Changes in the Composition of a Theoretical Freshwater Ecosystem Under Disturbances

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1. Introduction

Direct and indirect effects of the climate change on the terrestrial and oceanic ecosystems could also be observed in the last decades. Researches warn that there are significant changes in phenological, morphological and physiological properties of taxa and changes in spread of species, in frequency of epidemics. But the potential effects of climate change on natural ecosystems and the answers have been given indicated by the living communities which are less than the known of the complex natural ecosystems.

There is a dynamical equilibrium between the climate and ecosystems at natural systems. If the system is affected by anything, then there will be a response to maintain the equilibrium. This process can be a sudden or a gradual effect. Seems, nowadays the unpredictable, sudden changes will be the significant.

Our goal is to analyse the effect of some temperature-climate patterns on the production and community ecological relations in a strongly simplified theoretical model. This elaborated Theoretical Ecosystem Growth Model (TEGM) works as a freshwater algae ecosystem. The novelty of this modelling is characterized by a guild-specific approach at first (where competitive relationships can be manifested); on the other hand the population-dynamic model has been connected with the outputs of global circulation models. So this connection enables us to examine directly the effects of climate change.

Our expectations towards the climate-ecosystem model (TEGM) were as follows:

Depending on the adjusted constant temperature value the species which have optimum reproduction rate in that temperature let be with the largest number of specimens.

Increasing the daily random fluctuation species with narrow adaptation ability are extruded by the species with wide adaptation ability.

The diversity of the ecosystem with the increase of disturbances, to let change it according to the maximum curve, which refers the presence of Intermediate Disturbance Hypothesis.

In our earlier researches the distribution of the algae community of a theoretical freshwater ecosystem is examined by changing the temperature. The temperature was changed according to plan in order to estimate the various effects separately. The examined temperature patterns are as follows: constant temperature (293K, 294K, and 295K), the

temperature changes as a sine function over the year and historical and future climate patterns. (Drégelyi-Kiss & Hufnagel, 2009, 2010, Hufnagel et al., 2010)
In this work it was examined how the theoretical ecosystem growth model (TEGM) reaches the equilibrium in case of three signal such as unit impulse, unit step and unit ramp. The response of the theoretical ecosystem is analysed in case of these signals as disturbances. The daily random fluctuation is also examined on the basis of simulated ±1…±11 K random numbers.

2. Literature overview

The latest IPCC report (Fischlin et al., 2007) points out that a rise of 1.5-2.5 ^{0}C in global average temperature causes relevant changes in the structure and functioning of ecosystems, primarily with negative consequences for the biodiversity and goods and services of the ecological systems.
There are several consequences of the decrease in biodiversity. The most scenic is the decrease in the number of species. Secondly the decrease in genetic diversity has to be mentioned, there are a lot of cases where stands of the frequent species decrease. At the third case the contents of ecosystems change also, the various habitats allow of being and maintenance of creatures between different geological and climatic conditions. This kind of role of ecosystems is less known (Nechay 2002).
A natural system has a dynamic equilibrium between the climate and ecological systems. If the ecosystem is affected, then a response starts in order to keep the equilibrium. The degree of this reaction can be a sudden response by leaps or on the other hand gradual. Some variables such as the phenological properties follow the changing climatic conditions simply; in these cases gradual shifts could be expected (Fitter et al. 2002). In case of sudden responses there is a good example in the maritime tidal zone where the community significantly alters under small-scale temperature increase, which is caused by drastic decrease in the number of dominant predators (Sanford 1999).
According to the forecasts the probability of extreme weather conditions, the effects will be significant for the further occurrence of sudden effects. There are some quick extreme events and the given sudden responses behind the events which seemed to have experienced gradual changes (Easterling et al., 2000). In case of climate change this is not about the shift of the system being in equilibrium, but the succession could break or unhoped-for steps occur. In a mediterranean scrub regenerated after a fire the number of species does not change under artificial drought-treating while the number of species increases in the control parcel fluently (Penuelas et al., 2007). The reaction of the run-down, degrading and regenerated communities for the climate change differs significantly from the reaction of natural ecosystems. These processes are important because there are much more of these areas like natural.
The interpretation of the phenomena of disturbance has been changed with the development of the science. Earlier it is stated that the disturbance is a deviation from the equilibrium circumstances, nowadays it is as important factor to maintain the ecological integrity of the ecosystems. There are several definitions for the disturbance. (Laska, 2001) According to Grime (1973) the disturbance is such an event where the amount of the biomass decreases. It could also be stated that the disturbance differentiates in time, disturbs the life of a community, population or ecosystem, and changes the usability of the resources, environmental factors (Pickett & Parker, 1997). Summarizing it could be said that the

