Universidade Estadual Paulista
Instituto de Biociências

Comportamento dinâmico, estocaticidade e heterogeneidade ambiental em *Tribolium castaneum*

Aluna: Ana Rita Rocha Romão

Orientador: Prof. Dr. Wesley A. C. Godoy

Artigo apresentado ao Departamento de Parasitologia do Instituto de Biociências – UNESP - Botucatu, como exigência para obtenção do título de Bacharelado em Ciências Biológicas.

Botucatu – SP
2008

FICHA CATALOGRÁFICA ELABORADA PELA SEÇÃO TÉCNICA DE AQUISIÇÃO E TRATAMENTO
DA INFORMAÇÃO.
DIVISÃO DE BIBLIOTECA E DOCUMENTAÇÃO - CAMPUS DE BOTUCATU - UNESP

BIBLIOTECÁRIA RESPONSÁVEL: SELMA MARIA DE JESUS

Romão, Ana Rita Rocha.
Comportamento dinâmico, estocaticidade e heterogeneidade ambiental em *Tribolium castaneum* / Ana Rita Rocha Romão. – Botucatu : [s.n.], 2008.

Trabalho de conclusão (bacharelado – Ciências Biológicas) – Universidade Estadual Paulista, Instituto de Biociências de Botucatu, 2008
Orientador: Wesley A. C. Godoy

1. Genética de populações 2. Zoologia 3. Heterogeneidade

Palavras-chave: Dinâmica de populações; Estrutura espacial; *Tribolium castaneum*

Resumo:

Neste estudo analisamos a influência de parâmetros demográficos na dinâmica da população do *Trbibolium castaneum*, combinando empriricismo e teoria de populações para analisar os diferentes efeitos da heterogeneidade ambiental, empregando modelos de Ricker, designados ao estudo de um sistema de dois patches levando em conta análises determinísticas e estocásticas. Os resultados foram expressos através de diagramas de bifurcação e simulações estocásticas. O equilíbrio dinâmico foi amplamente investigado com resultados sugerindo espaços paramétricos específicos em resposta à heterogeneidade ambiental e à migração. Padrões de equilíbrio de população, sincronia e persistência em *T. castaneum* foram discutidos.

Dynamic behavior, stochasticity and environmental heterogeneity in *Tribolium castaneum*

A. R. R. Romão, M. I. S. Costa and W. A. C., Godoy

Abstract

In this study we analyzed the influence of demographic parameters on the population dynamics of *Tribolium castaneum*, combining empiricism and population theory to analyze the different effects of environmental heterogeneity, by employing Ricker models, designed to study a two-patch system taking into account deterministic and stochastic analysis. Results were expressed by bifurcation diagrams and stochastic simulations. Dynamic equilibrium was widely investigated with results suggesting specific parametric spaces in response to environmental heterogeneity and migration. Population equilibrium patterns, synchrony and persistence in *T. castaneum* were discussed.

Keywords: Population dynamics, spatial structure, *Tribolium castaneum*

Introduction

The red flour beetle *Tribolium castaneum* is an important pest of stored agricultural products (Jbilou *et al.* 2008), but it is also a genetic model for Coleoptera (Richards *et al.* 2008) and an useful model employed in several studies with emphasis in ecological modelling (Desharnais *et al.* 2006). Laboratory populations are easily cultured and many species can complete their life cycle in less than a month (Dennis *et al*., 1995). Population attributes such as density and age structure are readily measured and the populations themselves can be replicated. Some species of *Tribolium* are cannibalistic (Park *et al*., 1965). Adults feed on eggs, larvae, pupae, and callows while larvae eat eggs, pupae, and callows. Neither larvae nor adults eat mature adults and larvae do not feed on larvae (Dennis *et al*., 1995). *Tribolium castaneum* is commonly found in stored dried food, exhibiting high ability to live in dry environments (Richards *et al.* 2008). In addition, the species is able to interact with diverse chemical environment by using its odorant and gustatory receptors (Richards *et al.* 2008). These biological attributes make of the insect an interesting organism to be investigated as an ecological model for studies focused on population dynamics and conservation biology.

Spatial patterns have been considered of great importance for dynamic systems, mainly systems in which are involved organisms living in heterogeneous environments (Kendall & Fox, 1998; Tanabe, 2002). Spatial structure is known as an important component of animal populations and it has been employed to explain ecological patterns associated to regional persistence of populations and interactions such as competition, predation and parasitism (Comins *et al.* 1992; Day & Possingham, 1995).

Here we began from a deterministic model analyzing the variety of behavior between different environments going to another data approach with random values to understand the population dynamics of *T. castaneum* under different ecological aspects. Ricker models have shown to be efficient when used at combinations to include stochastic factors that could contribute significantly to the understanding about the processes that lead to the extinction of the animals. The objective of this study was to perform a sensitivity analysis with bifurcation diagrams in demographic parameters in order to know the parametrical space associated to stability in populations of *T. castaneum.* Stochastic simulations were also performed to compare oscillation patterns, synchrony and local persistence. The study was a combination between laboratory experiments and ecological modelling.

Material and methods

Experiments were previously set up (Godoy & Costa, 2005) at Department of Environmental Science and Policy at the University of California, Davis, USA, where beetle populations were established in small bottles with 5, 10, 15, 20, 30 and 35 grams of standard medium (95% flour, 5% brewer's yeast). All populations were housed in the same environmental chamber at 31^{o} C (Godoy & Costa, 2005).

Populations were paired with different amounts of food and four treatments were set up to compare different levels of environmental heterogeneity. High (vials with 5 and 35 g), moderate (10 and 30 g), low (15 and 25 g) and no heterogeneity (20 and 20 g), were established to compare the effects of different heterogeneity levels. The effect of corridors was achieved by exchanging a fixed percentage, 10 %, of the adult population between pairs of each generation. Initial populations in each pair of bottles totaled 50 ($N^1 + N^2 = 50$). From these 50, one bottle received the dispersing fraction and the other received the non-dispersing fraction. The initial sizes of paired populations were always 5 for vials with 5, 10, 15 and 20 grams, and 45 for vials with 35, 30, 25 and 20 grams. There were twelve replicate pairs per treatment.

The experimental protocol produced discrete generations at seven-week intervals. Adults were introduced to the medium for one week to oviposit and then removed. Removal simulated adult mortality, which destabilizes these populations (Costantino *et al.*, 1997). Seven weeks later, adults from the subsequent generation were counted. These output numbers were used to determine the initial size of the next generation, according to the following formula:

$$N^1_d = (1-d)N^1_{t+1} + dN^2_{t+1} \qquad (1a)$$

$$N^2_d = dN^1_{t+1}+(1-d)N^2_{t+1} \qquad (2a)$$

where d is the exchange rate, and N_d refers to the population size after dispersal. N_d is then used as N_t to begin the next generation. Six generations were investigated for a total period of 35 weeks.

