynamics of Other ESNIS Coalitions

The effect on an incumbent population in equilibrium when various other ESNIS coalitions enter was simulated. By varying the parameters σ_a, σ_k, and β it was possible to find other ESNIS coalitions when solving for the conditions given in Appendix 1. Table 1 contains ten such possible coalitions, and the parameter values which would result in the coalition. It is important to note that these ten possibilities are just a small sample of the many possibilities that could be found. In fact, taking any one of the ten points, and then varying just one of the parameters at a time will yield many more possibilities.

Of the ten coalitions given in Table 1, the dynamics of only four were looked at. The four looked at where coalitions 2, 3, 5 and 7, and these were selected to give a wide range of parameter values. Similar simulations can be carried out for the other six coalitions, as well as any other ESNIS coalition that can be found, and the results in each case should be similar. It is expected that every ESNIS coalition will displace all the incumbent populations, and stabilise at the ESNIS coalition's equilibrium population densities.

Coalition	β	σ_a	σ_k^2	$\check{u}_1$	$\check{u}_2$
1	0.8	0.525	13.0546	4.68824	3.49983
2	1	3.3	12.5	1.66494	-0.442381
3	1.5	3	12.5	2.34102	-0.535529
4	1.5	3.3	16	2.87159	-0.470848
5	1.75	1.5	12.5	3.27926	0.42584
6	2	1	12.5	2.2116	-1.54618
7	2	2.5	12.5	2.87702	-0.596216
8	2	3.2	12.5	2.01149	-1.94854
9	2.3	3	12.5	2.37989	-1.99306
10	2.5	2.5	12.5	2.83329	-1.60371

Table 1: Various parameter values for β, σ_a, and σ_k which give an ESNIS coalition ($\check{u}_1$, $\check{u}_2$).

4.3.1. Dynamics of the ESNIS Coalition (1.66494, -0.442381)

From Table 1, the ESNIS coalition (1.66494, -0.442381) is found when the parameter values are set as follows: $\beta = 1.0$; $\sigma_a = 3.3$; and $\sigma_k^2 = 12.5$. The equilibrium population densities of the ESNIS coalition are $\check{z}_1 = 66.7573$ and $\check{z}_2 = 33.1217$. The ESNIS coalition was allowed to enter into several different incumbent populations, as shown in Figures 9a-e.

In Figure 9a, there is only one incumbent population in equilibrium. It's phenotype is $u_3 = 3$ and the corresponding equilibrium population density is $z_3 = 69.7676$. The ESNIS coalition enters with initial population densities equal to 5.0, and the ESNIS coalition takes about 8000 generations to completely eliminate the incumbent population.

In Figure 9b, there are two incumbent populations, $u_3 = 3$ and $u_4 = 2.1$ with corresponding equilibrium population densities of $z_3 = 28.1217$ and $z_4 = 74.3435$. The ESNIS coalition again entered with initial population densities equal to 5.0, and in this case the ESNIS coalition took about 300 000 generations to eliminate the incumbent populations.

In Figure 9c, there are three incumbent populations in equilibrium, whose phenotypes are $u_3 = 3$, $u_4 = 2.1$ and $u_5 = -1.2$, with corresponding equilibrium densities of $z_3 = 9.02272$, $z_4 = 45.6072$, and $z_5 = 44.2492$. The ESNIS coalition is introduced into the system with initial population densities of 2.5. In this case, the ESNIS coalition took almost 600 000 generations to reach its equilibrium population densities after completely displacing the three incumbent populations.

In Figure 9d, a similar situation was simulated, with the three incumbent populations haveing phenotypes of $u_3 = 1.6$, $u_4 = -0.4$, and $u_5 = 2.0$, and corresponding equilibrium densities of $z_3 = 55.4791$, $z_4 = 33.5374$, and $z_5 = 10.7899$. The ESNIS coalition again entered with initial populations equal to 2.5, and over 3×10^7 generations pass before all the incumbents are finally displaced completely.

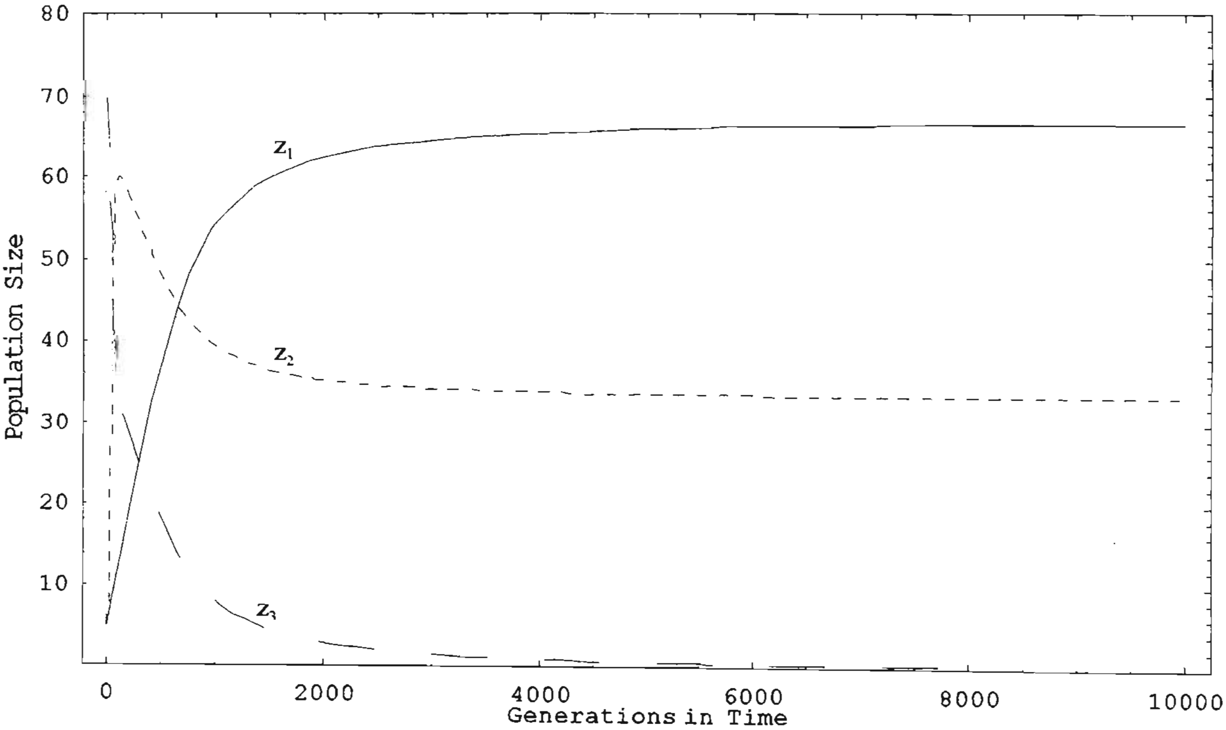

Figure 9a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (1.66494, -0.442381, 3)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3) is neither an ESS nor a NIS. The invader species 1, invader species 2, and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

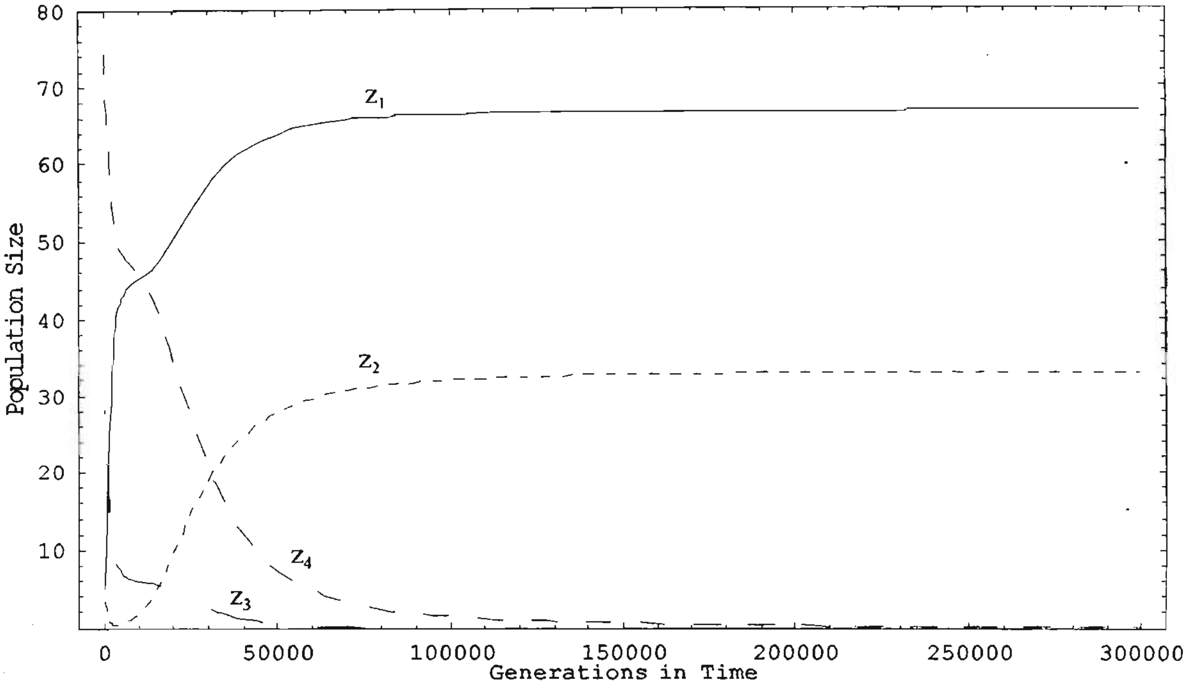

Figure 9b. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (1.66494, -0.442381, 3, 2.1). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1, and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

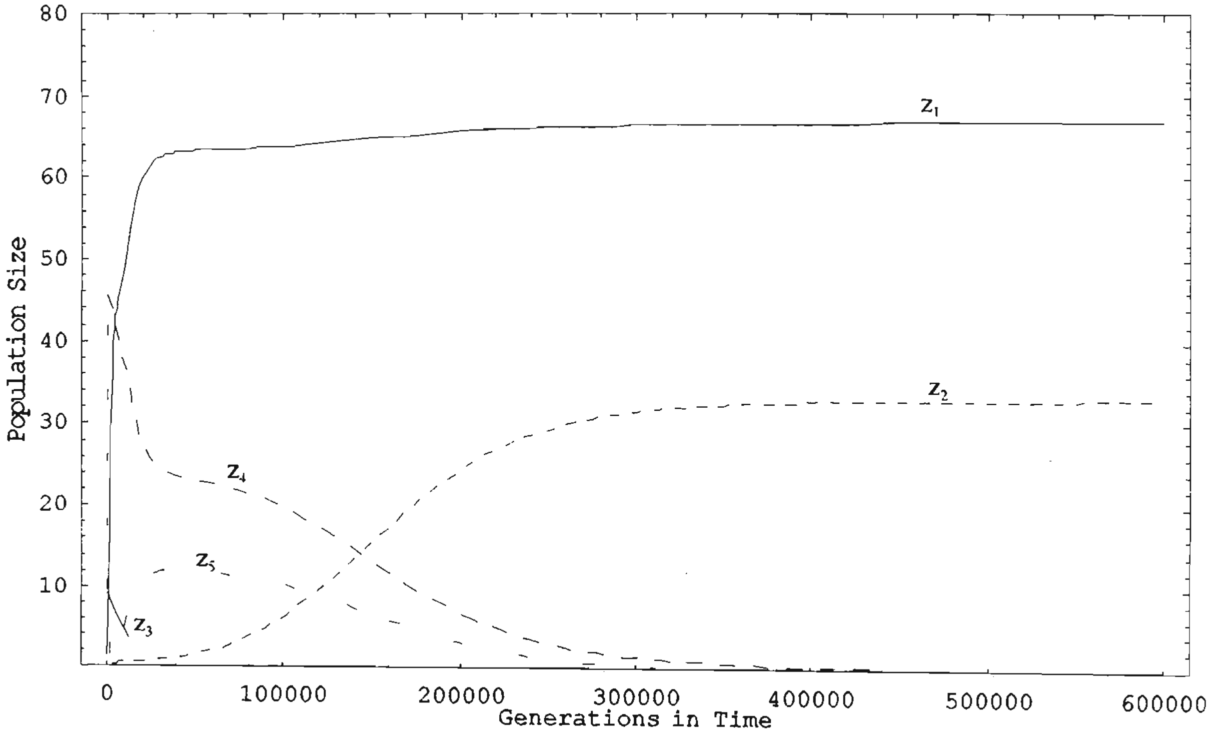

Figure 9c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5) = (1.66494, -0.442381, 3, 2.1, -1.2). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4, u_5) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4, and z_5.

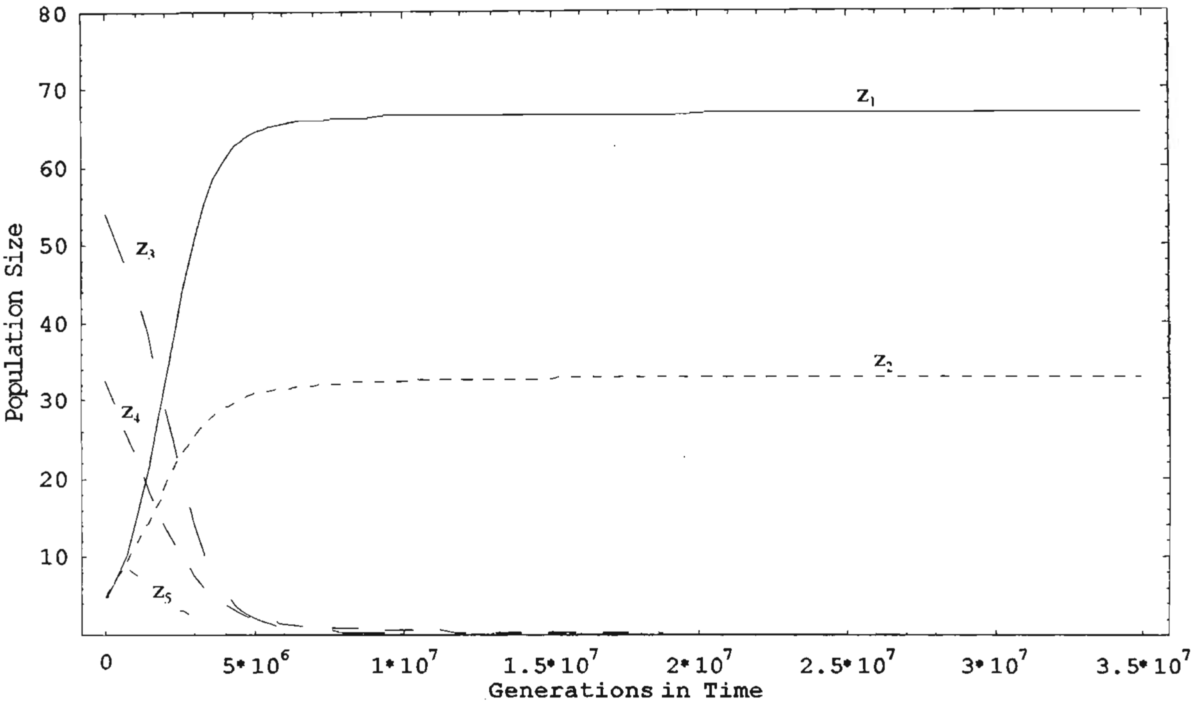

Figure 9d. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4, u_5) = (1.66494, -0.442381, 1.6, -0.4, 2.0)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4, u_5) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4, and z_5.

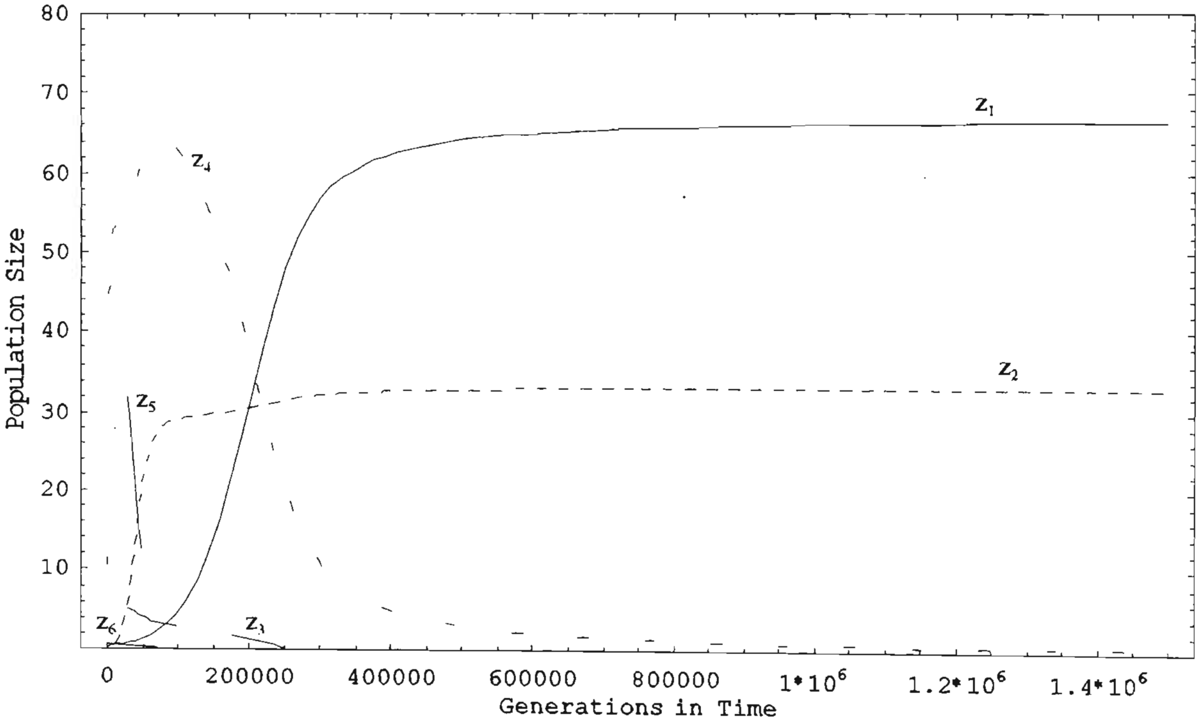

Figure 9e. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4, u_5, u_6) = (1.66494, -0.442381, 3, 2.1, 1.5, -3)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4, u_5, u_6) is neither an ESS nor a NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6.

In Figure 9e, there are four incumbent populations, using phenotypes $u_3 = 3.0$, $u_4 = 2.1$, $u_5 = 1.5$, and $u_6 = -3.0$. The corresponding equilibrium population densities are $z_3 = 11.4342$, $z_4 = 48.6541$, $z_5 = 38.9694$, and $z_6 = 0.526123$. The ESNIS coalition entered with population densities of 0.25, and took about 1 500 000 generations to stabilise and totally displace the incumbent populations.

Note that in Figures 9a-e, the final population densities of the ESNIS coalition are the same, regardless of how many incumbent populations were initially in residency. In §4.3.2., §4.3.3., and §4.3.4., similar simulations are run, with similar results.

4.3.2. Dynamics of the ESNIS Coalition (2.34102, −0.535529)

From Table 1, the ESNIS coalition (2.34102, −0.535529) is found when the parameter values are set as follows: $\beta = 1.5$; $\sigma_a = 3$; and $\sigma_k^2 = 12.5$. The equilibrium population densities of the ESNIS coalition are $\check{z}_1 = 66.7573$ and $\check{z}_2 = 33.1217$. The ESNIS coalition was allowed to enter into several different incumbent populations, as shown in Figures 10a-d.

In Figure 10a, there is one incumbent population with phenotype $u_3 = 1.5$ and a corresponding equilibrium population density of $z_3 = 91.3931$. The ESNIS coalition takes 50 000 generations to completely displace the incumbent, and to become stable.

In Figure 10b, the two incumbents with phenotypes $u_3 = 2.3$ and $u_4 = -0.5$ and having corresponding equilibrium population densities $z_3 = 66.2153$ and $z_4 = 30.9432$ are displaced completely by the ESNIS coalition, although it takes almost six million generations to do it.

In Figure 10c, the three incumbents $u_3 = 2.3$, $u_4 = -0.5$, and $u_5 = -0.8$, with equilibrium population densities $z_3 = 66.9253$, $z_4 = 17.3546$, and $z_5 = 13.4961$, are displaced by the ESNIS coalition over eight million generations.

Finally, in Figure 10d, the four incumbent phenotypes $u_3 = 4.0$, $u_4 = -4.0$, $u_5 = 1.3$ and $u_6 = 2.5$ have equilibrium population densities of $z_3 = 11.8074$, $z_4 = 4.54904$, $z_5 = 79.7616$, and z_6

= 1.44941, which are displaced in 400 000 generations by the ESNIS coalition.

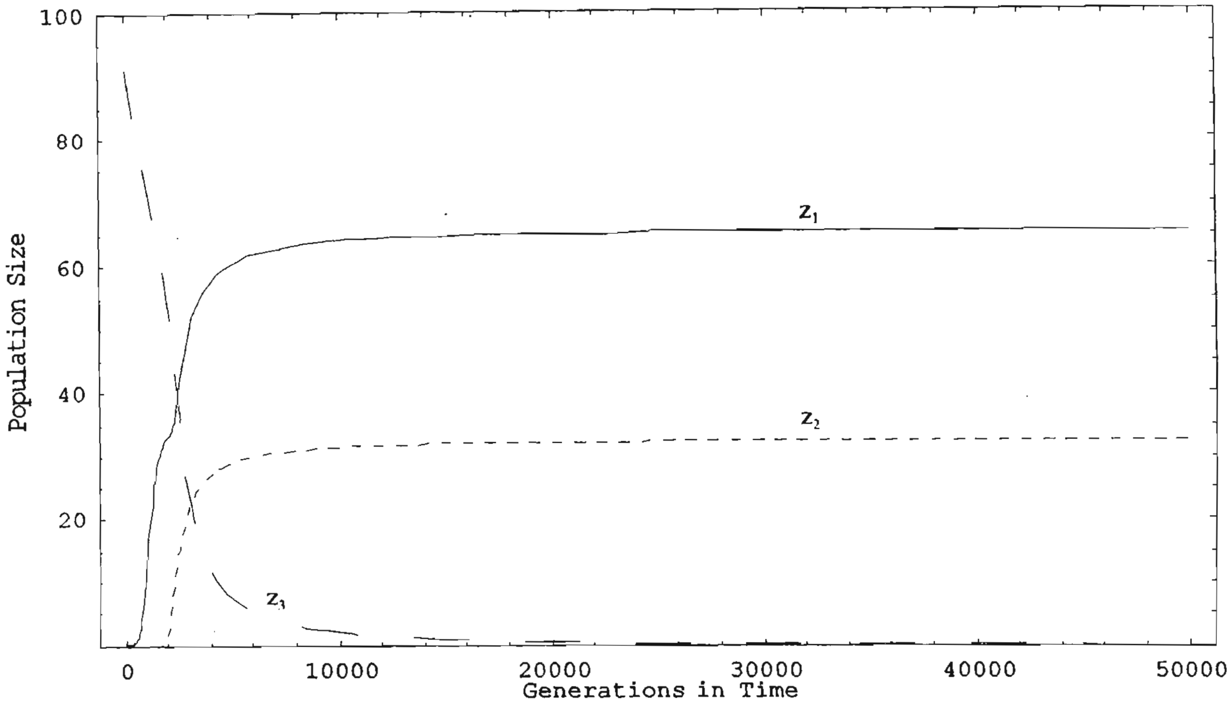

Figure 10a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (2.34102, -0.535529, 1.5)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3) is neither an ESS nor an NIS. The invader species 1, invader species 2, and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$, and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

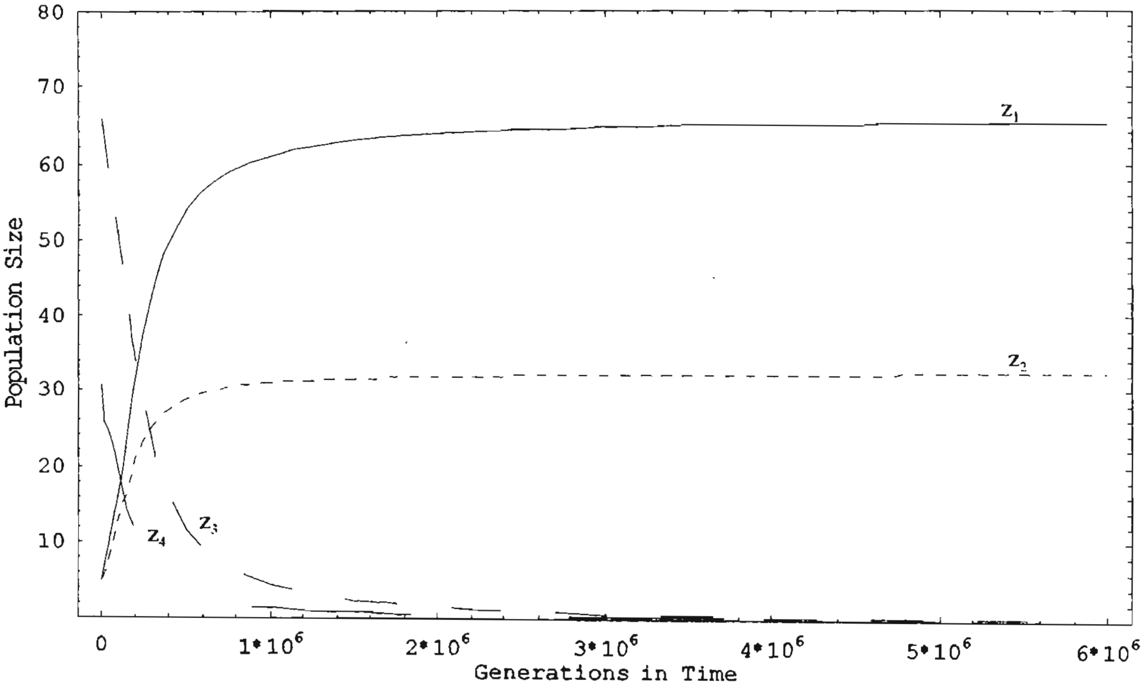

Figure 10b. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4) = (2.34102, -0.535529, 2.3, -0.5)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1, and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

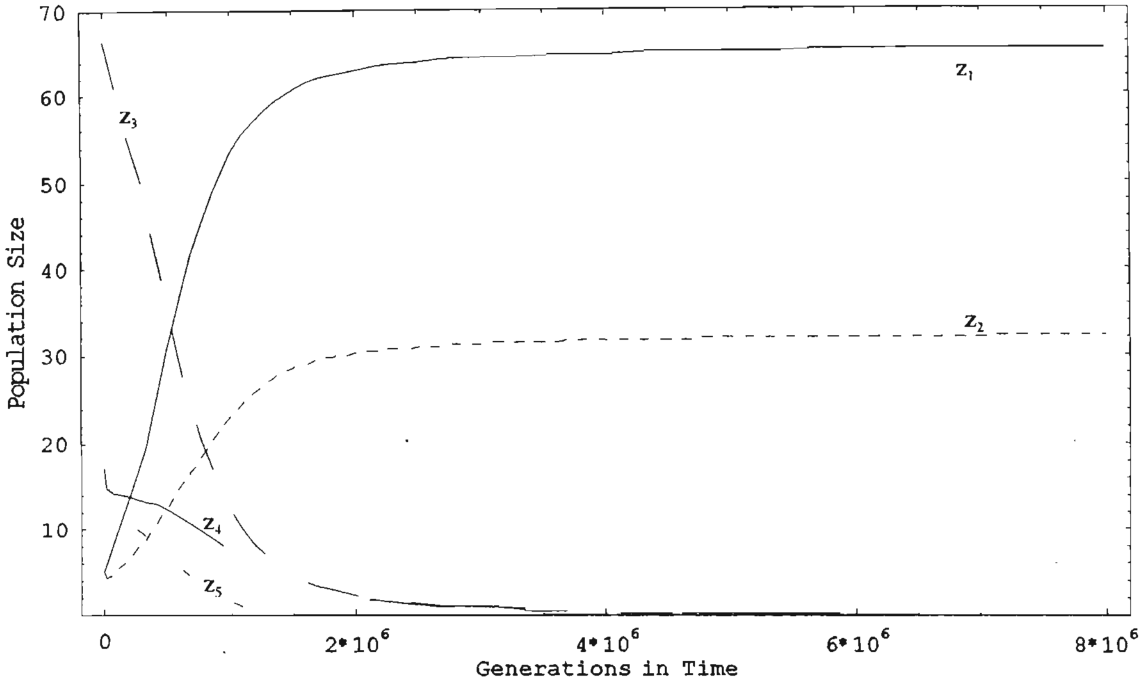

Figure 10c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5) = (2.34102, −0.535529, 2.3, −0.5, −0.8). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4, u_5) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4, and z_5.

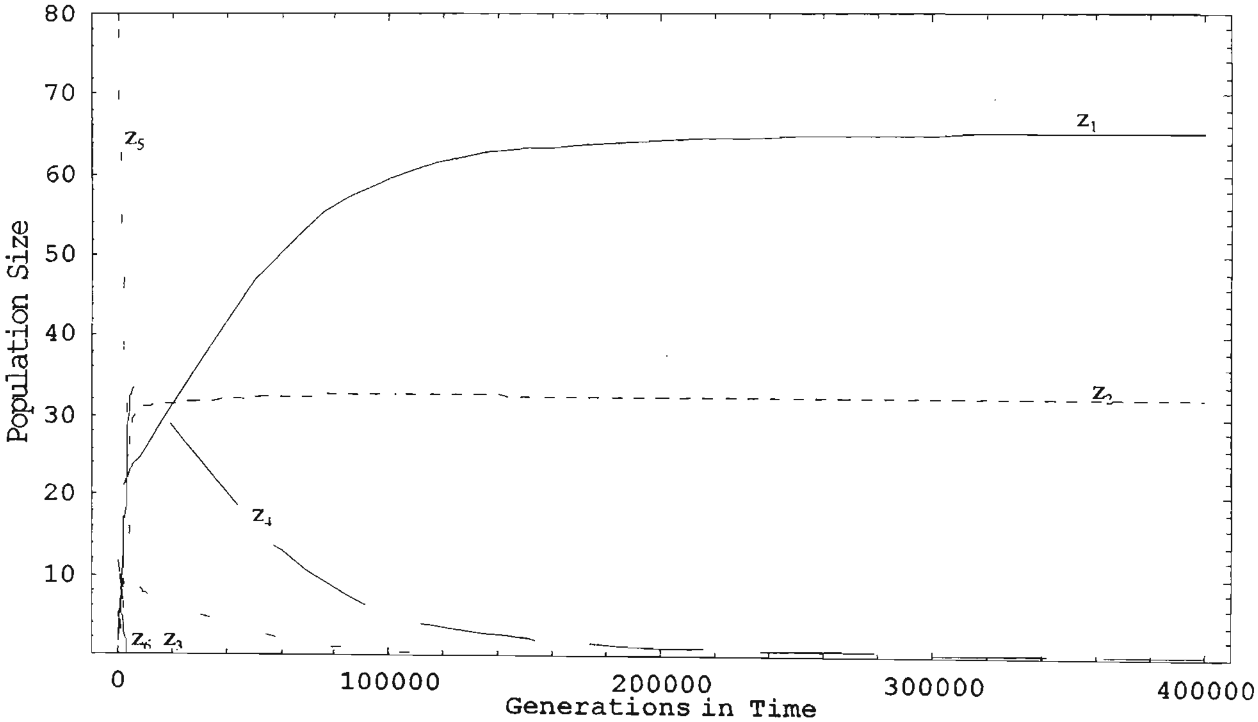

Figure 10d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (2.34102, −0.535529, 4, −4, 1.3, 2.5). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4, u_5, u_6) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6.

4.3.3. Dynamics of the ESNIS Coalition (3.27926, 0.42584)

From Table 1, the ESNIS coalition (3.27926, 0.42584) is found when the parameter values are set as follows: $\beta = 1.75$; $\sigma_a = 1.5$; and $\sigma_k^2 = 12.5$. The equilibrium population densities of the ESNIS coalition are $\check{z}_1 = 41.0973$ and $\check{z}_2 = 47.6339$. The ESNIS coalition was allowed to enter into several different incumbent populations, as shown in Figures 11a-d.

In Figure 11a, there is one incumbent population with phenotype $u_3 = 2.0$ and a corresponding equilibrium population density of $z_3 = 85.2144$. The ESNIS coalition takes only 700 generations to completely displace the incumbent, and to become stable.

In Figure 11b, the two incumbents with phenotypes $u_3 = 2.0$ and $u_4 = -2.0$ and having corresponding equilibrium population densities $z_3 = 72.3631$ and $z_4 = 25.9984$ are displaced completely by the ESNIS coalition, in only 2 000 generations.

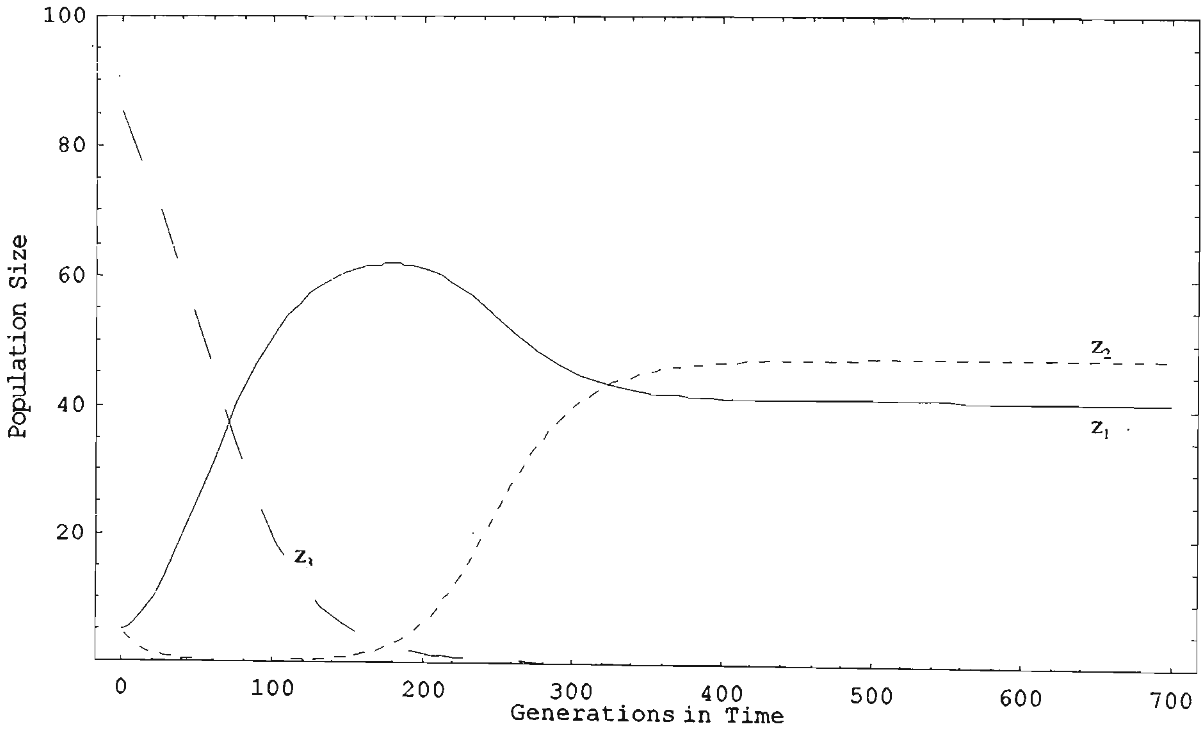

Figure 11a. Ecological dynamics of a community with phenotype $(\check{u}_1, \check{u}_2, u_3) = (3.27926, 0.42584, 2)$. The community phenotype $(\check{u}_1, \check{u}_2)$ is an ESNIS but (u_3) is neither an ESS nor an NIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\check{u}_1$, $\check{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

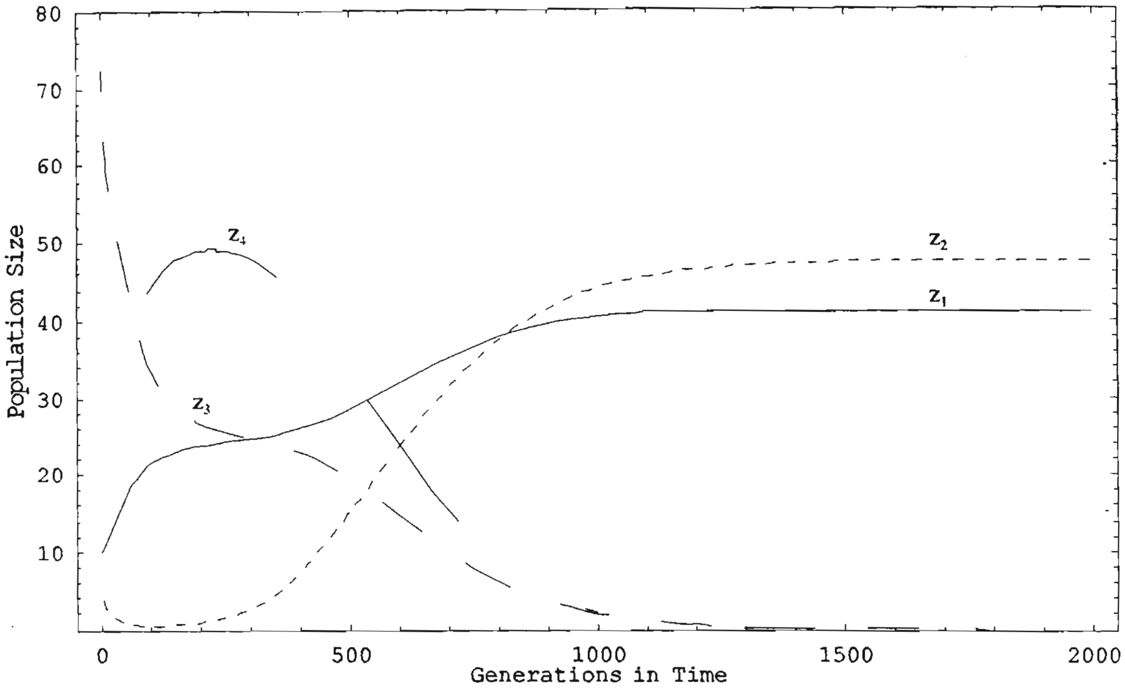

Figure 11b. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.27926, 0.42584, 2, −2). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

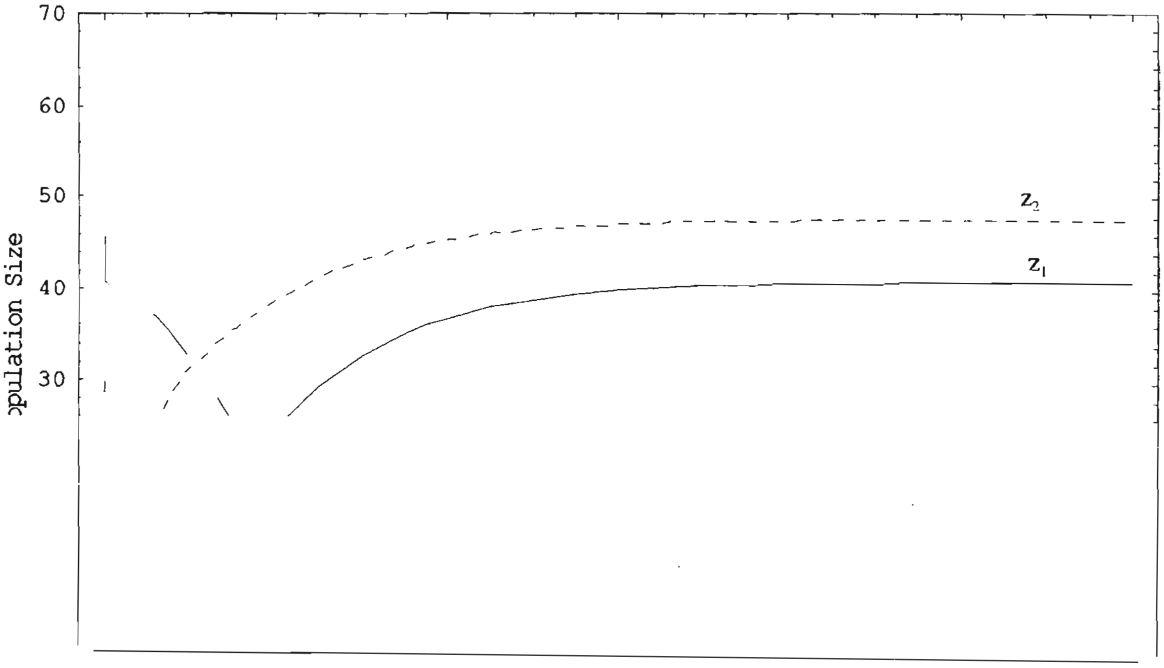

Figure 11c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5) = (3.27926, 0.42584, 3, 0.7, −3). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4, u_5) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4 and z_5.