disturbance does not mean decrease in biomass in all cases, this is a phenomenon well-bordered in time which results dynamic patch-pattern.
The type and the intensity of the disturbance affect the succession processes therefore seconder succession starts mostly (flood, hurricane, natural catastrophes). This is because certain elements of the original community could maintain in contrast with primer successions (such as volcano explosion) (Dobson et al., 1997). The spread and the amount of the disturbance could be very different which is affected by the heterogeneity of the environment. It is stated that the processes are usually unique and related to a given area (Pickett & Parker, 1997).
After the perturbation there is usually fast succession, where the surviving species and the members of the original community participate. Complex relations are developed to adapt to their new environment, biotic and abiotic factors (MacMahon, 1998). The rhythm of the changes slows down, and then the habitat gets into quasi equilibrium through continuous adaptation.
According to the Gause's Law of competitive exclusion (Gause, 1934; Hardin, 1960) the number of the limiting factors restrict the number of species coexisted which controls the composition of the communities and populations. The competition could not be maintained in the long run. There could be three types of processes, such as the more vulnerable species disappear, adapt or drift toward other environmental factors. There is stable state if every species are restricted by different environmental factors. If more species make a competition for the same resources, then the genre with the best adaptability will exclude the others, so the succession process tends to a climax state with small diversity.
The limiting resources are different in case of various living beings. The increase of the plants is restricted by nitrogen, phosphorus, soil humidity (in case of terrestrial plants), sunlight and other biologically important elements. For example, in case of phytoplankton in temperate zone it is rare that there is more than three restriction parameter at the same time. So the phytoplankton community has to tend to his equilibrium with 1-3 dominant species during the succession process by competitive exclusion principle. But it is observed that the phytoplankton communities have much more species than expected. This phenomenon is known as "plankton paradox". It could be explained that the boundary conditions (e.g. continuous changes in environment, sunlight, turbulence) change faster than the competitive exclusion may occur. (Hutchinson, 1957). Summarizing the theory and the observations do not agree with each other. (Padisák, 1998)
Some researchers state that the ecological and environmental factors are in continuous interaction, the habitats of plankton do not reach the equilibrium state where only one genre is dominant. (Scheffer, 2006).
There are several hypotheses where the relationship between the disturbance and diversity are examined (Magura et al., 2006). The most spread theory is the Intermediate Disturbance Hypothesis (IDH). It is stated that the diversity increases in case of small or moderate disturbances (Connell, 1978; Grime, 1973). According to Increasing Disturbance Theory the smallest diversity exists in strongly disturbed areas (Gray, 1989). The Habitat-Specialist Hypothesis states that the diversity of living beings of original habitats decreases with reaching the strongly disturbed areas (Magura et al., 2004).
The species richness in tropical forests as well as that of the atolls is unsurpassable, and the question arises why the theory of competitive exclusion does not prevail here. Trees often fall and perish in tropical rainforests due to storms and landslide, and corals often perish as a result of freshwater circulation and predation. It can be said with good reason that

disturbances of various quality and intensity appear several times in the life of the above mentioned communities, therefore these communities cannot reach the state of equilibrium. The Intermediate Disturbance Hypothesis (IDH) (Connell, 1978) is based on this observation and states the following:
In case of no disturbance the number of the surviving species decreases to minimum due to competitive exclusion.
In case of large disturbance only pioneers are able to grow after the specific disturbance events.
If the frequency and the intensity of the disturbance are medium, there is a bigger chance to affect the community.
There are some great examples of IDH in the case of phytoplankton communities in natural waters (Haffner et al., 1980; Sommer 1995; Viner & Kemp, 1983, Padisák 1998, Olrik & Nauwerck, 1993). Nowadays it is accepted that diversity is the biggest in the second and the third generations after the disturbance event (Reynolds, 2006).

3. Material and methods

3.1 The elaborated Theoretical Ecosystem Growth Model (TEGM)

An algae community consisting of 33 species in a freshwater ecosystem was modelled (TEGM; Drégelyi-Kiss & Hufnagel, 2009, 2010). During the examinations the behaviour of a theoretical ecosystem was studied by changing the temperature variously. Several author draw attention to the temperature as main control factor in case of freshwater ecosystems (Christou & Moraitou-Apostolopoulou, 1995; Iguchi 2004; Dippner et al. 2000, Vadadi-Fülöp et al., 2009).
The conceptual diagram of the TEGM model (Fig. 1) describes the mathematical calculations during the modelling process (Sipkay et al., 2010). The model has two important input parameters. One is the various reproductive functions; the other is functions of the temperature patterns.
Rivalry begins among the species with the change of temperature. In every temperature interval, there are dominant species which win the competition. The increase of the population is not infinite because of the restrictive function of the model. The ecosystem reaches a dynamic equilibrium state for an input temperature. In the course of this equilibrium the following output parameters are examined: the dominant species and their numbers, the value of use of resources, the diversity of the ecosystem and the duration of reaching the equilibrium.
Algae species are characterised by the temperature interval in which they are able to reproduce. This reproductive feature depends on their temperature sensitivity. There are four types of species based on their sensitivity: super generalists (SG0, SG1), generalists (G1-G5), transitional species (T1-T9) and specialists (S1-S14). The temperature-optimum curve originates from the normal (Gaussian) distribution, where the expected value is the temperature optimum (Drégelyi-Kiss & Hufnagel, 2010). The used temperature range for the optimum values is from 277K to 301K, and the lay of the optimum curves is symmetrical in this range.
The restrictive value of reaching the sunlight (K_k) was set to 10^7 value in the first phase of the simulation studies (TEGMa model), in the second phase the intensity of the sunlight changing during a year was considered (TEGMb model):

$$K_k = d_1 \cdot \sin\left(d_2 \cdot k + d_3\right) + d_4 + \varepsilon \qquad (1)$$

where d_1=4950000, d_2=0,0172, d_3=1,4045, d_4=5049998, ε: has uniform distribution in the interval of (-50000,50000).
The constant values of the K_j restrictive function is set in a way where the period of the function is 365.25, the maximum place is on 23rd June and the minimum place is on 22nd December. (These are the most and the least sunny days.)