Sensitivity analysis with bifurcation diagram

Bifurcation diagrams were used to describe possible behavior for different parameter values of the Ricker Model (Ricker, 1952). Ricker model is a formalism proposed to investigate the population growth, assuming an exponential growth in discrete time, governed by a growth rate (r) and a carrying capacity (K). The Ricker equation may be written as

$$n_{t+1} = n_t e^{r(1 - \frac{n_t}{K})} .$$

The sensitivity analysis was conduced by employing the bifurcation theory (May & Oster, 1976), since the dynamic behavior from Ricker model depends essentially of the *r* values (growing rate) and *K* (carrying capacity). When the spatial dimension is introduced in discrete growth models, migration can also influence the population behavior. The variation in parameter values usually generates qualitative changes in the population dynamic behavior, since monotonic equilibrium, going through cycles until chaos. The monotonic equilibrium characterizes a constant trajectory over the time. The limit cycles express the oscillatory nature of population between fixed limits and chaos reflects uncertain fluctuations through time. The migration value used for bifurcation diagrams was 0.1. Stochastic simulations were performed using maximum and minimum *r* and *K* values experimentally obtained. Stochastic migration was investigated with uniform distribution for values between 0.0 and 0.2 by using the *rand* module of MATLAB 5.3.

Results

Table 1 shows the growth rate (*r*) and carrying capacity (*K*) for N_1 and N_2 populations of *T. castaneum.* A comparison between dynamic behaviors from migrant populations with non migrant populations under high environmental heterogeneity showed that without migration *T. castaneum* exhibits stable equilibrium for N_1 and a cascade of behaviors such as stable equilibrium, limit cycles and chaotic behavior for N_2 (Fig. 1A). With migration, N_1 and N_2 exhibited the cascade of behaviors above mentioned, but with spectral difference (Fig. 1B). With low heterogeneity and no migration, N_1 populations exhibited a two-point limit cycle and N_2 the cascade of behaviors (Fig. 2A). With migration the two-point limit cycle observed in N_1 was changed to two cascades with equilibrium points below 1000 (Fig. 2B). N_2 exhibited only one cascade with wide spectrum, from 0 to 4000 (Fig. 2B).

For moderate heterogeneity non-migrant populations exhibited an eight-point limit cycle for N_1 and a complete cascade of behaviors for N_2 (Fig. 3A). With migration N_1 and N_2 exhibited cascades (Fig. 3B). For the control group (no heterogeneity) without migration N_1 resulted in a four-limit cycle and N_2 the same cascade previously cited (Fig. 4A). However, with migration, both N_1 and N_2 resulted in cascades showing periodicity windows for r values between 2.8 and 3.4 (Fig. 4B).

Deterministic interactions with the Ricker coupled model for two patches resulted in stable equilibrium for high heterogeneity populations (Fig. 5A), stable equilibrium and two-point limit cycle for low heterogeneity populations (Fig. 5B), stable equilibrium and unpredictable fluctuations for moderate heterogeneity populations (Fig. 5C) and stable equilibrium and four-point limit cycle for no heterogeneity populations (Fig. 5D). Of the two populations, one exhibited always stable equilibrium in response to $r < 1$ for all treatments. However, the other population showed different equilibria in response to different environmental heterogeneities. With migration of 0.1, all populations exhibited two-point limit cycles (Fig. 6 B, C, and D), except populations obtained from high heterogeneity (Fig. 6 A).

For stochastic migration simulations (Figs. 7A, B, C, D) the treatments: low, moderate and no heterogeneity exhibited the same synchronous pattern for N_1 and N_2 , differing from the high environmental heterogeneity (Fig. 7A), which showed asynchrony on fluctuations. For all treatments with stochastic carrying capacity the populations exhibited no synchronic fluctuations (Fig. 8 A, B, C, D). However, incorporating migration the synchrony was observed again (Fig. 9 A, B, C, D).

Discussion

Bifurcation diagrams performed to investigate the sensitivity of the growth rate (*r*) in isolated populations show a stable equilibrium for N_1 and a cascade of behaviors for N_2. These results indicate that if r_1 is set to 1.9067 and N_1 receive no migrant, *T. castaneum* will maintain the stable equilibrium. For different values of r_2 *T. castaneum* could exhibit a cascade of behaviors, since stable equilibrium to chaos. However, with migration N_1 could exhibit other behavior besides stable equilibrium because even with its growth rate set to 1.9067, the population would receive migrants from N_2. The same result was found analyzing low and moderate heterogeneity. Populations without migration resulted in limit cycles for N_1 and a cascade of behaviors for N_2. However, with migration N_1 and N_2 exhibited cascades in response to migrants, which allowed that N_2 qualitatively influenced N_1.

For the control group the result was slightly different from the results obtained from the populations with environmental heterogeneity. Without migration, limit cycles were obtained for N_1 and a cascade for N_2. However, with migration N_1 and N_2 exhibited a complete cascade, but with periodicity windows appearing for $2.8 < r < 3.3$. This behavior was observed only for the control group.

Migration is recognized as a stabilizing factor in insect populations (Godoy *et al.* 1997). The stabilization takes place in response to emigration of individuals from a fragment to another one, since few individuals living in a system trend to produce low offspring, leading to low population growth (Castanho *et al.* 2006). Isolated populations have no chance of rescuing empty or extinct patches. Then, populations characterized by patches connected by migration are known as persistent systems because populations may recolonise each other (Serra *et al.* 2007). The way in which the graphics were exhibited in this paper show the effect of migration on two populations, however the results appear throughout a bifurcation diagram with *'r"* as the *X* axis . Bifurcation diagrams with points produced in response to growth rate are commonly shown to analyse the equilibrium in nonlinear systems, such as populations described by the Ricker Model. However, in this study there are two populations connected by migration, which can influence each other. Then, the growth rate that appears in the graphics is also influenced by the migration.

The results found with deterministic and stochastic simulations suggest a significant difference among the treatments, mainly with respect to high environmental heterogeneity. The oscillation patterns found in this treatment was very different from the other cases. This result is probably due to the spectrum of the parameter values observed in populations, which had high environmental heterogeneity. In addition, the synchrony patterns observed in the stochastic simulations were also different for this treatment, suggesting that in this case the synchrony is rare.

The results obtained suggest that the dynamic behavior variation on population depend on different factors. Demographic parameters seem exerts significant influence on the system and the heterogeneity of environments may alter or invert patterns of population dynamics. Spatial synchrony had been observed in many ecological systems, but the cause of the phenomena remains not clear (Serra *et al.* 2007). The Moran effect has been cited as the most common cause, running as a group of exogenous ecological factors that acts stochastically over population, taking to simultaneous flouting (Moran, 1953).

Recently Godoy & Costa (2005) analyzed *Tribolium* populations with a independent density model, combining migration with environmental heterogeneity and found that stochasticity occurs more substantially in coupled environments with high heterogeneity levels. We believe that the balance between temporal and environmental variability can determine the level of local population variability and synchrony, with implications for the dynamics of both local and global extinction. Hence, the global extinction risk can be directly determined by features of local population dynamics.

References

Bret A. M. & Hastings, A. (2008) Extinction risk depends strongly on factors contributing to stochasticity. *Nature* **454**:100-103.