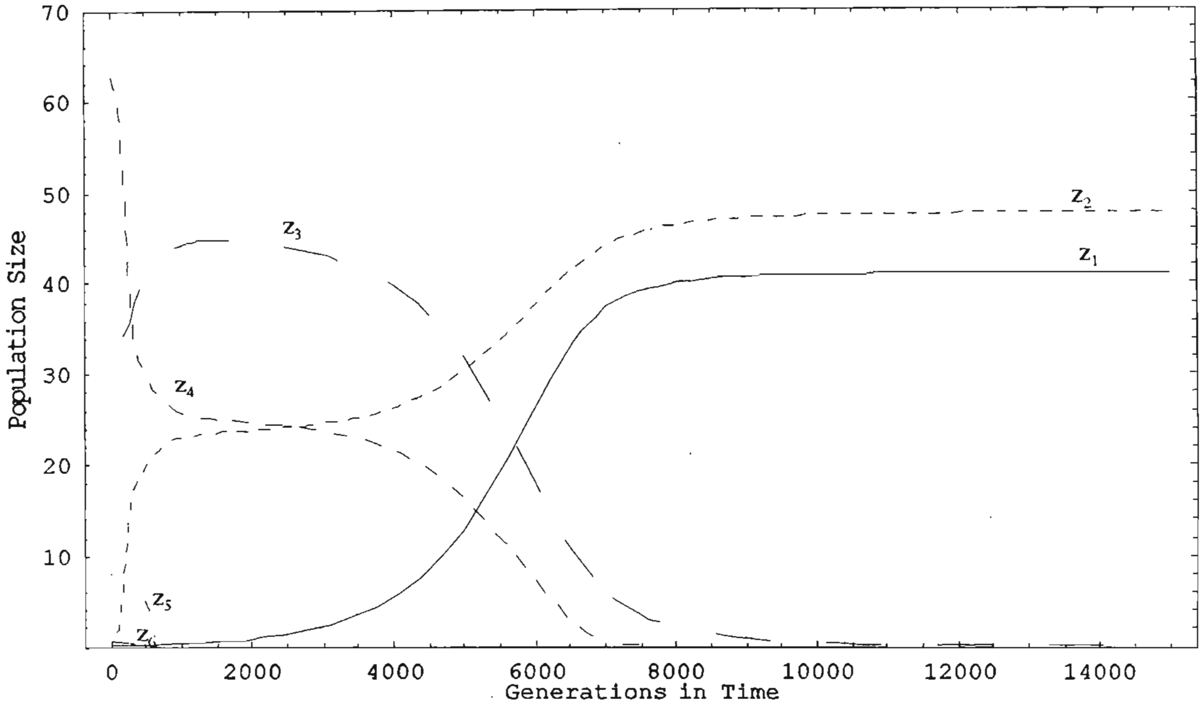

Figure 11d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (3.27926, 0.42584, 3,−1.2, 2.6, 2.1). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4, u_5, u_6) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6.

In Figure 11c, the three incumbents phenotypes are $u_3 = 3.0$, $u_4 = 0.7$, and $u_5 = -3.0$, with equilibrium population densities $z_3 = 45.7229$, $z_4 = 18.0167$, and $z_5 = 29.7366$, are displaced by the ESNIS coalition in 12 000 generations.

Finally, in Figure 11d, the four incumbent phenotypes $u_3 = 3.0$, $u_4 = -1.2$, $u_5 = 2.6$ and $u_6 = 2.1$ have equilibrium population densities of $z_3 = 31.4274$, $z_4 = 62.725$, $z_5 = 8.08399$, and $z_6 = 0.662655$, which are displaced in 15 000 generations by the ESNIS coalition.

4.3.4. Dynamics of the ESNIS Coalition (2.87702, −0.596216)

From Table 1, the ESNIS coalition (2.87702, −0.596216) is found when the parameter values are set as follows: $\beta = 2.0$; $\sigma_a = 2.5$; and $\sigma_k^2 = 12.5$. The equilibrium population densities of the ESNIS coalition are $\check{z}_1 = 60.4037$ and $\check{z}_2 = 31.2709$. The ESNIS coalition was allowed to enter into several different incumbent populations, as shown in Figures 12a-d.

In Figure 12a, there is one incumbent population with phenotype $u_3 = 1.2$ and a corresponding equilibrium population density of $z_3 = 92.4595$. The ESNIS coalition takes only 4 000 generations to completely displace the incumbent, and to become stable.

In Figure 12b, the two incumbents with phenotypes $u_3 = 1.2$ and $u_4 = 3.4$ and having corresponding equilibrium population densities $z_3 = 42.0265$ and $z_4 = 41.2199$ are displaced completely by the ESNIS coalition, in only 9 000 generations to do it.

In Figure 12c, the three incumbents $u_3 = 3.0$, $u_4 = 2.1$, and $u_5 = -1.0$, with equilibrium population densities $z_3 = 55.8964$, $z_4 = 21.6266$, and $z_5 = 13.7129$, are displaced by the ESNIS coalition over 200 000 generations.

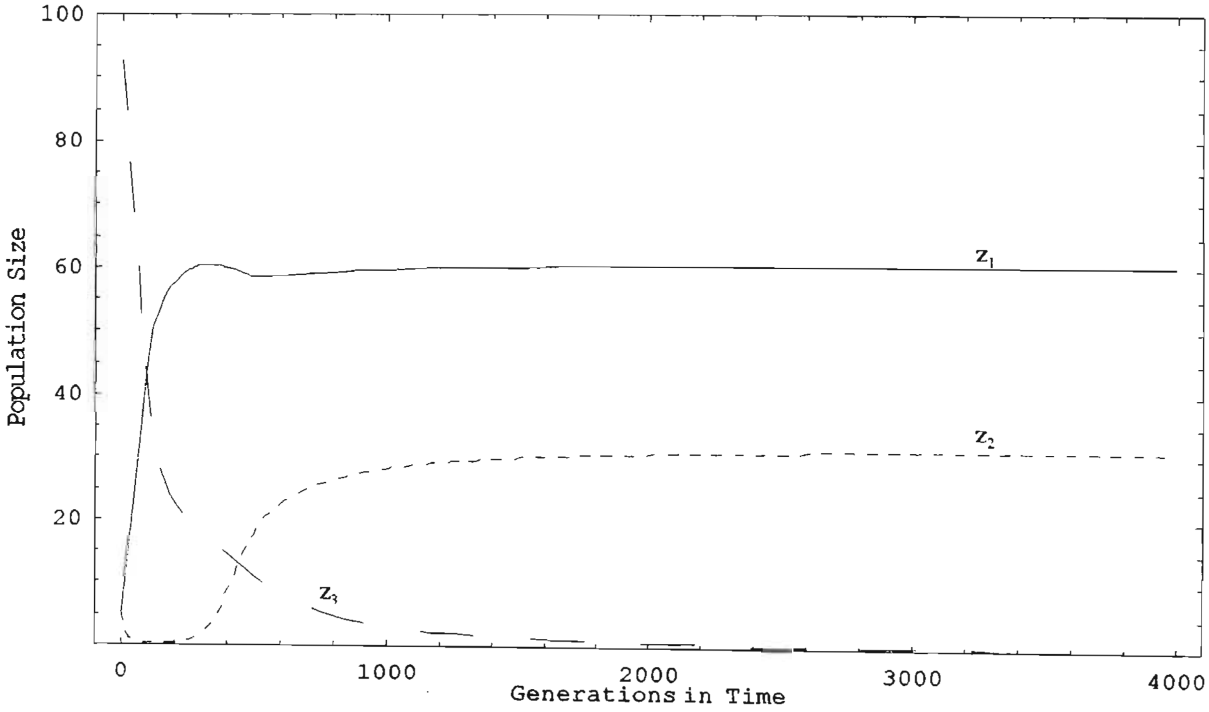

Figure 12a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (2.87702, -0.596216, 1.2)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3) is neither an ESS nor an NIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$, and u_3 respectively. The respective population densities are z_1, z_2, and z_3.

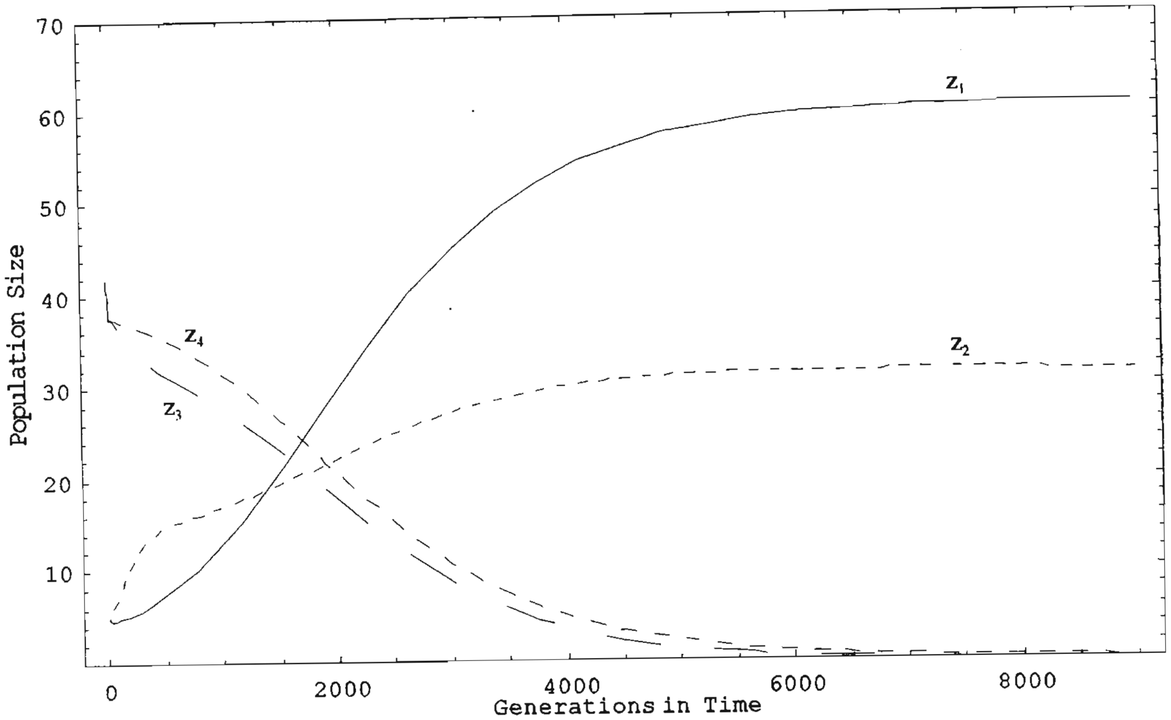

Figure 12b. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4, u_5, u_6) = (2.87702, -0.596216, 1.2, 3.4)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, and u_4 respectively. The respective population densities are z_1, z_2, z_3, and z_4.

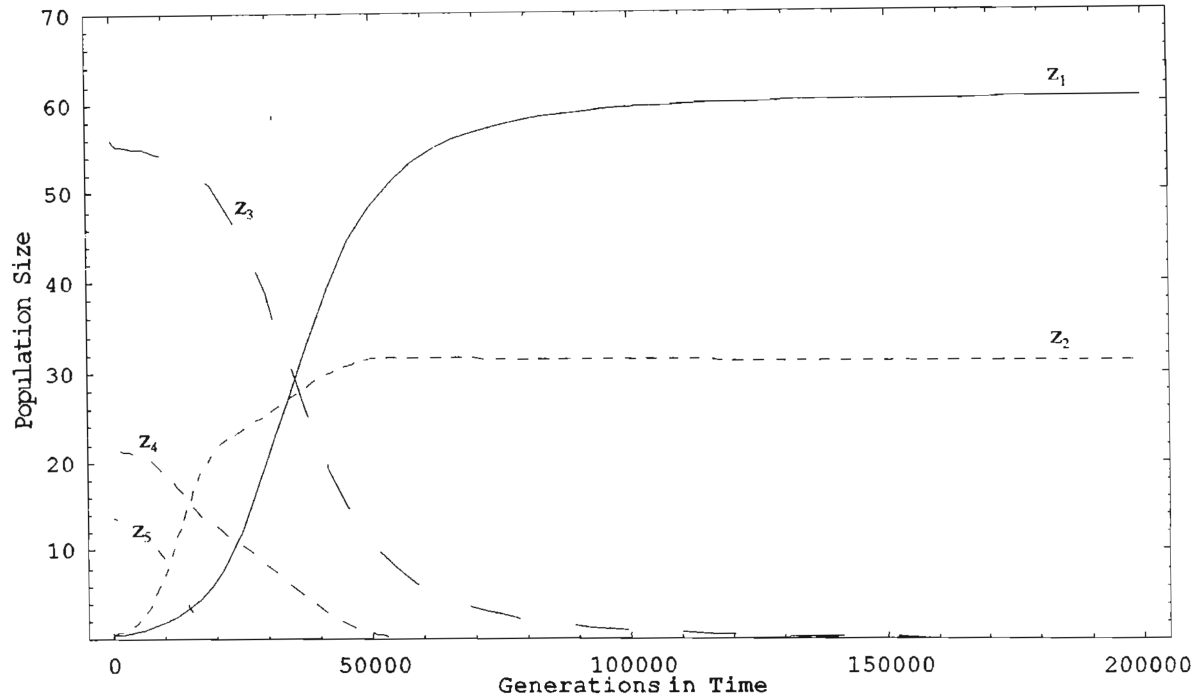

Figure 12c. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4, u_5) = (2.87702, -0.596216, 3, 2.1, -1)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an ESNIS but (u_3, u_4, u_5) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4 and z_5.

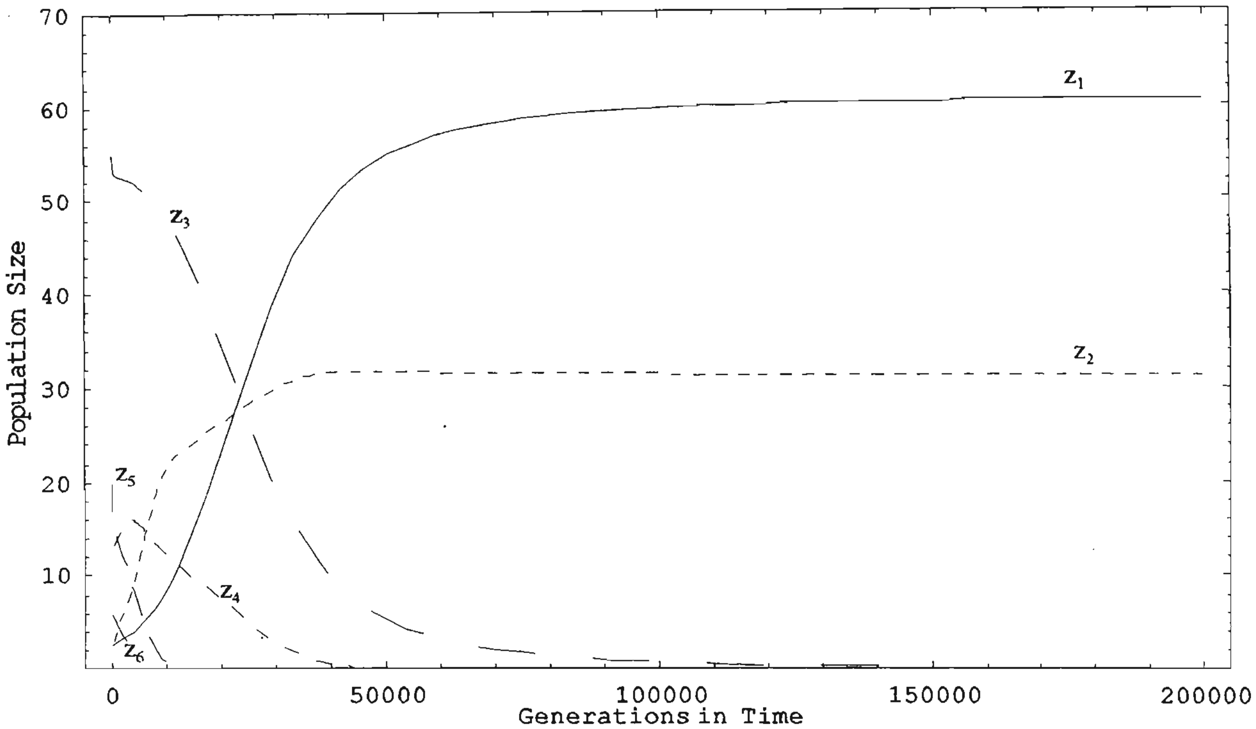

Figure 12d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (2.87702, -0.596216, 3, 2.1, - 1.1, 0.8). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an ESNIS but (u_3, u_4, u_5, u_6) is neither an ESS nor an NIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6.

Finally, in Figure 12d, the four incumbent phenotypes $u_3 = 3.0$, $u_4 = 2.1$, $u_5 = -1.1$ and $u_6 = 0.8$ have equilibrium population densities of $z_3 = 55.0366$, $z_4 = 11.8396$, $z_5 = 20.3525$, and $z_6 = 5.80211$, which are displaced in 200 000 generations by the ESNIS coalition.

4.3.5. Conclusion of Dynamics of Other ESNIS Coalitions

The simulations carried out in §4.3.1, §4.3.2, §4.3.3, and §4.3.4 lead one to believe that any ESNIS coalition will invade and displace the incumbent community, regardless of the composition of the incumbent community, which agrees with the theory of Chapter 3

4.4 Dynamics of NIS Coalitions Which are Not Also ESS Coalitions

The effect on an incumbent population in equilibrium if an NIS coalition which is not also an ESS coalition was introduced was simulated for four different NIS coalitions. In this case when solving for the conditions given in Appendix 1, the coalition had to be a NIS, but not an

ESS. Coalitions 1, 5, 9, and 10, were selected to give a wide range of parameter values, and therefore allow generalisations to be made about the other coalitions based on the four coalitions looked at. In each case, the NIS coalition should invade the incumbent population, but not necessarily eliminate the incumbents, as would happen if the NIS coalition was also an ESS coalition.

Coalition	β	σ_a	σ_k^2	$\breve{u}_1$	$\breve{u}_2$
1	0.25	3.3	12.5	1.45106	-0.897655
2	0.5	3	12.5	2.20454	-0.933304
3	0.75	3	12.5	2.37022	-0.667883
4	1	1.5	12.5	4.30407	1.61949
5	1.1	1.5	12	4.06368	1.46587
6	1.1	1.5	13	4.33521	1.69794
7	1.1	1.5	100	26.0583	22.8906
8	1.25	1.5	12.5	4.00158	1.44136
9	1.5	1.5	12	3.51864	0.920606
10	2	3.3	30.5	5.52008	0.560477

Table 2: Various parameter values for β, σ_a, and σ_k which give an NIS coalition ($\breve{u}_1$, $\breve{u}_2$) which is not also an ESS coalition.

In order to find NIS coalitions which were not also ESS coalitions, the parameters mentioned in §4.1 had to be changed. Table 2 above gives ten combinations of parameter values which give NIS but not ESS coalitions, as well as the phenotypes for the NIS coalitions. The table does not give all the possibilities, and slight variations in the parameter values will give other possible NIS coalitions. The parameters r and k_m were left as 0.25 and 100 respectively.

4.4.1. Dynamics of the NIS Coalition (1.45106, -0.897655)

The NIS coalition (1.45106, -0.897655), which is not also an ESS, has corresponding equilibrium population densities of $\check{z}_1 = 52.0433$ and $\check{z}_2 = 54.1647$, when interacting with no other communities.

In Figure 13a, the NIS coalition is introduced into a community which has one incumbent population at an equilibrium density of $z_3 = 82.1079$, and its phenotype is $u_3 = 2.22$. The NIS coalition invades the incumbent as expected, and the three populations settle down to their equilibrium densities of $z_1 = 51.7995$, $z_2 = 54.227$, and $z_3 = 0.199754$, taking 200 000 generations to do so. In this case, the incumbent is almost, but not completely displaced.

In Figure 13b, the incumbent population's phenotypes are $u_3 = 2.0$, and $u_4 = -0.5$, and the corresponding equilibrium population densities are $z_3 = 34.3635$ and $z_4 = 71.6701$. In this case the system takes two million generations to stabilise after the introduction of the NIS coalition. The incumbent populations are pushed aside by the invaders, and are greatly reduced in size, while the NIS coalition almost reaches the equilibrium values it has when not interacting with any other populations. The final stable population densities are $z_1 = 49.5417$, $z_2 = 51.7006$, $z_3 = 1.67429$ and $z_4 = 3.29031$.

In Figure 13c, the three incumbent phenotypes $u_3 = 5.0$, $u_4 = 0.9$, and $u_5 = -3.0$ have corresponding equilibrium population densities of $z_3 = 5.42481$, $z_4 = 39.175$, $z_5 = 60.2458$. When the NIS coalition is introduced into the community, the system takes 800 000 generations to stabilise, and the stable population densities are $z_1 = 48.2424$, $z_2 = 53.3814$, $z_3 = 0.428684$, $z_4 = 4.22688$, and $z_5 = 0$. Thus the incumbent population with phenotype u_5 has been eliminated.

Finally, in Figure 13d, the NIS coalition enters into a community with four populations whose phenotypes are $u_3 = 4.0$, $u_4 = 2.2$, $u_5 = -2.0$, and $u_6 = -5.0$. The corresponding incumbent population densities are $z_3 = 15.2197$, $z_4 = 28.708$, $z_5 = 46.6298$, and $z_6 = 260.23$. The introduction of the NIS coalition upsets the equilibrium, and it takes 80 000 generations for stability to return. At that time, two of the original incumbent populations, whose phenotypes were u_4 and u_5 have been eliminated. The remaining population densities are $z_1 = 51.9987$, $z_2 = 54.0586$, $z_3 = 0.117073$, and $z_6 = 0.23431$.

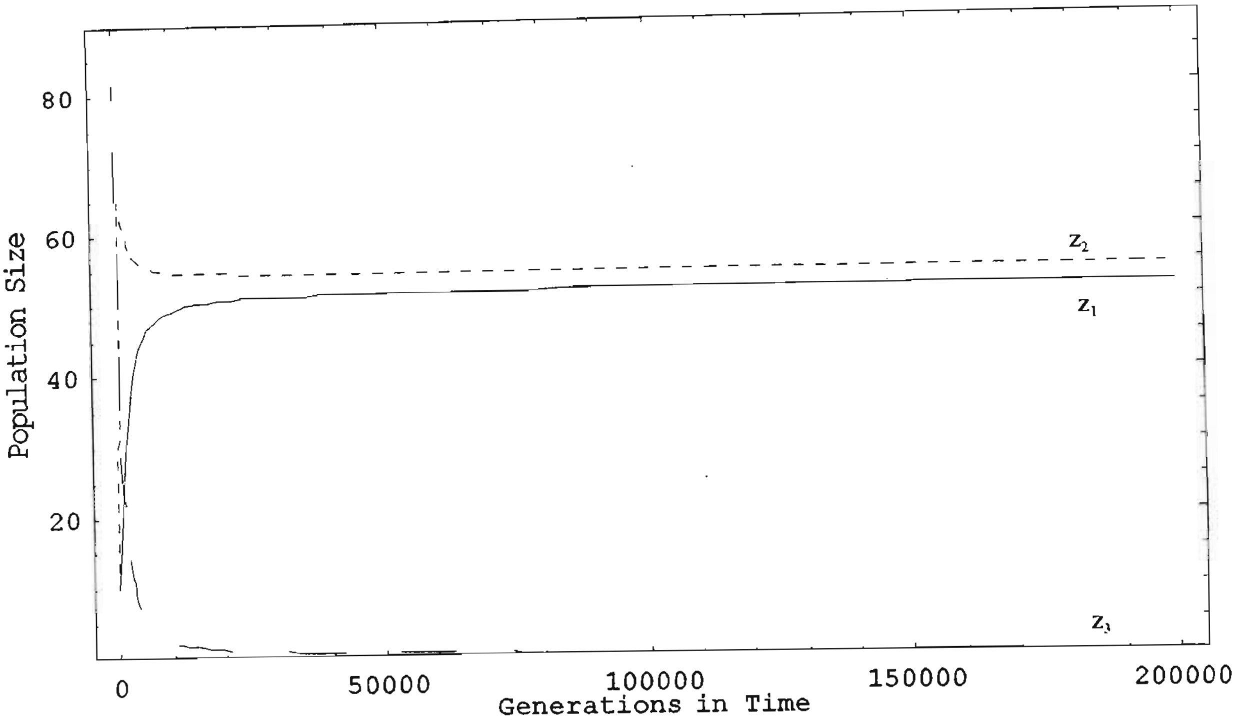

Figure 13a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (1.45106, -0.897655, 2.22)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an NIS but (u_3) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2, and z_3. (Note: z_3 has not been eliminated)

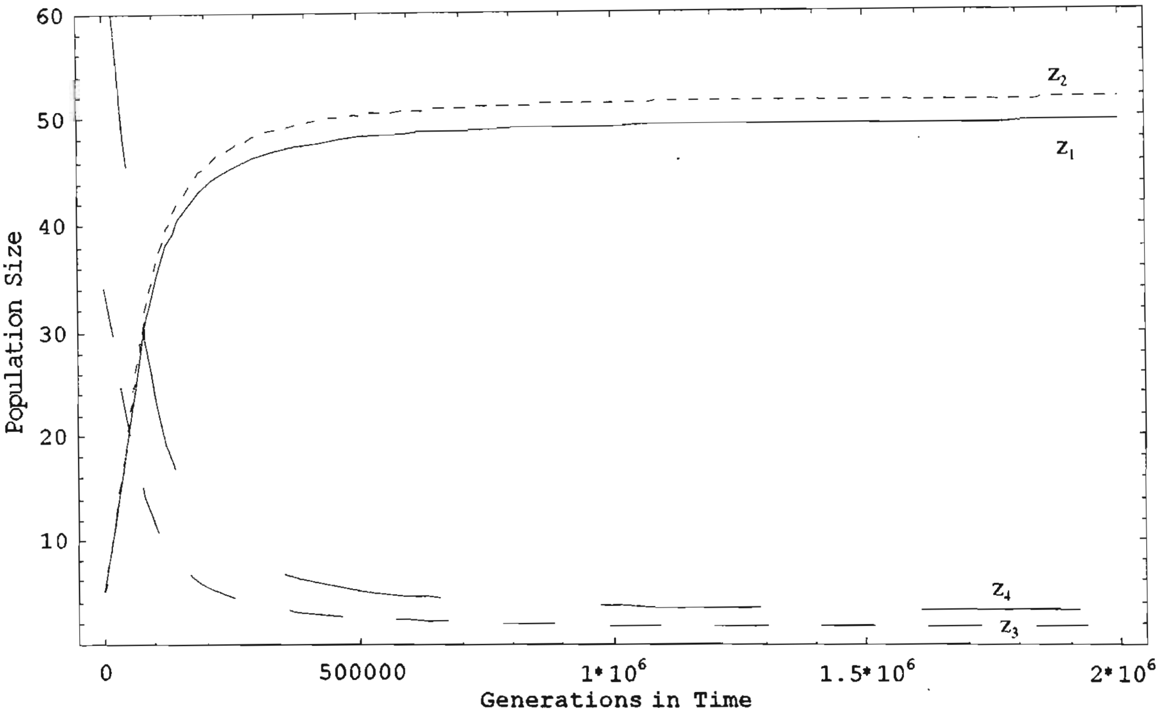

Figure 13b. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4) = (1.45106, -0.897655, 2, -0.5)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an NIS but (u_3, u_4) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3 and z_4.

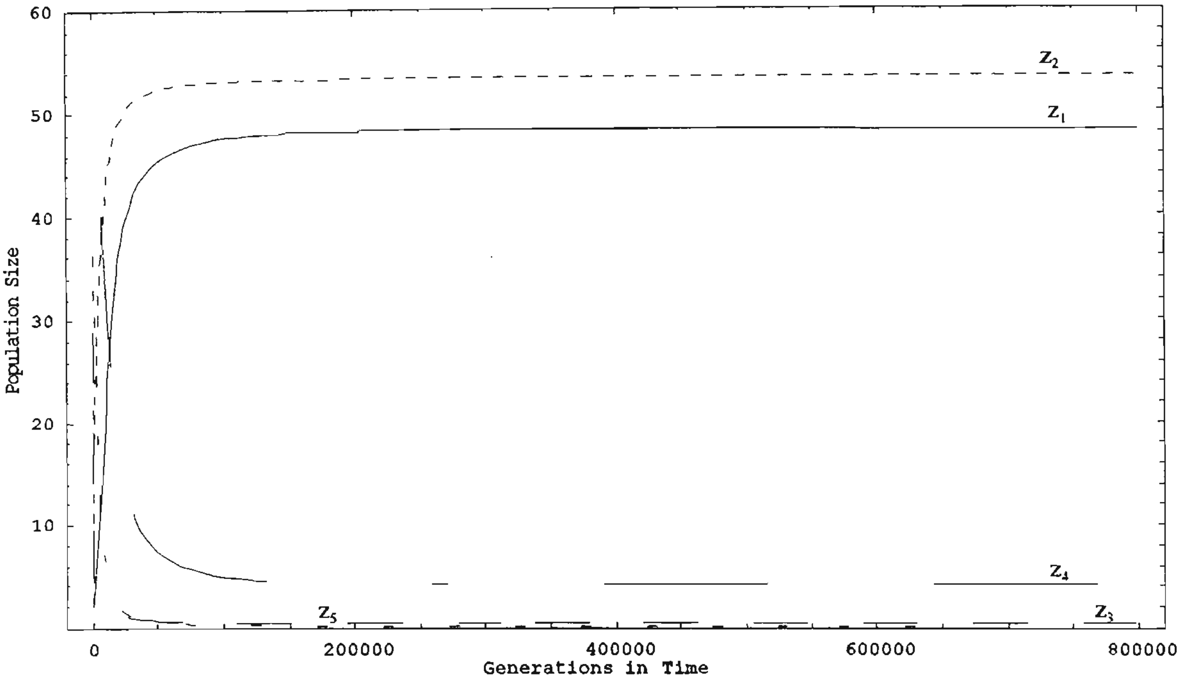

Figure 13c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (1.45106, -0.897655, 5, 0.9, -3). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4 and z_5. (Note z_5 is eliminated).

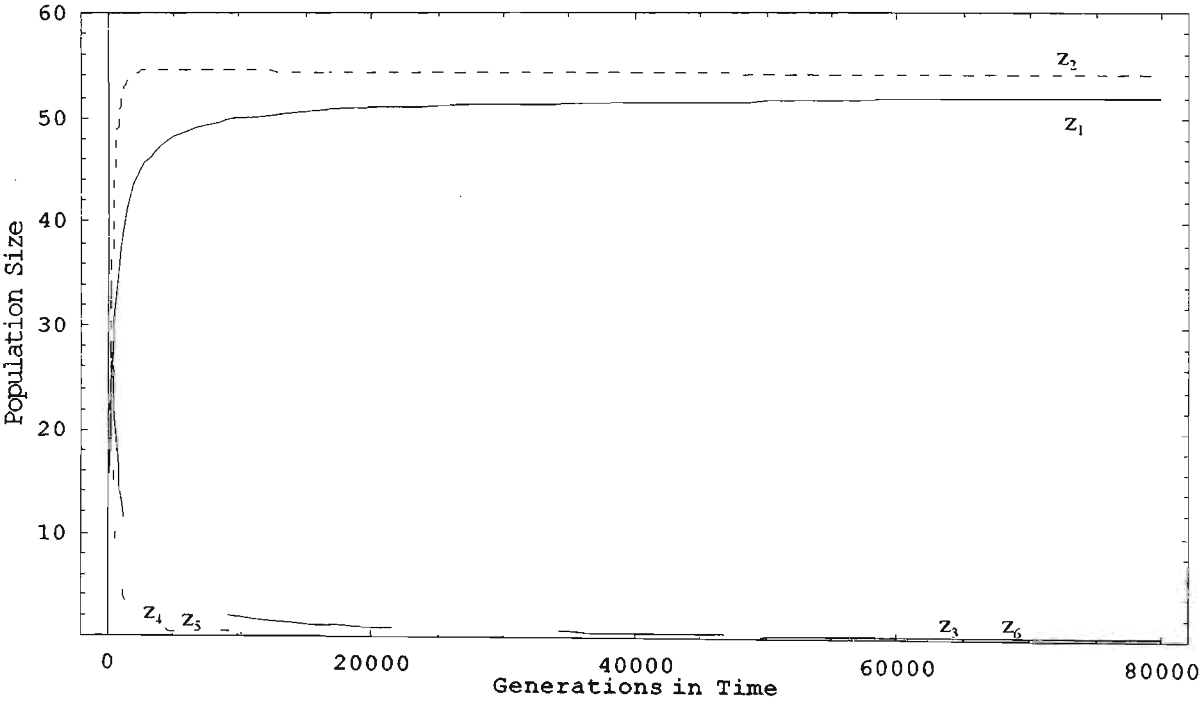

Figure 13d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (1.45106, -0.897655, 4, 2.2, -2, -5). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5, u_6) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6. (Note that z_4 and z_5 are both eliminated, while z_3 and z_6 are not)

Thus in all four cases, the NIS coalition invaded the incumbent population, and in all cases, the incumbents suffered badly, with some being totally eliminated, and the rest being drastically reduced.

4.4.2. Dynamics of the NIS Coalition (4.06368, 1.46587)

The NIS coalition (4.06368, 1.46587), which is not also an ESS, has corresponding equilibrium population densities of $\check{z}_1 = 31.962$ and $\check{z}_2 = 64.4859$, when interacting with no other communities. Examples of the interaction of the NIS coalition with other communities are given in Figures 14a-d.

In Figure 14a, the NIS coalition enters a community with one incumbent phenotype $u_3 = -3.5$ whose corresponding equilibrium population density is $z_3 = 60.0245$. The system takes 200 generations to stabilise after the introduction of the NIS coalition, at which stage the three populations are $z_1 = 23.6617$, $z_2 = 62.6542$, and $z_3 = 37.4089$.

In Figure 14b, the phenotypes $u_3 = 3.1$ and $u_4 = -3.1$ with corresponding equilibrium populations $z_3 = 54.2619$ and $z_4 = 54.0431$ are incumbent. After the introduction of the NIS coalition, stability returns after 1 500 generations, at which stage the new equilibrium population densities are $z_1 = 15.642$, $z_2 = 47.962$, $z_3 = 16.79$ and $z_4 = 44.6697$.

In Figure 14c, three incumbent populations of $z_3 = 35.9005$, $z_4 = 57.4896$, and $z_5 = 33.1799$ whose phenotypes are $u_3 = 3.5$, $u_4 = 0.9$, and $u_5 = -1.9$ are in residence. The NIS coalition enters the community, and the new five population communities take 1 500 generations to stabilise. At that time the new community population densities are $z_1 = 16.0042$, $z_2 = 36.0177$, $z_3 = 19.6353$, $z_4 = 20.5719$, and $z_5 = 29.0228$.

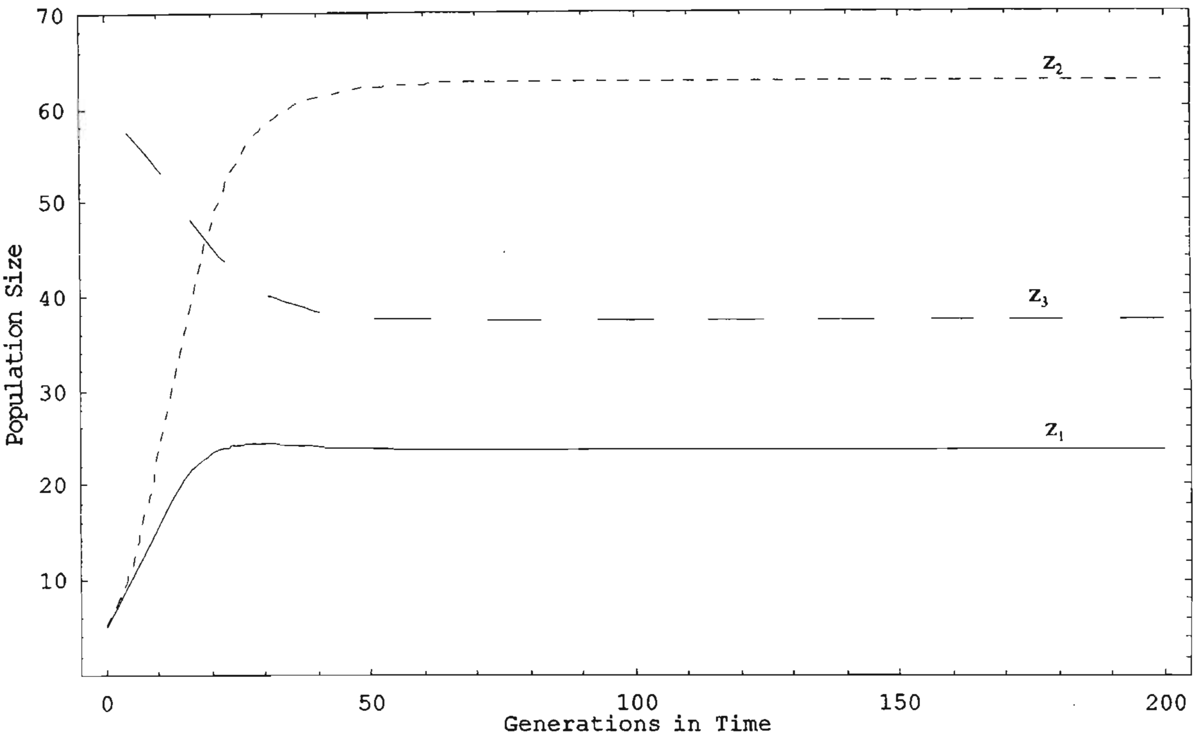

Figure 14a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (4.06368, -1.46587, -3.5)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an NIS but (u_3) is neither an ESS nor an ESNIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2 and z_3.

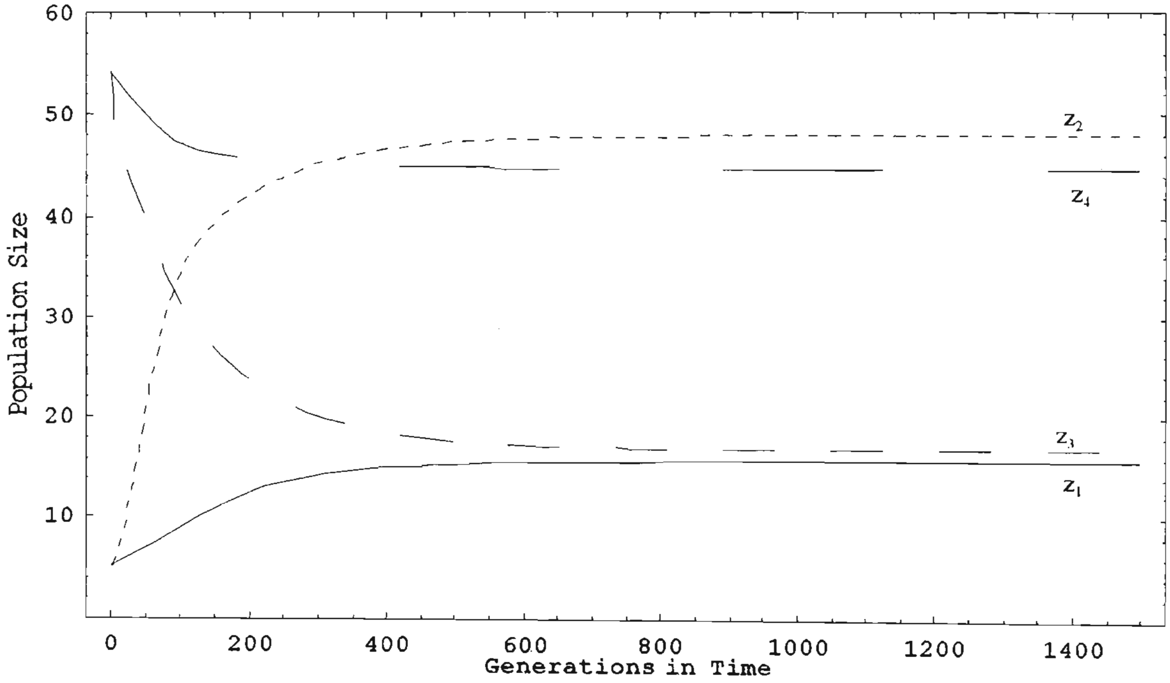

Figure 14b. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3, u_4) = (4.06368, -1.46587, 3.1, -3.1)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an NIS but (u_3, u_4) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3 and z_4.