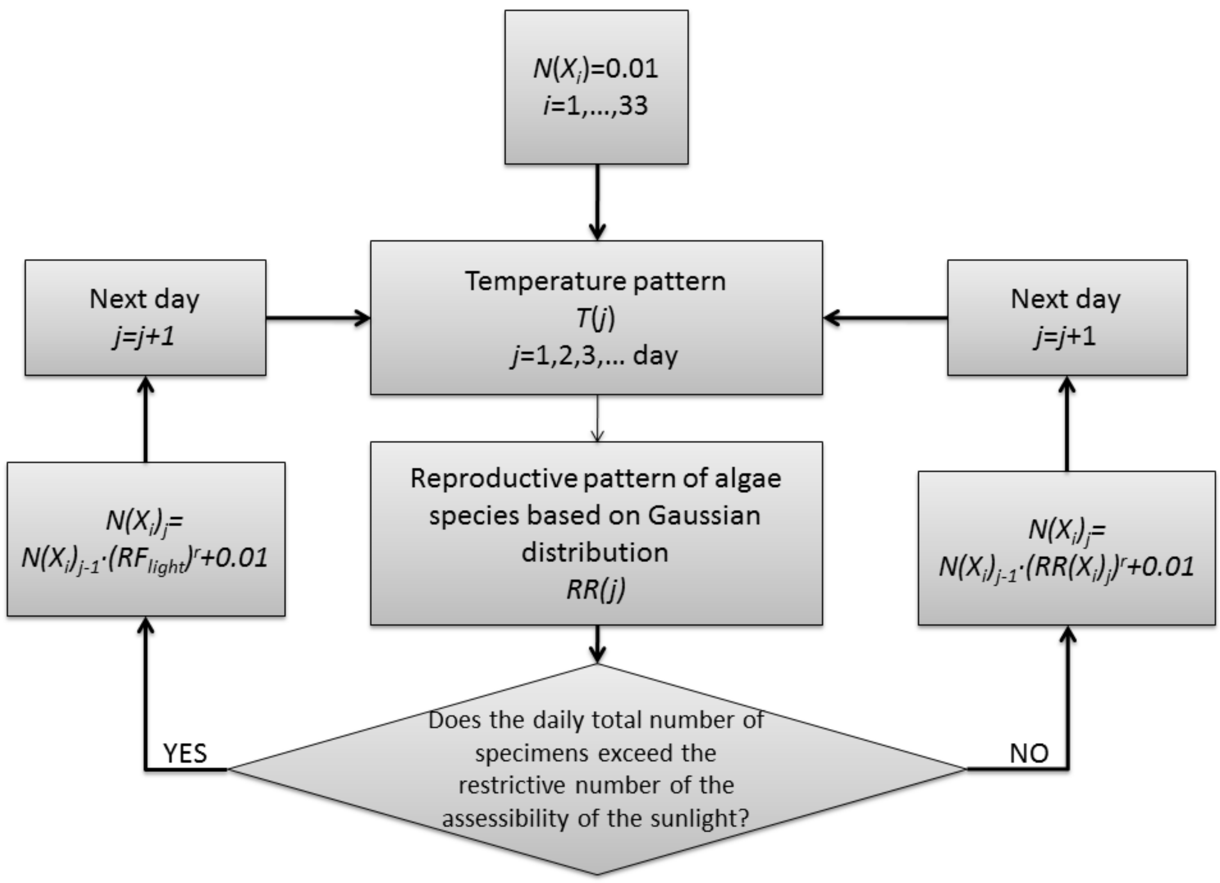

Fig. 1. Conceptual diagram of the TEGM model (RR: reproduction rate, RF: restriction function related to the accessibility of the sunlight, N(Xi): the number of the ith algae species, r: velocity parameter)

3.2 Special functions

The dynamic state of a system depends on the stationary state before the disturbance and the type and amount of the perturbation. Under special signals the composition of the theoretical ecosystem changes and new equilibrium state evolves. It is important to examine the way of reaching the new balance regarding the stability of the system.
The reaching of the equilibrium state of the theoretical ecosystem model was examined by three special functions. One of them is the Dirac delta function, which can be modelled as a large change in temperature lasted small time. The other is the step function which modelling the remaining significant change in temperature. The third one represents the slowly increasing temperature day by day. (Pokorádi, 2008)
Dirac-delta means an impulse, which has zero value always except for one moment, when it takes infinite large value:

$$\int_{-\infty}^{+\infty} \delta(t)dt = 1 \tag{2}$$

The unit impulse-like signal is modelled by an increase in the temperature in a day which throws the ecosystem off balance. The theoretical ecosystem is in equilibrium at constant temperature (293K, 294K and 295K), then on the 1001^{th} day of the simulation the temperature has a sudden higher value, and the next day of the simulation the temperature pattern sets back the constant temperature which had before the disturbance. The magnitude of the temperature impulse is between 1K and 100K values.
The unit step function (Heaviside function) could be understand as "power-on" phenomena:

$$1(t) = \begin{cases} 0, & t < 0 \\ 1, & t > 0 \end{cases} \tag{3}$$

During the unit step-like examination the value of constant temperature is changed on the 1001^{th} day of the simulation with 1K or 2K temperature up or down.
The unit ramp function could be described by the following equation:

$$t1(t) = \begin{cases} 0, & t < 0 \\ t, & t > 0 \end{cases} \tag{4}$$

The unit ramp-like study is modelled as the temperature increases slowly with consecutive days through 10 years. The following cases are examined:
T = 294 K – 294.365 K (the gradient of temperature is 0.0001 K/day)
T = 294 K – 297.652 K (the gradient of temperature is 0.001 K/day)
T = 268 K – 286.26 K (the gradient of temperature is 0.005 K/day)
T = 268 K – 304.52 K (the gradient of temperature is 0.01 K/day)
It is important to study the effects of daily temperature fluctuations. This was modelled as the disturbance has a uniform distribution (between ±1K… ±11K). During the simulation the given random fluctuation on the constant and increasing temperature pattern was analysed.

4. Results

4.1 Examination of impulse unit

The theoretical ecosystem is in equilibrium at constant temperature (293K, 294K and 295K), then on the 1001^{th} day of the simulation the temperature has a sudden higher value, and the next day of the simulation the temperature pattern sets back the constant temperature which had before the disturbance. The magnitude of the temperature impulse is between 1K and 100K values.
Making the impulse unit-like simulations with TEGMa model the time of reaching the new equilibrium state depends on the magnitude of the given temperature impulse (1-100K) (Table 1). The first row of the table shows the duration of reaching the equilibrium at the beginning of the simulation. This time is 32 days and 34 days in case of faster ecosystem depending on the used constant temperature pattern. The ecosystem which has smaller reproducibility (r=0.1) the time is 151 days and 187 days, respectively.