Castanho, M. J. P., Magnago, K. F., Bassanezi, R. C. & Godoy, W. A. C. (2006) Fuzzy subset approach in coupled population dynamics of blowflies. *Biological. Research* **39:** 341-352.

Comins, H. N., Hassell, M. P. & May, R. M. (1992) The spatial dynamics of host-parasitoid systems. *Journal of Animal Ecollogy* **61**:735-748.

Costantino, R.F., Desharnais R. A., Cushing, J.M. & Dennis, B. (1997) Chaotic dynamics in an insect population. *Science* **275**:389-391.

Day, J.R., & Possingham, H. P. (1995) A stochastic metapopulation model with variability in patch size and position. *Theoretical Population Biology* **48**:333-360.

Den Boer, P. J. (1981) On the survival of populations in a heterogeneous and variable environment. *Oecologia* **50**: 39-53.

Dennis, B. R., Desharnais, A., Cushing, J. M. & Costantino, R. F. (1995) Nonlinear demographic dynamics: mathematical models, statistical methods and biological experiments. *Ecological Monographs* **65**:261-281.

Desharnais, R. A. (2005) **Advanced in ecological research**. Elsevier Academic Press, Amsterdam.

Godoy W.A.C., Von Zuben C.J., Reis S.F. & Von Zuben F.J. (1997) The spatial dynamics of native and introduced blowflies (Dip., Calliphoridae). *Journal of Applied Entomology* **121**: 305-309.

Godoy W.A.C., Von Zuben F.J., Von Zuben C.J. & Reis S.F. (2001) Spatio-temporal dynamics and transition from asymptotic equilibrium to bounded oscillations in *Chrysomya albiceps* (Diptera, Calliphoridae). *Memórias do Instituto Oswaldo Cruz* **96**: 627-634.

Godoy W.A.C. & Costa M.I.S. (2005). Dynamics of extinction in coupled populations of the flour beetle Tribolium castaneum. *Brazilian Journal of Biology* **65:** 271-280.

Goldwyn E. E. & Hastings A. (2008). When can dispersal synchronize populations? *Theoretical Population Biology* **73**: 395-402.

Jbilou, R., Amri, H., **Bouayad, N**., **Ghailani, N**. **et al.** (2008). Insecticidal effects of extracts of seven plant species on larval development, alpha-amylase activity and offspring production of *Tribolium castaneum* (Herbst) (Insecta: Coleoptera: Tenebrionidae.) *Bioresource Technology* **99**:959-64.

Kendall, B. E. & Fox, G. A. (1998). Spatial structure, environmental heterogeneity, and population dynamics: analysis of the coupled logistic map. *Theoretical Population Biology* **54**: 11-37.

Liebhold, A., Sork, V., Peltonen, M., Koenig, W., et al. (2004). Within-population spatial synchrony in mast seeding of North American oaks. *Oikos* **104**: 156–64.

May, R. M. & Oster, G. F. (1976). Bifurcations and dynamic complexity in simple ecological models. *American Nauralist* **110***:* 573-599.

Moran, P.A.P. (1953). The statistical analysis of the Canadian Lynx cicle: II – Synchronization and meteorology. *Australian Journal of Zoology* **1**: 291-298.

Park, T., Mertz, D. B., Grodzinski, W. & Prus, T. (1965). Cannibalistic predation in population of flour beetles. *Physiological Zoology* **38**: 289-321.

Richards, S., Gibbs, R.A., Weinstock, G.M., Brown, S.J. et al. (2008). The genome of the model beetle and pest *Tribolium castaneum*. *Nature*. **452**:949-55.

Ricker, E. L. (1952). Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**:559-623.

Serra, H., Silva, I. C. R., Mancera, P. F. A., Faria, L. D. B., et al. (2007). Stochastic dynamics in exotic and native blowflies: an analysis combining laboratory experiments and a two-patch metapopulation model. *Ecological Research* **22**:686-695.

Tanabe, S. I. (2002). Between-forest variation in vertical stratification of drosophilid populations. *Ecological Entomology* **27**:720–731.

Figure Legends

Fig.1. Bifurcation diagram of r (growth rate) in T. castaneum for high environmental heterogeneity with no migration (a) and 0.1 of migration (b)

Fig.2. Bifurcation diagram of r in T. castaneum for low heterogeneity with no migration (a) and 0.1 of migration (b)

Fig.3. Bifurcation diagram of r in T. castaneum for moderate heterogeneity with no migration (a) and 0.1 of migration (b)

Fig.4. Bifurcation diagram of r in T. castaneum for no heterogeneity with no migration (a) and 0.1 of migration (b)

Fig. 5. Deterministic iterations in T. castaneum comparing high (A), low (B), moderate (C) and no heterogeneity (D) without migration

Fig. 6. Deterministic iterations in T. castaneum comparing high (A), low (B), moderate (C) and no heterogeneity (D) with migration

Fig. 7. Stochastic migration in T. castaneum comparing high (A), low (B), moderate (C) and no heterogeneity (D)

Fig. 8. Stochastic carrying capacity in T. castaneum comparing high (A), low (B), moderate (C) and no heterogeneity (D) without migration

Fig. 9. Stochastic carrying capacity in T. castaneum comparing high (A), low (B), moderate (C) and no heterogeneity (D) with migration

Table 1

Parameters for N1	**High heterogeneity**	**Low heterogeneity**	**Moderate heterogeneity**	**No heterogeneity**
R1min	0.14	0.14	0.14	0.14
R1max	0.44	0.44	0.44	0.44
K1*	153	456	294	654
Parameters for N2	**High heterogeneity**	**Low heterogeneity**	**Moderate heterogeneity**	**No heterogeneity**
R2min	1.81	1.73	1.78	1.51
R2max	1.90	2.37	3.45	2.65
K2*	1053	804	950	698