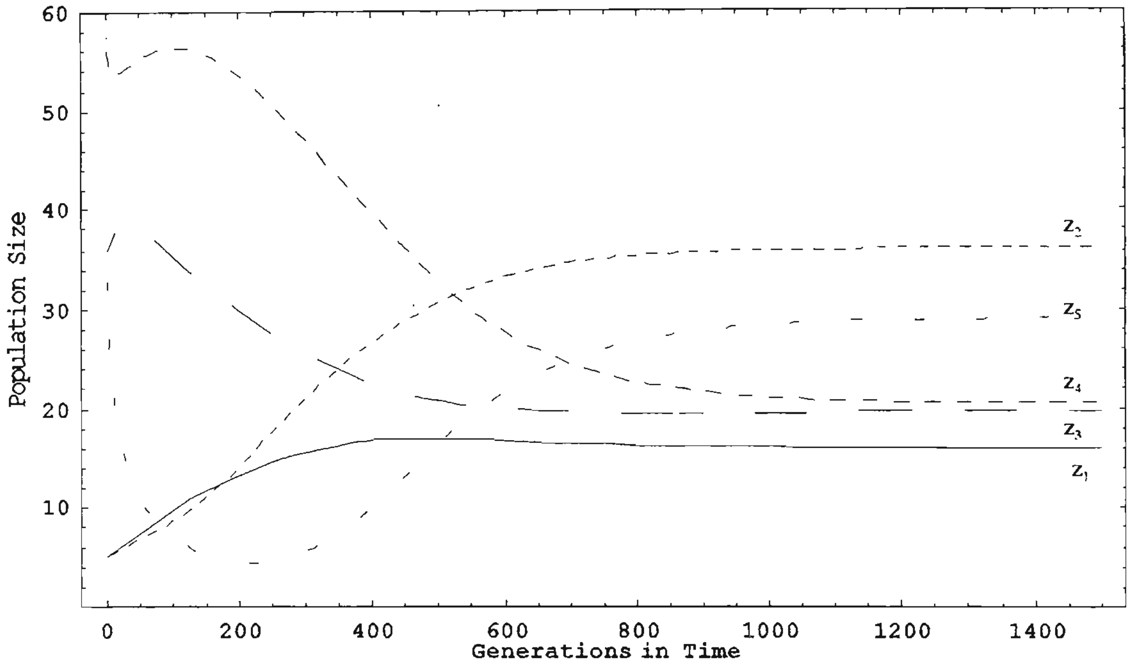

Figure 14c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (4.06368, − 1.46587, 3.5, 0.9, − 1.9). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4 and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4 and z_5.

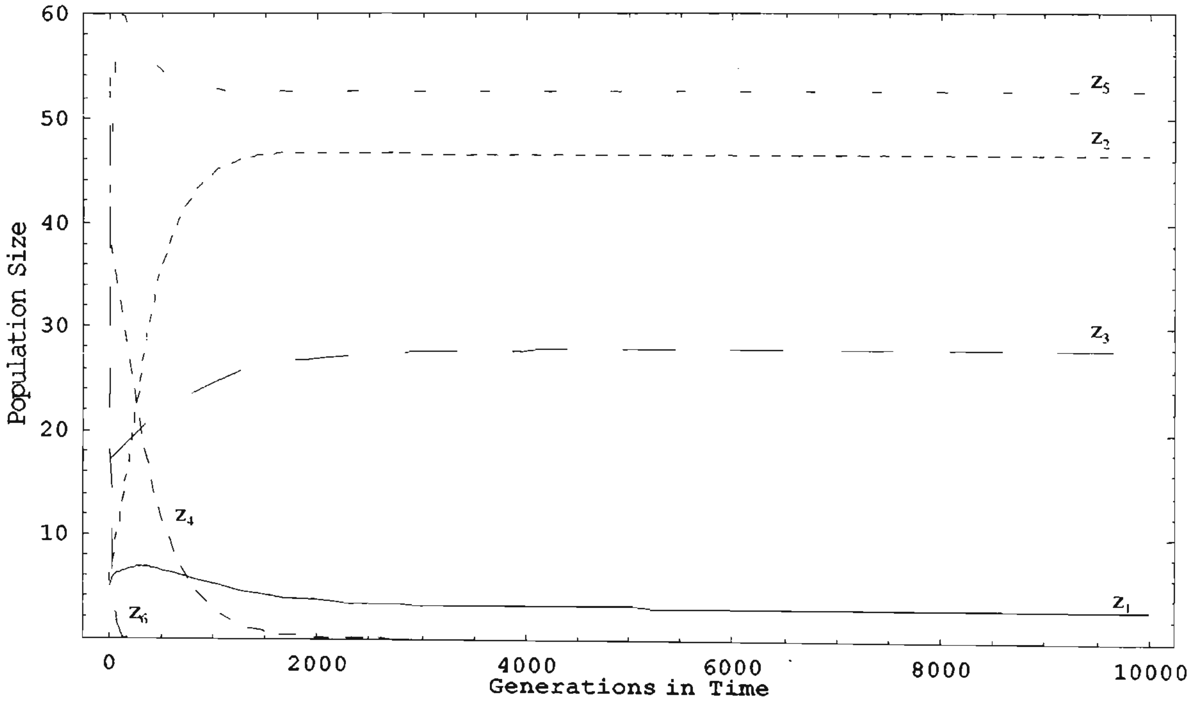

Figure 14d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (4.06368, − 1.46587, 3.5, 2, −2, −2.5). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5, u_6) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6. (Note z_4 and z_6 are both eliminated)

Finally in Figure 14d, the NIS coalition invades a community with four incumbent populations whose densities are $z_3 = 17.1883$, $z_4 = 38.7055$, $z_5 = 52.5041$, and $z_6 = 53.9096$ and whose phenotypes are $u_3 = 3.5$, $u_4 = 2.0$, $u_5 = -2.0$ and $u_6 = -2.5$ respectively. The interaction with the NIS coalition eliminates two of the incumbent populations, and takes 10 000 generations to stabilise. The populations which survive are $z_1 = 3.05927$, $z_2 = 46.4429$, $z_3 = 27.8349$ and lastly $z_5 = 52.6365$, while z_4 and z_6 both die out.

Thus in all four cases the NIS coalition invaded, but unlike the previous section (§4.4.1.) the NIS does not take over the system to the same degree. In Figures 14a-c, the incumbent populations are displaced, but they are not overwhelmed by the NIS coalition. Only in Figure 14d are some of the incumbents eliminated, but even here the NIS coalition has one of its populations which has just managed to enter the system, and is much lower in magnitude than any of the other populations at the new stable equilibrium point.

4.4.3. Dynamics of the NIS Coalition (3.51864, 0.920606)

If the NIS coalition (3.51864, 0.920606) enters into a system with no incumbent populations, then the NIS will attain equilibrium population densities of $\check{z}_1 = 37.5737$ and $\check{z}_2 = 53.0038$.

In Figure 15a, the incumbent population has phenotype $u_3 = -3$ and the corresponding equilibrium population $z_3 = 68.7289$. After 250 generations the population densities are stable at $z_1 = 28.4839$, $z_2 = 55.4236$, and $z_3 = 20.5349$.

In Figure 15b the two incumbent populations with phenotypes $u_3 = 3.1$ and $u_4 = -0.2$ with respective densities of $z_3 = 41.8354$ and $z_4 = 63.009$ are invaded by the NIS with the result that after 20 000 generations the stable populations densities are $z_1 = 37.3861$, $z_2 = 52.8009$, $z_3 = 0.0$ and $z_4 = 0.6877$. Thus the one incumbent has been totally displaced, while the other has been largely reduced, but is still in evidence.

In Figure 15c there are three incumbent populations using phenotypes $u_3 = 3.5$, $u_4 = 0.9$, and $u_5 = -1.9$ with populations of $z_3 = 31.9678$, $z_4 = 53.8606$ and $z_5 = 14.1784$ respectively. The invading and incumbent phenotypes are stable after 50 000 generations, at which time the populations of the five phenotypes have changed to $z_1 = 22.0091$, $z_2 = 40.741$, $z_3 = 15.759$, $z_4 = 4.7752$ and $z_5 = 14.2813$. In this case the NIS invades the incumbents as expected, but none of the incumbents are completely displaced.

In Figure 15d we have four incumbent populations using phenotypes $u_3 = 3.5$, $u_4 = 0.9$, $u_5 = -1.9$ and $u_6 = -1$. Their respective populations are $z_3 = 29.7154$, $z_4 = 53.3746$, $z_5 = 11.4576$, and $z_6 = 8.9532$. After the NIS phenotypes are introduced to the system, it takes 20 000 generations for the system to stabilize, at which stage the population densities are $z_1 = 16.435$, $z_2 = 28.136$, $z_3 = 22.4353$, $z_4 = 22.7928$, $z_5 = 0.0$ and $z_6 = 9.382$. As in Figure 15b one of the incumbent populations has been completely displaced.

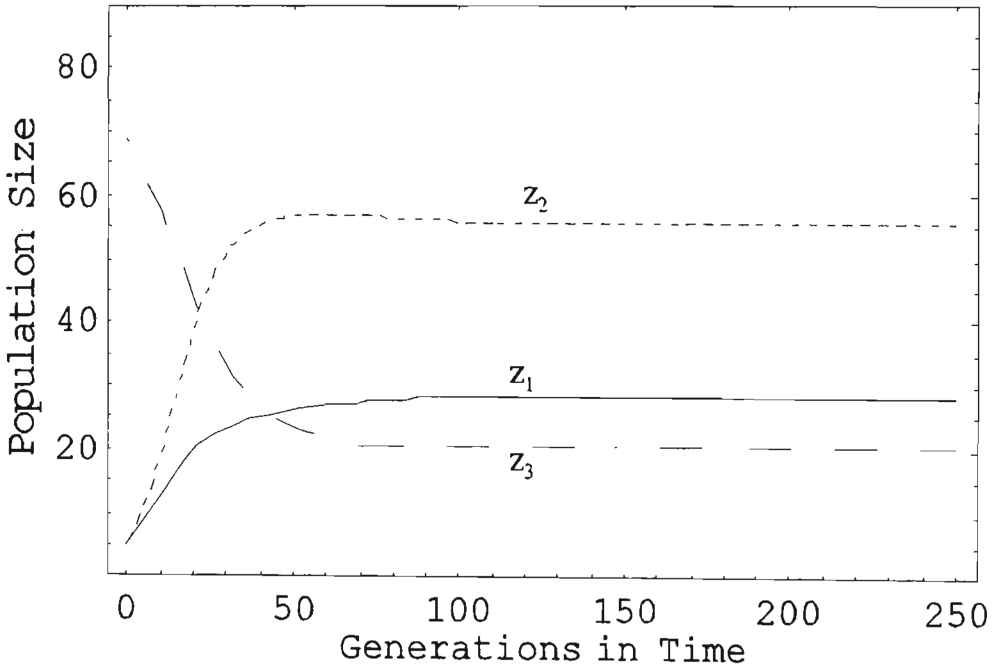

Figure 15a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (3.51864, 0.920606, -3)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an NIS but (u_3) is neither an ESS nor an ESNIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$, and u_3 respectively. The respective population densities are z_1, z_2 and z_3.

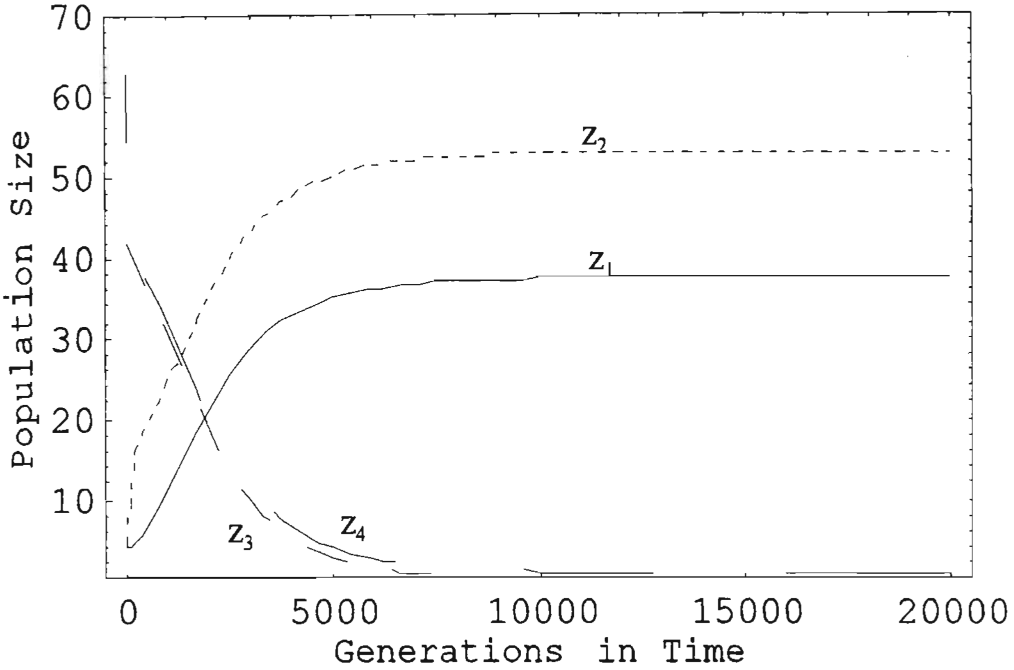

Figure 15b. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.51864, 0.920606, 3.1, −0.2). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3 and z_4.

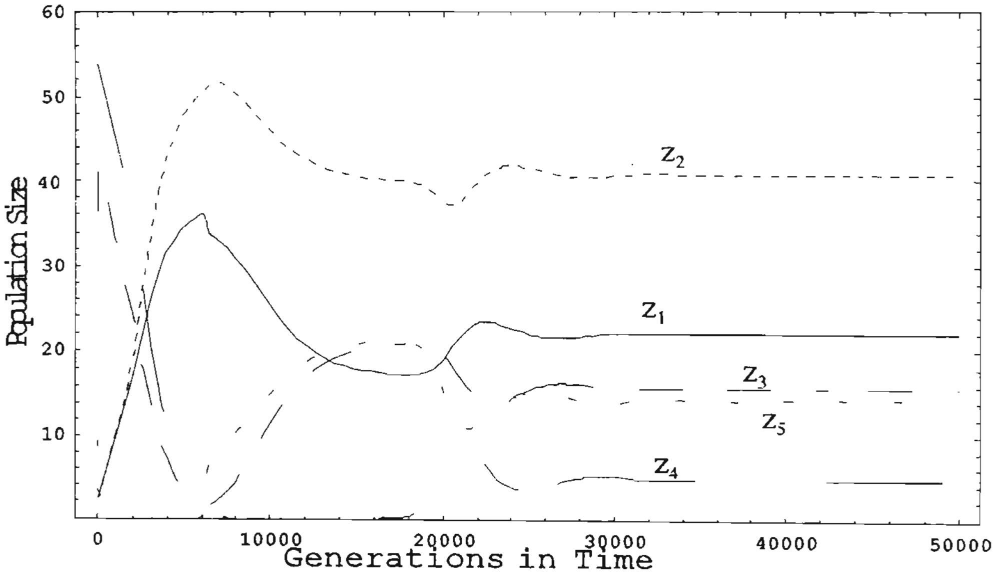

Figure 15c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5) = (3.51864, 0.920606, 3.5, 0.9, −1.9). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4 and z_5.

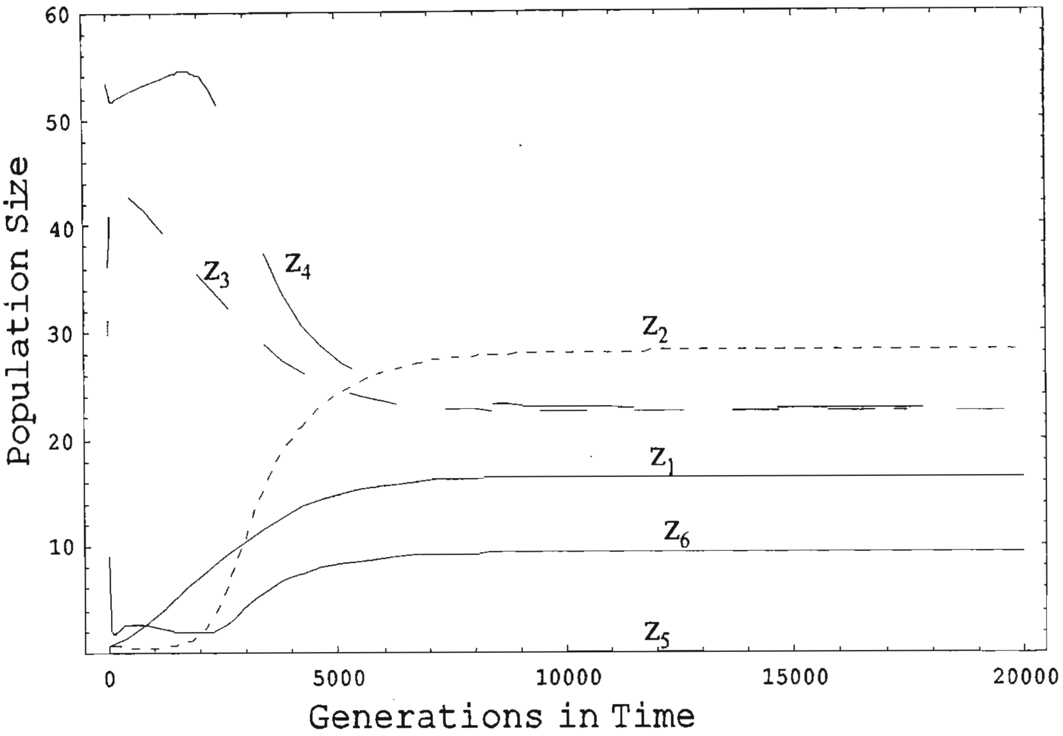

Figure 15d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (3.51864, 0.920606, 3.5, 0.9, −1.9, −1). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5, u_6) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6.

4.4.4. Dynamics of the NIS Coalition (5.52008, 0.560477)

When left to evolve without any other influences being brought to bear on it, the NIS coalition (5.52008, 0.560477) has equilibrium population densities of $\check{z}_1 = 43.2014$ and $\check{z}_2 = 63.3422$. The dynamics of evolution when the NIS coalition enters an incumbent community are shown in Figures 16a-d.

In Figure 16a, one incumbent population of $z_3 = 81.806$ which uses phenotype $u_3 = 3.5$ is invaded by the NIS coalition takes 30 000 generations to stabilise, at which stage the new equilibrium population densities are $z_1 = 42.9502$, $z_2 = 62.8973$ and $z_3 = 0.580649$. In this case the incumbent population has almost, but not quite, been eliminated with the introduction of the NIS coalition.

In Figure 16b, the incumbent phenotypes of $u_3 = 2.8$ and $u_4 = -2.8$ with corresponding equilibrium population densities $z_3 = 80.8408$ and $z_4 = 29.7891$ interact with the NIS coalition, resulting in a new stable community 5 000 generations later. The new stable community has population densities of $z_1 = 39.3972$, $z_2 = 48.0451$, $z_3 = 10.0227$, and $z_4 = 15.6331$.

A community with three incumbent populations using phenotypes $u_3 = 3.5$, $u_4 = -1.3$, $u_5 = -3.2$, whose corresponding equilibrium populations are $z_3 = 71.4422$, $z_4 = 19.7092$, and $z_5 = 23.6425$, interacts with the NIS coalition for 10 000 generations before stability returns. At that stage, the new population densities are $z_1 = 38.7203$, $z_2 = 53.1265$, $z_3 = 7.52556$, $z_4 = 0.0$, and $z_5 = 14.1956$. The dynamics are shown in Figure 16c.

Finally the dynamics of the community whose members use $u_3 = 3.5$, $u_4 = -1.3$, $u_5 = -3.8$, and $u_6 = 1.4$ as their phenotypes, and whose corresponding equilibrium populations are $z_3 = 69.1047$, $z_4 = 22.225$, $z_5 = 16.8314$, and $z_6 = 5.03473$, are shown in Figure 16d. The interaction with the NIS coalition takes 100 000 generations to stabilise, and the final stable populations are $z_1 = 39.7077$, $z_2 = 21.5382$, $z_3 = 0.0$, $z_4 = 6.19569$, $z_5 = 16.126$, and $z_6 = 31.9002$.

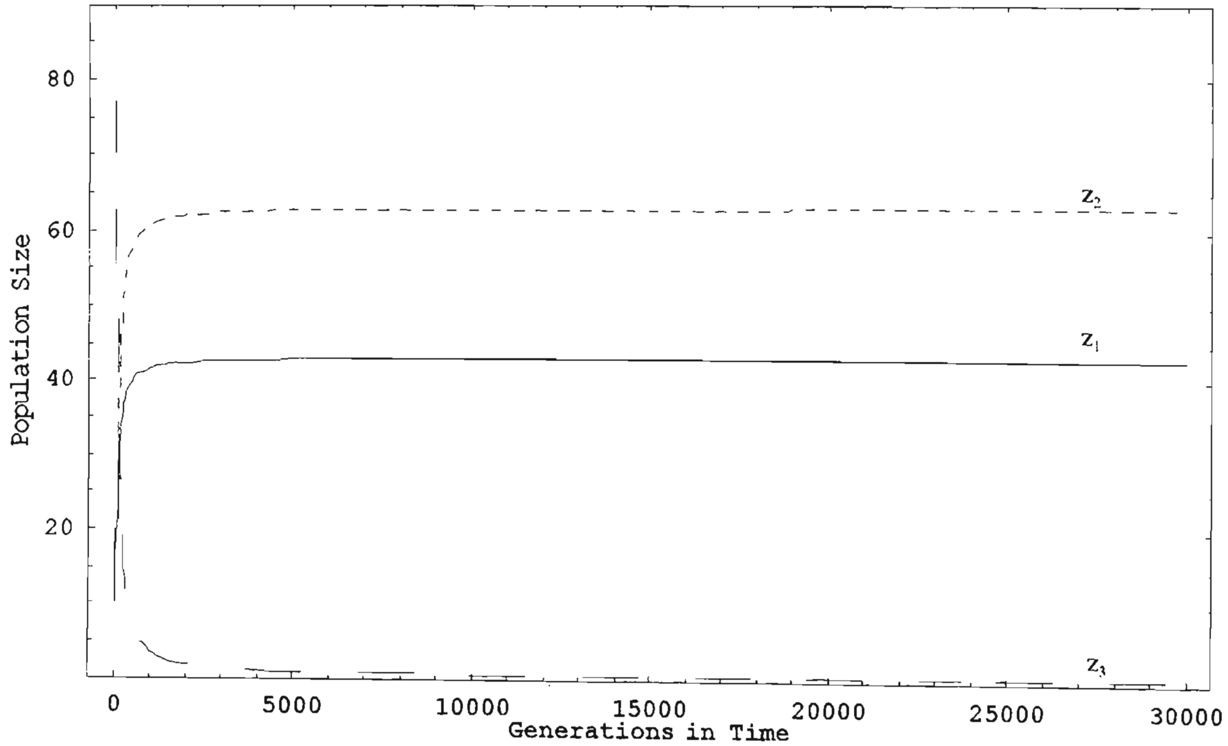

Figure 16a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2, u_3) = (5.52008, 0.560477, 3.5)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is an NIS but (u_3) is neither an ESS nor an ESNIS. The invader species 1, invader species 2 and incumbent species 1 phenotypes are $\breve{u}_1$, $\breve{u}_2$ and u_3 respectively. The respective population densities are z_1, z_2 and z_3.

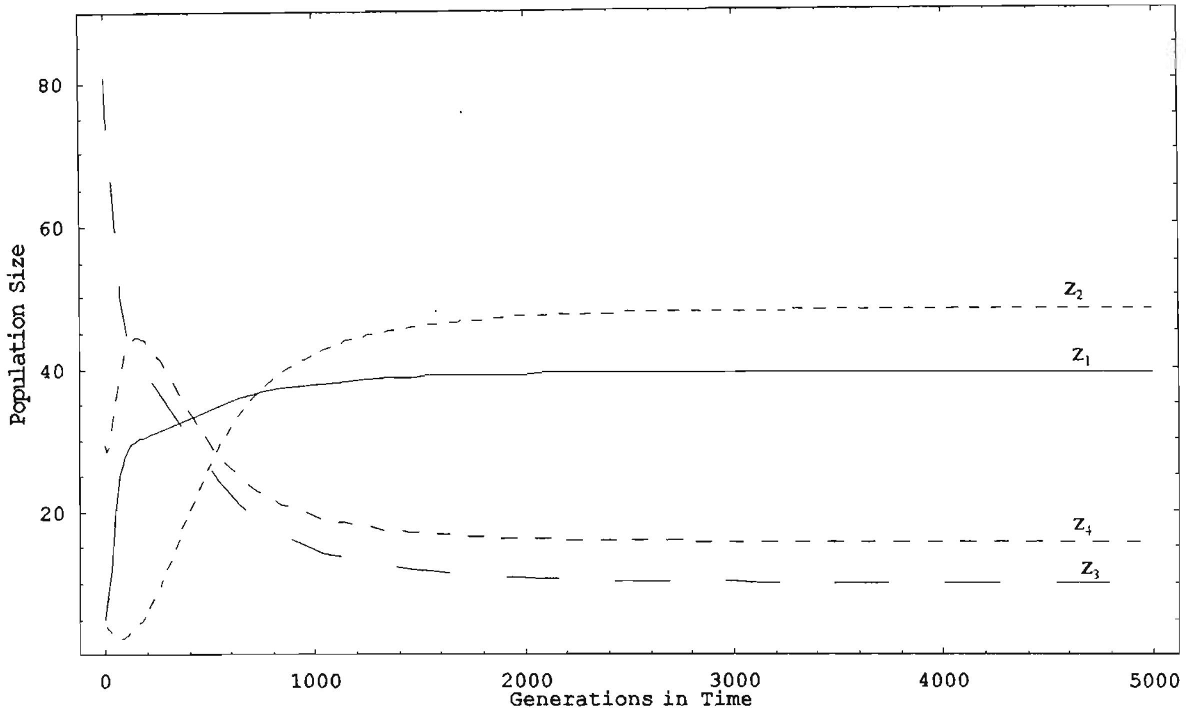

Figure 16b. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (5.52008, 0.560477, 2.8, −2.8). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1 and incumbent species 2 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3 and u_4 respectively. The respective population densities are z_1, z_2, z_3 and z_4.

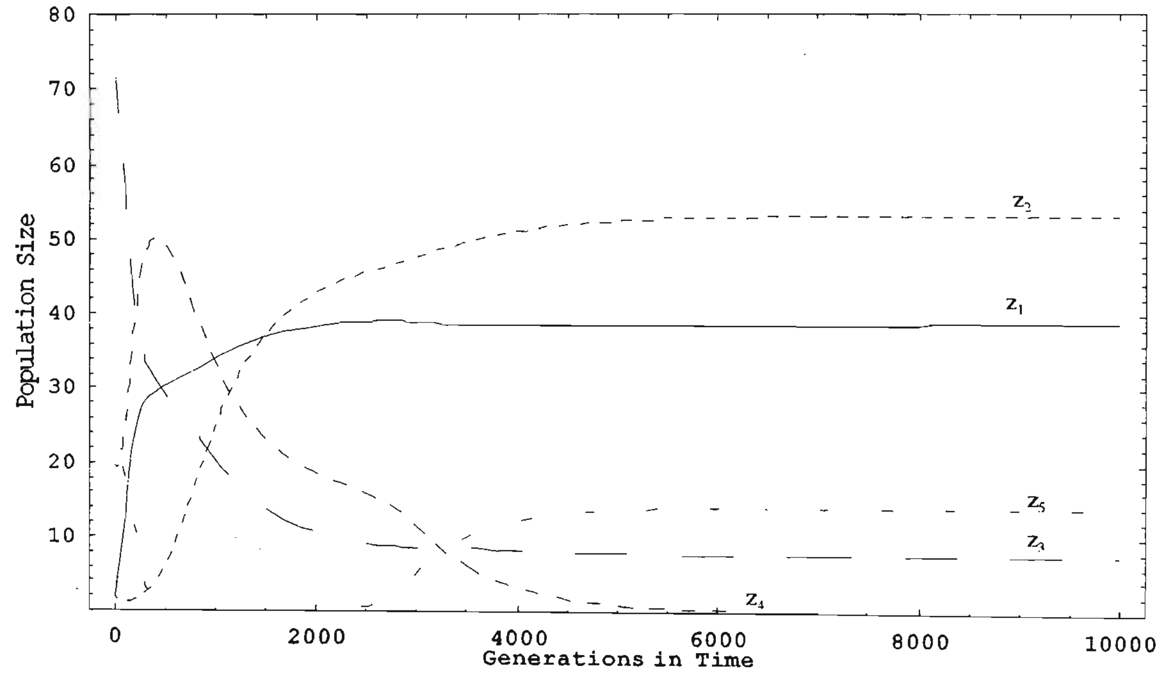

Figure 16c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5) = (5.52008, 0.560477, 3.5, −1.3, −3.2). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2 and incumbent species 3 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, and u_5 respectively. The respective population densities are z_1, z_2, z_3, z_4 and z_5. (Note that z_4 is eliminated)

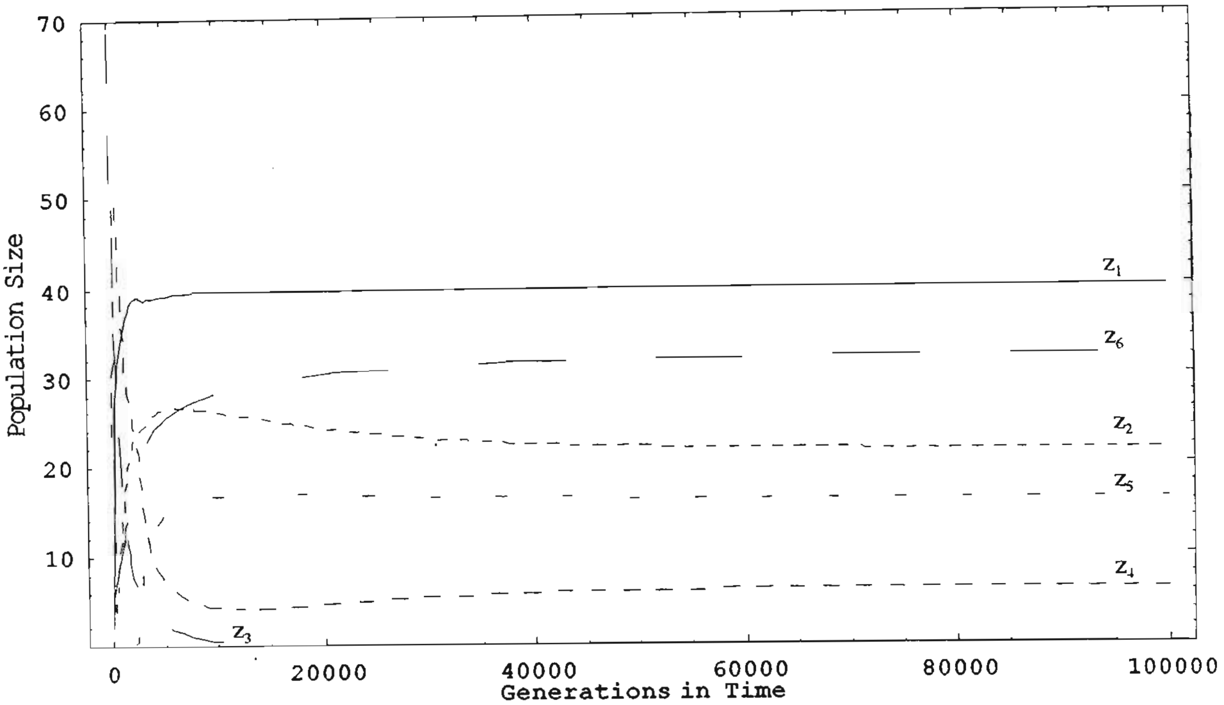

Figure 16d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5, u_6) = (5.52008, 0.560477, 3.5, - 1.3, -3.8, - 1.4). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is an NIS but (u_3, u_4, u_5, u_6) is neither an ESS nor an ESNIS. The invader species 1, invader species 2, incumbent species 1, incumbent species 2, incumbent species 3 and incumbent species 4 phenotypes are $\breve{u}_1$, $\breve{u}_2$, u_3, u_4, u_5 and u_6 respectively. The respective population densities are z_1, z_2, z_3, z_4, z_5 and z_6. (Note that z_3 is eliminated)

Thus in this section, all the incumbent communities are displaced to some degree by the interaction with the NIS coalition, with the coalition generally stabilising at population densities which are greater than those the incumbents stabilise to.

4.4.5. Conclusion of NIS Coalitions Which are Not ESS's

In all four sections, the NIS coalition has invaded the incumbent community. If the incumbent community consists of more than one population, some of the incumbent populations might be displaced, but not all of them. Thus the NIS coalition invades, but does not eliminate the incumbent community, which is what one would expect as the NIS coalition is not also an ESS. It is also apparent that the final population densities are hard to predict, unlike the case where the ESNIS coalition invaded an incumbent community, where it was possible to predict the final stable state (which were just the ESNIS equilibrium populations, all incumbents having been displaced).

4.5 Dynamics of An ESS Coalition Which is Not A NIS

It was hoped that the dynamics of an ESS which was not also a NIS could be explored in a similar manner to the simulations above. Unfortunately, many hours spent searching for an ESS which was not also a NIS proved fruitless. In Table 3 below, a selection of parameter values which gave candidate ESS's is given.

A candidate ESS meets the criterion for an ESS, except that it is not stable, but does not meet the criterion for a NIS. In other words, it meets the sufficient conditions for the ESS and not for the NIS which are found in Appendix 1. However, when the candidate ESS was left to evolve without any outside influence, one of the members of the coalition always became extinct, so the candidate ESS failed to meet the stability condition which is inherent in the definition of the ESS.

Coalition	β	σ_a	σ_k^2	$\breve{u}_1$	$\breve{u}_2$
1	0.7	0.4	12.5	3.93849	2.87995
2	0.8	0.5	12.5	4.1912	2.99557
3	0.8333	0.3	13.0546	0.991844	-0.568283
4	0.8333	0.52	13.0546	4.20634	2.95895
5	0.9	0.4	12.5	0.130838	1.67632

Table 3: Various parameter values for β, σ_a, and σ_k which give a candidate ESS coalition ($\breve{u}_1$, $\breve{u}_2$).

As with Tables 1 and 2, this table is not complete. Any one of these candidates can, by changing one of the parameters slightly, give many other candidate ESS's. For instance, if $\beta = 0.8333$, and $(\sigma_k)^2$ is fixed at 13.0546, then for any value of σ_a where $0.30 \leq \sigma_a \leq 0.5229426$, a candidate ESS exists.

The number of candidate ESS's which exist lead one to conclude that there should exist ESS coalitions which are not also NIS coalitions. However, such an example was not found in this work. The behaviour of one of the candidate ESS's is shown in Figures 17a-e. In Figures 17a-c, the candidate ESS is left to evolve without any outside influences. In Figure 17a, the

ESS coalition's initial populations are larger than the expected equilibrium populations. In 17b, the ESS coalition's initial populations are the expected equilibrium populations, and in Figure 17c, the ESS coalition's initial populations are both set at 5.0. Then in Figure 17d and Figure 17e, the candidate ESS was set at its equilibrium populations, and left to interact with two other populations, which themselves were at equilibrium before the introduction of the candidate ESS coalition in Figure 17d, and which were not at equilibrium in Figure 17e. The candidate ESS coalition chosen for these simulations was (3.93849, 2.87995) which is found when the parameters are set at $\beta = 0.7$, $\sigma_a = 0.4$, and $\sigma_k^2 = 12.5$.

In all Figures except for Figure 17b, at least one of the candidate ESS coalition populations became extinct.

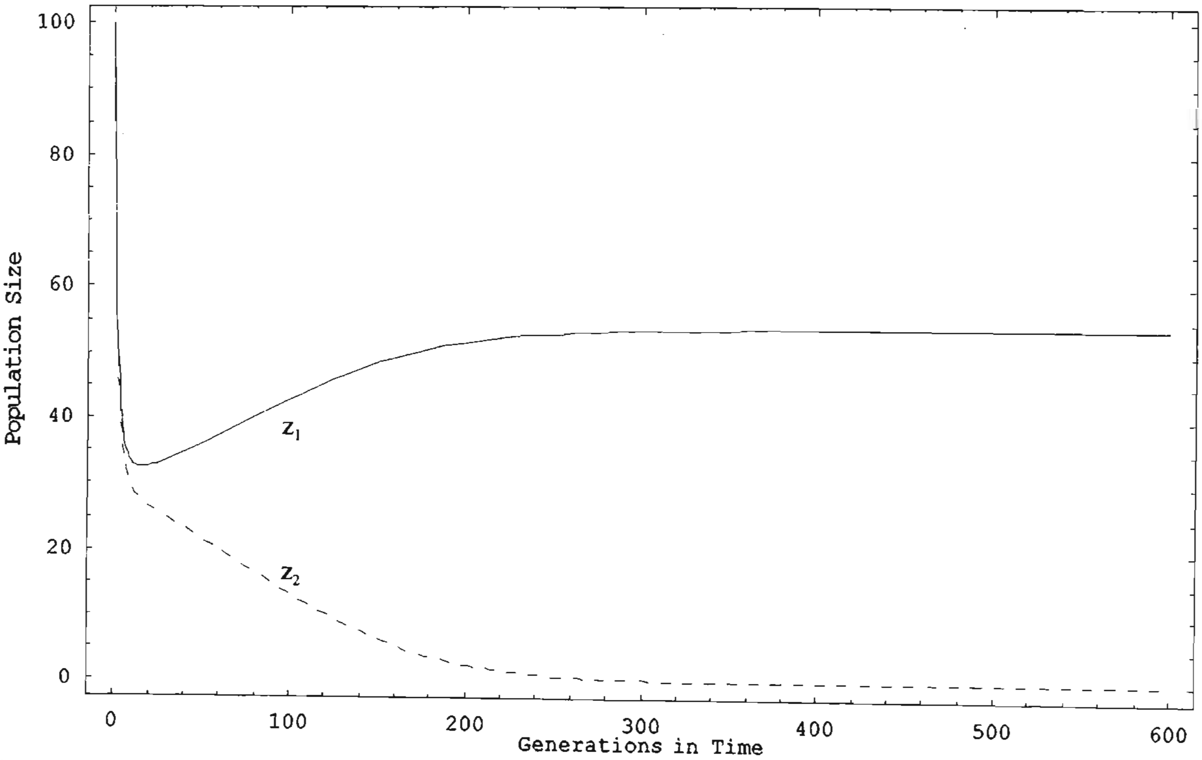

Figure 17a. Ecological dynamics of a community with phenotype $(\breve{u}_1, \breve{u}_2) = (3.93849, 2.87995)$. The community phenotype $(\breve{u}_1, \breve{u}_2)$ is a candidate ESS but it is not an NIS. The respective population densities are z_1 and z_2. Both z_1 and z_2 have initial population densities of 100. Note that z_2 becomes extinct, implying that $(\breve{u}_1, \breve{u}_2)$ is not an ESS.

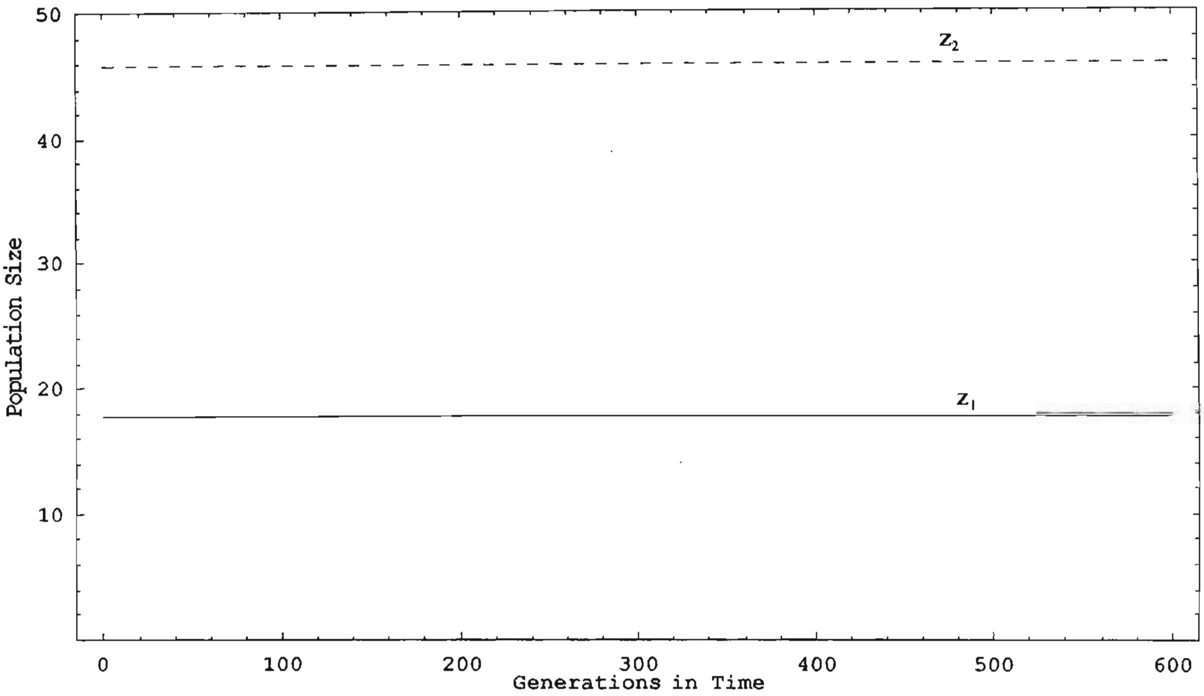

Figure 17b. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$) = (3.93849, 2.87995). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is a candidate ESS but it is not an NIS. The respective population densities are z_1 and z_2. Both z_1 and z_2 initially are at their equilibrium population densities. Note that both remain at equilibrium.