T_{impulse}	*r*=1			*r*=0.1		
	T=293K	*T*=294K	*T*=295K	*T*=293K	*T*=294K	*T*=295K
at the beginning	32 days	34 days	32 days	151 days	187 days	151 days
1 K	0 day	21 days	0 day	0 day	36 days	0 day
3 K	23 days	21 days	24 days	51 days	50 days	51 days
5 K	28 days	18 days	22 days	62 days	59 days	62 days
10 K	32 days	31 days	32 days	88 days	82 days	89 days
15 K	32 days	34 days	32 days	114 days	103 days	132 days
20 K	32 days	34 days	32 days	136 days	131 days	151 days
30 K	32 days	34 days	32 days	151 days	183 days	151 days
100 K	32 days	34 days	32 days	151 days	187 days	151 days

Table 1. The time of reaching the equilibrium at various temperatures at the beginning and on the effect of the $T_{impulse}$ temperature on the 1001th day of the simulation study (different velocity parameters, TEGMa model)There are two groups according to the setting temperature.

The simulations made at 293K and 295K with r=1 parameter are similar, the duration of reaching the equilibrium is the longest in case of 10K or larger temperature impulse. In case of slower ecosystem 20K and 30K impulse is essential to get the desired time. The other group is related to the simulations made at 294K. During these simulations there must be more time to reach the new evolved equilibrium state in every case.

On the effect of small temperature impulse there are not changes in the composition of the theoretical ecosystem. In case of moderate impulses (3K, 5K, 10K, 15K) it is stated that the distribution of the species are not the same before and after the interference. At 293K and 295K the transient (T7) extrudes the specialist (S13 and S14, respectively), and the number of specimens of generalist (G4) and supergeneralist (SG1) increase. For example at 293K temperature in case of 5K impulse on the 1001th day of the simulation with TEGMb, r=1, it requires almost 30 years to reach the equilibrium state had been before the 1000th day (Figure 2).

There are similar patterns in the change of the composition of the theoretical ecosystem at 294 K temperature, also. If the system is affected by 3K impulse in case of r=1, and 3K or 5K impulse in case of r=0.1, respectively, then the specialist (S14) which has higher optimum temperature for the reproduction extrudes the other one (S13), while they share the resources on a fifty-fifty way before the interference. To take into account that the composition of the theoretical ecosystem is totally symmetric the temperature impulses are examined toward the lower temperature value (i.e. negative impulses), also. In case of -3K temperature impulse the S13 genre is the dominant. In case of faster ecosystem on the effect of 5K temperature impulse and with r=0.1 and 10K impulse parameters the T7 transient genre wins the competition, the productivity of the generalist increases.

Comparing the faster and the slower ecosystems it is stated that the change in the composition of the equilibrium state is similar, in case of *r*=1 and 3K impulse; and in case of *r*=0.1 and 10 K temperature impulse. If 15 K or more impulse is given in case of faster ecosystem, then the composition of the species are the same before and after the interference. (Fig. 3-4)

It is important to study how the diversity and the adaptability work out in the course of smaller impulses. The distribution of species and the diversity of the theoretical ecosystem

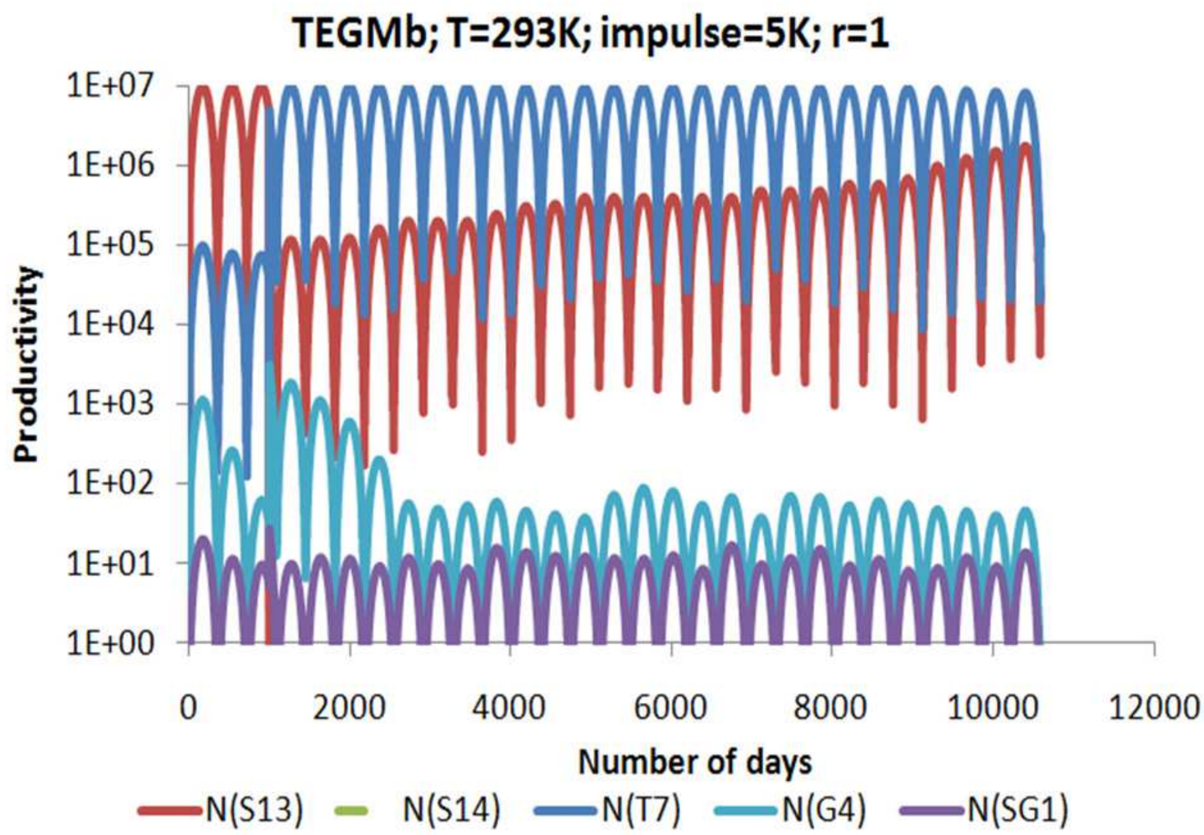

Fig. 1. The results of TEGMb simulation in case of the given 5K temperature impulse with r=1 velocity parameter

strongly depend on the setting value of the velocity parameter. The diversity of the faster ecosystem increases with smaller temperature impulses (3K, 5K) during TEGMa simulation. The diversity continuously increases during the 30 years of simulation in case of 5 K impulse and decreases in case of 3 K impulse using the TEGMb model. There are an increase in the diversity value in the course of larger impulses (10K, 15K, and 20K) for the slower ecosystem in both, TEGMa and TEGMb cases. The evolving time of the new equilibrium state is the slower where the simulation has *r*=0.1, *T*=294 parameters.
Summarizing it is stated that the new equilibrium state evolved on the effects of small and medium temperature impulses differs significantly from the state before the interference.