*** K min = 1**

Fig.1

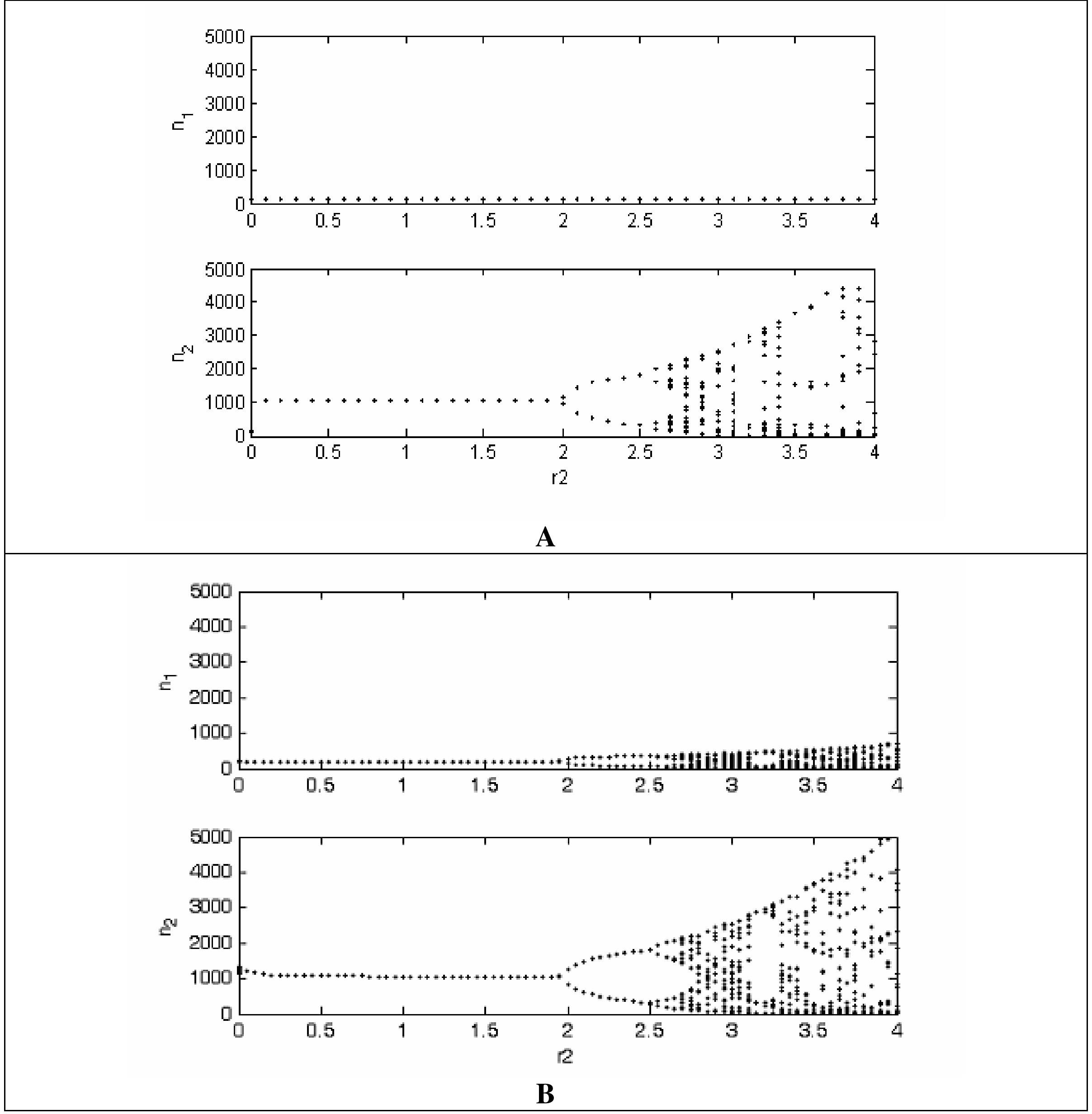


Fig.2

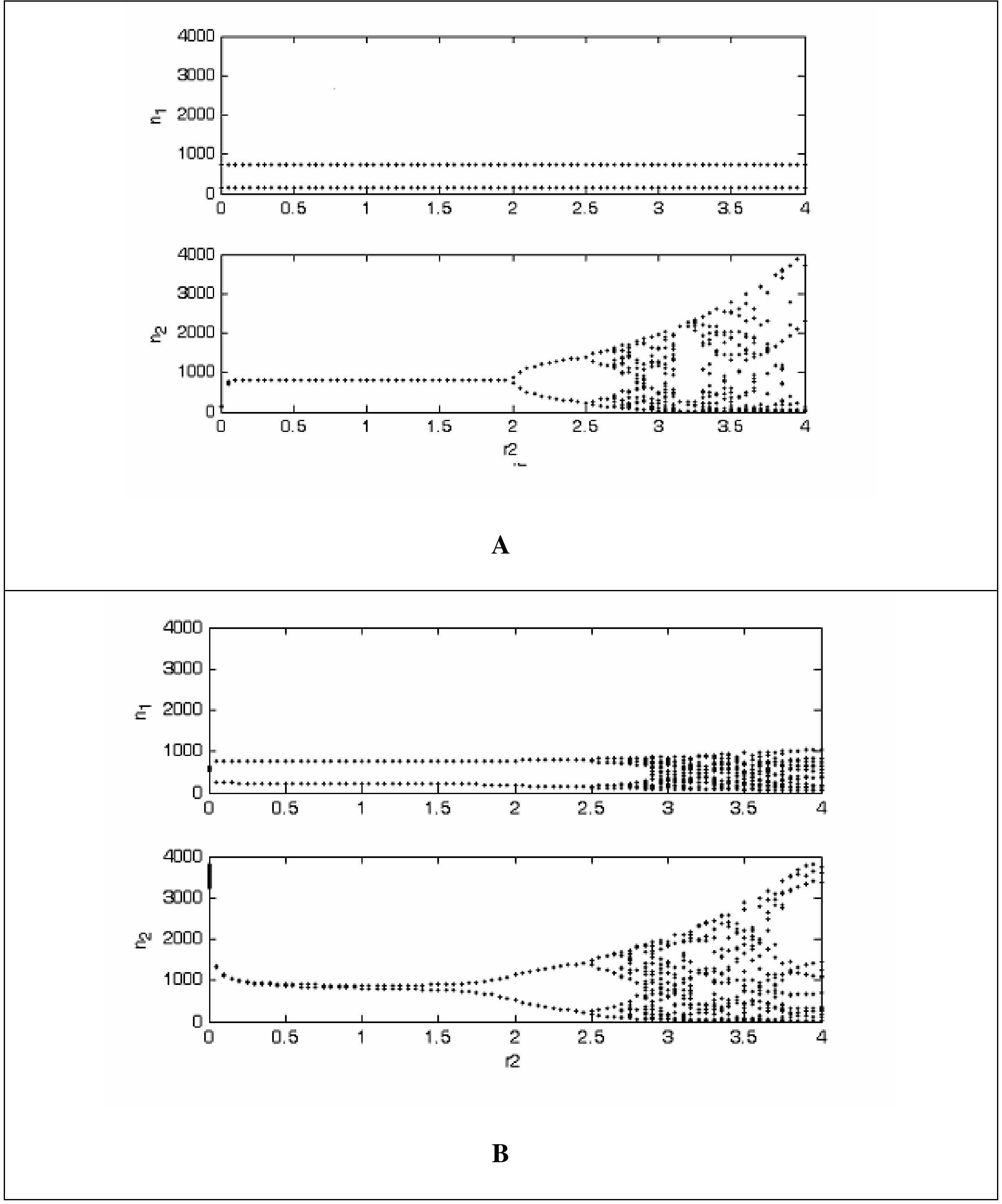
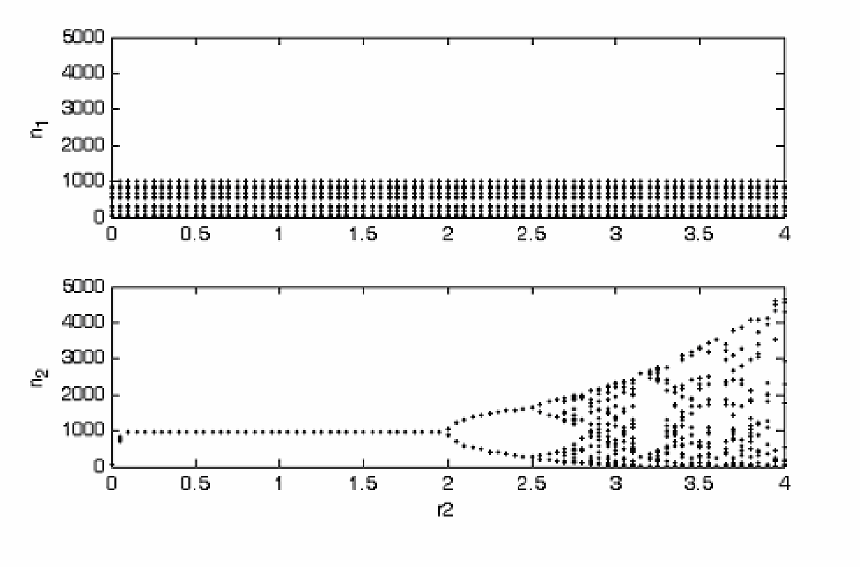
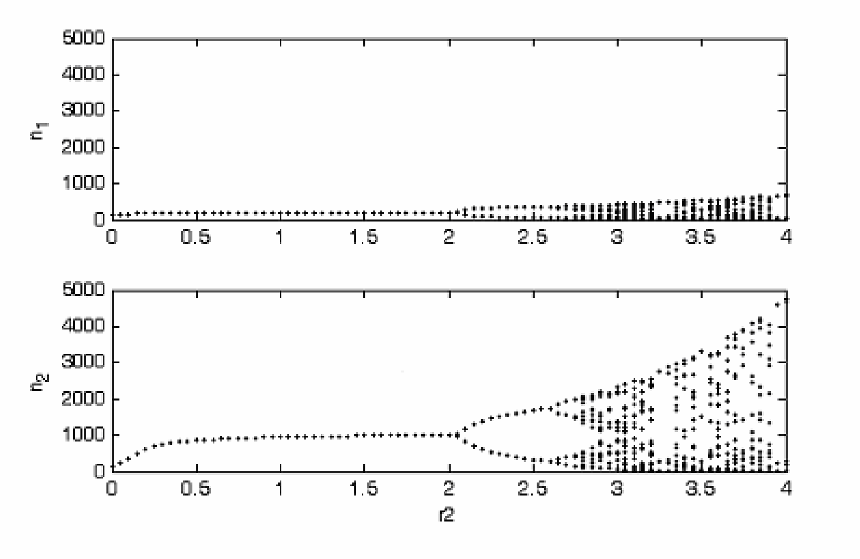