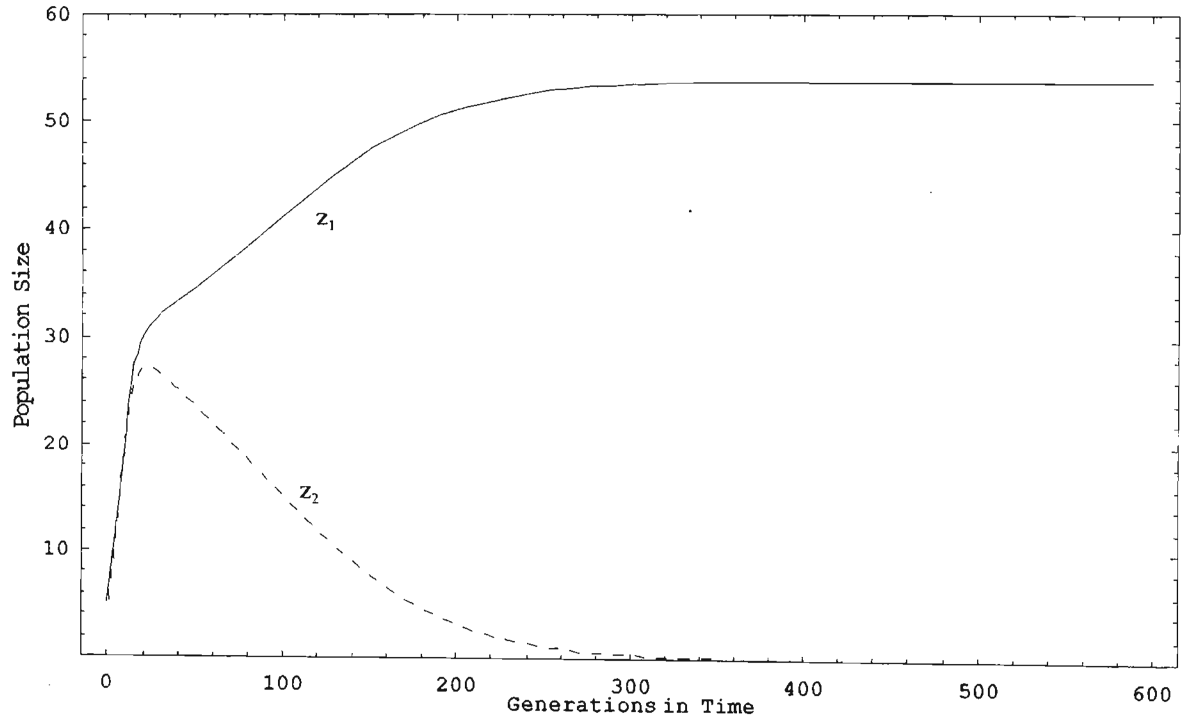

Figure 17c. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$) = (3.93849, 2.87995). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is a candidate ESS but it is not an NIS. The respective population densities are z_1 and z_2. Both z_1 and z_2 have initial population densities of 5.0. Note that z_2 becomes extinct, implying that ($\breve{u}_1$, $\breve{u}_2$) is not an ESS.

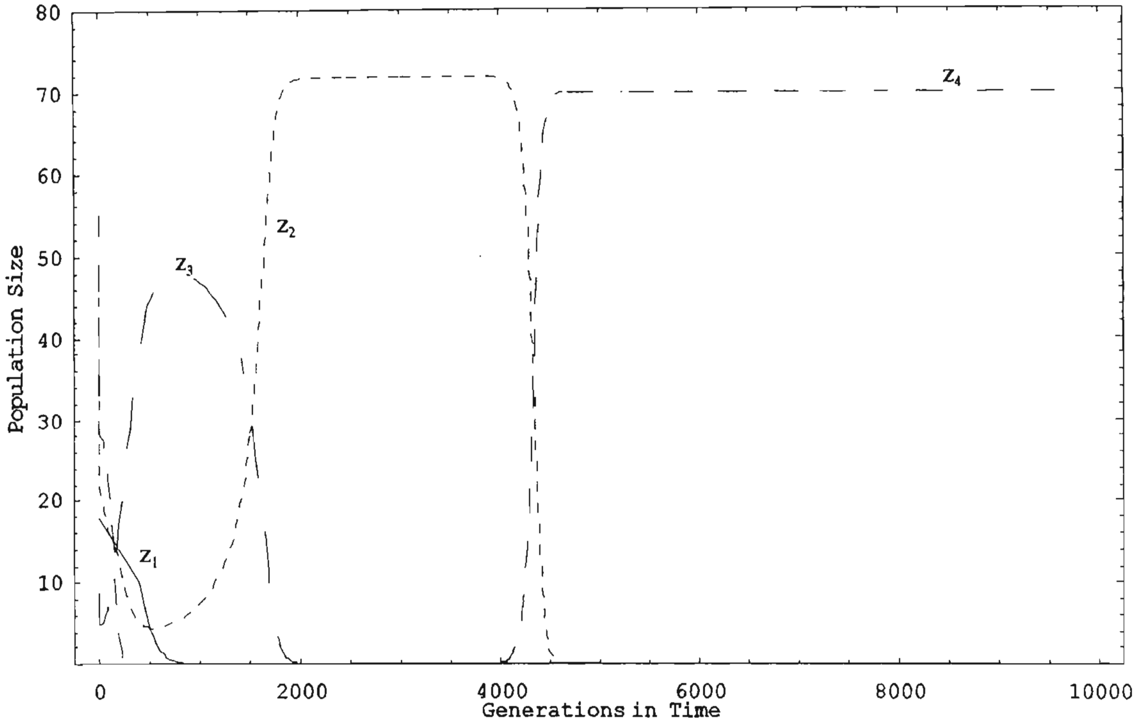

Figure 17d. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.93849, 2.87995, 4, 3). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is a candidate ESS but it is not an NIS, and (u_3, u_4) is neither an ESS nor an NIS. The respective population densities are z_1, z_2, z_3 and z_4. Note that z_1 and z_2 become extinct, so ($\breve{u}_1$, $\breve{u}_2$) is not an ESS.

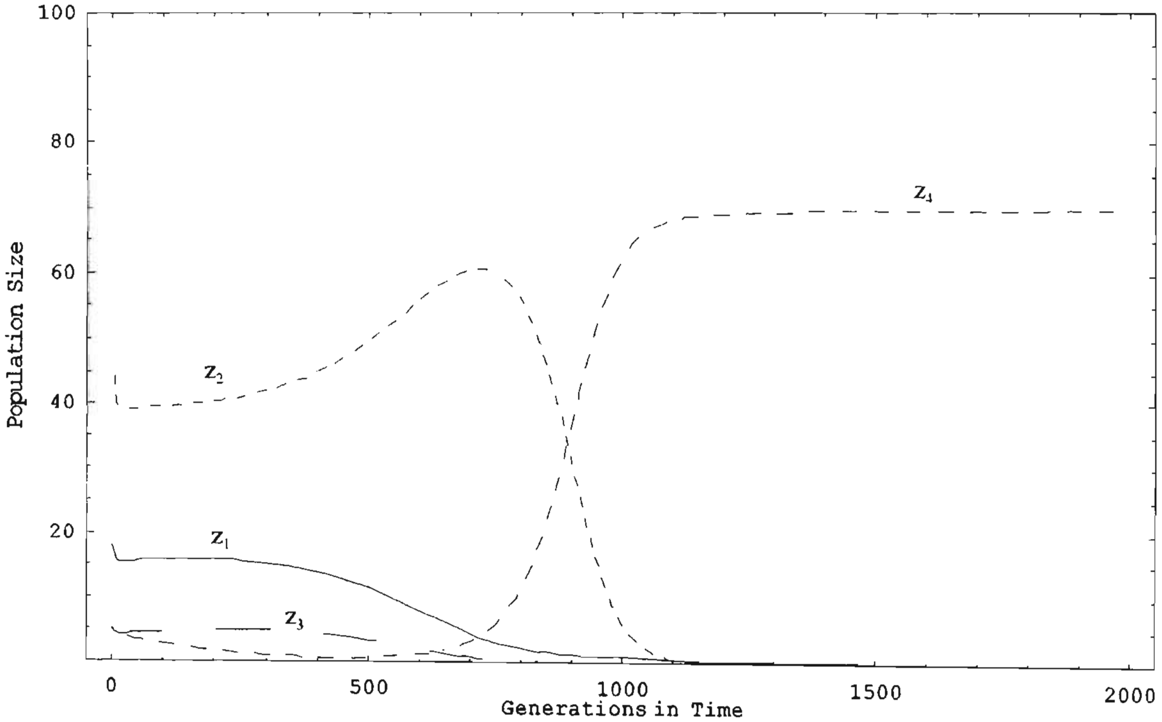

Figure 17e. Ecological dynamics of a community with phenotype ($\breve{u}_1$, $\breve{u}_2$, u_3, u_4) = (3.93849, 2.87995, 4, 3). The community phenotype ($\breve{u}_1$, $\breve{u}_2$) is a candidate ESS but it is not an NIS, and (u_3, u_4) is neither an ESS nor an NIS. The respective population densities are z_1, z_2, z_3 and z_4. Note that both z_1 and z_2 become extinct, so ($\breve{u}_1$, $\breve{u}_2$) is not an ESS.

Thus the candidate ESS coalition (3.93849, 2.87995) is not an ESS. Similar conclusions can be reached about the other candidates in Table 3, however, it seems likely that there are ESS coalitions which are not also NIS coalitions. They just remain to be found.

Chapter 5: Non Lotka-Volterra Example

Having looked at the effects of an ESNIS coalition invading incumbent populations where the population dynamics were given by Lotka-Volterra competition models, it was of interest to simulate the effects when the population dynamics were not Lotka-Volterra in nature. Although the results of chapter three have not been proven to apply to systems which are not governed by the Lotka-Volterra competition models, it is of interest to see whether or not the results hold. This would give a better understanding of the theory presented, and could lead to the theorem proven in chapter three being extended to all dynamic systems, regardless of the equations used to model them. Thus a search was made for a non Lotka-Volterra example. There were three criteria the example had to meet. Firstly, the paper had to present a mathematical model. Secondly, an ESS had been found, and thirdly the ESS had to be a coalition allowing coexistence. Many examples were found which including only one or two of the criteria, while meeting all three proved more difficult.

The idea was to set up the model used in the paper, and then reproduce the results of the paper which were relevant. Having found an ESS, the next step would be to run simulations to determine whether or not the ESS could invade established communities. Obviously if the ESS could always invade the established community, and in doing so eliminate the incumbent communities, then the ESS would be displaying the characteristics of an ESNIS. If every simulation ended with the same ESS coalition reaching its equilibrium populations, then it would seem that the ESS coalition was globally stable, and unique. If the theorem presented in chapter 3 is valid for non Lotka-Volterra systems, then there should exist a globally stable ESS which is able to invade any incumbent community.

5.1. Definition of the Example

The system chosen was designed for modeling biomass allocation to roots and leaves. The model was simulated by Vincent and Vincent, 1996. In their paper, they dealt mainly with a one-dimensional system, but they did include a section on coexistence, which was why the paper was chosen. The original model is presented first, along with Vincent and Vincent's results, followed by the changes made in order to turn the model into a coexistence model.

5.1.1. The One Dimensional Model

The growth rate of a plant population is given by

$$\frac{d\,B_p}{d\,t}\,\frac{1}{B_p} = \mathrm{MIN}\begin{bmatrix} G_1(u_p) \\ G_2(u_p) \end{bmatrix} \qquad p = 1 \cdots n \tag{1}$$

where

B_p = biomass of population p

$$G_1(u) = \frac{r\,N\,u}{N + k_N} - R - d \tag{2}$$

$$G_2(v) = \frac{r\,L\,(1 - v)}{L + k_L} - R - d \tag{3}$$

N = available soil nutrient

L = light availability

u_p = fraction of biomass allocated to root by population p

r = per capita maximal rate of plant growth

k_N = ½ saturation constant for nutrient

k_L = ½ saturation constant for light

R = density independent per capita respiration rate

d = density independent per capita loss rate

u, v = dummy variables which are replaced by the strategy u_p for population p.

The strategy u_p may be chosen over the fixed interval $0 \le u_p \le 1$. N and L are not constants, but rather are a function of resource supply and consumption. Note that the G-function's are linear. The MIN function acts in such a way that the "nutrient-limited growth curve" ($G_1(u)$) will be chosen for values of u_p between

$$0 \le u_p \le u_m \tag{4}$$

and the "light-limited growth curve" ($G_2(v)$) will be chosen for values of u_p between

$$u_m \le u_p \le 1. \tag{5}$$

The equation for u_m is found by setting the right hand sides of $G_1(u_m)$ and $G_2(u_m)$ equal to each other, and solving for u_m. The resulting equation is

$$u_m = \frac{L(N + k_N)}{L\,k_N + 2\,L\,N + N\,k_L} \tag{6}$$

In order to be able to use the ESS maximum principle, equation (1) had to be expressed in term of two separate differential equations. The *n* species were divided into two groups: nutrient-limited types, 1, and light-limited types, 2. Nutrient-limited species *i* have biomass given by b_{1i} and allocation to root fraction given by u_{1i} with dynamics given by

$$\frac{db_{1i}}{dt}\,\frac{1}{b_{1i}} = \frac{r\,N\,u_{1i}}{N + k_N} - R - d \tag{7}$$

and light-limited species *j* have biomass b_{2j} and allocation to root fraction given by u_{2j} with dynamics given by

$$\frac{db_{2j}}{dt}\,\frac{1}{b_{2j}} = \frac{r\,L(1 - u_{2j})}{N + k_N} - R - d. \tag{8}$$

The allocation fractions are required to satisfy the constraints (4) and (5) with u_p replaced by u_{1i} in (4) and by u_{2j} in (5).

The nutrient dynamics are given by

$$\frac{dN}{dt} = a(T - N - \sum_{i=1}^{n_i} pb_{1i} + \sum_{j=1}^{n_j} pb_{2j}) - \sum_{i=1}^{n_i} pb_{1i}\,[G_1(u_{1i}) + d] - \sum_{j=1}^{n_j} pb_{2j}\,[G_2(u_{2j}) + d] \tag{9}$$

and the light availability by

$$L = \frac{L_0}{1 + \sum_{i=1}^{n_i} \alpha\, b_{1i}\,(1 - u_{1i}) + \sum_{j=1}^{n_j} \alpha\, b_{2j}\,(1 - u_{2j})} \tag{10}$$

where

T = total soil nutrient in habitat

a = mineralisation rate

p = plant tissue nutrient concentration

L_0 = solar constant

α = light decay rate per unit leaf biomass

and where $n_i + n_j = n$ (total number of species) with the understanding that if $n_i = 0$ then the summation is zero and likewise for n_j. Note that G_1 is evaluated at u_{1i} and G_2 at u_{2j}. The constants were given the following values:

$a = 0.3$, $r = 5$, $k_N = k_L = 1$, $p = 0.1$, $R = 0.5$, $\alpha = 0.001$, $L_0 = 2$, $T = 5$ and $d = 0.5$.

The ESS maximum principle was then used to calculate the ESS strategy. u_m* can be calculated by solving four equilibrium equations which are (6), (10), the r.h.s. of (7) or (8) set equal to zero with the u_{1i} and u_{2j} set equal to u_m and $b_{1i} = b_{2j} = b$, the r.h.s. of (9) set equal to zero with u_{1i} or u_{2j} set equal to u_m and $b_{1i} = b$, $b_{2j} = 0$ or $b_{1i} = 0$, $b_{2j} = b$, depending on whether (7) or (8) is used. Whichever of (7) or (8) were used, the same results should be obtained.

Vincent and Vincent solved these equations simultaneously and got the following equilibrium values: $u_m^* = 0.700517$, $b^* = 17.2515$, $N^* = 0.399587$, and $L^* = 2.01039$.

Vincent and Vincent then simulated the system, and got equilibrium values of $u_m^* = 0.699$, $b^* = 17.247$, $N^* = 0.401$, and $L^* = 1.990$.

5.1.2. The Coexistence Model

The G-functions change as follows:

$$G_1(u) = \frac{r\,N\,(u - u^2 + 0.2)}{N + k_N} - R - d \qquad (11a)$$

$$G_2(v) = \frac{r\,L\,(-1 + v + (1 - v)^2 + 0.5)}{L + k_L} - R - d \qquad (11b)$$

The strategy u_p is still chosen over the fixed interval $0 \leq u_p \leq 1$, but the MIN function acts in such a way that the "nutrient-limited growth curve" ($G_1(u)$) will be chosen for values of u_p between

$$0 \leq u_p \leq u_{m1} \quad \text{and}$$

$$u_{m2} \leq u_p \leq 1$$

and the "light-limited growth curve" ($G_2(v)$) will be chosen for values of u_p between

$$u_{m1} \leq u_p \leq u_{m2}.$$

It is also given that $u_{m1} \leq u_{m2}$, where u_{m1} and u_{m2} can be found at the points of intersection of the two curves, that is

$$u_{m1} = \frac{0.5\, k_N L + 0.5\, k_L N + L N - 0.5\,[1.8\, N^2(L + k_L)^2 + 0.8\, L N\, (N + k_N)(L + k_L) - L(N + k_N)]^{½}}{L k_N + 2 L N + N k_L} \tag{12a}$$

and

$$u_{m2} = \frac{0.5\, k_N L + 0.5\, k_L N + L N + 0.5\,[1.8\, N^2(L + k_L)^2 + 0.8\, L N\, (N + k_N)(L + k_L) - L(N + k_N)]^{½}}{L k_N + 2 L N + N k_L} \tag{12b}$$

All the other equations from §5.1.1. remain the same. Unfortunately, Vincent and Vincent only gave graphical results for this section.

5.2. Problems Encountered with the Model

The first problem with Vincent and Vincent's analysis is in their solving of the four equilibrium equations to find the ESS. Equation (10) has a numerator of 2, and every term in its denominator is positive, giving the denominator a magnitude that is greater than one. It is thus impossible for L to have a value greater than 2, and so Vincent and Vincent's value of $L^* = 2.01039$ is impossible to attain analytically. (A numerical solution could yield a value of L^* slightly greater than 2).

A second problem arises when trying to solve the four equilibrium equations to get the equilibrium solutions. Whether one uses equation (7) or (8) the same results should be obtained. With the form of the equations presented in the paper, this does not happen. Two separate sets of equilibrium solutions are attained. Using equation (7) gives $u_m^* = 0.699482$, $b^* = 17.2484$, N^*

= 0.400415, and $L^* = 1.98969$, while using equation (8) gives the equilibrium solutions $u_m^* = 0.697616$, $b^* = 68.9749$, $N^* = 0.401674$, and $L^* = 1.95918$.

If equation (9) is changed so that there are no positive signs in the first bracket, that is the "+" sign in the first bracket is replaced by a "–", then the same results are obtained for both sets of four equilibrium equations. The equilibrium solutions in this case are $u_m^* = 0.699482$, $b^* = 17.2484$, $N^* = 0.400415$, and $L^* = 1.98969$. These solutions are close to the solutions obtained by Vincent and Vincent.

Finally, if equation (9) is changed so the only negative sign in the first bracket is between the terms T and N (so the other negative sign becomes positive), the same results are obtained for both sets of four equilibrium equations. The equilibrium solutions in this case are $u_m^* = 0.697616$, $b^* = 68.9749$, $N^* = 0.401674$, and $L^* = 1.95918$.

The MATHEMATICA code used to solve for these equilibrium solutions is found in Figure 18 below, before any changes were made to equation (9). The variable "N" is written in lower case as "N" is a function in MATHEMATICA.

```
(* Set the Parameter Values *)
a = 0.3; r = 5; kn = 1; kl = 1; p = 0.1; R = 0.5; alpha = 0.001; Lo = 2; T = 5; d = 0.5;
g1[u_] := (r n u/(n + kn)) - R - d;
g2[u_] := (r L(1 - u)/(L + kl)) - R - d;
(* Using equation (7) *)
Solve[{um == L(n + kn)/(2 n L + n kl + L kn), L == Lo/(1 +  alpha b(1 - um)), g1[um] == 0,
   a(T - n - p b) - p b (g1[um] + d) == 0}, {um, b, n, L}]
(* Using equation (8) *)
Solve[{um == L(n + kn)/(2 n L + n kl + L kn), L == Lo/(1 + alpha b(1 - um)),
   g2[um] == 0, a(T - n + p b) - p b (g2[um] + d) == 0}, {um, b, n, L}]
```

Figure 18. Code to solve the four equilibrium equations in the one-dimensional case.

The equations in the "Solve" function are given in the following order: (6), (10), r.h.s. of (7) (or (8)) set equal to zero, and the r.h.s. of (9) set equal to zero.

5.3. The Non Lotka-Volterra Model

If equation (9) was changed so that the first bracket had no positive signs in it, then the same results are obtained when using equation (7) as when using equation (8). The equilibrium plant biomass is 17.2484, compared with Vincent and Vincent's value of 17.2515. Thus it seems that the presence of a positive sign in the first bracket of equation (9) was a typographical error.

Equation (9) was changed to

$$\frac{dN}{dt} = a(T - N - \sum_{i=1}^{n_i} pb_{1i} - \sum_{j=1}^{n_j} pb_{2j}) - \sum_{i=1}^{n_i} pb_{1i}\,[G_1(u_{1i}) + d] - \sum_{j=1}^{n_j} pb_{2j}\,[G_2(u_{2j}) + d] \qquad (13)$$

The one-dimensional model was set up and simulated before moving onto the coexistence model. This was done so that the nature of the new one-dimensional problem could be compared to that of the one-dimensional problem as presented by Vincent and Vincent. Once this had been done, the new coexistence model could be set up and simulated.

5.3.1. The New One-Dimensional Model

Solving the four equations simultaneously using equation (13) in place of equation (9) resulted in the equilibrium solutions $u_m^* = 0.699482$, $b^* = 17.2484$, $N^* = 0.400415$, and $L^* = 1.98969$ A simulation of the one-dimensional model was then set up and run. The strategy dynamic used in both this and the coexistence model was

$$u_i = \sigma^2 \left[\frac{\partial G_i}{\partial u_i}\right] \qquad (14)$$

where σ is the variance in strategy about the mean u_i. The MIN function is simulated by calculating G_1 and G_2 for a given value of u and v, and adding the requirement that

$$\text{IF } G_1 < G_2 \text{ THEN } G = G_1 \text{ ELSE } G = G_2. \qquad (15)$$

The same process used by Vincent and Vincent was now used to simulate the system. While the same results would have been obtained using only one species, it is more interesting to simulate two species. Using (14) as the strategy dynamic and choosing initial parameter values of $\sigma^2 = 0.005$, $b_1(0) = b_2(0) = 0.5$, $N(0) = 10$, $u_1(0) = 0.3$, $u_2(0) = 0.6$ the following results were obtained.

Figure 19 shows the evolution of the strategies over time. Both strategies evolve to a value of 0.695 (compared with u_m^* = 0.699 from the direct calculation) because the ESS is a coalition of one. Figure 20 illustrates the nutrient and light dynamics of the situation. Nutrient levels dropped rapidly while light levels remained nearly constant. The equilibrium values for N and L from the simulation are $N^* = 0.404$ and $L^* = 1.990$ (compared with 0.400 and 1.990 respectively).

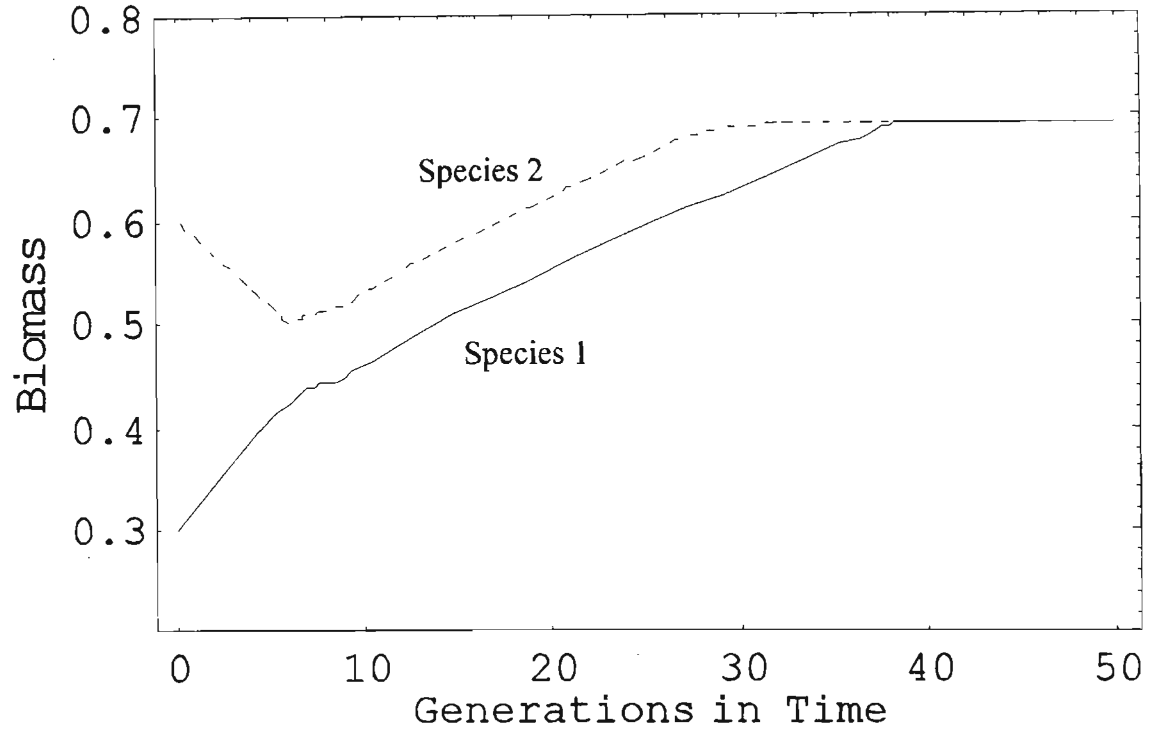

Figure 19. The evolution over time of the initial strategies $u_1 = 0.3$ (species 1) and $u_2 = 0.6$ (species 2) are shown as solid and dotted lines respectively. Note that both strategies evolved to the same solution.

In Figure 21, the population dynamics of the two species are shown. Both species start from 0.5 and end with populations of 0.9055 and 16.0138 for species one and two respectively. Both plants obtain the ESS strategy with a combined equilibrium population $b_1^* + b_2^* = 16.9193$ (compared with $b^* = 17.2484$). Although there was some discrepancy in the results of the simulation as compared to the direct calculation, they were not too large to prohibit looking at the coexistence model, and in fact similar sized discrepancies were found by Vincent and Vincent. For example, Vincent and Vincent calculated a population of 17.252 and by simulation, obtained a population of 17.247.

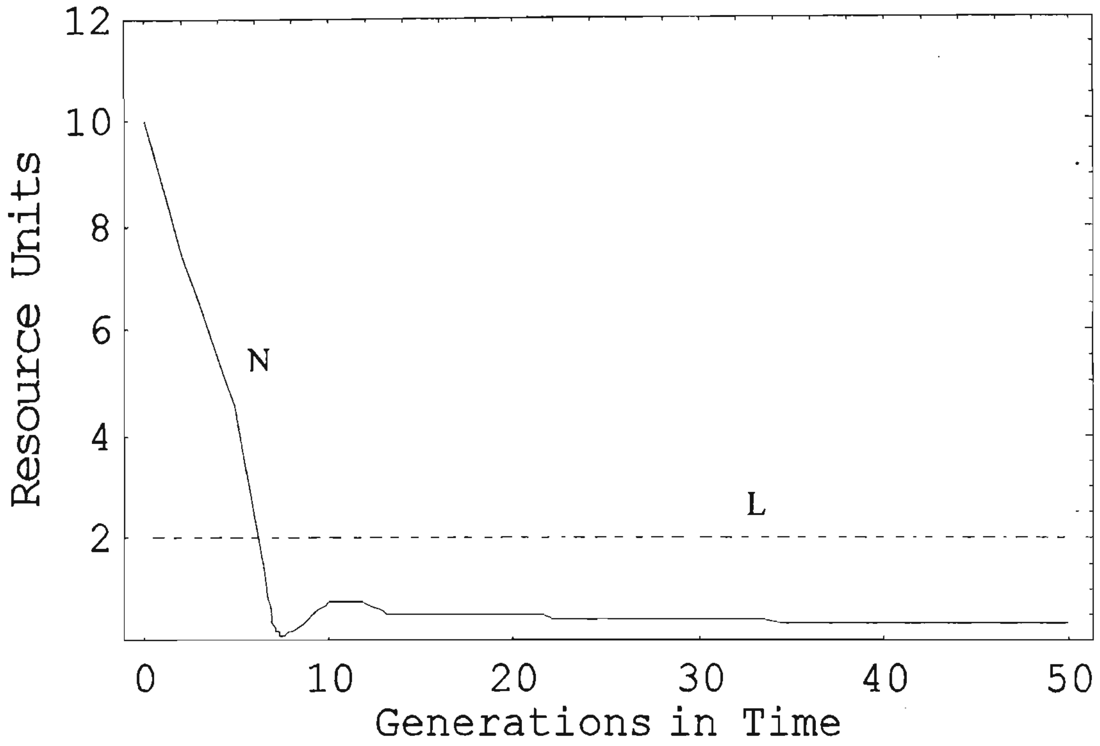

Figure 20. The change in nutrients (solid line) and the change in light (dotted line) over time are taken from equations (13) and (10), respectively.

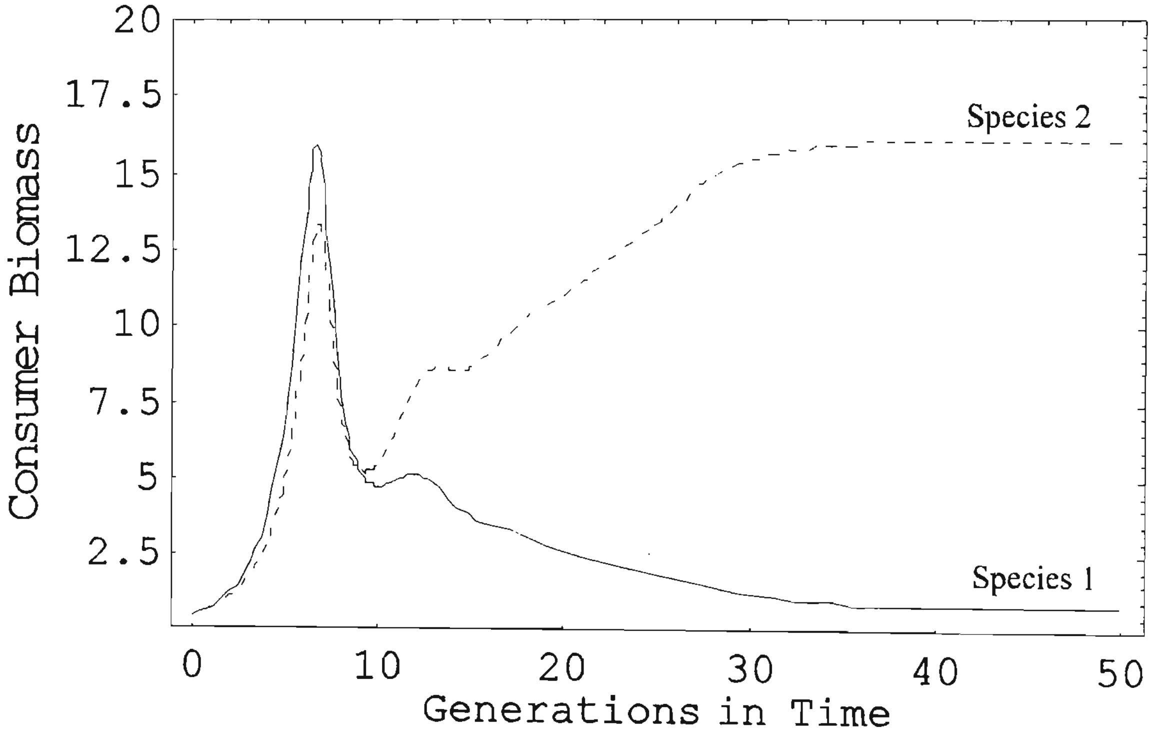

Figure 21. Populations of species 1 (solid) and species 2 (dotted) are shown against time. Since both species 1 and species 2 evolved to the same strategy, their populations can be summed to give the equilibrium population of the ESS strategy, u_m^*.

Having found an ESS strategy, namely $u_m = 0.695$, it was of interest to see whether or not this strategy had any invasive properties before moving on to the coexistence model. Three different incumbent populations which were initially at equilibrium were invaded by the ESS. The results are shown in the figures below. In each case, the invading ESS strategy $u_2 = 0.695$ has an initial population of $b_2 = 0.5$.

In Figure 22a, the incumbent strategy $u_1 = 0.5$ has an initial equilibrium population of $b_1 = 8.879$. The invading ESS strategy stabilises to a final population of $b_2 = 17.234$ after 700 generations, and completely displaces the incumbent population. In Figure 22b, the incumbent strategy $u_1 = 0.65$ has an initial equilibrium population of $b_1 = 14.166$. The final population sizes are $b_1 = 0$ and $b_2 = 17.234$, which are obtained after 400 generations. Finally in Figure 22c, the incumbent population has an initial size of $b_1 = 16.566$, using strategy $u_1 = 0.69$. The invading population takes 2000 generations to stabilise at $b_2 = 17.234$, having eliminated the incumbent population.

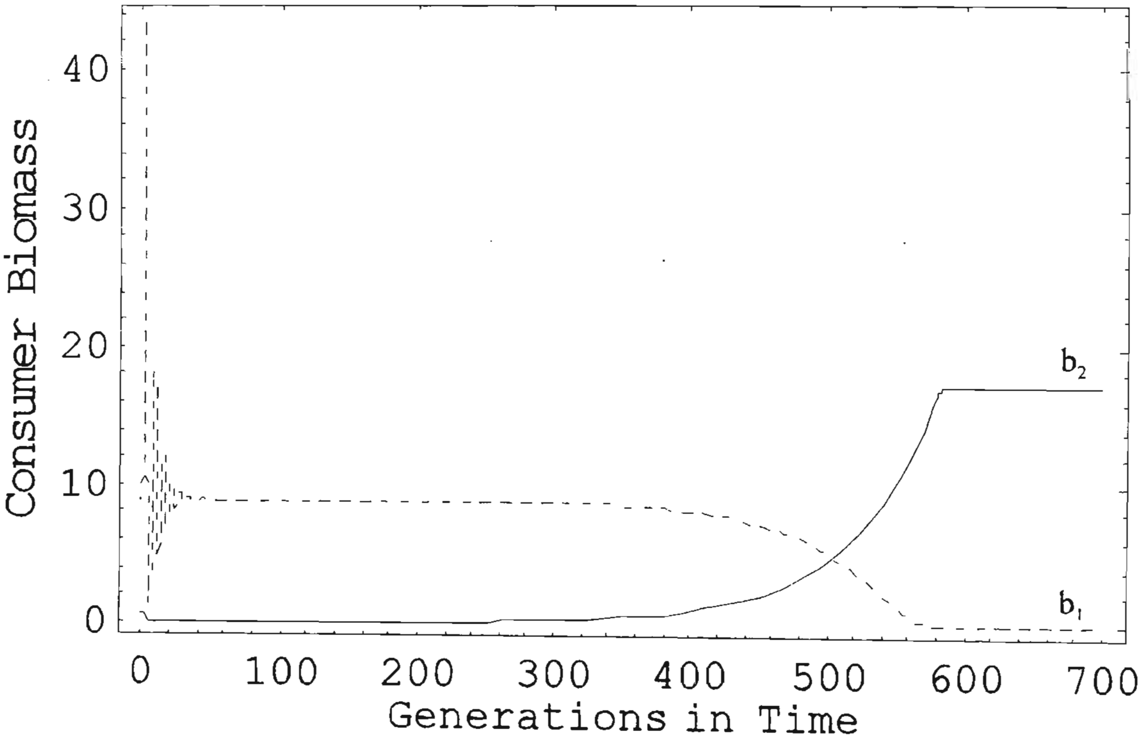

Figure 22a. The invading strategy $u_2 = 0.695$ which is the ESS strategy invades and displaces the incumbent population whose strategy is $u_1 = 0.5$ in 700 generations at which time the invader's population has stabilised at 17.2341.

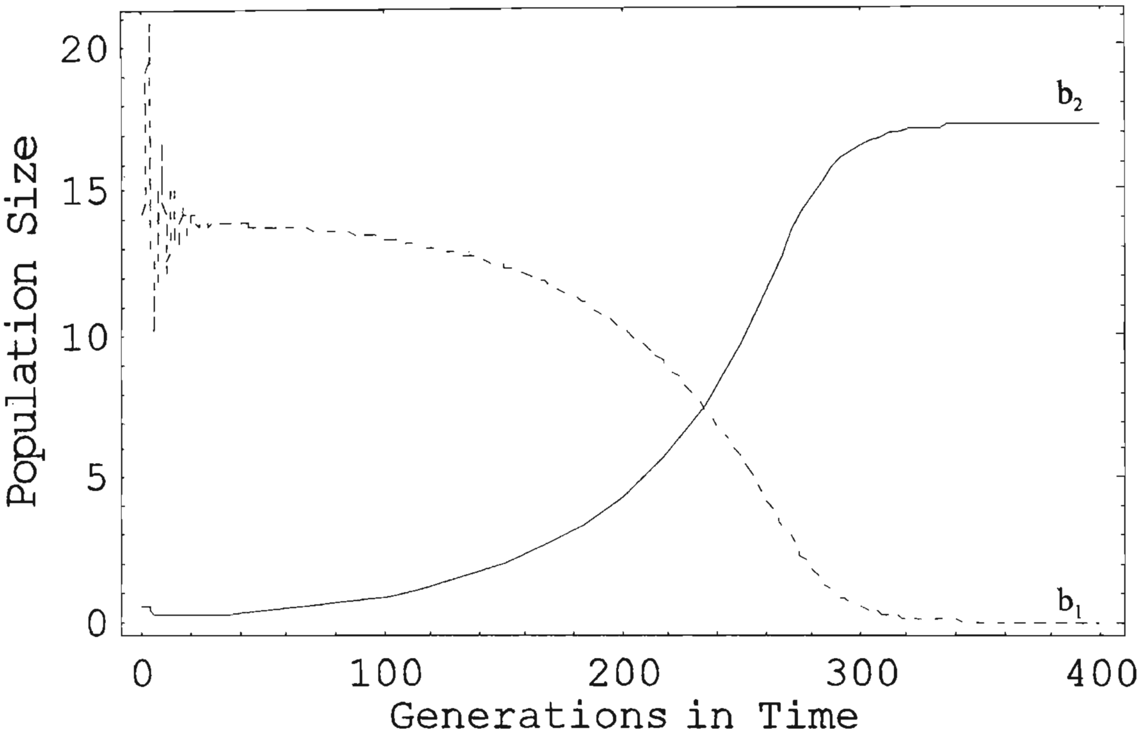

Figure 22b. The invading strategy $u_2 = 0.695$ which is the ESS strategy invades and displaces the incumbent population whose strategy is $u_1 = 0.65$ in 400 generations at which time the invader's population has stabilised at 17.2341.