4.2 Examination of step unit

During the unit step-like examination the value of constant temperature is changed on the 1001th day of the simulation with 1K or 2K temperature up or down.
The value of the constant temperature function (293K, 294K, and 295K) is changed at the 1001th day of the simulation. At 293 K temperature the conditions are suited for the S13, K7, G4 and SG1 species optimum reproducibility. In this temperature the composition does not change in case of 1K temperature step. (Table 2)

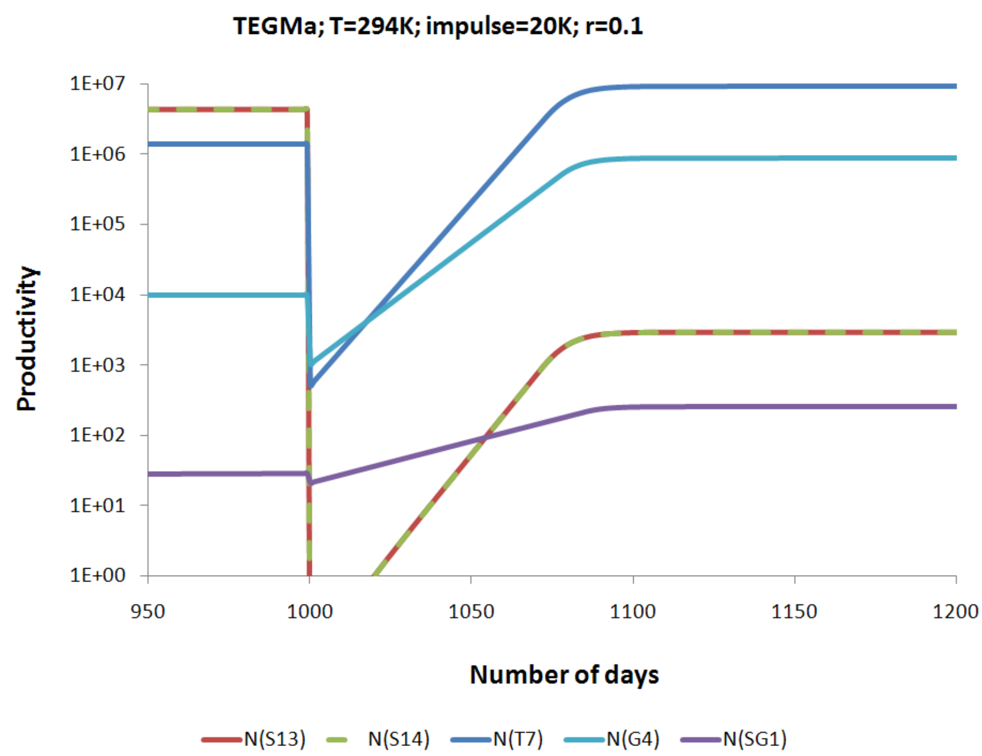

Fig. 3. The effect of 20 K temperature impulse on the 1001th day of the simulation (in case of *r*=0.1, TEGMa model, T=294K)

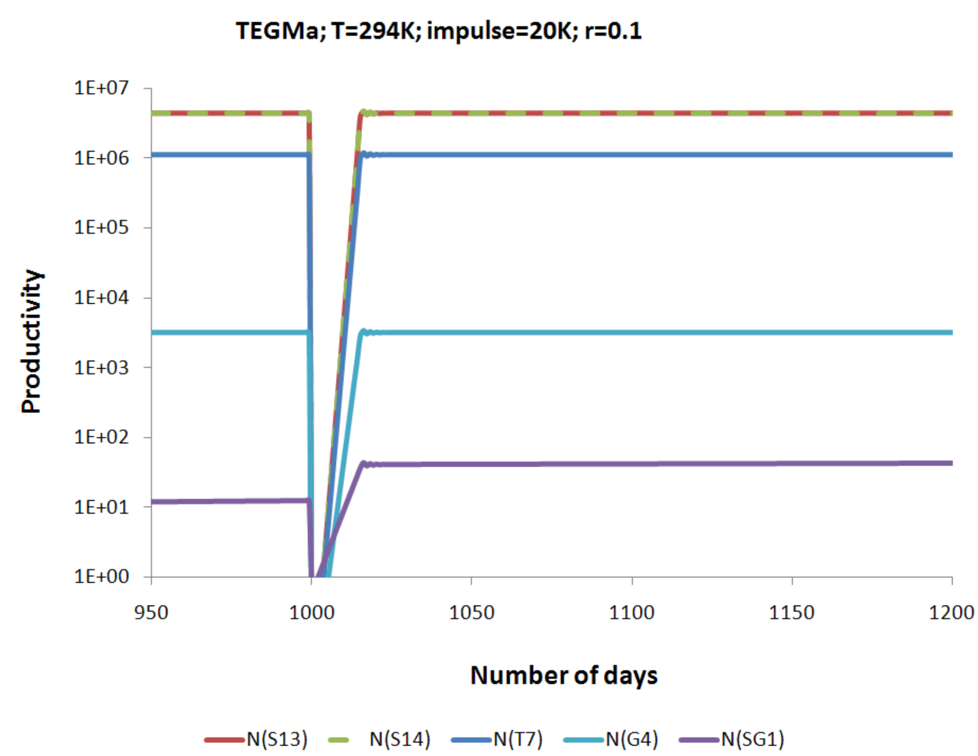

Fig. 4. The effect of 20 K temperature impulse on the 1001th day of the simulation (in case of *r*=1, TEGMa model, T=294K)

r	T1	T2	Duration of reaching the equilibrium state	Speciality after the unit step
1	293	294	-	the composition does not change
0.1	293	294	-	the composition does not change
1	294	293	20 days (and S14 disappears)	S14 disappears, S13 increases
0.1	294	293	200 days (and S14 disappears)	S14 disappears, S13 increases
1	293	295	10 days (S13 disappears in 20 days)	T7 win the competition, not the specialist as could be expected
0.1	293	295	80 days (S13 disappears after 200 days)	
1	295	293	10 days (S14 disappears in 20 days)	
0.1	295	293	80 days (S14 disappears after 200 days)	