Fig. 3


n1
n2
r2
0
1000
2000
3000
4000
5000
0.5
1
1.5
2
2.5
3
3.5
4

A


n1
n2
r2
0
1000
2000
3000
4000
5000
0.5
1
1.5
2
2.5
3
3.5
4

B

Fig.4

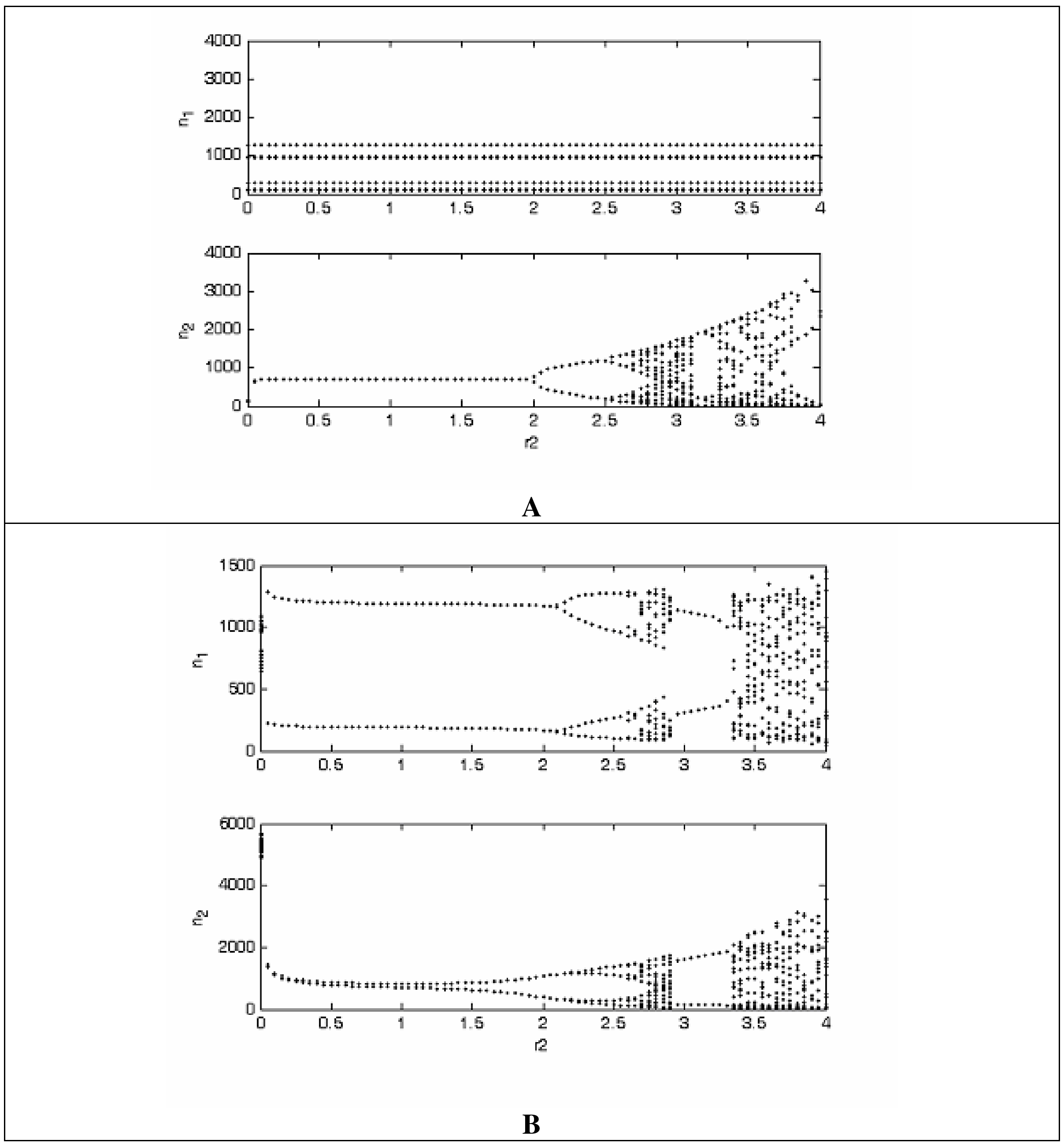
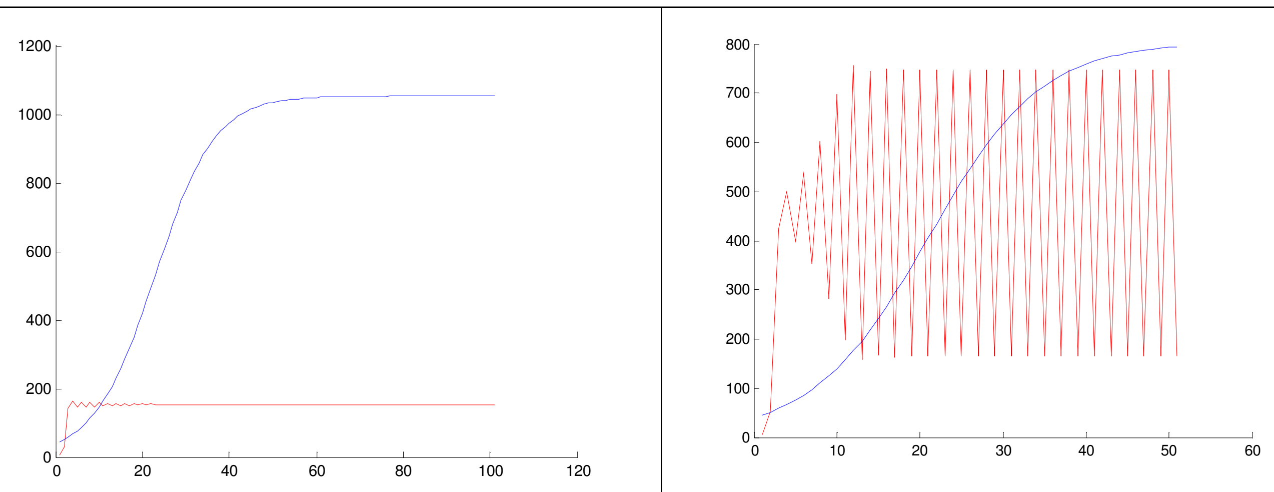
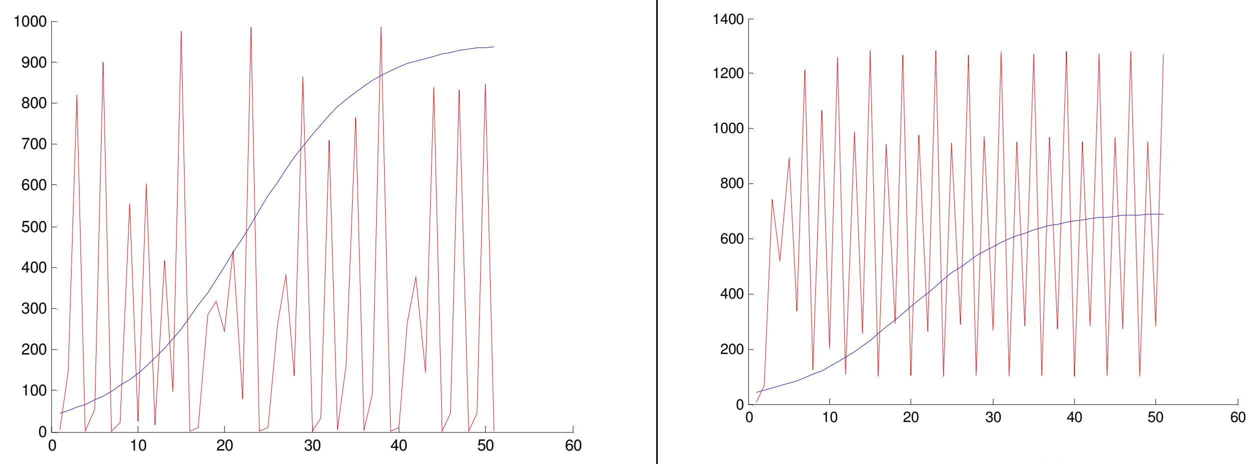