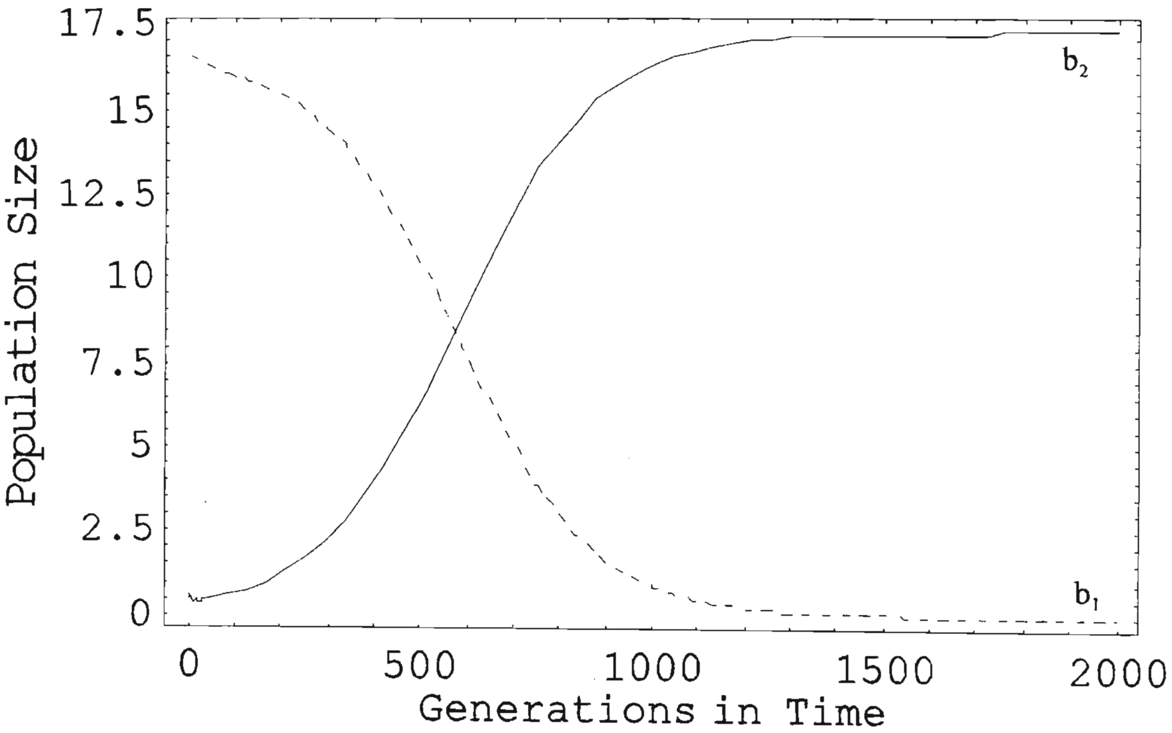

Figure 22c. The invading strategy $u_2 = 0.695$ which is the ESS strategy invades and displaces the incumbent population whose strategy is $u_1 = 0.69$ in 2000 generations at which time the invader's population has stabilised at 17.2341.

The three simulations whose results are given in Figures 22a-c imply that the ESS strategy $u_m = 0.695$ is also an NIS strategy because it can invade established communities. Although the simulations done for the one-dimensional case are not extensive, they seem to support the notion that there is an ESS which is also an NIS.

5.3.2. The New Coexistence Model

Similar to the one-dimensional model, six equations had to be solved simultaneously. They were (12a), (12b), (10), the right-hand side of (11a) or (11b) set equal to zero with u or v set equal to u_{m1}, then the right-hand side of (11a) or (11b) set equal to zero with u or v set equal to u_{m2}, and the right-hand side of (13) set equal to zero with u_{1i} or u_{2j} set equal to u_{mk}, where the subscript $k = 1, 2$ and has the same value as either i or j, and $b_{1i} = b_i$, $b_{2j} = 0$ or $b_{1i} = 0$, $b_{2j} = b_j$ depending on whether (11a) or (11b) was used.

Solving these two sets of equations simultaneously should give the same values for the six variables, namely N, L, u_{m1}, u_{m2}, b_1, and b_2. Both sets of equations have the following values: $N^* = 1.00463$; $L^* = 1.98174$; $u_{m1}^* = 0.274342$; $u_{m2}^* = 0.725658$; $b_1^* = 11.3124$; and $b_2^* = 3.67028$.

Equations (12a) and (12b) were used to generate Figure 23 on the next page with $N = 1.0046$ and $L = 1.9817$. The equilibrium strategies are found where the G*-functions have a value of zero, that is where the two curves intersect with the horizontal line. From Figure 23 it is easy to see that there are two possible biomass allocation to root proportions which will give the G-function a value of zero, which occurs at equilibrium.

The next step was to set up the simulation. Using (14) as the strategy dynamic, and choosing the initial parameter values as $\sigma^2 = 0.005$, $b_1(0) = b_2(0) = 0.5$, $N(0) = 5$, $u_1(0) = 0.32$, $u_2(0) = 0.7$ the following results were obtained. In Figure 24 and Figure 25 on the following pages the dynamics of the coexistence model are shown. In Figure 24 the evolution of the two strategies from 0.32 and 0.7 to 0.2714 (species 1, compared with $u_{m1}^* = 0.2743$) and 0.7286 (species 2, compared with $u_{m2}^* = 0.7257$), respectively. The dynamics of the population sizes are shown in Figure 25. Both populations start from initial values of 0.5 and species 1 evolves to $b_1^* = 10.8498$ (compare with

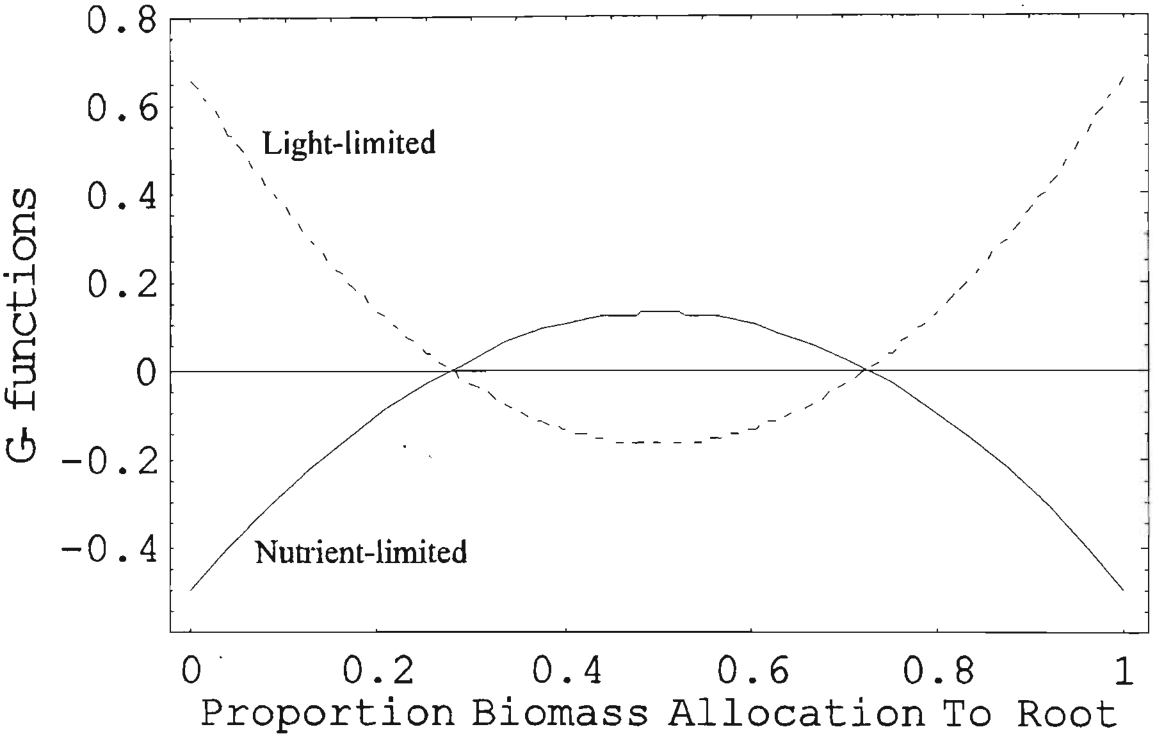

Figure 23. The solid line depicts equation (12a) and the dotted line depicts equation (12b) for the G-functions as a function of root allocation strategy at equilibrium.

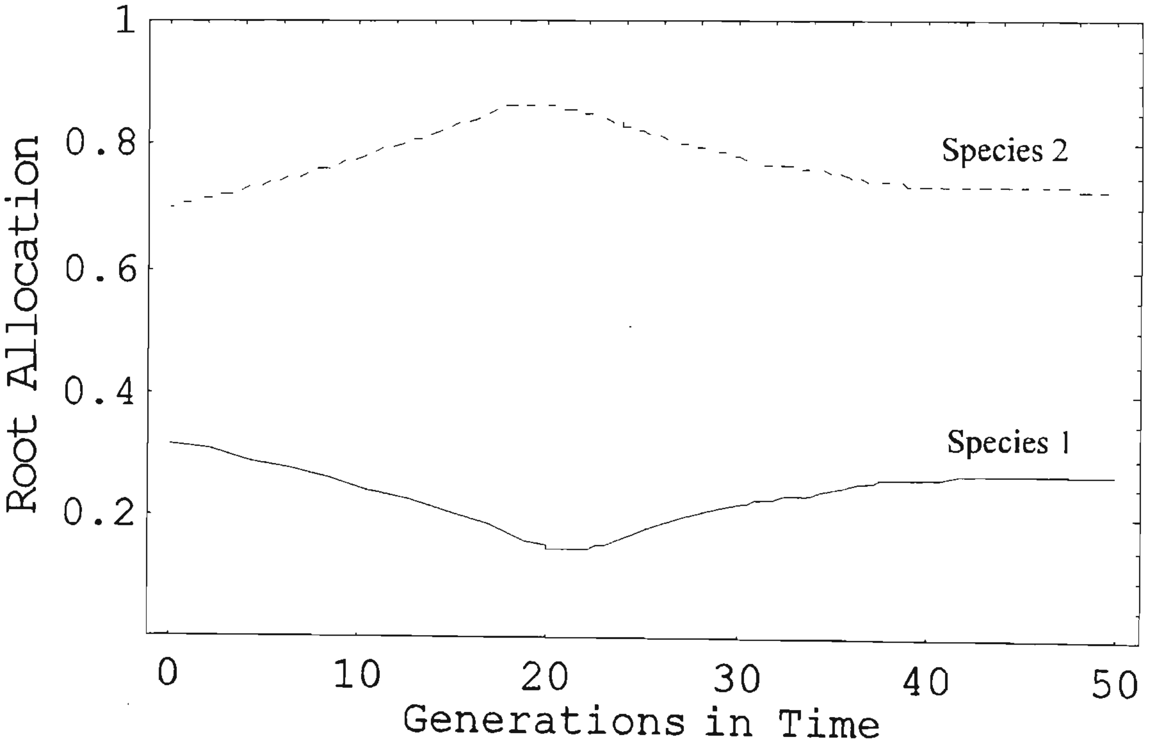

Figure 24. Initial strategies $u_1 = 0.32$ and $u_2 = 0.7$ for species 1 and 2, respectively, evolved to two different strategies and are shown as solid and dotted lines respectively.

11.3123) and species 2 evolves to $b_2^* = 4.0322$ (compare with 3.6703). The simulation results for N and L are $N^* = 1.011$ and $L^* = 1.988$ (compared with 1.005 and 1.982, respectively). While these results are different, the difference was not so great as to prevent further simulations to be carried out. It is worth noting that the results presented by Vincent and Vincent also showed similar discrepancies.

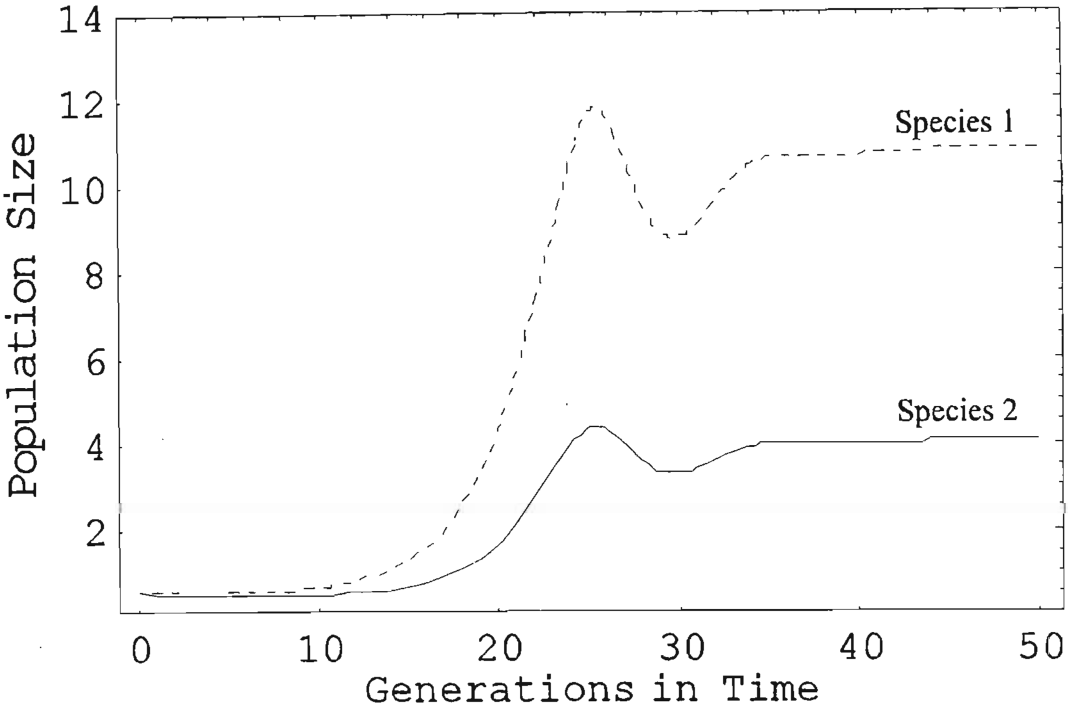

Figure 25. Populations of species 1 (solid) and species 2 (dotted) shown over time.

Unfortunately the coexistence model is such that while the two species compete for the resources, the two ESS strategies do not always evolve to the same population sizes. The combined population stays fairly constant, regardless of the initial population and strategy choices. However, if the initial strategy choices are all above 0.729 or all below 0.271 then only one strategy will evolve. If the initial strategies are changed from the values used to generate Figures 24 and 25, the composition of the population changes, but the equilibrium strategies reached remain the same. As the final population solution for the one species increases, the final composition of the other species decreases, while the sum of the populations remains constant.

If, for example, the initial strategies for the two species are changed to 0.4 and 0.6 respectively, then the populations evolved to are $b_1 = 7.4516$ and $b_2 = 7.4516$. The sum of these populations is 14.9031, compared with 14.8820 which is the sum of the populations reached in Figure 25 while 14.9827 is the sum of the equilibrium populations obtained by direct calculation. This seems to imply that there will not be a globally stable and unique ESS, because even though the same strategies are always optimal, the population distribution changes depending on the initial strategy choice. However, the simulations were still carried out in order to determine if any of the characteristics of a globally stable strategy coalition were present.

5.4. The Simulations

Table 4 below gives a set of equilibrium populations for various strategies which were not allowed to evolve with time. In other words, the strategy for the incumbent population was fixed, and then with only the incumbent populations being present, the system was allowed to evolve until the population stabilised. These populations and strategies were then chosen as the incumbent communities. The behaviour of these incumbent communities in five different situations was then modelled. In each of the five situations there are two invading populations, whose initial strategies vary in each of the five situations.

1. The invading species had initial strategy values of $u_3 = 0.32$ and $u_4 = 0.7$, and both had initial populations of 0.5. These strategies were allowed to change with time.
2. The invading species used the ESS strategies and equilibrium populations. In this situation the ESS strategies could change with time.
3. Similar to situation two, except the invading species both had initial populations of 0.5.
4. Situation three was repeated where the ESS strategies were fixed.
5. Situation two was repeated where the ESS strategies were fixed.

Number	u_1	u_2	b_1	b_2
1	0.2	–	14.0625	–
2	0.8	–	14.0625	–
3	0.2	0.8	6.4996	6.4996
4	0.15	0.85	5.5966	5.5966
5	0.27	0.73	7.4391	7.4391

Table 4. Equilibrium populations corresponding to strategies u_1 and u_2.

From Figures 24 and 25, the ESS strategies are $u_3 = 0.271$ and $u_4 = 0.729$ with corresponding equilibrium populations $b_3 = 10.850$ and $b_4 = 4.032$.

The results of the simulations for the five situations can be summarised as follows. In all situations for all cases, the incumbent populations are eliminated, and the invading populations stabilise and their final strategies are the ESS strategies. The combined sum of the stable populations remains fairly constant for all cases. For situations three and four, the two invading populations stabilise to the same size, while in the other three situations this is not the case.

The results are now presented in greater detail. Note that for situations four and five that the dynamics of the strategies are not presented as they do not change over time.

5.4.1. Situation One

The invading species have initial strategies $u_3 = 0.32$ and $u_4 = 0.7$, which are introduced with initial populations of 0.5 into a situation where the incumbent populations are at equilibrium, and the invading strategies were allowed to evolve. In all cases it is expected that the invading strategies will evolve into the ESS strategies, and eliminate the incumbent populations.

Case 1: One Incumbent Using Strategy $u_1 = 0.2$

In Figure 26a, there is only one incumbent population using strategy $u_1 = 0.2$ which has an initial population of 14.0625, which is eliminated in 175 generations by the invading species using initial strategies $u_3 = 0.32$ and $u_4 = 0.7$. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = 6.82$ and $b_4 = 8.04$. Note the combined population is 14.86, compared with the combined ESS equilibrium populations from Figure 25 which is 14.88.

In Figure 26b, the dynamics of the strategies are shown. u_1 remains constant at 0.2, while u_3 initially decreases from 0.32, and then increases again to 0.271. u_4 initially increases from 0.7, and then decreases slightly again to stabilise at a value of 0.729. Note the invading strategies stabilise at the ESS strategies.

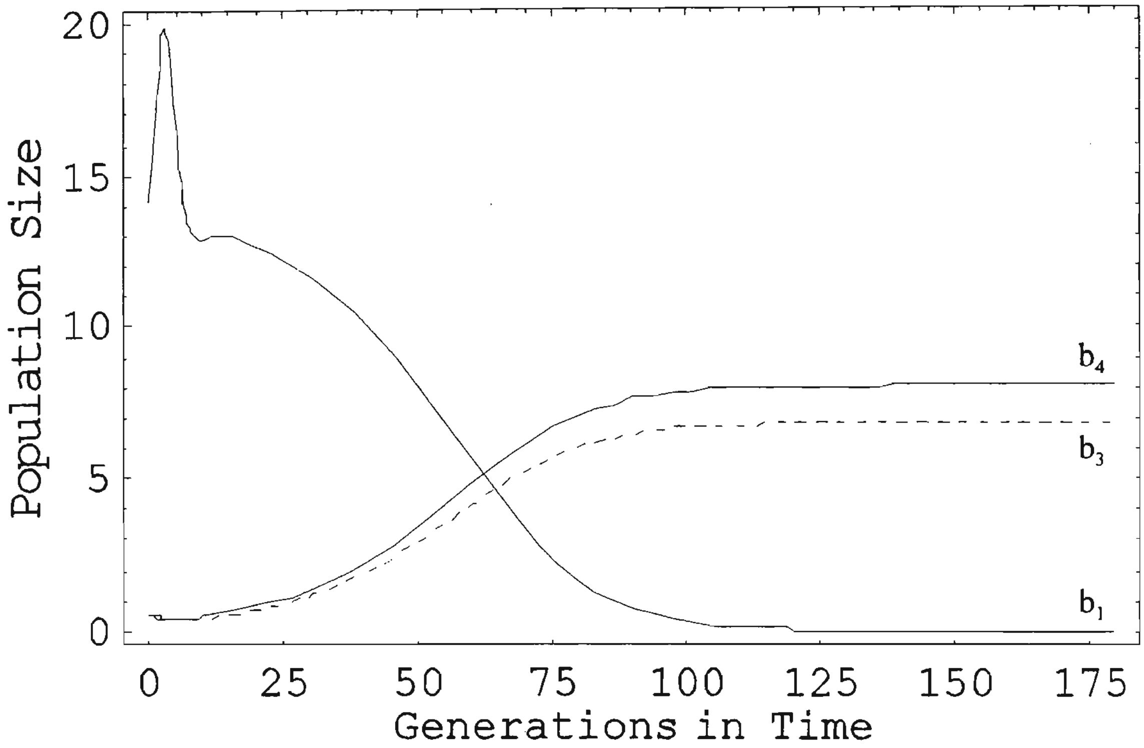

Figure 26a. Situation 1, Case 1: One incumbent and two invaders with the initial population $b_1 = 14.0625$ for the incumbent. Note the incumbent is eliminated, while the final populations for the invaders are $b_3 = 6.816$ and $b_4 = 8.036$.

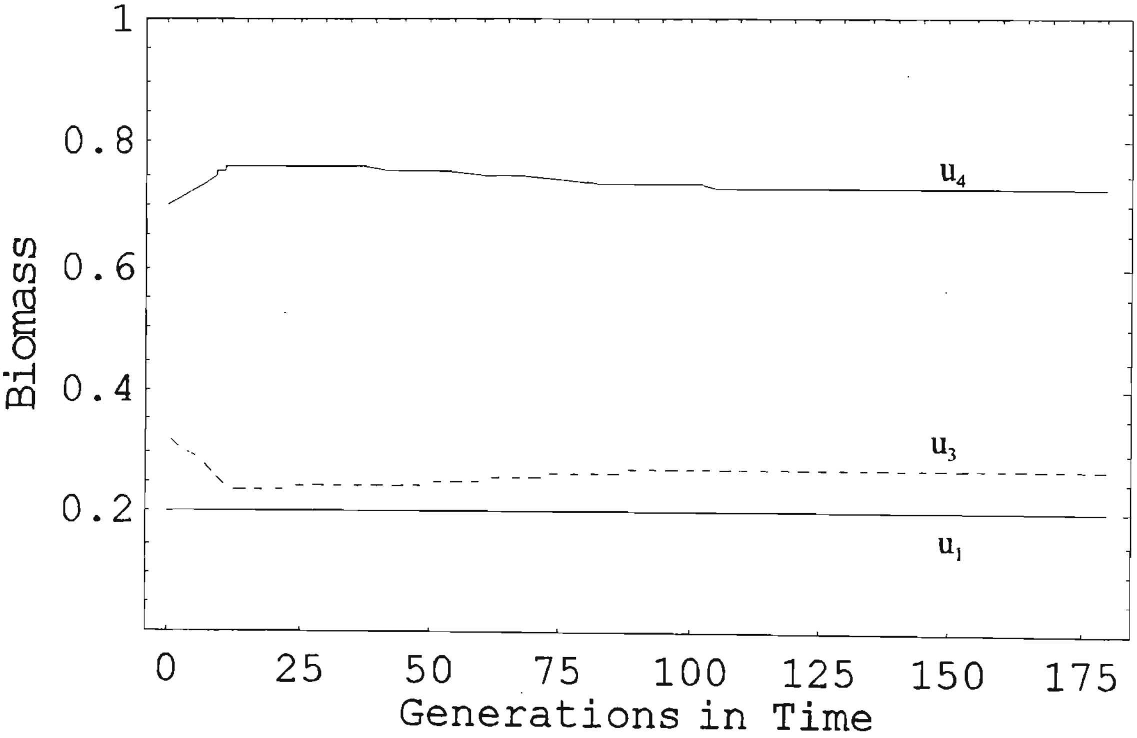

Figure 26b. Situation 1, Case 1: The invading strategies $(u_3, u_4) = (0.32, 0.7)$ evolve to the ESS coalition (0.271, 0.729).

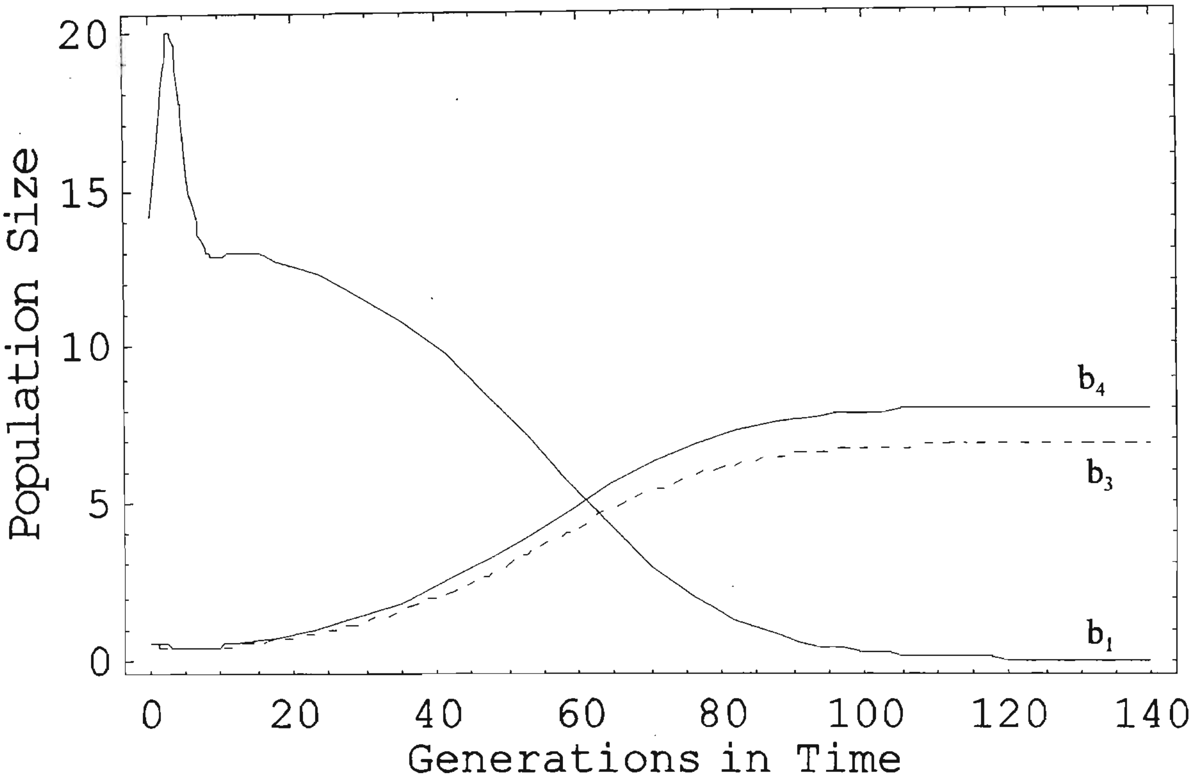

Figure 27a. Situation 1, Case 2: One incumbent and two invaders with the initial population b_1 = 14.0625 for the incumbent. Note the incumbent is eliminated, while the final populations for the invaders are b_3 = 6.836 and b_4 = 8.010.

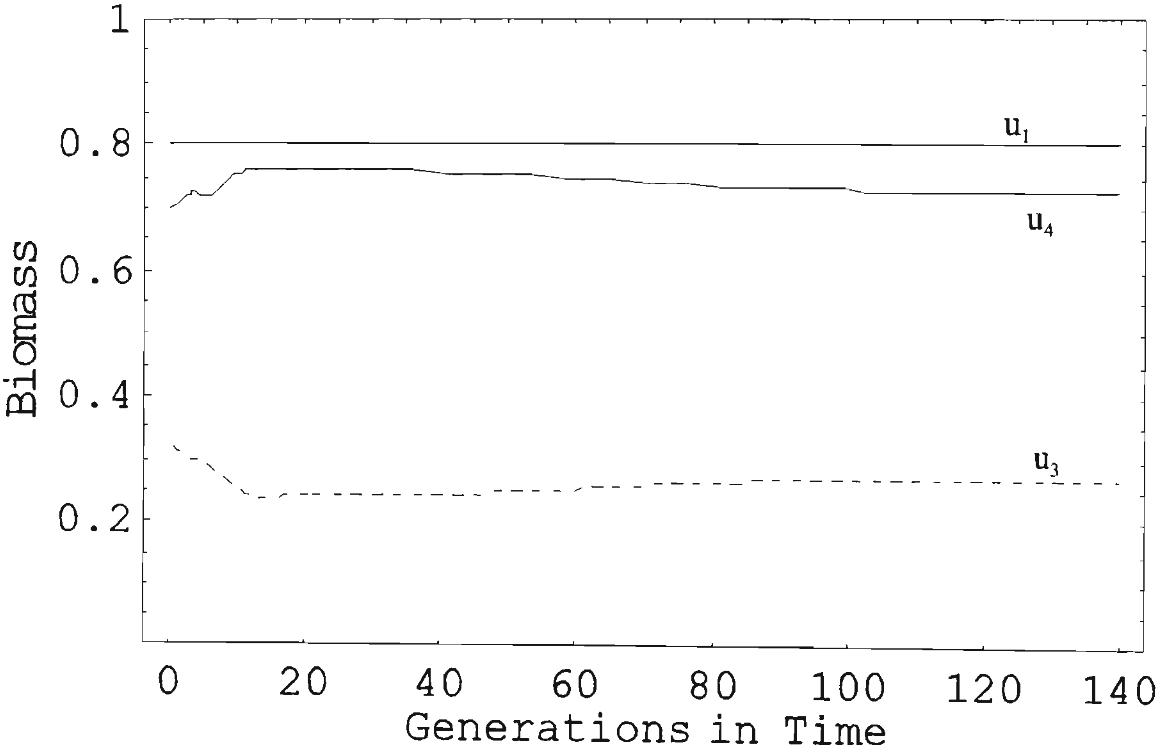

Figure 27b. Situation 1, Case 2: The invading strategies (u_3, u_4) = (0.32, 0.7) evolve to the ESS coalition (0.271, 0.729)

Case 2: One Incumbent Using Strategy $u_1 = 0.8$

In Figure 27a on the previous page, there is only one incumbent population using strategy $u_1 = 0.8$ which has an initial population of 14.0625, which is eliminated in 140 generations by the invading species using initial strategies $u_3 = 0.32$ and $u_4 = 0.7$. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = 6.836$ and $b_4 = 8.010$. Note the combined population is 14.846, compared with the combined ESS equilibrium populations from Figure 25 which is 14.882.

In Figure 27b on the previous page, the dynamics of the strategies are shown. u_1 remains constant at 0.8, while u_3 initially decreases from 0.32, and then increases again to 0.271. u_4 initially increases from 0.7, and then decreases slightly again to stabilise at a value of 0.729. Note the invading strategies stabilise at the ESS strategies, and that the dynamics of the invading strategies is similar to that of Case One.

Case 3: Two Incumbents Using Strategies $u_1 = 0.2$ and $u_2 = 0.8$

In Figure 28a on the following page, there are two incumbent populations using strategies $u_1 = 0.2$ and $u_2 = 0.8$ where both have initial populations of 6.4996, which are eliminated in 200 generations by the invading species using initial strategies $u_3 = 0.32$ and $u_4 = 0.7$. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = 6.810$ and $b_4 = 8.043$. Note the combined population is 14.853.

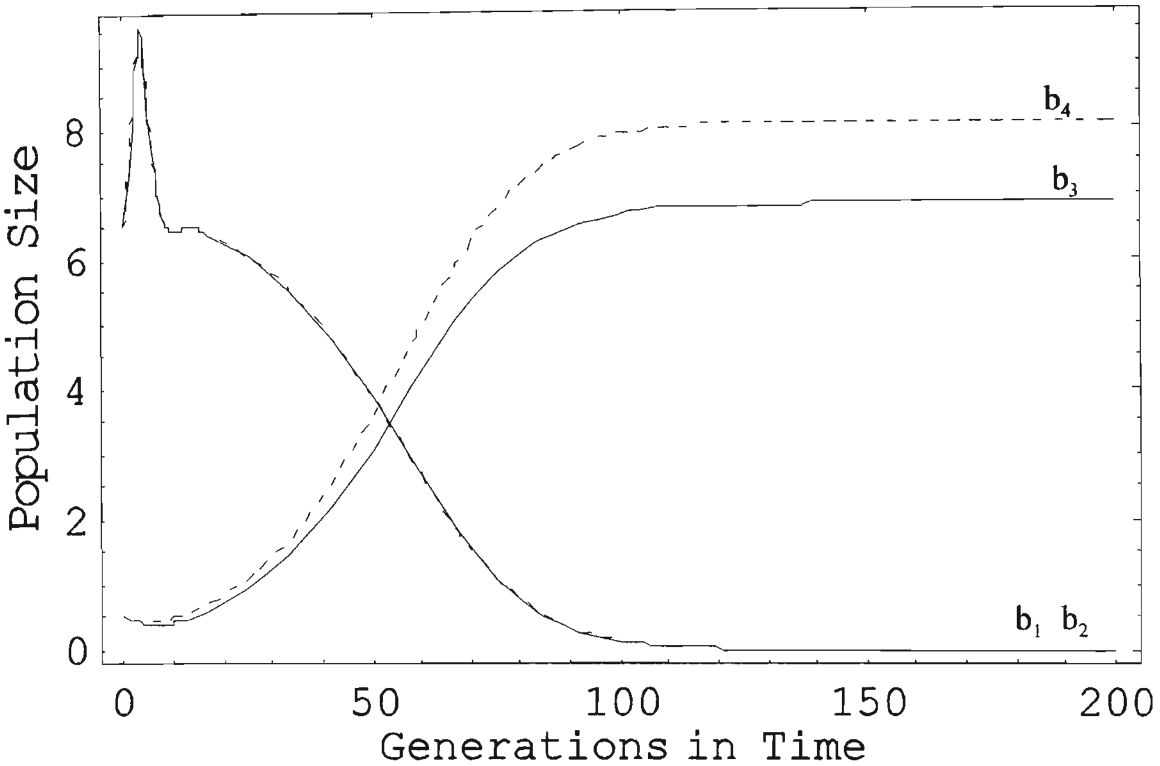

Figure 28a. Situation 1, Case 3: Two incumbent and two invaders with the initial populations $b_1 = 6.4996$ and $b_2 = 6.4996$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = 6.810$ and $b_4 = 8.043$.

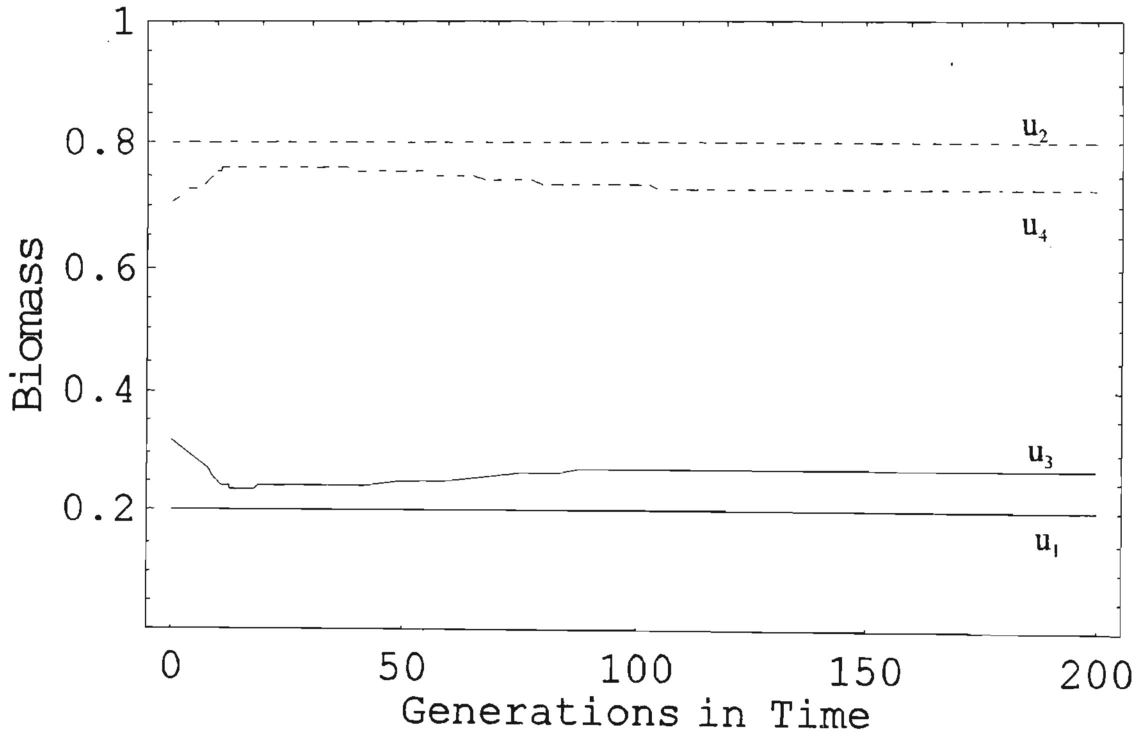

Figure 28b. Situation 1, Case 3: The invading strategies $(u_3, u_4) = (0.32, 0.7)$ evolve to the ESS coalition (0.271, 0.729)

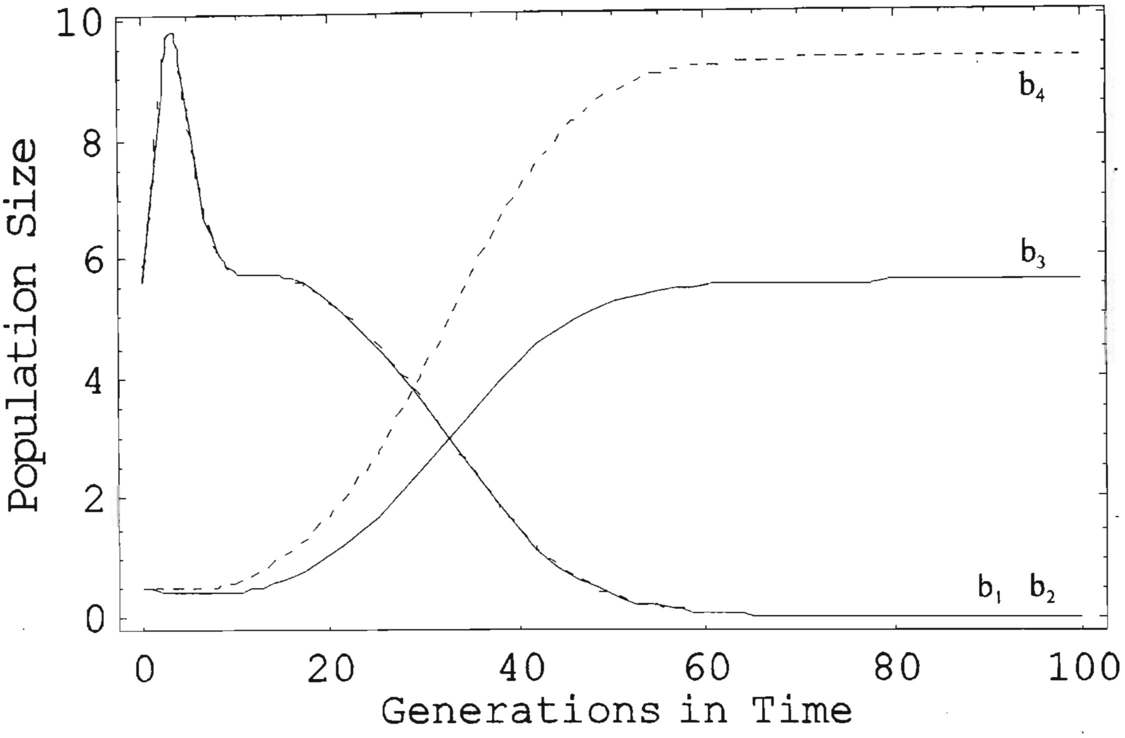

Figure 29a. Situation 1, Case 4: Two incumbent and two invaders with the initial populations $b_1 = 5.5966$ and $b_2 = 5.5966$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = 5.562$ and $b_4 = 9.292$.