Table 2. Examination of T1 →T2 unit step in case of ecosystems having different velocity parameters (TEGMa model)

On the effect of +1 K temperature ramp at 294 K constant temperature the composition of equilibrium does not change significantly in case of both the slower or the faster ecosystem (S14 appears with 10 number of specimens). In case of 294K→293K change the S13 specialist win the competition in 20 days, as expected.
In can be seen in Figure 5 that the productivity decreases strongly in case of 2K change. The slower ecosystem reaches the equilibrium later than the faster type. There is no noticeable change in productivity in cases of 1K temperature step.

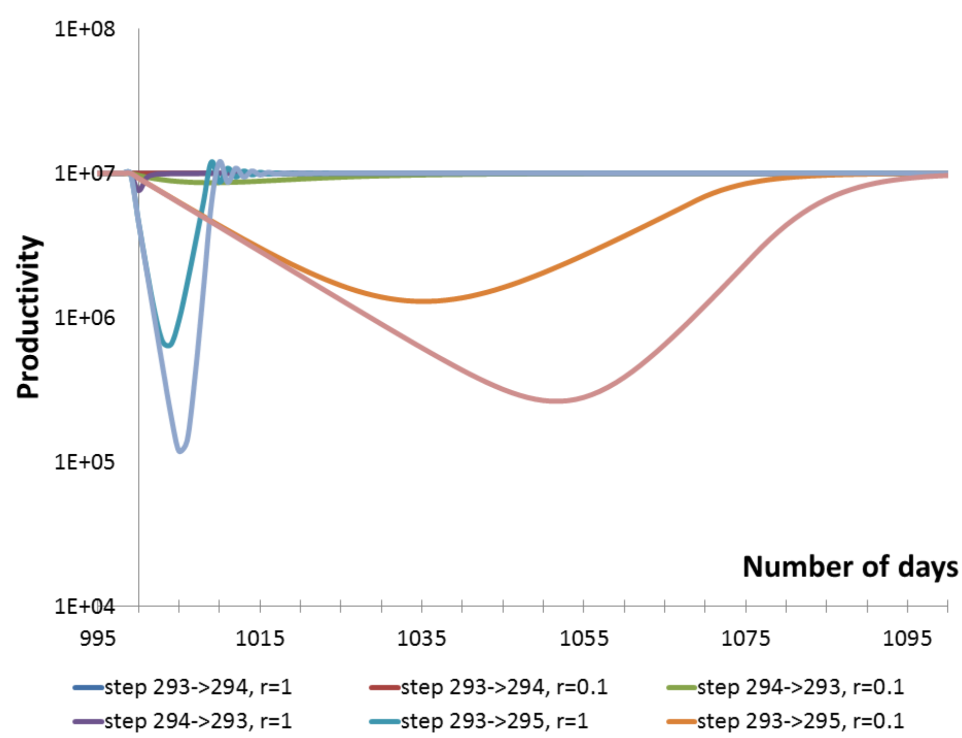

Fig. 5. The number of days of simulation versus the productivity of the theoretical ecosystem due to temperature step signal (TEGMa)

Observing the Shannon diversity values of the ecosystem it is stated (Figure 6) that the diversity value, which belongs to the new equilibrium state, moves through a local maximum value depending on the temperature.
Summarizing the effect of temperature step it is stated that the composition of the ecosystem being equilibrium at base temperature determines, what kind of the diversity of the ecosystem will be.