4000
3000
2000
1000
0
n_1
0
0.5
1
1.5
2
2.5
3
3.5
4
4000
3000
2000
1000
0
n_2
r2
A
1500
1000
500
0
n_1
6000
4000
2000
0
n_2
r2
B

Fig.5



A: High Heterogeneity: r1=1.90;r2= 0.14;K1=153;K2=1053;nit=100;m = 0,0

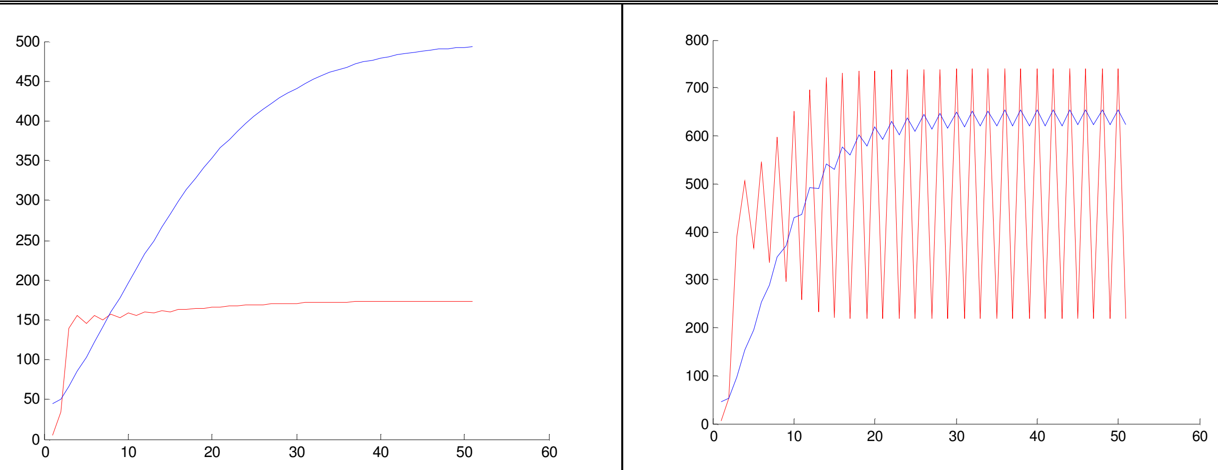
B: Low Heterogeneity: r1=2.37;r2= 0.14;K1=456;K2=804;nit=50;m=0,0



C: Moderate Heterogenity: r1=3.45;r2= 0.14;K1=294;K2=950;nit=50;m=0,0

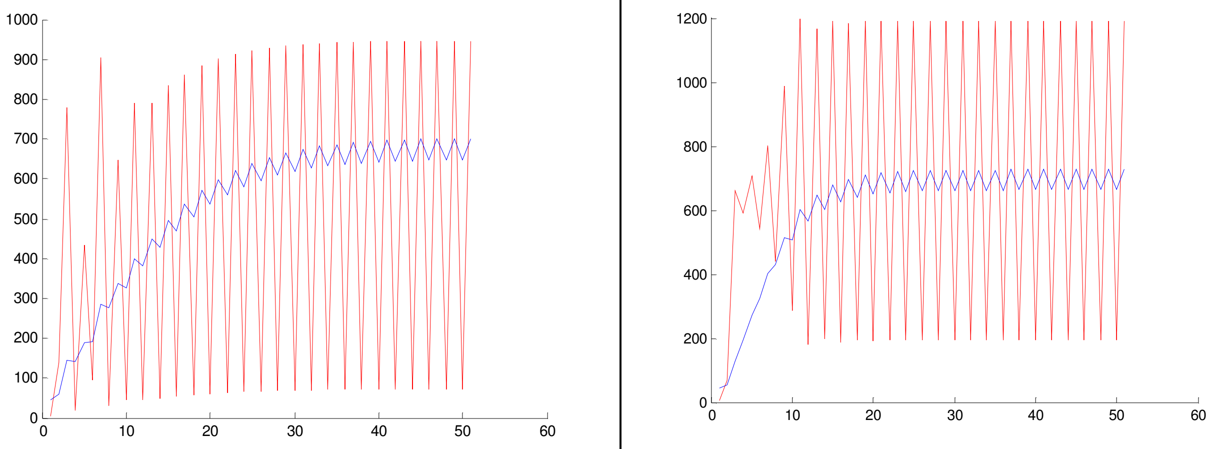
D: No Heterogeneity: r1=2.65;r2= 0.14;K1=654;K2=698;nit=50;m0,0