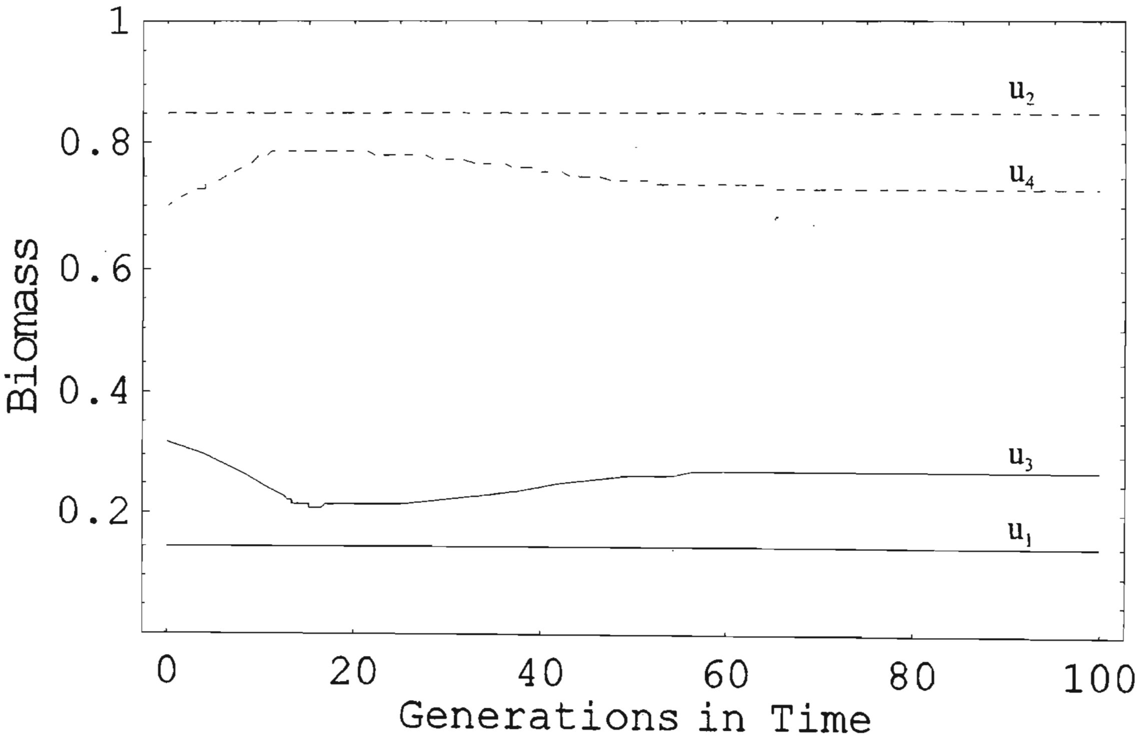

Figure 29b. Situation 1, Case 4: The invading strategies $(u_3, u_4) = (0.32, 0.7)$ evolve to the ESS coalition (0.271, 0.729)

In Figure 28b two pages previously, the dynamics of the strategies are shown. u_1 and u_2 remain constant at 0.2 and 0.8 respectively, while u_3 initially decreases from 0.32, and then increases again to 0.271. u_4 initially increases from 0.7, and then decreases slightly again to stabilise at a value of 0.729. Note the invading strategies stabilise at the ESS strategies, and that the invading strategies show similar patterns of evolution as found in Cases One and Two.

Case 4: Two Incumbents Using Strategies $u_1 = 0.15$ and $u_2 = 0.85$

In Figure 29a on the previous page, there are two incumbent populations using strategies $u_1 = 0.2$ and $u_2 = 0.8$ which both have initial populations of 5.5966, which are both eliminated in 100 generations by the invading species using initial strategies $u_3 = 0.32$ and $u_4 = 0.7$. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = 5.562$ and $b_4 = 9.292$. Note the combined population is 14.854, compared with 14.882 from Figure 25.

In Figure 29b on the previous page, the dynamics of the strategies are shown. u_1 remains constant at 0.15, u_2 remains constant at 0.85, while u_3 and u_4 show similar dynamics as in the previous cases. Note the invading strategies stabilise at the ESS strategies.

Case 5: Two Incumbents Using Strategies $u_1 = 0.271$ and $u_2 = 0.729$

In Figure 30a on the following page, there are two incumbent populations using strategies u_1 = 0.27 and $u_2 = 0.73$ which both have initial populations of 7.4391, which are both eliminated in 12 000 generations by the invading species using initial strategies $u_3 = 0.32$ and $u_4 = 0.7$. This is a much longer time period than the previous cases, as would be expected considering that the incumbent strategies were chosen so close to the ESS strategies. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = 6.296$ and $b_4 = 8.556$ Note the combined population is 14.852.

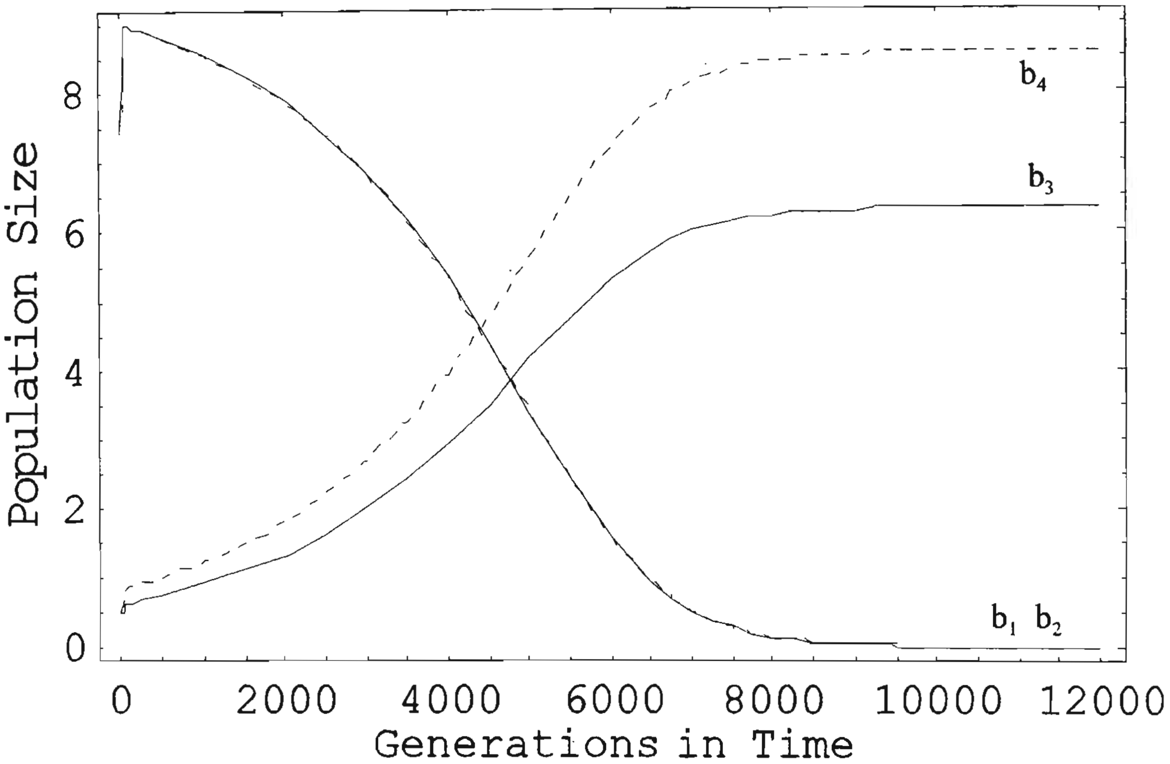

Figure 30a. Situation 1, Case 5: Two incumbent and two invaders with the initial populations $b_1 = 7.4391$ and $b_2 = 7.4391$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = 6.296$ and $b_4 = 8.556$.

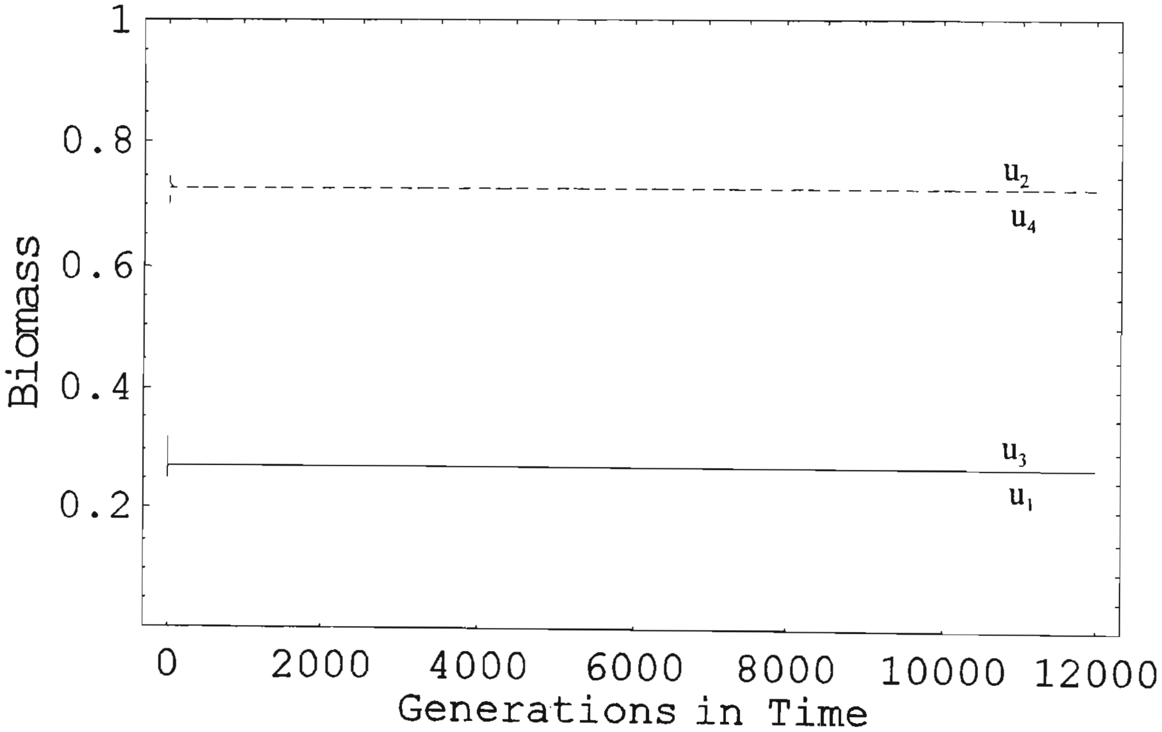

Figure 30b. Situation 1, Case 5: The invading strategies $(u_3, u_4) = (0.32, 0.7)$ evolve to the ESS coalition (0.271, 0.729)

In Figure 30b on the previous page, the dynamics of the strategies are shown. u_1 remains constant at 0.27, u_2 remains constant at 0.73, while u_3 and u_4 take less than 1000 generations to stabilise, compared with the 12000 generations required before the populations stabilised. Note the invading strategies stabilise at the ESS strategies.

In this situation the incumbent populations were eliminated in each case. The invading species evolved to the ESS strategies, but not to the ESS equilibrium populations. This was not unexpected, due to the fact that the ESS equilibrium populations as determined from Figure 25 were very dependent on the initial strategy choice.

5.4.2. Situation Two

The incumbent populations were allowed to interact with the two invading populations which were using the ESS strategies and starting from the ESS equilibrium populations. In all the cases in this situation, the invading populations have initial strategies of $u_3 = 0.271$ and $u_4 = 0.729$, and initial populations of $b_3 = 10.850$ and $b_4 = 4.032$ respectively. The invading species strategies, although starting from the ESS strategies, were allowed to evolve. In this situation, it is expected that the ESS will eliminate the incumbent population and settle to its equilibrium populations, although some initial deviation of the invading species from their initial values might be expected.

Case 1: One Incumbent Using Strategy $u_1 = 0.2$

In Figure 31a, on the next page, there is only one incumbent population using strategy $u_1 = 0.2$ which has an initial population of 14.0625, which is eliminated in 120 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle within 100 generations into equilibrium populations, which are quite different to the ESS equilibrium populations, of $b_3 = 13.557$ and $b_4 = 1.290$. Note the combined population is 14.847, compared with the combined ESS equilibrium population from Figure 25 which is 14.882.

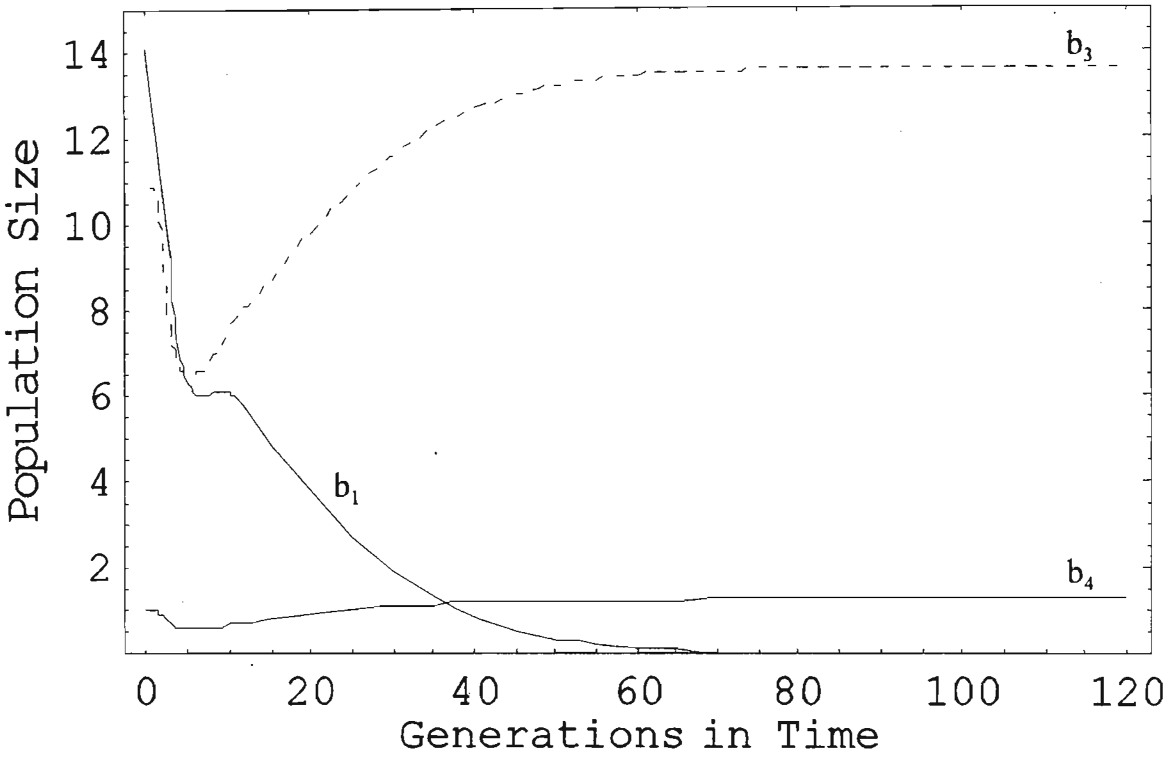

Figure 31a. Situation 2, Case 1: One incumbent and two invaders with the incumbent's initial population b_1 = 14.0625 Note the incumbent is eliminated, while the final populations for the invaders are b_3 = 13.557 and b_4 = 1.290

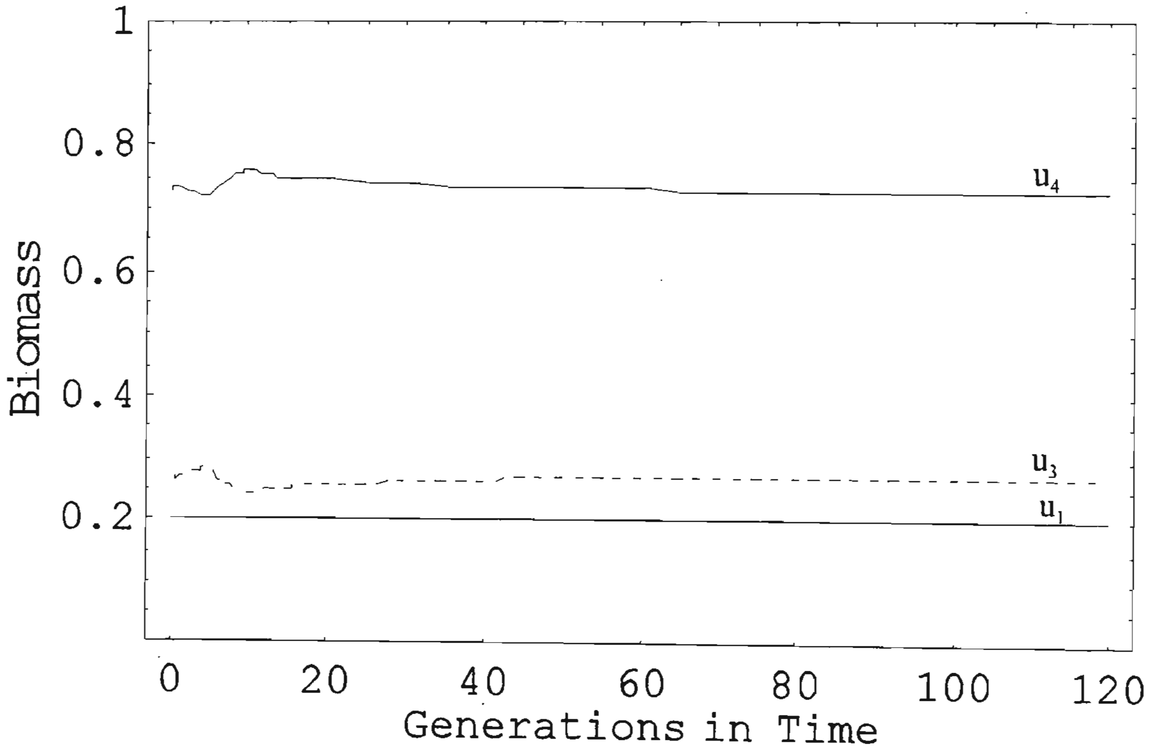

Figure 31b. Situation 2, Case 1: The invading strategies (u_3, u_4) = (0.271, 0.729) take less than 80 generations to settle down to the equilibrium strategies, which are the ESS strategies.

In Figure 31b, the dynamics of the strategies are shown. u_1 remains constant at 0.2, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies. The strategies stabilise within 80 generations.

Case 2: One Incumbent Using Strategy $u_1 = 0.8$

In Figure 32a on the next page, there is only one incumbent population using strategy $u_1 = 0.8$ which has an initial population of 14.0625, which is eliminated in 80 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$. The invading species stabilise to the equilibrium populations of $b_3 = 10.806$ and $b_4 = 4.016$, compared with the ESS equilibrium populations of 10.850 and 4.032 respectively. Note the combined population is 14.822, the same as the combined ESS equilibrium populations from Figure 25.

In Figure 32b on the following page, the dynamics of the strategies are shown. u_1 remains constant at 0.8, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies. The strategies stabilise within 80 generations.

Case 3: Two Incumbents Using Strategies $u_1 = 0.2$ and $u_2 = 0.8$

In Figure 33a, there are two incumbent populations using strategies $u_1 = 0.2$ and $u_2 = 0.8$ which both have initial populations of 6.4996, which are eliminated within 100 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations of $b_3 = 10.823$ and $b_4 = 4.022$, which are slightly smaller than the ESS equilibrium populations. Note the combined population is 14.845, compared with the combined ESS equilibrium population from Figure 25 which is 14.882.

In Figure 33b, the dynamics of the strategies are shown. u_1 and u_2 remain constant at 0.2 and 0.8 respectively, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies. The strategies stabilise within 80 generations.

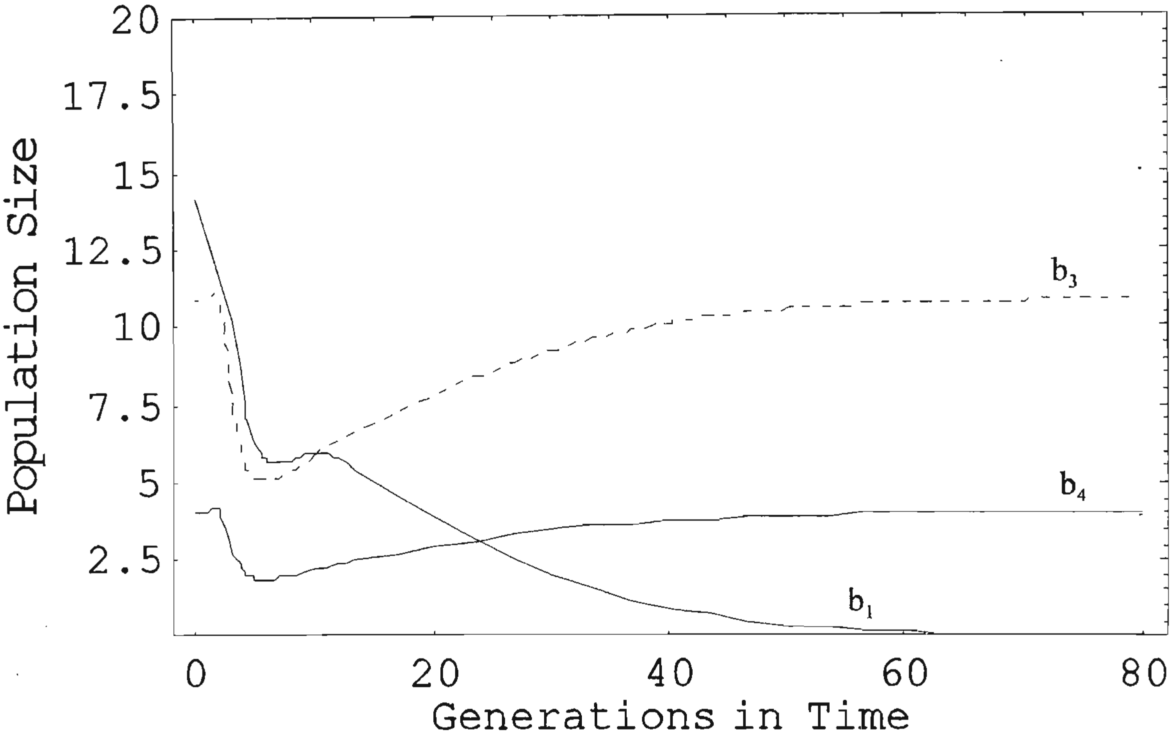

Figure 32a. Situation 2, Case 2: One incumbent and two invaders with the incumbent's initial population b_1 = 14.0625 Note the incumbent is eliminated, while the final populations for the invaders are b_3 = 10.806 and b_4 = 4.016.

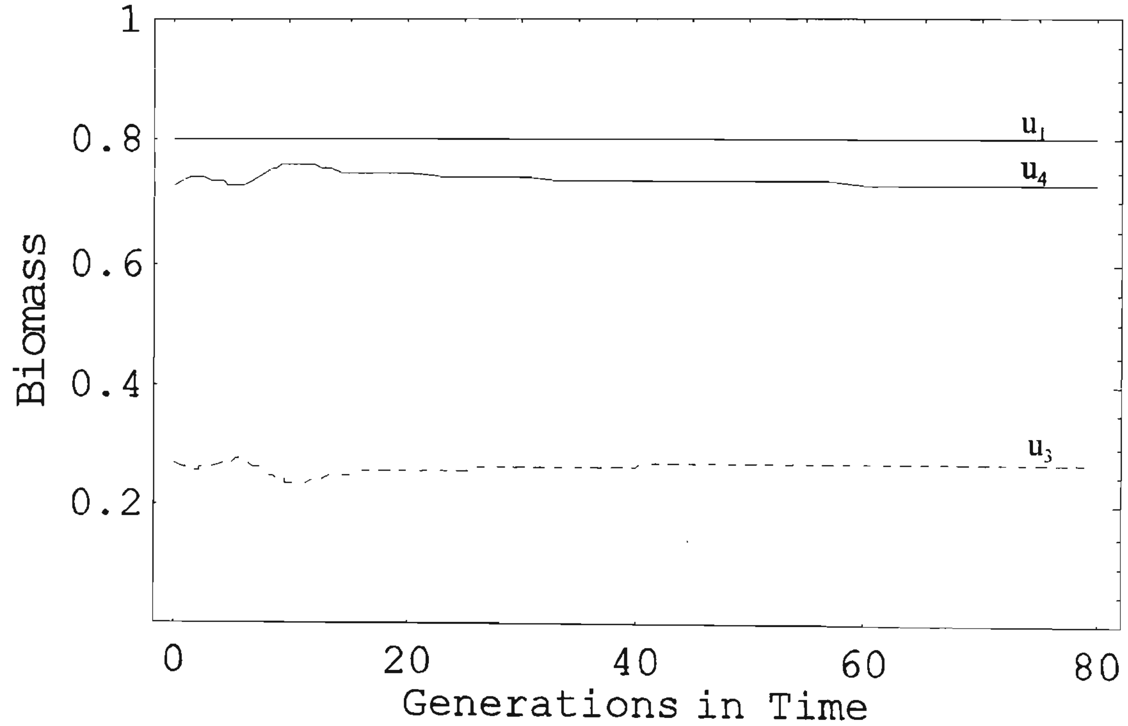

Figure 32b. Situation 2, Case 2: The invading strategies (u_3, u_4) = (0.271, 0.729) take less than 80 generations to settle down to the equilibrium strategies, which are the ESS strategies.

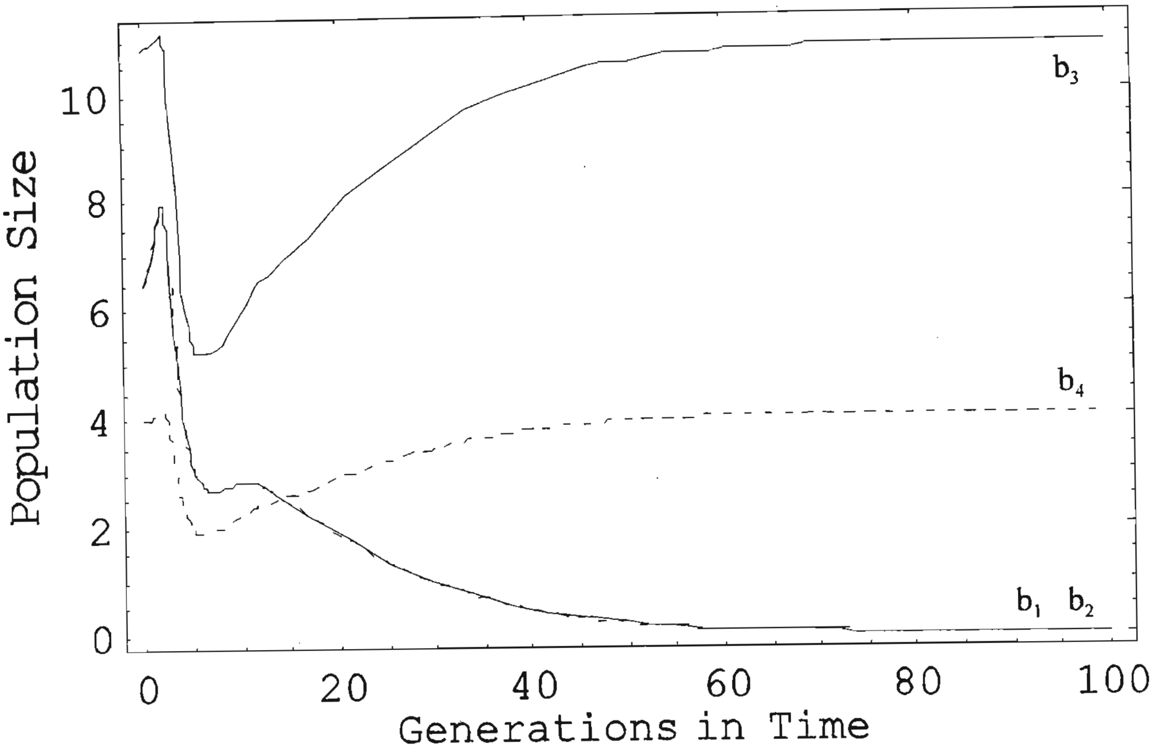

Figure 33a. Situation 2, Case 3: Two incumbent and two invaders with the initial populations $b_1 = 6.4996$ and $b_2 = 6.4996$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = 10.823$ and $b_4 = 4.022$.

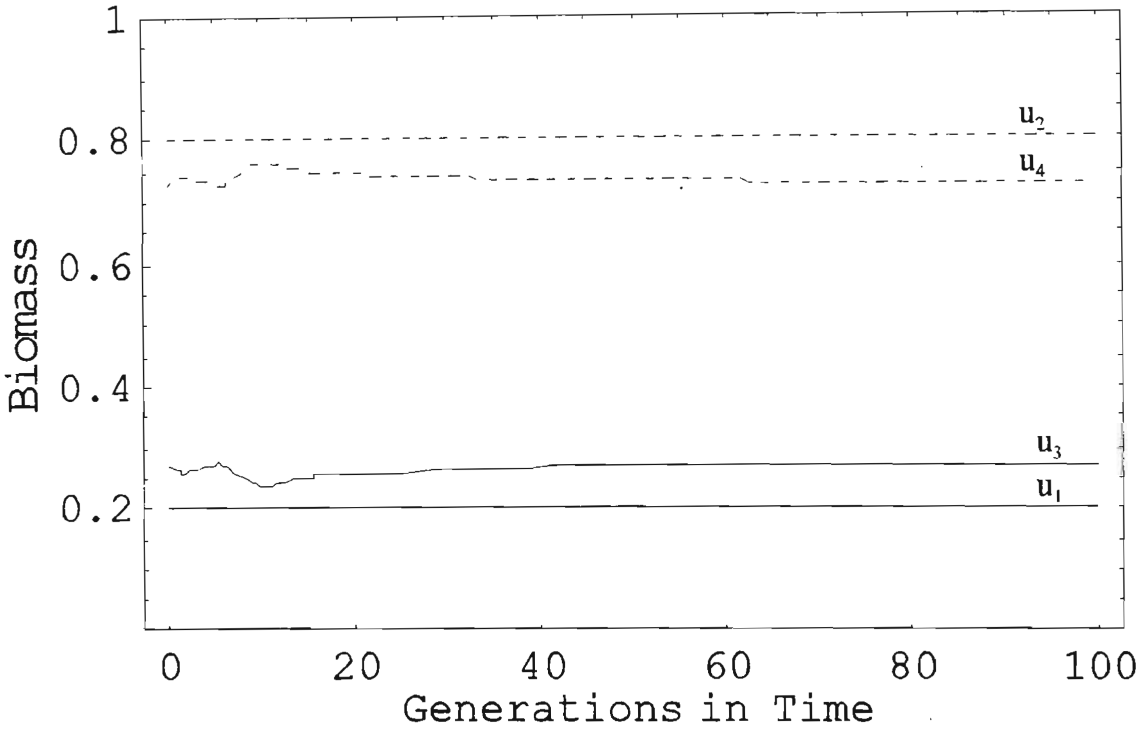

Figure 33b. Situation 2, Case 3: The invading strategies $(u_3, u_4) = (0.271, 0.729)$ take less than 60 generations to settle down to the equilibrium strategies, which are the ESS strategies.

Case 4: Two Incumbents Using Strategies $u_1 = 0.15$ and $u_2 = 0.85$

In Figure 34a, there are two incumbent populations using strategies $u_1 = 0.15$ and $u_2 = 0.85$ which both have initial populations of 5.5966, which are eliminated within 60 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations of $b_3 = 10.824$ and $b_4 = 4.023$, which are slightly smaller than the ESS equilibrium populations. Note the combined population is 14.847.

In Figure 34b, the dynamics of the strategies are shown. u_1 and u_2 remain constant at 0.15 and 0.85 respectively, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies. The strategies stabilise within 30 generations.

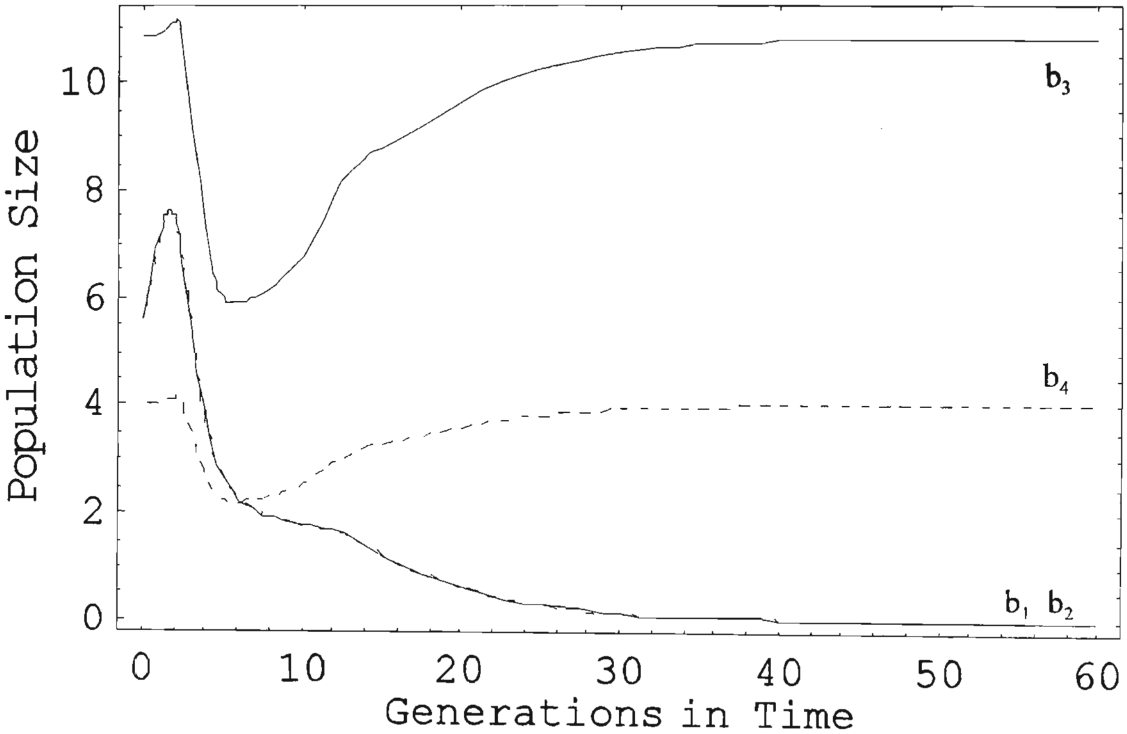

Figure 34a. Situation 2, Case 4: Two incumbent and two invaders with the initial populations $b_1 = 5.5966$ and $b_2 = 5.5966$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = 10.824$ and $b_4 = 4.023$.

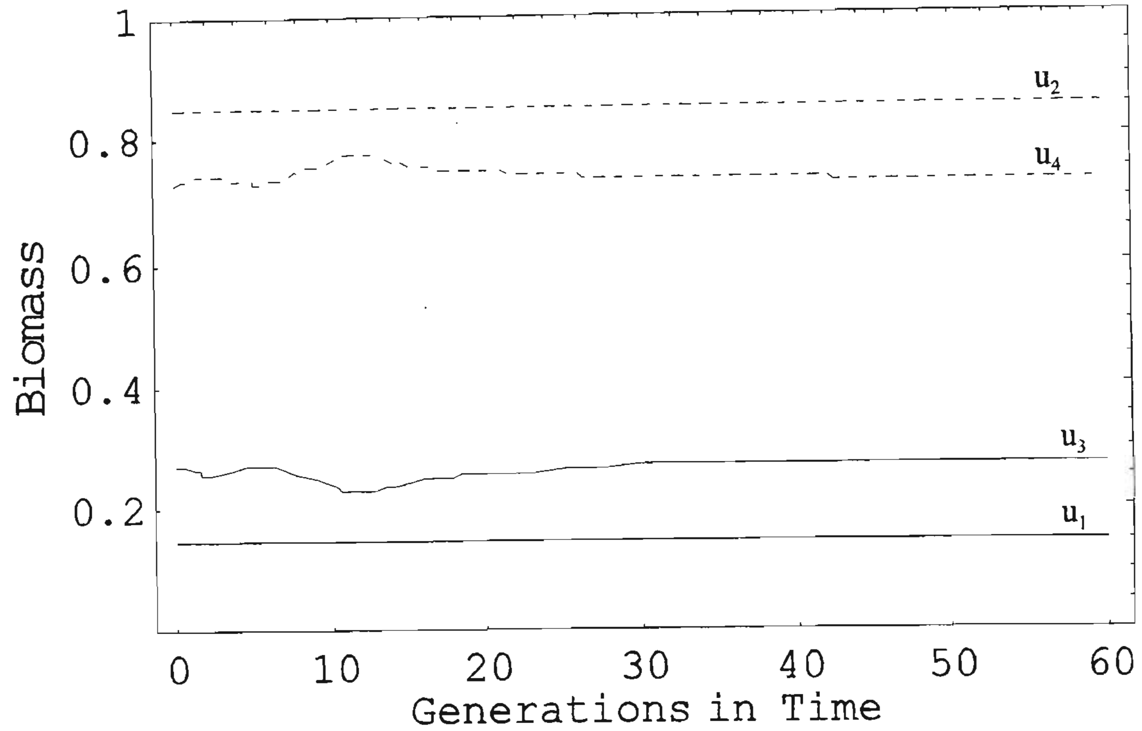

Figure 34b. Situation 2, Case 4: The invading strategies ($(u_3, u_4) = (0.271, 0.729)$) take less than 30 generations to settle down to the equilibrium strategies, which are the ESS strategies.

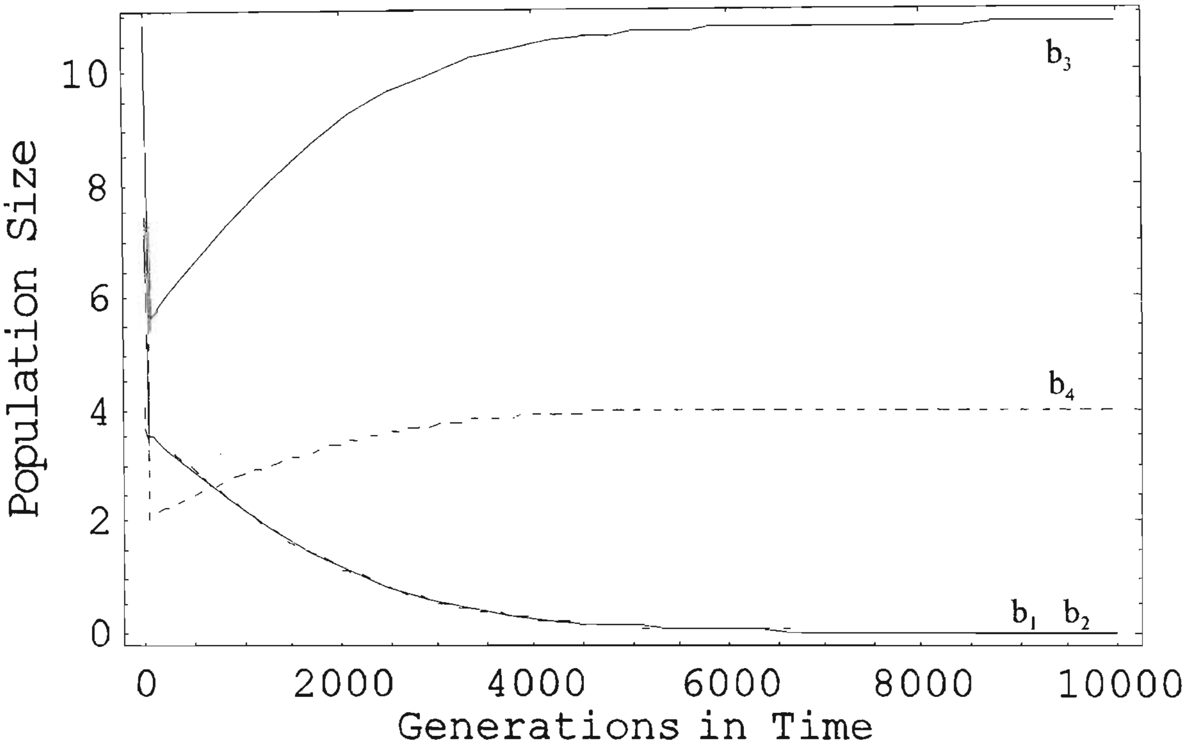

Figure 35a. Situation 2, Case 5: Two incumbent and two invaders with the initial populations $b_1 = 7.4391$ and $b_2 = 7.4391$ for the incumbents. Note the incumbents are eliminated, and the final populations for the invaders are $b_3 = 10.824$ and $b_4 = 4.023$.

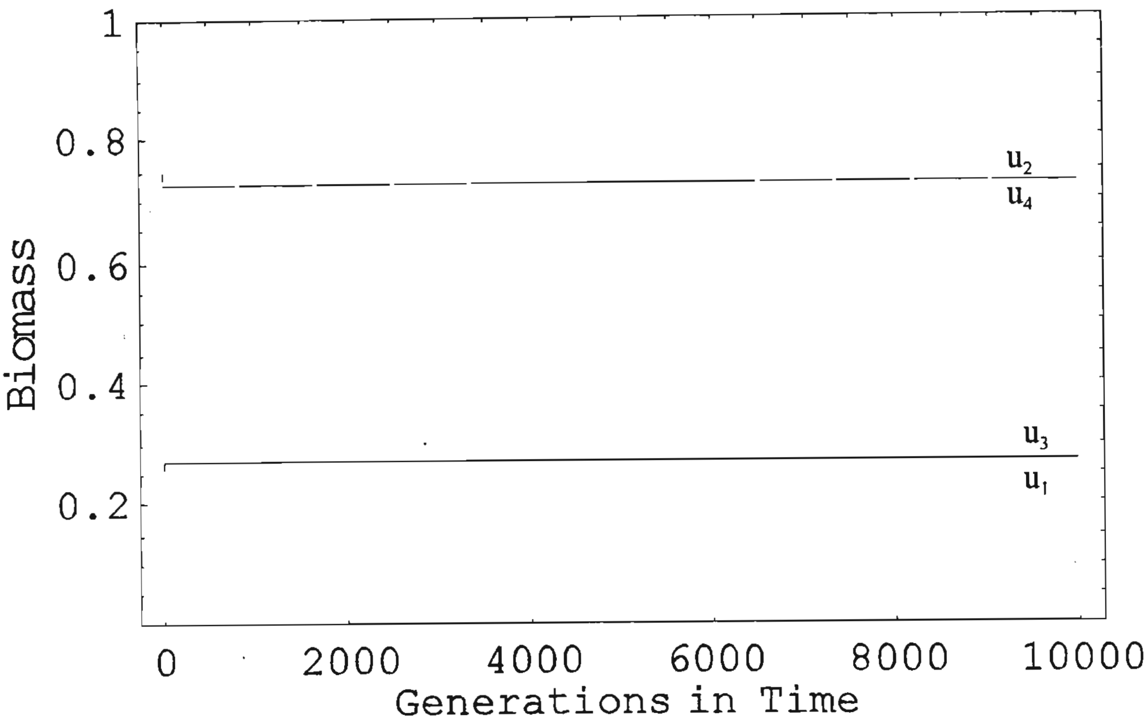

Figure 35b. Situation 2, Case 5: The invading strategies (u_3, u_4) = (0.271, 0.729) take very few generations, compared with the populations, to settle down to the equilibrium strategies, which are the ESS strategies.