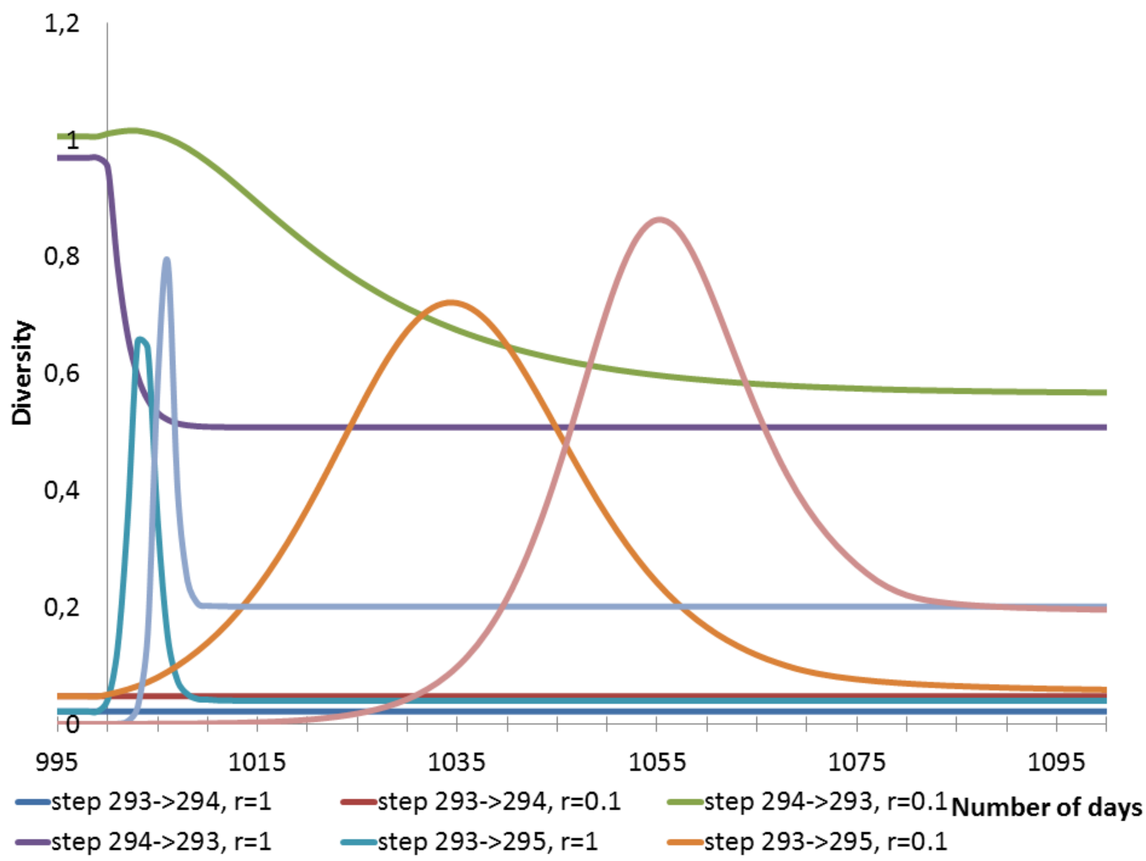

Fig. 6. Diversity of the theoretical ecosystem versus the number of days of simulation due to temperature step (TEGMa)

4.3 Examination of ramp temperature function

During ramp temperature function the value was daily increased from 268K continuously with various amounts (0.0001K…0.01K). It can be seen the appearance of some species depending on gradient. The local maximum values of the diversity exist where the specialist and the generalists have just exchanged with each other. (Figure 7-8.)

4.4 Daily random fluctuation

The daily random fluctuation was modelled as the disturbance has a uniform distribution (between ±1K… ±11K). In case of constant temperature pattern the results of the simulation study can be seen in Fig. 8, which is the part of the examinations where the random fluctuations were changed until ± 11K. The number of specimens in the community is

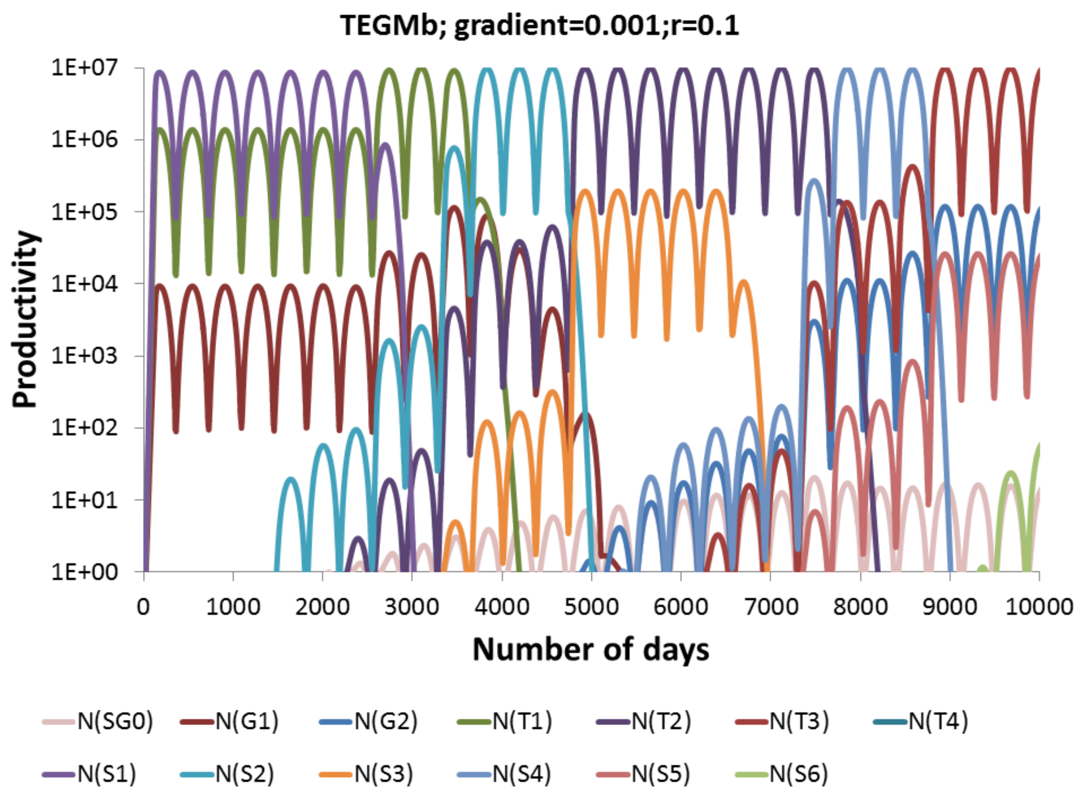

Fig. 7. The productivity results of TEGMb simulation with r=0.1 parameter in case of increasing temperature pattern (gradient=0.001K/day, T_0=268K)