Fig. 6



A: High Heterogeneity: r1=1.90;r2= 0.14;K1=153;K2=1053;nit=50;m = 0,1

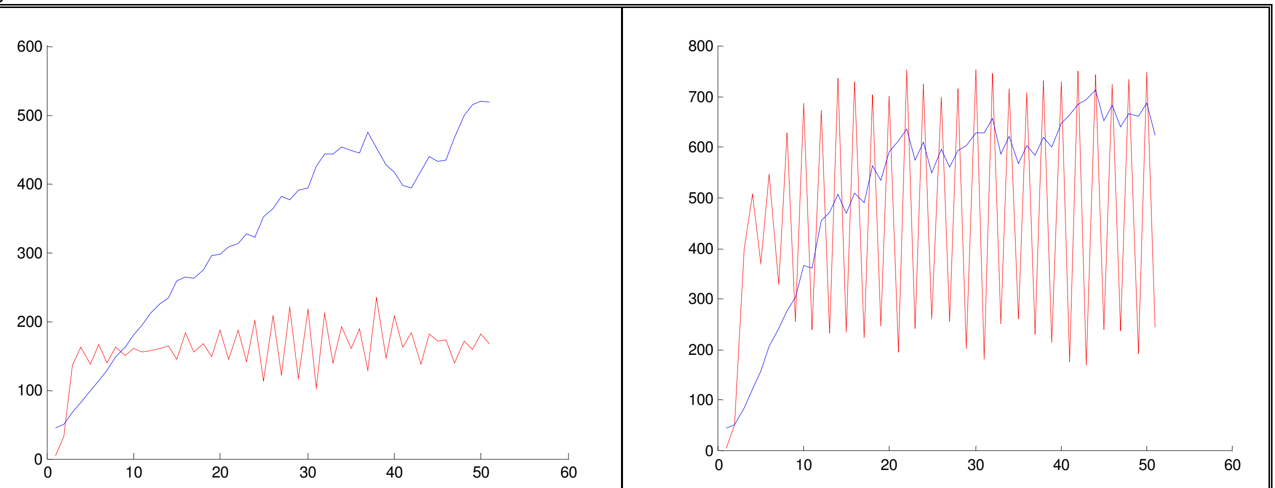
B: Low Heterogeneity: r1=2.37;r2= 0.14;K1=456;K2=804;nit=50;m=0,1



C: Moderate Heterogenity: r1=3.45;r2= 0.14;K1=294;K2=950;nit=50;m=0,1

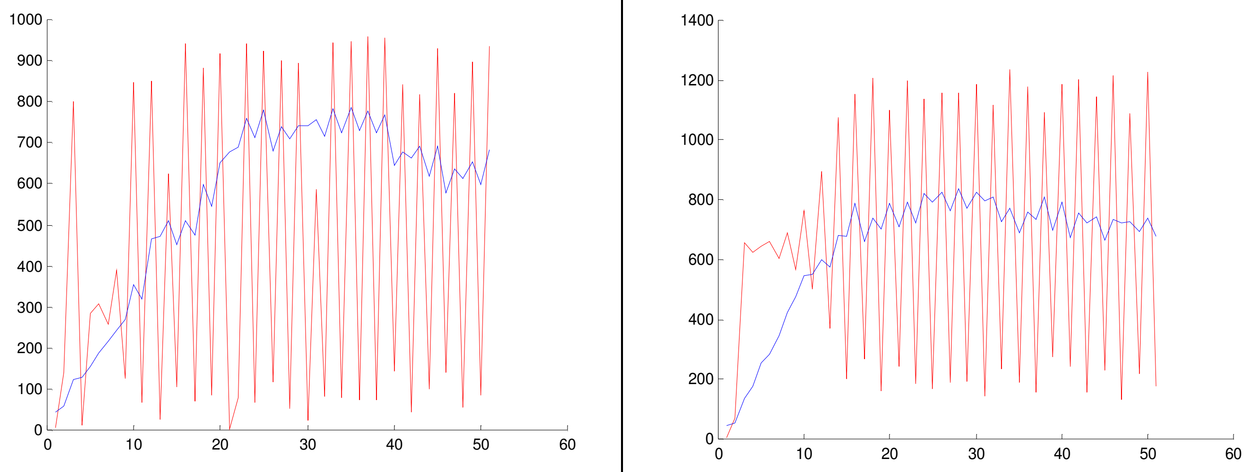
D: No Heterogeneity: r1=2.65;r2= 0.14;K1=654;K2=698;nit=50;m0,1

Fig 7



A: High Heterogeneity: r1=1.90;r2= 0.14;K1=153;K2=1053;nit=50;mmin=0,0;mmax=0,2

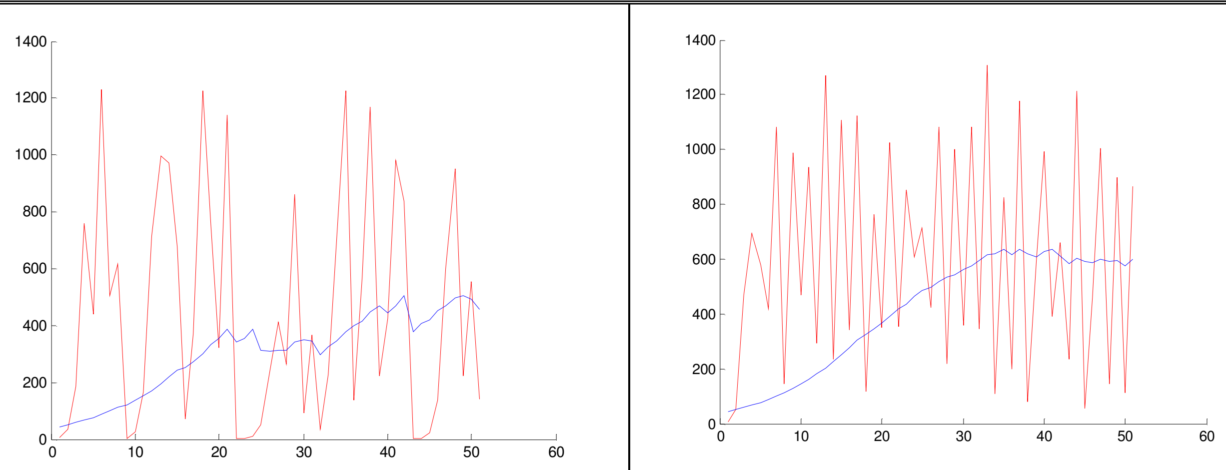
B: Low Heterogeneity: r1=2.37;r2= 0.14;K1=456;K2=804;nit=50;mmin=0,0;mmax= 0,2