Case 5: Two Incumbents Using Strategies $u_1 = 0.27$ and $u_2 = 0.73$

In Figure 35a on the previous page, there are two incumbent populations using strategies $u_1 = 0.27$ and $u_2 = 0.73$ which both have initial populations of 7.4391. The invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies eliminate the incumbent populations. The system takes 10 000 generations to eliminate the incumbents and the final equilibrium solutions for the invaders are $b_3 = 10.824$ and $b_4 = 4.023$. Note the combined population is 14.847, the same as the previous case.

In Figure 35b above, the dynamics of the strategies are shown. u_1 and u_2 remain constant at 0.27 and 0.73 respectively, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies.

5.4.3. Situation Three

The incumbent populations were allowed to interact with the two invading populations which were using the ESS strategies, but with small initial populations. In all the cases in this situation, the invading populations have initial strategies of $u_3 = 0.271$ and $u_4 = 0.729$, and initial populations of $b_3 = 0.5$ and $b_4 = 0.5$ respectively. The invading species strategies, although starting from the ESS strategies, were allowed to evolve. In this situation, it is expected that the ESS will eliminate the incumbent population, although the ESS equilibrium populations might not be reached, which is what happened.

Case 1: One Incumbent Using Strategy $u_1 = 0.2$

In Figure 36a below, there is only one incumbent population using strategy $u_1 = 0.2$ which has an initial population of 14.0625, which is eliminated in 140 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = b_4 = 7.423$. Note the combined population is 14.846, compared with the combined ESS equilibrium populations from Figure 25 which is 14.882.

In Figure 36b on the next page, the dynamics of the strategies are shown. u_1 remains constant at 0.2, while u_3 and u_4 change initially, and then settle into the ESS strategy values.

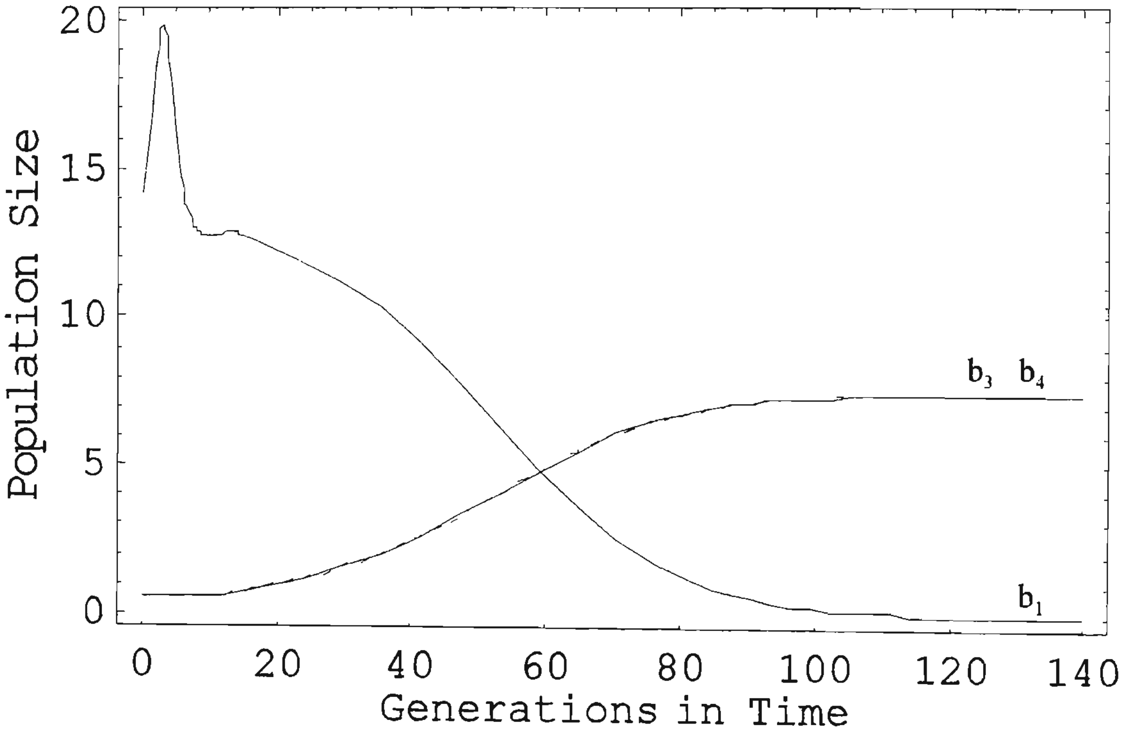

Figure 36a. Situation 3, Case 1: One incumbent and two invaders with the incumbent's initial population b_1 = 14.0625 Note the incumbent is eliminated, while the final populations for the invaders are b_3 = 7.423 and b_4 = 7.423.

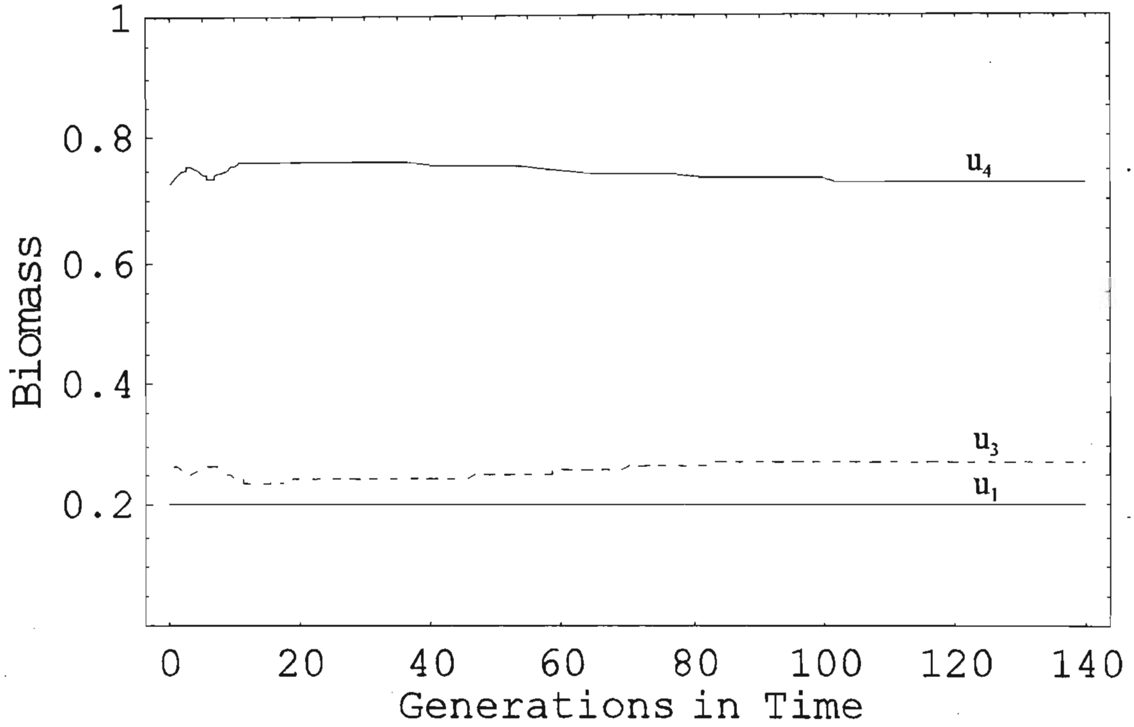

Figure 36b. Situation 3, Case 1: The invading strategies (u_3, u_4) = (0.271, 0.729) take less than 120 generations to settle down to the equilibrium strategies, which are the ESS strategies.

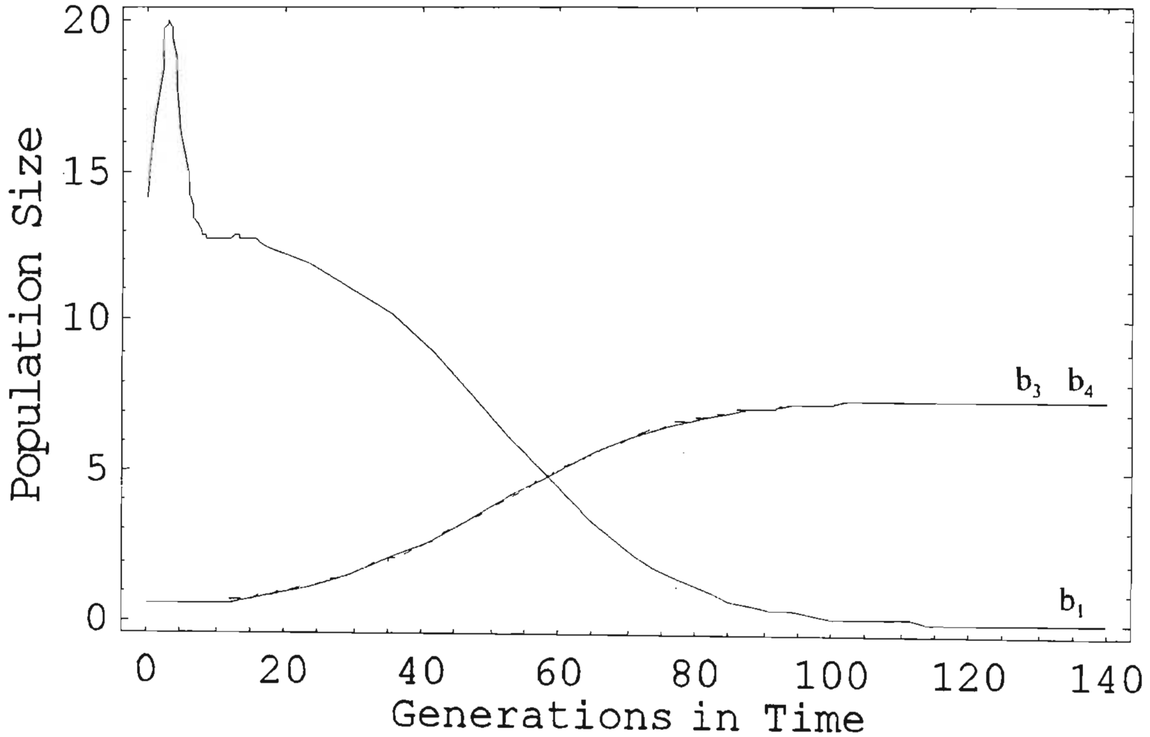

Figure 37a. Situation 3, Case 2: One incumbent and two invaders with the incumbent's initial population b_1 = 14.0625 Note the incumbent is eliminated, while the final populations for the invaders are b_3 = 7.424 and b_4 = 7.424.

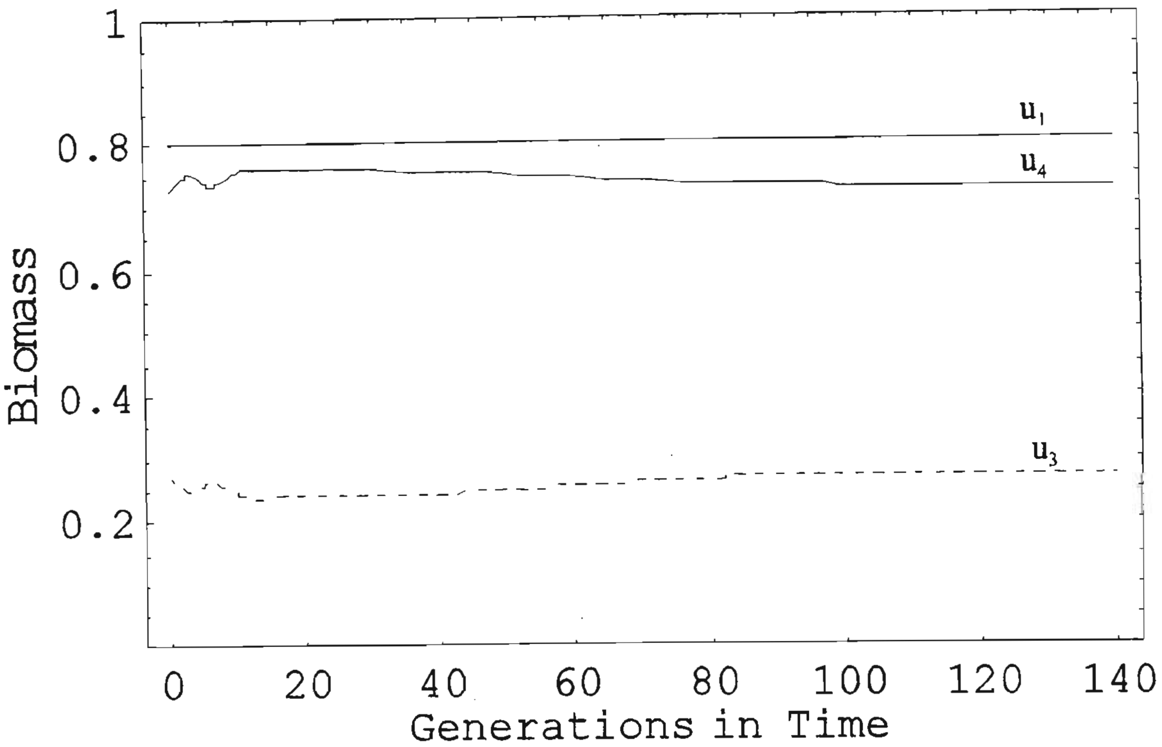

Figure 37b. Situation 3, Case 2: The invading strategies (u_3, u_4) = (0.271, 0.729) take less than 120 generations to settle down to the equilibrium strategies, which are the ESS strategies.

Case 2: One Incumbent Using Strategy $u_1 = 0.8$

In Figure 37a on the previous page, there is only one incumbent population using strategy $u_1 = 0.8$ which has an initial population of 14.0625, which is eliminated in 140 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = b_4 = 7.424$. Note the combined population is 14.848, compared with the combined ESS equilibrium populations from Figure 25 which is 14.882.

In Figure 37b, the dynamics of the strategies are shown. u_1 remains constant at 0.8, while u_3 and u_4 change initially, and then settle into the ESS strategy values.

Case 3: Two Incumbents Using Strategies $u_1 = 0.2$ and $u_2 = 0.8$

In Figure 38a on the following page, there are two incumbent populations using strategies u_1 =

0.2 and $u_2 = 0.8$ which both have initial populations of 6.4996, which are eliminated within 140 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species stabilise to populations of $b_3 = b_4 = 7.425$. Note the combined population is 14.850.

In Figure 38b, the dynamics of the strategies are shown. u_1 and u_2 remain constant at 0.15 and 0.85 respectively, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies.

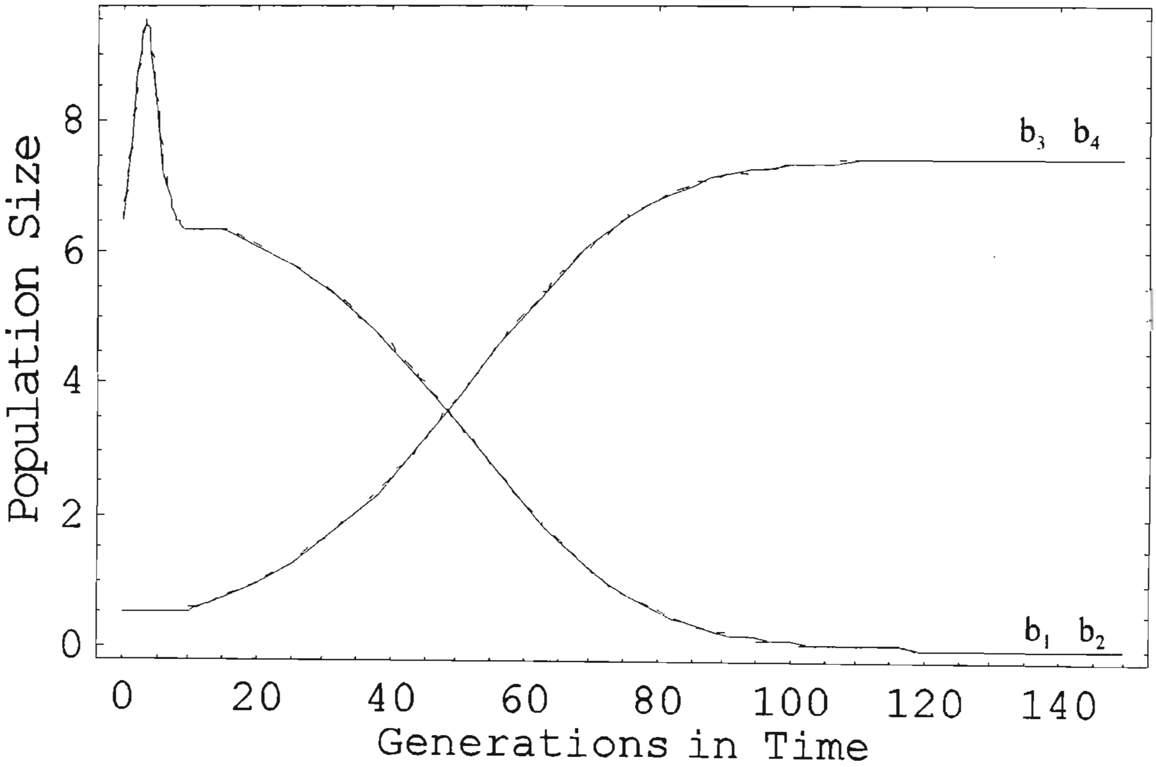

Figure 38a. Situation 3, Case 3: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 6.4996$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.425$.

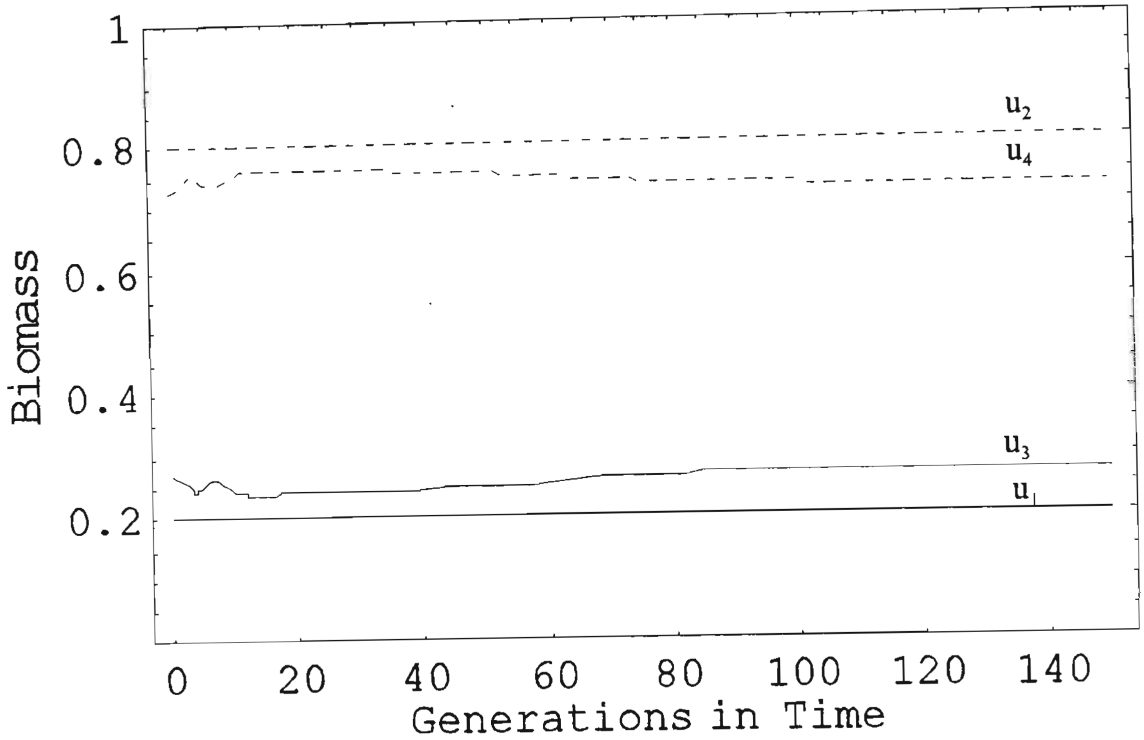

Figure 38b. Situation 3, Case 3: The invading strategies (u_3, u_4) = (0.271, 0.729) take less than 120 generations to settle down to the equilibrium strategies, which are the ESS strategies.

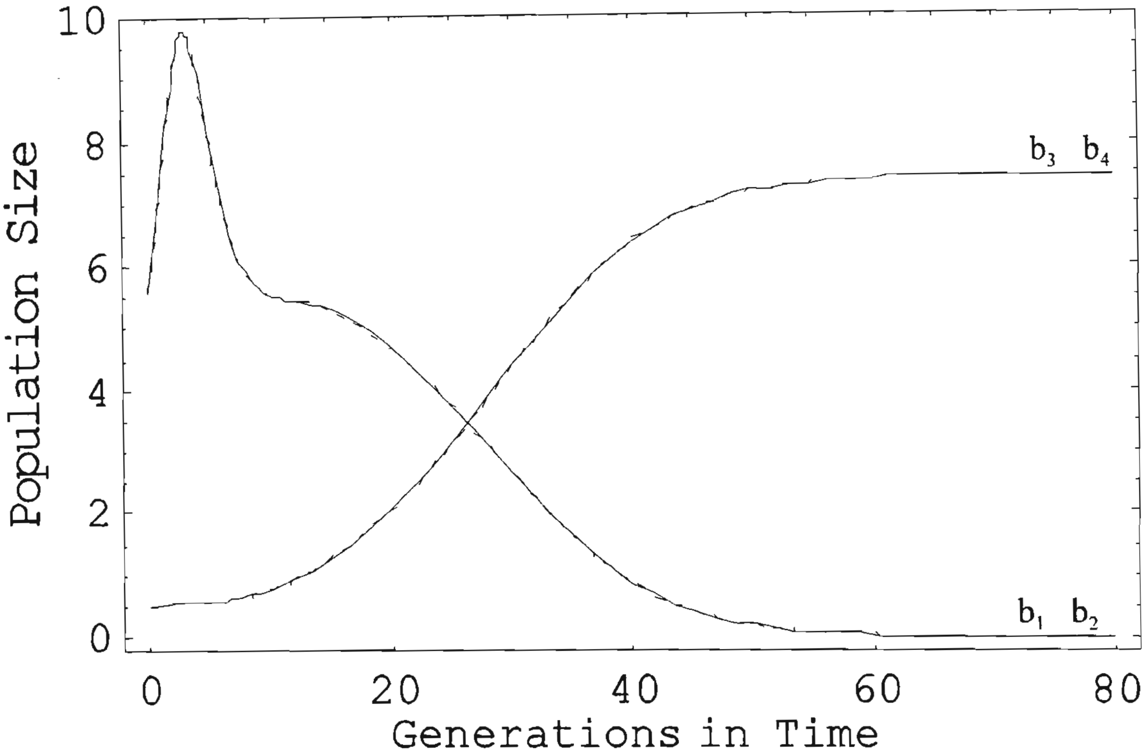

Figure 39a. Situation 3, Case 4: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 5.5966$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.424$.

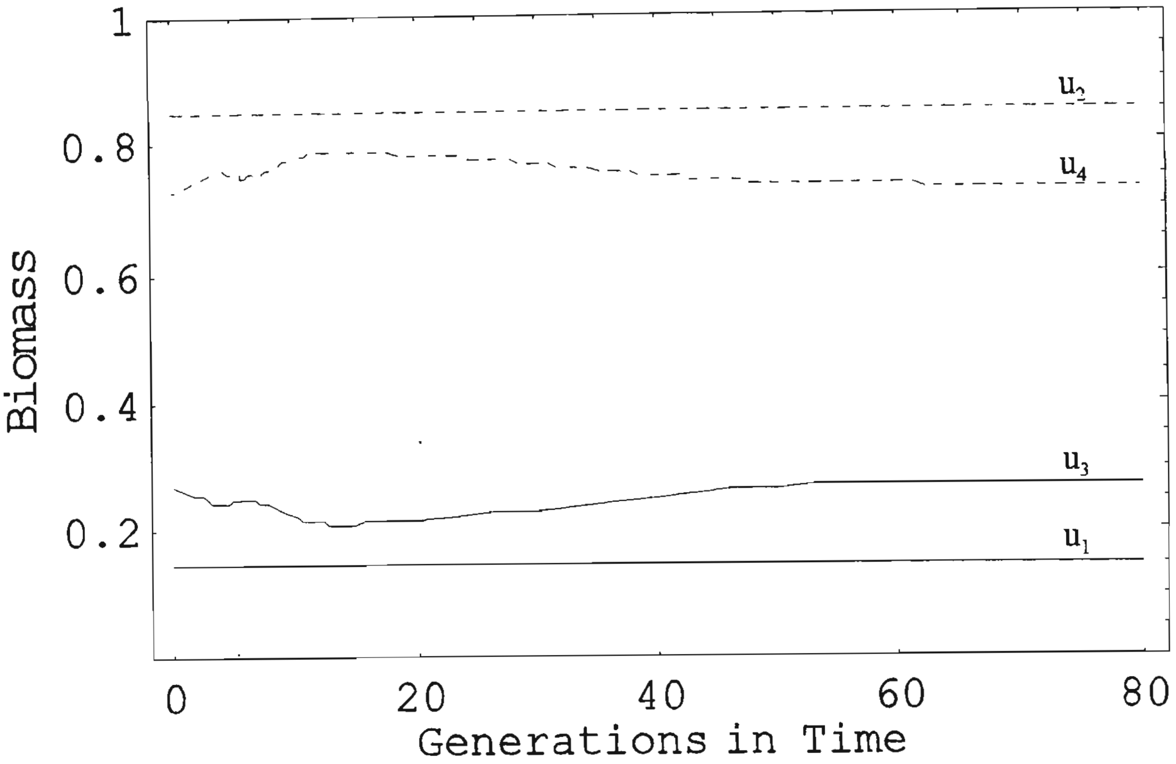

Figure 39b. Situation 3, Case 4: The invading strategies (u_3, u_4) = (0.271, 0.729) take less than 80 generations to settle down to the equilibrium strategies, which are the ESS strategies.

Case 4: Two Incumbents Using Strategies $u_1 = 0.15$ and $u_2 = 0.85$

In Figure 39a on the previous page, there are two incumbent populations using strategies $u_1 = 0.15$ and $u_2 = 0.85$ which both have initial populations of 5.5966, which are eliminated within 80 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species stabilise to populations of $b_3 = b_4 = 7.424$. Note the combined population is 14.848, the same as case two.

In Figure 39b, the dynamics of the strategies are shown. u_1 and u_2 remain constant at 0.15 and 0.85 respectively, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies. The strategies stabilise within 80 generations.

Case 5: Two Incumbents Using Strategies $u_1 = 0.27$ and $u_2 = 0.73$

In Figure 40a on the following page, there are two incumbent populations using strategies $u_1 = 0.27$ and $u_2 = 0.73$ which both have initial populations of 7.4391, which are eliminated over the course of 10 000 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations of $b_3 = b_4 = 7.423$. Note the combined population is 14.846.

In Figure 40b on the next page, the dynamics of the strategies are shown. u_1 and u_2 remain constant, while u_3 and u_4 undergo slight deviations before returning to their initial values, which are the ESS strategies. The strategies stabilise within 1000 generations, one fifth of the time it takes for the populations to stabilise.

In conclusion of situation three, all the incumbent populations were eliminated, as was expected. In each case the final stable populations were identical for both of the invading species, and the combined population total stayed fairly constant with the combined populations which were reached in situations one and two.

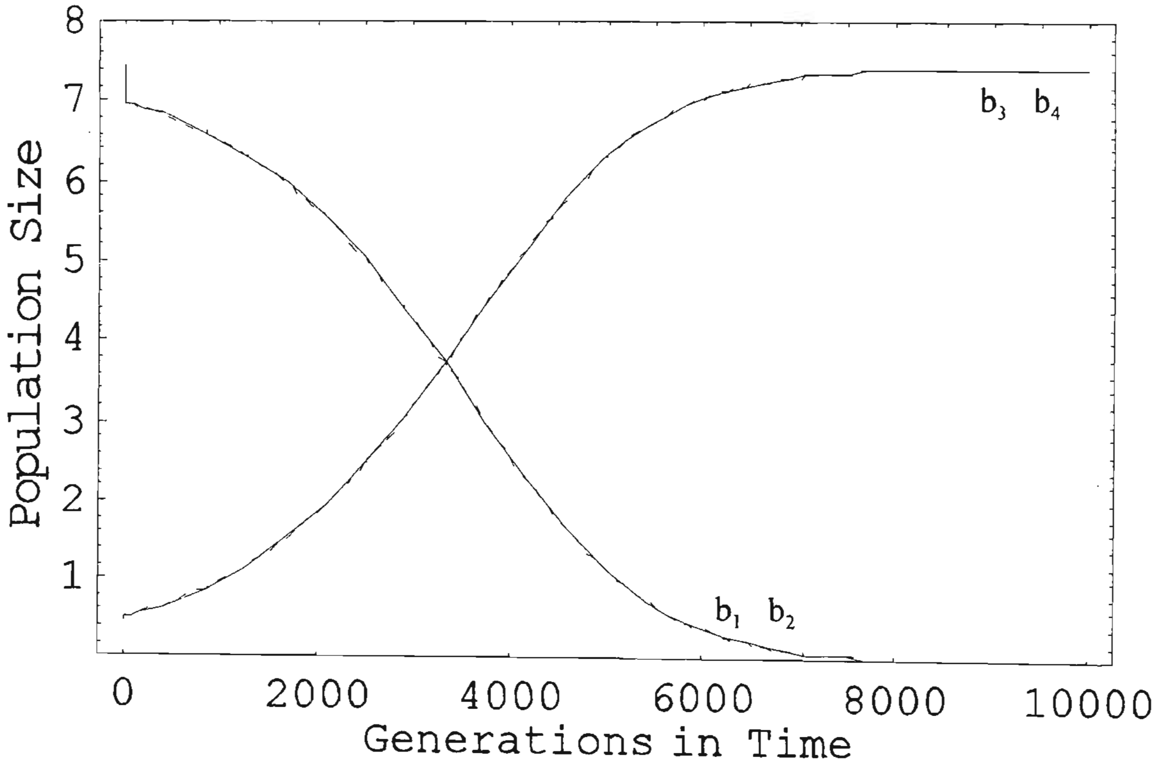

Figure 40a. Situation 3, Case 5: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 7.4391$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.423$.

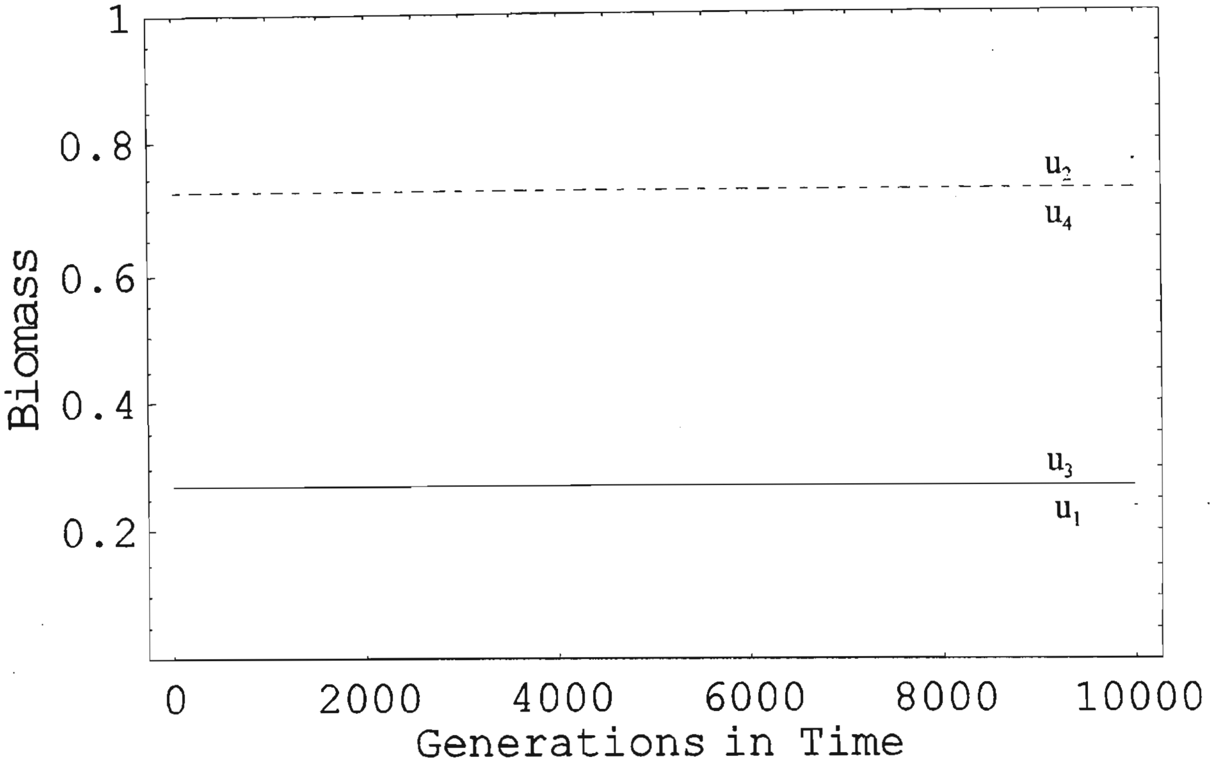

Figure 40b. Situation 3, Case 5: The invading strategies (u_3, u_4) = (0.271, 0.729) take much less than 10 000 generations to settle down to the equilibrium strategies, which are the ESS strategies.

5.4.4. Situation Four

This situation is similar to situation three, except that the invading strategies are not allowed to evolve at all. In other words, all the strategies are fixed, and only the populations can change. In this situation, it is expected that the incumbent populations will be eliminated, with similar results to those of situation three. As the strategies are all fixed, the strategy dynamics were not plotted.

Case 1: One Incumbent Using Strategy $u_1 = 0.2$

In Figure 41 on the next page, there is only one incumbent population using strategy $u_1 = 0.2$ which has an initial population of 14.0625, which is eliminated in 800 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$. Thus it takes more than four times as long for the incumbent to be eliminated when the invading strategies are not allowed to evolve. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = b_4 = 7.432$. Note the combined population is 14.864, compared with the combined ESS equilibrium populations from Figure 25 which is 14.882.

Case 2: One Incumbent Using Strategy $u_1 = 0.8$

In Figure 42 on the next page, there is only one incumbent population using strategy $u_1 = 0.8$ which has an initial population of 14.0625, which is eliminated in 600 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$. Thus it takes more than three times as long for the incumbent to be eliminated when the invading strategies are not allowed to evolve. The invading species start with initial populations of 0.5, and settle into equilibrium populations of $b_3 = b_4 = 7.432$. Note the combined population is 14.864, compared with the combined ESS equilibrium populations from Figure 25 which is 14.882.

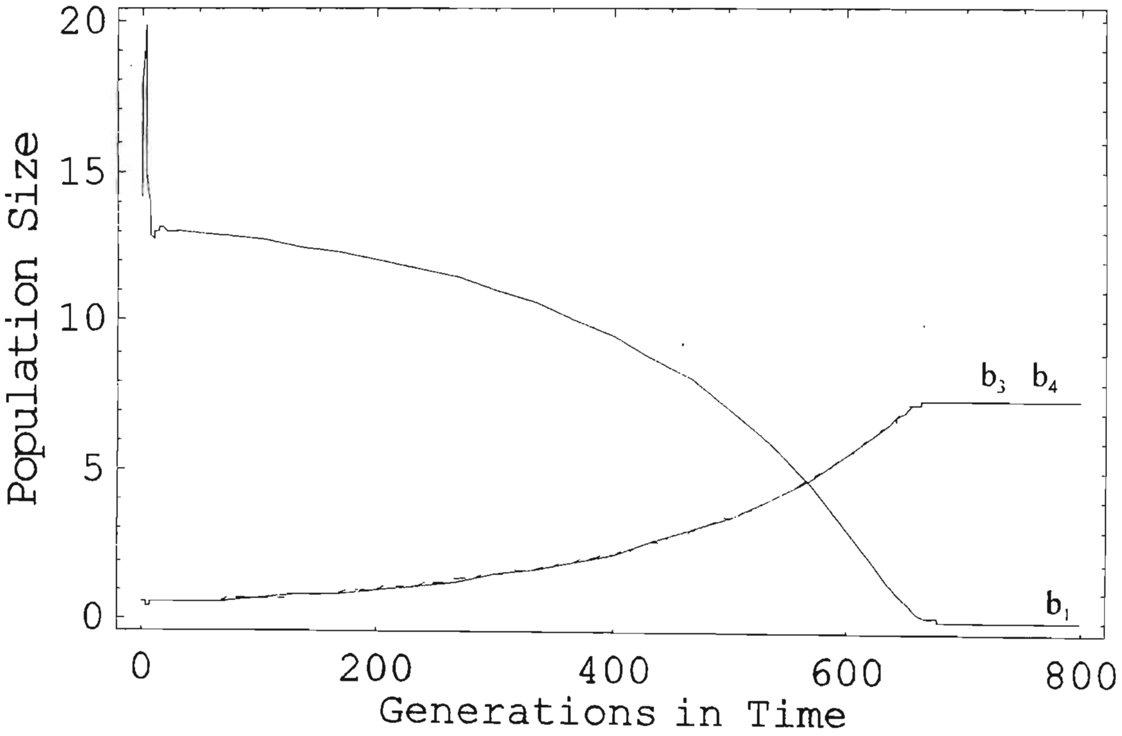

Figure 41. Situation 4, Case 1: One incumbent and two invaders with the incumbent's initial population $b_1 = 14.0625$. Note the incumbent is eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.432$.

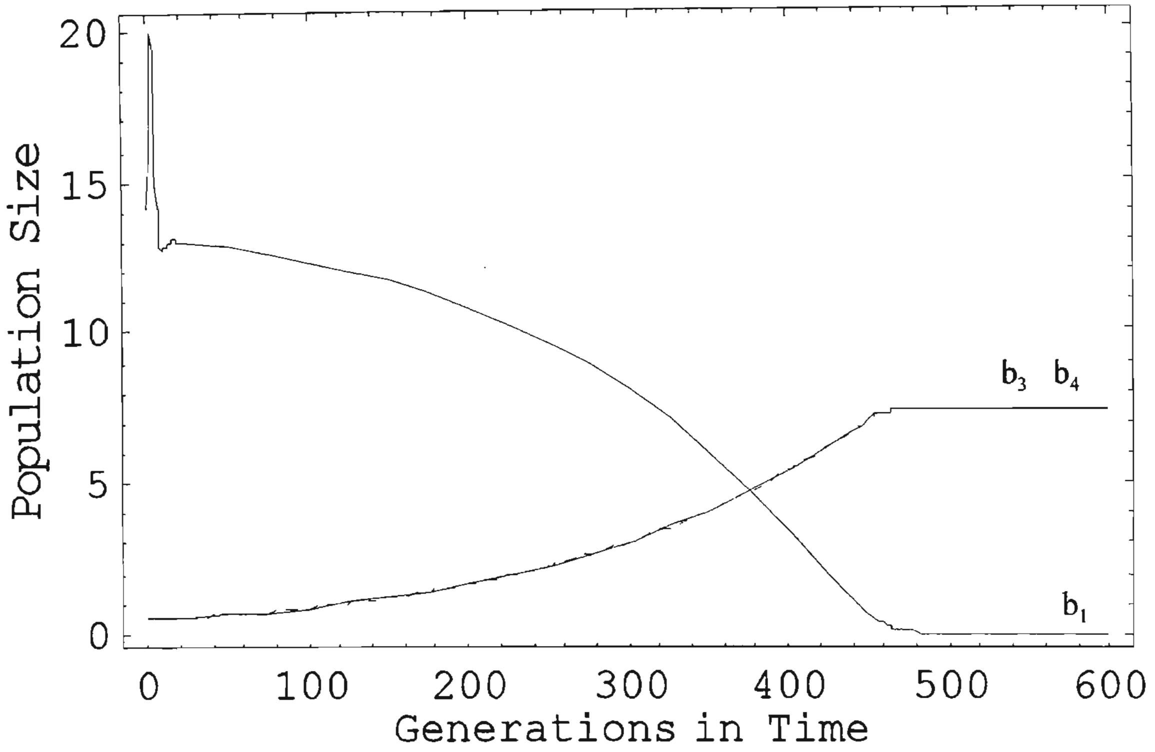

Figure 42. Situation 4, Case 2: One incumbent and two invaders with the incumbent's initial population $b_1 = 14.0625$. Note the incumbent is eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.432$.

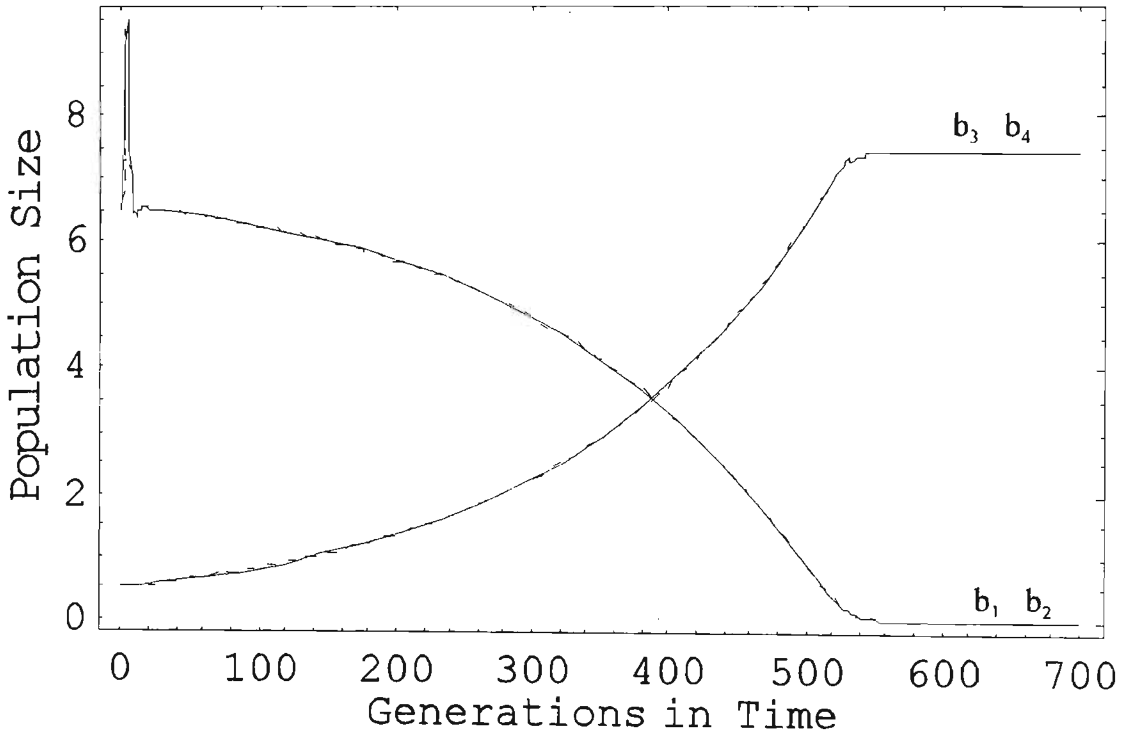

Figure 43. Situation 4, Case 3: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 6.4996$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.432$.

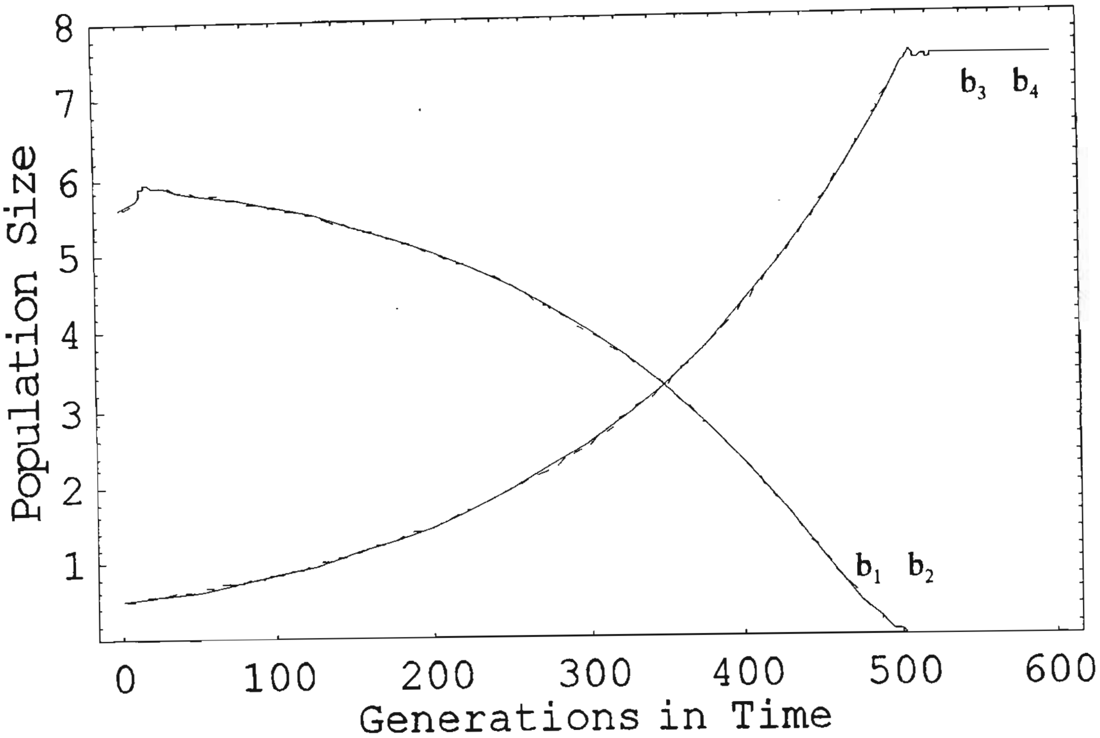

Figure 44. Situation 4, Case 4: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 5.5966$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.432$.

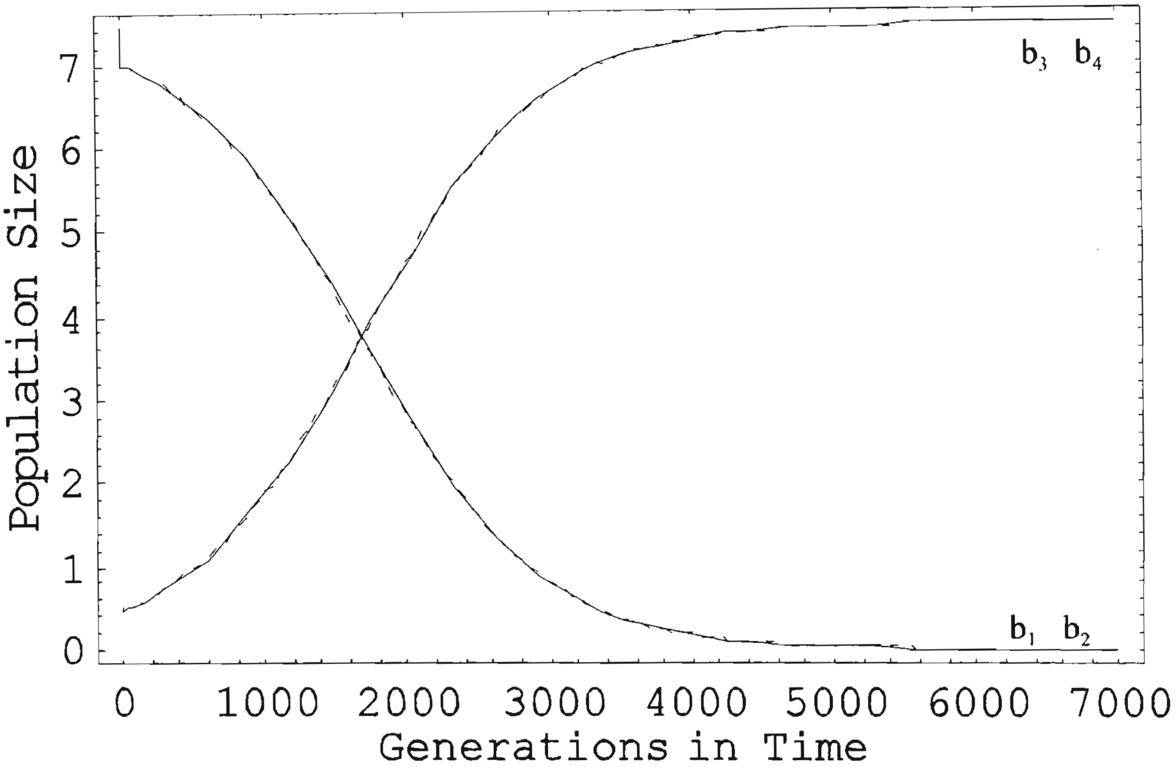

Figure 45. Situation 4, Case 5: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 7.4391$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = b_4 = 7.432$.

Case 3: Two Incumbents Using Strategies $u_1 = 0.2$ and $u_2 = 0.8$

In Figure 43, there are two incumbent populations using strategies $u_1 = 0.2$ and $u_2 = 0.8$ which both have initial populations of 6.4996, which are eliminated within 700 generations, five times as long as the same case in situation three, by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species stabilise to populations of $b_3 = b_4 = 7.432$, which is the same as the populations in cases one and two. Note the combined population is 14.864.

Case 4: Two Incumbents Using Strategies $u_1 = 0.15$ and $u_2 = 0.85$

In Figure 44 on the previous page, there are two incumbent populations using strategies $u_1 = 0.15$ and $u_2 = 0.85$ which both have initial populations of 5.5966, which are eliminated within 600 generations, which is more than seven times as long as for case four in situation three, by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species stabilise to populations of $b_3 = b_4 = 7.432$. Note this is the same as the previous cases.

Case 5: Two Incumbents Using Strategies $u_1 = 0.27$ and $u_2 = 0.73$

In Figure 45, there are two incumbent populations using strategies $u_1 = 0.27$ and $u_2 = 0.73$ which both have initial populations of 7.4391, which are eliminated over the course of 7 000 generations, the same as the previous situation, by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations of $b_3 = b_4 = 7.432$. Note the combined population is 14.864.

In situation four, all the incumbent populations were eliminated, as was expected. In each case the final stable populations were identical for both of the invading species, and the combined population total stayed fairly constant with the combined populations which were reached in situations one, two and three. However, the combined population was much closer to that of the

ESS combined populations. It is also worth noting that the results in situation four are almost identical to those in situation three, but except in case five, they all take more time to stabilise.

5.4.5. Situation Five

This situation is similar to situation two, except that all the strategies are fixed, and only the populations can change. In this situation, it is expected that the results will be similar to those of situation two. Due to the similarities between this situation and situation two, it is expected that the incumbents will be eliminated, and the system will stabilise to the ESS equilibrium populations. It is also expected, due to the results in situation four, that the time taken for stability in each case will be longer than the time taken for the same case in situation two. As the strategies are all fixed, the strategy dynamics were not plotted.

Case 1: One Incumbent Using Strategy $u_1 = 0.2$

In Figure 46 on the next page, there is only one incumbent population using strategy $u_1 = 0.2$ which has an initial population of 14.0625, which is eliminated in 250 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations, which are slightly smaller than the ESS equilibrium populations, of $b_3 = 10.843$ and $b_4 = 4.030$. Note the combined population is 14.873, compared with the combined ESS equilibrium population from Figure 25 which is 14.882. Also note that this case takes twice the time to stabilise as case one in situation two.

Case 2: One Incumbent Using Strategy $u_1 = 0.8$

In Figure 47 on the following page, there is only one incumbent population using strategy $u_1 = 0.8$ which has an initial population of 14.0625, which is eliminated in 200 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations, which are slightly smaller than the ESS equilibrium populations, of $b_3 = 10.842$ and $b_4 = 4.029$. Note the combined population is 14.871, compared with the combined ESS equilibrium population from Figure 25 which is 14.882. Also note that this case takes over twice the time to stabilise as case two in situation two.

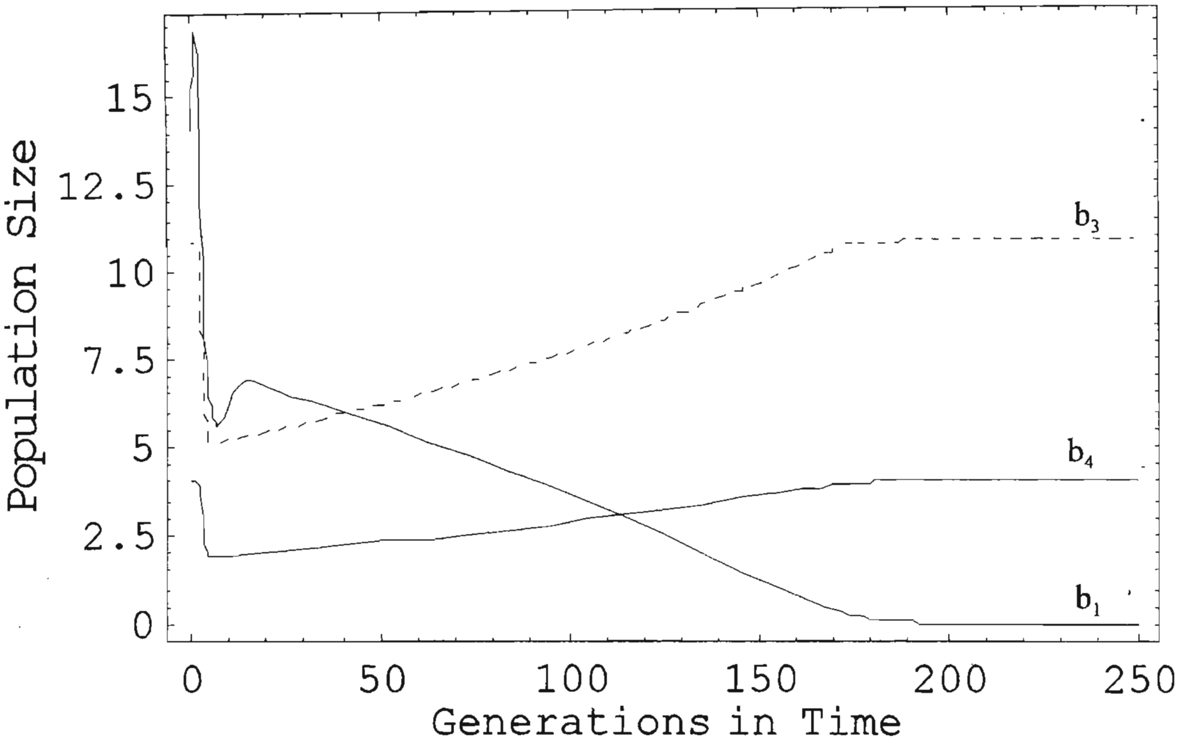

Figure 46. Situation 5, Case 1: One incumbent and two invaders with the incumbent's initial population b_1 = 14.0625 Note the incumbent is eliminated, while the final populations for the invaders are b_3 = 10.843 and b_4 = 4.030.

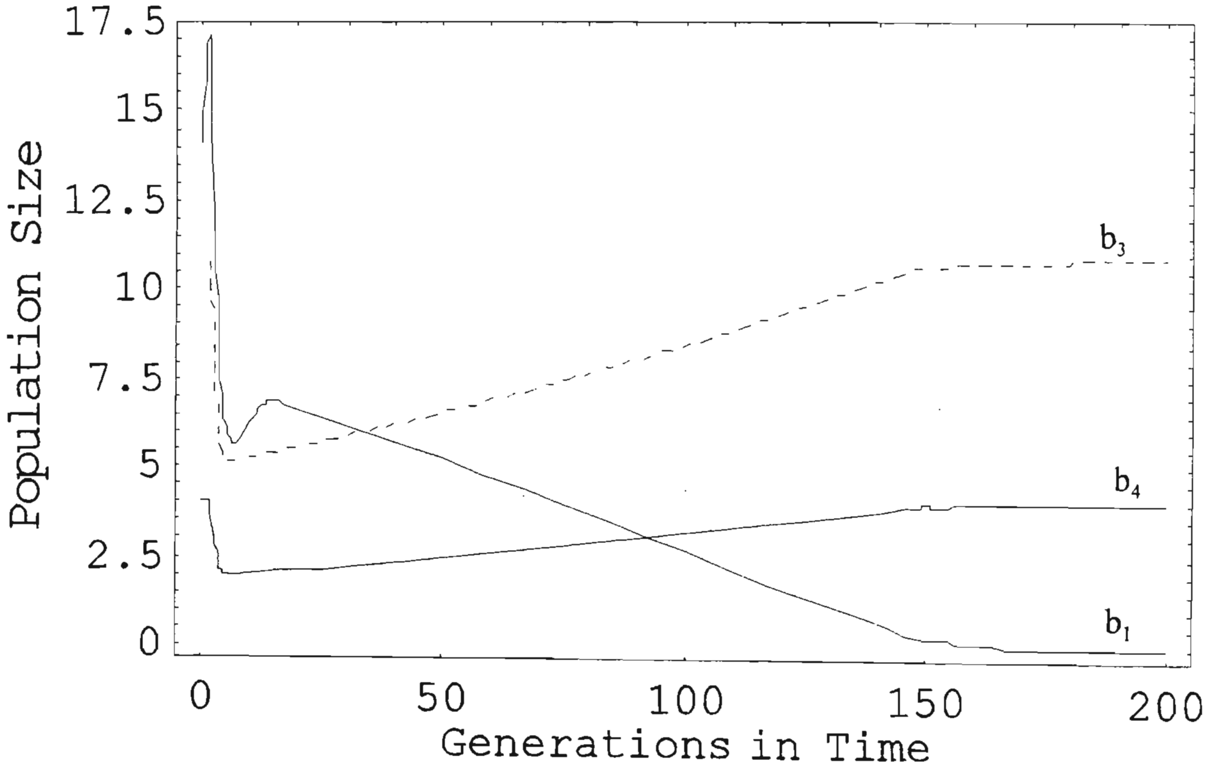

Figure 47. Situation 5, Case 2: One incumbent and two invaders with the incumbent's initial population b_1 = 14.0625 Note the incumbent is eliminated, while the final populations for the invaders are b_3 = 10.842 and b_4 = 4.029.

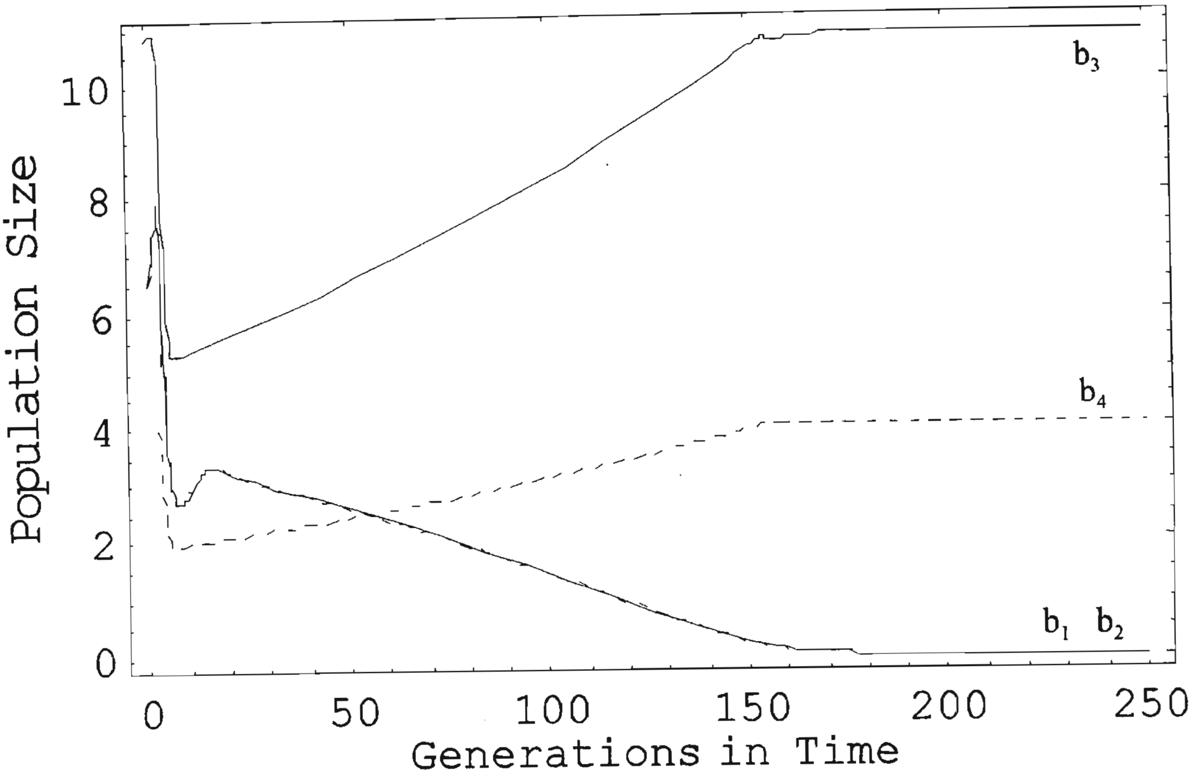

Figure 48. Situation 5, Case 3: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 6.4996$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = 10.843$ and $b_4 = 4.030$.

Case 3: Two Incumbents Using Strategies $u_1 = 0.2$ and $u_2 = 0.8$

In Figure 48 above, there are two incumbent populations using strategies $u_1 = 0.2$ and $u_2 = 0.8$ which both have initial populations of 6.4996, which are eliminated within 250 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations of $b_3 = 10.843$ and $b_4 = 4.030$, which are slightly smaller than the ESS equilibrium populations. Note the combined population is 14.873.

Case 4: Two Incumbents Using Strategies $u_1 = 0.15$ and $u_2 = 0.85$

In Figure 49 on the next page, there are two incumbent populations using strategies $u_1 = 0.15$ and $u_2 = 0.85$ which both have initial populations of 5.5966, which are eliminated within 200 generations by the invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies. The invading species settle into equilibrium populations of $b_3 = 10.843$ and $b_4 = 4.030$, which are slightly smaller than the ESS equilibrium populations. Note the combined population is 14.873.

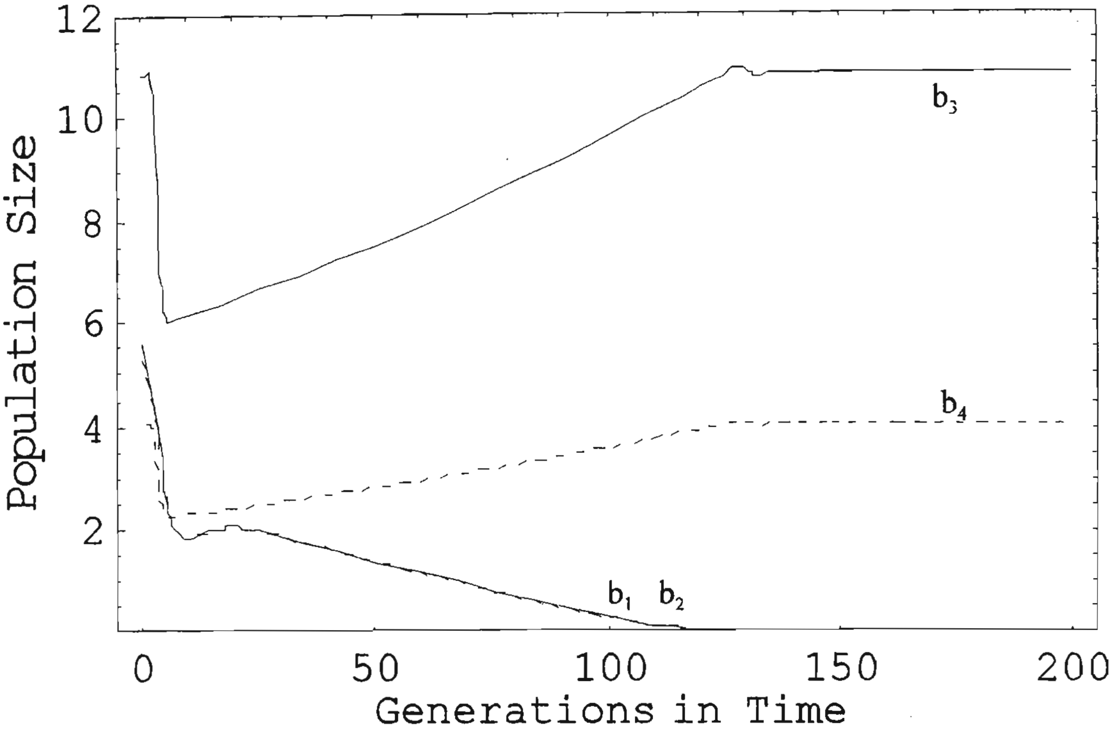

Figure 49. Situation 5, Case 4: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 5.5966$ for the incumbents. Note the incumbents are eliminated, while the final populations for the invaders are $b_3 = 10.843$ and $b_4 = 4.030$.

Case 5: Two Incumbents Using Strategies $u_1 = 0.27$ and $u_2 = 0.73$

In Figure 50 on the following page, there are two incumbent populations using strategies $u_1 = 0.27$ and $u_2 = 0.73$ which both have initial populations of 7.4391. The invading species using initial strategies $u_3 = 0.271$ and $u_4 = 0.729$, which are the ESS strategies eliminate the incumbent populations. The system takes 4 000 generations to stabilise to the equilibrium solutions of $b_3 = 10.825$ and $b_4 = 4.023$. Note the combined population is 14.848, compared with the combined ESS equilibrium population from Figure 25 which is 14.882.

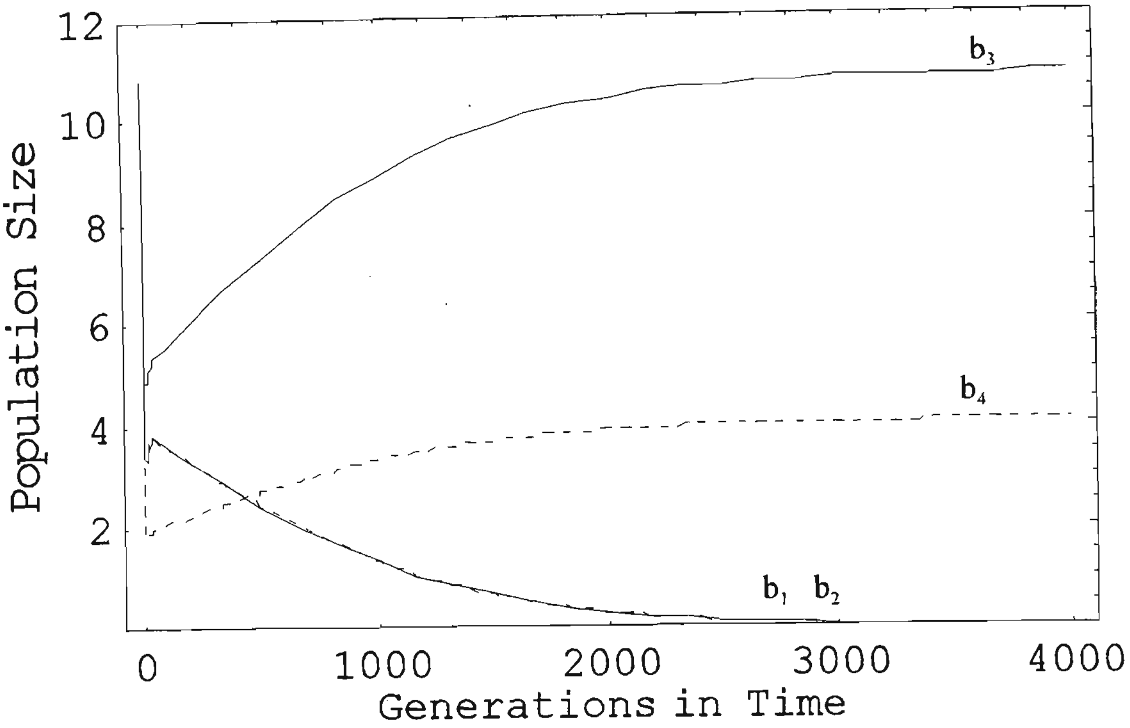

Figure 50. Situation 5, Case 5: Two incumbent and two invaders with the initial populations $b_1 = b_2 = 7.4391$ for the incumbents. Note the incumbents are eliminated, and the final populations for the invaders are $b_3 = 10.825$ and $b_4 = 4.023$.

Also note, that for all the cases in this situation, it took more time for the system to stabilise than taken in situation two, with the exception of case five. Thus, in situation five, the results were almost identical to those obtained in situation two.

5.5. Conclusion of the Model

In this chapter, a dynamic system which was not Lotka-Volterra in nature was found, with the intention of discovering whether or not the results of the previous chapters were still relevant. An example of such a model was found, and presented in §5.1. When trying to duplicate the analysis which had already been done on the model in order to better understand the model, some problems were encountered. These were presented in §5.2. A slight change in one of the equations presented in the paper allowed the analysis to go forward, and the nature of the results found in §5.3. was similar to those presented in the original paper.

Five different situations were simulated in §5.4. A problem was that although the combined population kept almost constant, how the population was shared between the two evolutionary stable strategies depended largely on the initial population and strategy chosen in the simulation.

In §5.4. it was expected that in each of the five situations that the incumbent populations would be eliminated, and the ESS strategies would be attained by invading species. The only area of doubt was as to how the population would be distributed between the two equilibrium species. In fact, the results could be broken down into two broad categories. If the invading populations were initially small, then the final populations would be between the two ESS equilibrium populations. If the invading populations started as the ESS equilibrium populations, then they also ended as the ESS equilibrium populations, with the exception of case one in situation two.

For all of the cases, the ESS was able to eliminate the incumbent populations regardless of its initial population size. This seems to imply that the ESS was also an NIS, and that there was only one such strategy choice. However, the fact that there seems to be a great number of different population distributions between the two equilibrium species, leads one to conclude that either the simulation was not accurate enough or an unique globally stable strategy coalition does not exist. The discrepancies found between the direct calculation and the simulation results, although in keeping with the nature of the results published by Vincent and Vincent, suggest that the simulation was not accurate enough.

Chapter 6: Conclusion

Ever since the concept of an evolutionary stable strategy was first introduced by Maynard-Smith and Price in 1973, there has been a growing body of work concerning this concept. A large volume of work has been produced by various authors, who often introduced their own concepts, for which they had their own acronyms. This has led to a fair amount of duplication, leading some authors trying to collect and collate the various terms (for example Lessard, 1990 & Eshel, 1996) in order to promote better understanding of the topic. Several of the terms, and their relationship to each other, were introduced in order to give a general background to the whole area of evolutionary stability, and to give an idea of what work had already been covered. The terms that were necessary for this work were presented and mathematically defined.

This work has tried to extend what has already been done in this field by investigating the dynamics of coexisting species. The evolutionary dynamics of single species has already been looked at (Apaloo, in preparation a). It has been proved in this work that an ESNIS coalition is an optimal strategy which will displace any size and composition of incumbent populations when Lotka-Volterra competition models are used, and which will be immune to invasion by any other mutant populations, because the ESNIS coalition, where it exists, is unique. In other words, it has been shown that an ESNIS coalition cannot exist in an ecologically stable state with any finite number of strategies in its neighbourhood. It has also been shown in this work that the equilibrium population, when the ESNIS coalition is the only population present, is globally stable in a n-dimensional system (for n finite), where the ESNIS coalition interacts with $n - 2$ other strategies in its neighbourhood.

The behaviour of different incumbent communities of various sizes and composition when made to interact with an invading coalition of species was simulated. Although an ESS coalition which was not also an NIS coalition was not found, it is likely that one does exist, although locating it might be extremely difficult. The equilibrium populations of the various incumbent populations were found, and then made to interact with the ESNIS and NIS coalitions which entered with populations which were small compared with those of the incumbent communities.

This resulted in the incumbent community, whether it consisted of one or four species, being completely eliminated if the coalition interacting with the incumbent community was an ESNIS coalition. The only difference between the one incumbent specie and the four incumbent species scenarios was the number of generations in time which the ESNIS took to establish itself, and to stabilise. In each case, the outcome of the interaction could be predicted. However, the results when one of the two members of the ESNIS coalition interacted with the incumbent populations showed that although the ESNIS coalition is globally stable, the ability of one member of the coalition being able to invade an incumbent population when the other member of the coalition is not present depends largely on the phenotypes of the incumbent populations.

However, if the invading coalition was an NIS coalition which was not also an ESS coalition, then the results of the interaction with the incumbent populations were predictable only in that the NIS coalition would enter the incumbent population, and at least one of the incumbents would remain in equilibrium with the invaders, although sometimes all of them did.

The dynamic behaviour of coexisting systems has been covered in this work quite extensively, especially for Lotka-Volterra competition models. The proof that the ESNIS coalition is globally stable has only been proven for systems of coexisting species whose dynamics are given by Lotka-Volterra competition models. While the results may well hold for non Lotka-Volterra evolution, this remains to be proven. Simulations of a non Lotka-Volterra system gave mixed results. The results seemed to support the idea of a globally stable ESNIS coalition, except for the distribution of the population between the two species. If the simulation could be refined so that the ESS strategies always evolved to the same equilibrium populations, regardless of the initial population size, and regardless of the initial strategy choice, the same simulations could be rerun and similar results would strongly support the existence of a globally stable ESNIS coalition for a non Lotka-Volterra system.

The proof presented in this work, has the weakness that it relies on an assumption of equilibrium points being regular. This assumption needs to be proven, or alternatively the consequences to the proof if the equilibrium points are not regular needs to be examined.

Also, an ESS coalition which is not also an NIS coalition needs to be found, and then simulated interacting with incumbent populations. If the author is incorrect, and there is no ESS coalition which is not also an NIS coalition, then this needs to be proven.

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Appendices

Appendix 1: Sufficient Conditions for ESS and NIS

For the Lotka-Volterra equations used in chapters three and four, the following sufficient conditions are valid for the two-dimensional case.

ESS: Sufficient conditions for an interior community phenotype $(\breve{u}_1, \breve{u}_2)$ with corresponding equilibrium population sizes $(\check{z}_1, \check{z}_2)$ to be an ESS are

$$k(\breve{u}_1) = \check{z}_1 + \alpha(\breve{u}_1 - \breve{u}_2)\check{z}_2$$

$$k(\breve{u}_2) = \alpha(\breve{u}_2 - \breve{u}_1)\check{z}_1 + \check{z}_2$$

$$k'(\breve{u}_1) = \alpha'(0)\check{z}_1 + \alpha'(\breve{u}_1 - \breve{u}_2)\check{z}_2$$

$$k'(\breve{u}_2) = \alpha'(\breve{u}_2 - \breve{u}_1)\check{z}_1 + \alpha'(0)\check{z}_2$$

$$k''(\breve{u}_1) - [\alpha''(0)\check{z}_1 + \alpha''(\breve{u}_1 - \breve{u}_2)\check{z}_2] < 0$$

$$k''(\breve{u}_2) - [\alpha''(\breve{u}_2 - \breve{u}_1)\check{z}_1 + \alpha''(0)\check{z}_2] < 0$$

NIS: Sufficient conditions for an interior community phenotype $(\breve{u}_1, \breve{u}_2)$ with corresponding equilibrium population sizes $(\check{z}_1, \check{z}_2)$ to be an NIS are

$$k(\breve{u}_1) = \check{z}_1 + \alpha(\breve{u}_1 - \breve{u}_2)\check{z}_2$$

$$k(\breve{u}_2) = \alpha(\breve{u}_2 - \breve{u}_1)\check{z}_1 + \check{z}_2$$

$$k'(\breve{u}_1) = \alpha'(0)\check{z}_1 + \alpha'(\breve{u}_1 - \breve{u}_2)\check{z}_2$$

$$k'(\breve{u}_2) = \alpha'(\breve{u}_2 - \breve{u}_1)\check{z}_1 + \alpha'(0)\check{z}_2$$

$$k''(\breve{u}_1) - \alpha''(0)\check{z}_1 - \alpha''(\breve{u}_1 - \breve{u}_2)\check{z}_2 - 2[-\alpha''(0)\check{z}_1 + \alpha'(0)\frac{\partial z_1}{\partial u_1} + \alpha'(\breve{u}_1 - \breve{u}_2)\frac{\partial z_2}{\partial u_1}] < 0$$

$$k''(\breve{u}_2) - \alpha''(\breve{u}_2 - \breve{u}_1)\check{z}_1 - \alpha''(0)\check{z}_2 - 2[-\alpha''(0)\check{z}_2 + \alpha'(0)\frac{\partial z_2}{\partial u_2} + \alpha'(\breve{u}_2 - \breve{u}_1)\frac{\partial z_1}{\partial u_2}] < 0$$

where the partials of z_1 and z_2 satisfy

$$k'(\breve{u}_1) = \alpha'(\breve{u}_1 - \breve{u}_2)\check{z}_2 + \frac{\partial z_1}{\partial u_1} + \alpha(\breve{u}_1 - \breve{u}_2)\frac{\partial z_2}{\partial u_1}$$

$$0 = -\alpha'(\breve{u}_1 - \breve{u}_2)\check{z}_2 + \frac{\partial z_1}{\partial u_2} + \alpha(\breve{u}_1 - \breve{u}_2)\frac{\partial z_2}{\partial u_2}$$

$$0 = -\alpha'(\breve{u}_2 - \breve{u}_1)\check{z}_1 + \alpha(\breve{u}_2 - \breve{u}_1)\frac{\partial z_1}{\partial u_1} + \frac{\partial z_2}{\partial u_1}$$

$$k'(\breve{u}_2) = \alpha'(\breve{u}_2 - \breve{u}_1)\check{z}_1 + \alpha(\breve{u}_2 - \breve{u}_1)\frac{\partial z_1}{\partial u_2} + \frac{\partial z_2}{\partial u_2}$$

at $(\breve{u}_1, \breve{u}_2)$.

Appendix 2: The Index Theorem (Hofbauer and Sigmund, 1988)

Definition A1: Suppose that $\mathbf{y} \notin \mathbf{f}(\mathrm{bd}\,\bar{U})$. Then the Brouwer degree of $\mathbf{f}$ at the value $\mathbf{y} \in R^n$ is defined by

$$\deg(\mathbf{f}, \mathbf{y}) = \sum_{\mathbf{f}(z) = \mathbf{y}} \mathit{sign} \det D_z\mathbf{f}$$

if $\mathbf{y}$ is a regular value, and by

$$\deg(\mathbf{f}, \mathbf{y}) = \lim_{n \to \infty} \deg(\mathbf{f}, \mathbf{y}_n)$$

if $\mathbf{y}$ is not a regular value, where $\mathbf{y}_n$ is a sequence of regular values converging to $\mathbf{y}$.

Definition A2: Let $\check{z}$ be an isolated equilibrium of the differential equation (I) defined on the open set $U \subseteq R^n$. The Poincaré index of $\check{z}$, $i(\check{z})$, with respect to the vector field $\mathbf{f}$ is defined as

$$i(\check{z}) = \deg(\mathbf{f}, \mathbf{0}).$$

Definition A3: If $\check{z}$ is regular, then the Poincaré index of $\check{z}$, $i(\check{z})$ is given by

$$i(\check{z}) = (-1)^\sigma$$

where σ is the number of negative eigenvalues of the Jacobian matrix $D_{\check{z}}\mathbf{f}$.

Theorem A4 (Index Theorem for system (I)): If the *n*-dimensional system (I) has uniformly bounded orbits then it has a saturated fixed point, and if all saturated fixed points are regular then the sum of the indices is $(-1)^n$.

□

Theorem A5: Let $\check{z} \in R^n_+$ be an isolated fixed point of (I) and *U* the intersection of an isolating neighbourhood of $\check{z}$ with interior of R^n_+. Let $-\boldsymbol{\varepsilon}$ be the vector field with components $-\varepsilon_i < 0$ and **h** the vector field with components $z_i f_i(\mathbf{z})$ on *U*. Then

(a) $\text{bd-ind}(\check{z}) = \lim_{\varepsilon \to 0} \deg(\mathbf{h}, -\boldsymbol{\varepsilon})$ is well defined

(b) $\text{bd-ind}(\check{z}) = \begin{cases} i(\check{z}) & \text{if } \check{z} \text{ is saturated and regular} \\ 0 & \text{if } \check{z} \text{ is not saturated} \end{cases}$

(c) index theorem for (I) extends to isolated fixed points for this "boundary-index"

(d) if $\text{bd-ind}(\check{z}) \neq 0$, then there exist points $\mathbf{z} \in R^n_+$ arbitrarily close to $\check{z}$ such that $f_i(\mathbf{z}) < 0$ for all *i* with $\check{z}_i = 0$.