C: Moderate Heterogenity: r1=3.45;r2= 0.14;K1=294;K2=950;nit=50;mmin=0,0;mmax=0, 2

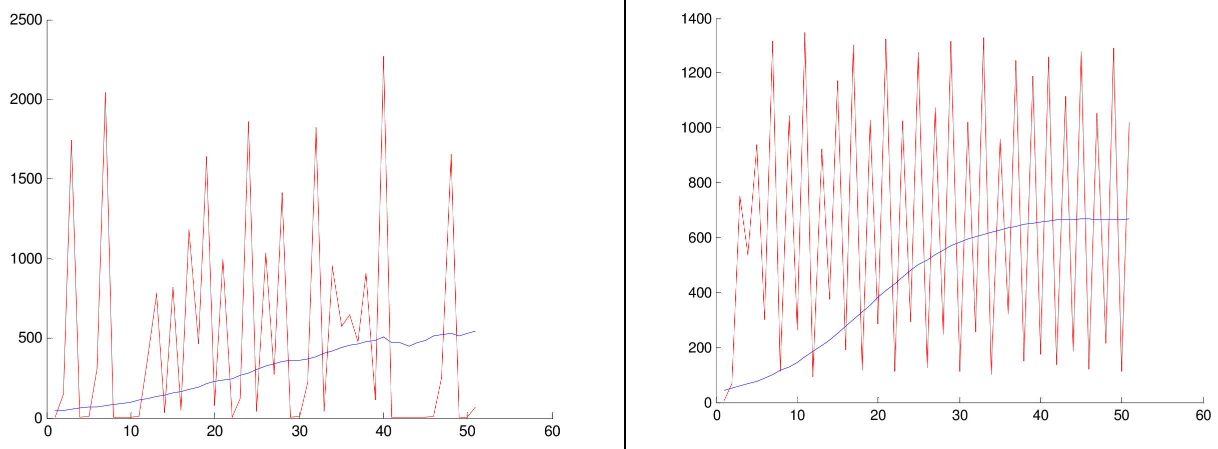
D: No Heterogeneity: r1=2.65;r2= 0.14;K1=654;K2=698;nit=50;mmin=0,0;mmax= 0,2

Fig. 8



A: High Heterogeneity: r1=1.90;r2= 0.14;Kmin=153;Kmax=1053;nit=50;m = 0,0

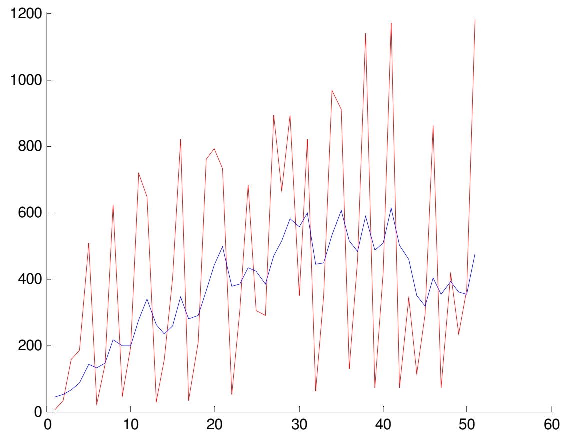
B: Low Heterogeneity: r1=2.37;r2= 0.14;Kmin=456;Kmax=804;nit=50;m=0,0



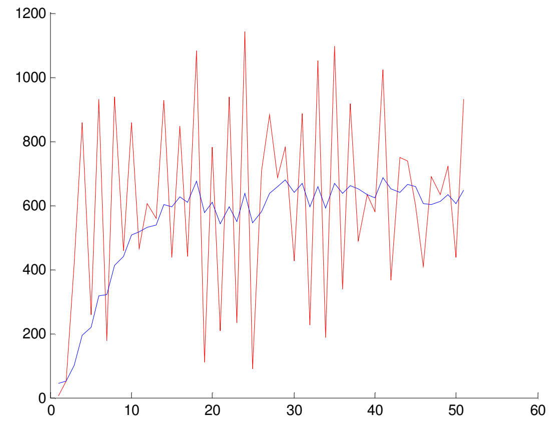
C: Moderate Heterogenity: r1=3.45;r2= 0.14;Kmin=294;Kmax=950;nit=50;m=0,0

D: No Heterogeneity: r1=2.65;r2= 0.14;Kmin=654;Kmax=698;nit=50;m0,0

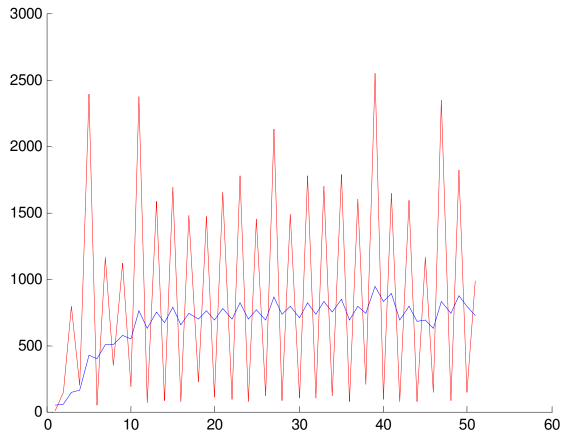
Fig 9



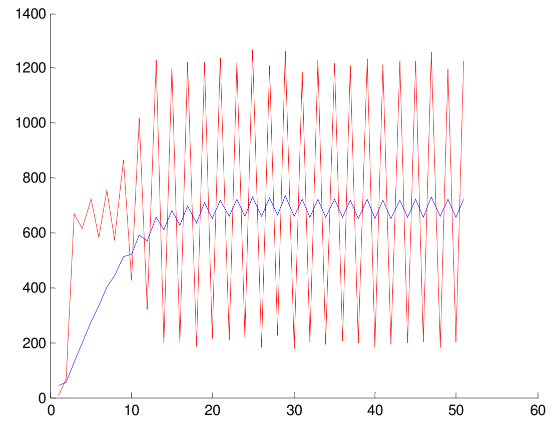
A: High Heterogeneity: r1=1.90;r2= 0.14;Kmin=153;Kmax=1053;nit=50;m = 0,1



B: Low Heterogeneity: r1=2.37;r2= 0.14;Kmin=456;Kmax=804;nit=50;m=0,1



C: Moderate Heterogenity: r1=3.45;r2= 0.14;Kmin=294;Kmax=950;nit=50;m=0,1



D: No Heterogeneity: r1=2.65;r2= 0.14;Kmin=654;Kmax=698;nit=50;m0,1