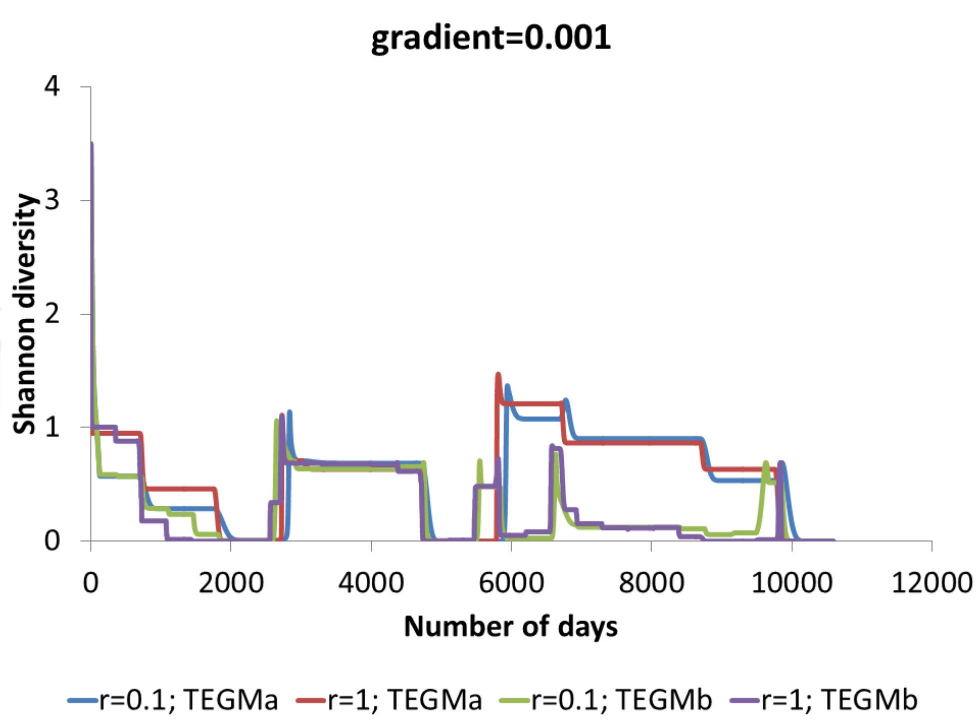

Fig. 8. The daily diversity value with TEGMb simulation and r=0.1 parameter in case of increasing temperature pattern (gradient=0.001K/day, T_0=268K)

permanent and maximum until the daily random fluctuation values are between 0 and ±2K. Significant decrease in the number of specimens depends on the velocity factor of the ecosystem which has faster reproductive ability shows lower local maximum values than the slower system in the experiments. The degree of the diversity is greater in the case of r=0.1 velocity factor than in the case of the faster system. If there is no disturbance, the largest diversity can be presented found at 294 K for both speed values. If the fluctuation is between ± 6K and ± 9K, the diversity values are nearly equally low. In case of the biggest variation (± 11K) the degree of the diversity increases strongly.

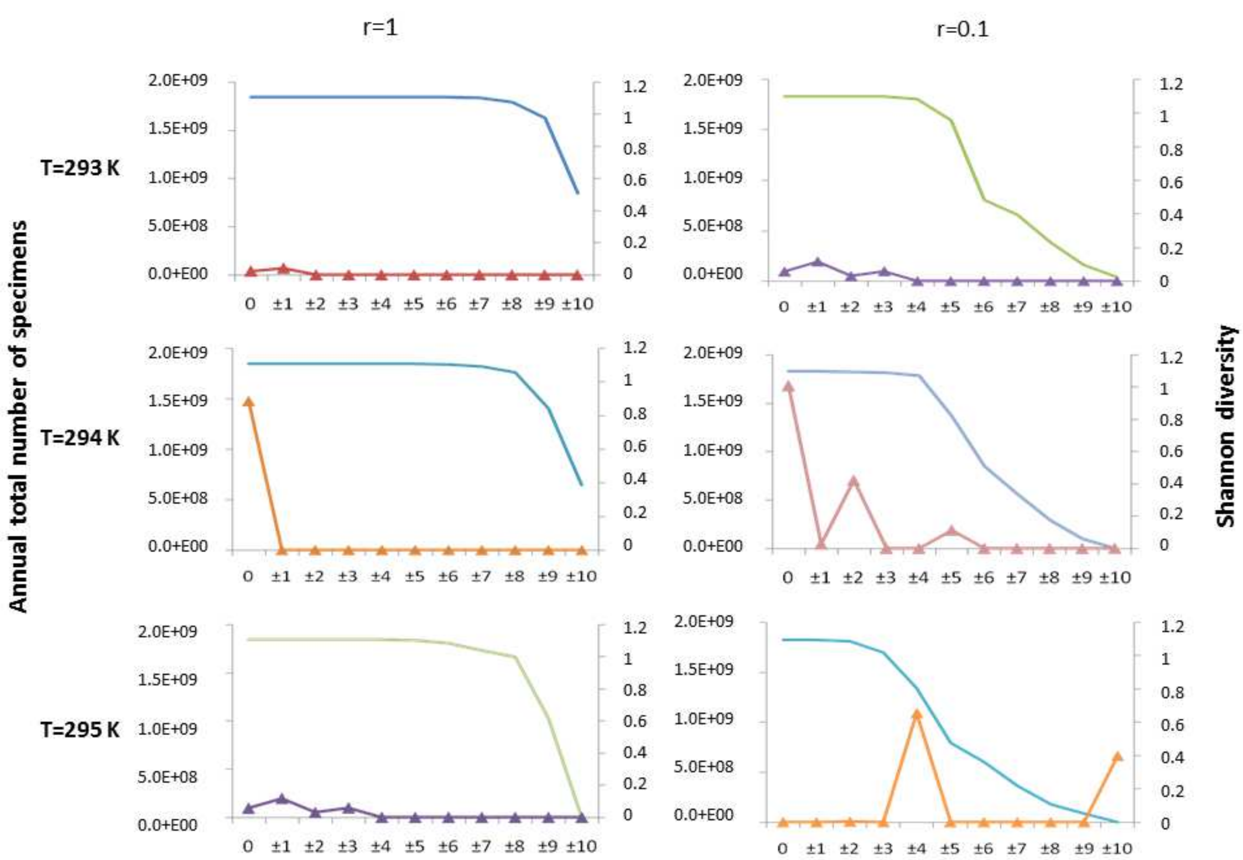

Fig. 9. The change in productivity and diversity value of the theoretical ecosystem in the function of daily random fluctuation in constant temperature environment with TEGMb model (The signed plots show the diversity values.)

At linear increasing temperature pattern the value of the use of resources does not decrease to zero value in case or larger gradients (0.005K/day and 0.01 K/day) and large random daily fluctuation (±7K). This decrease happens in case of smaller gradients. This is because the supergeneralists are less sensitive for the daily random fluctuation. This does not appear in case of slower ecosystems. (Figure 10)

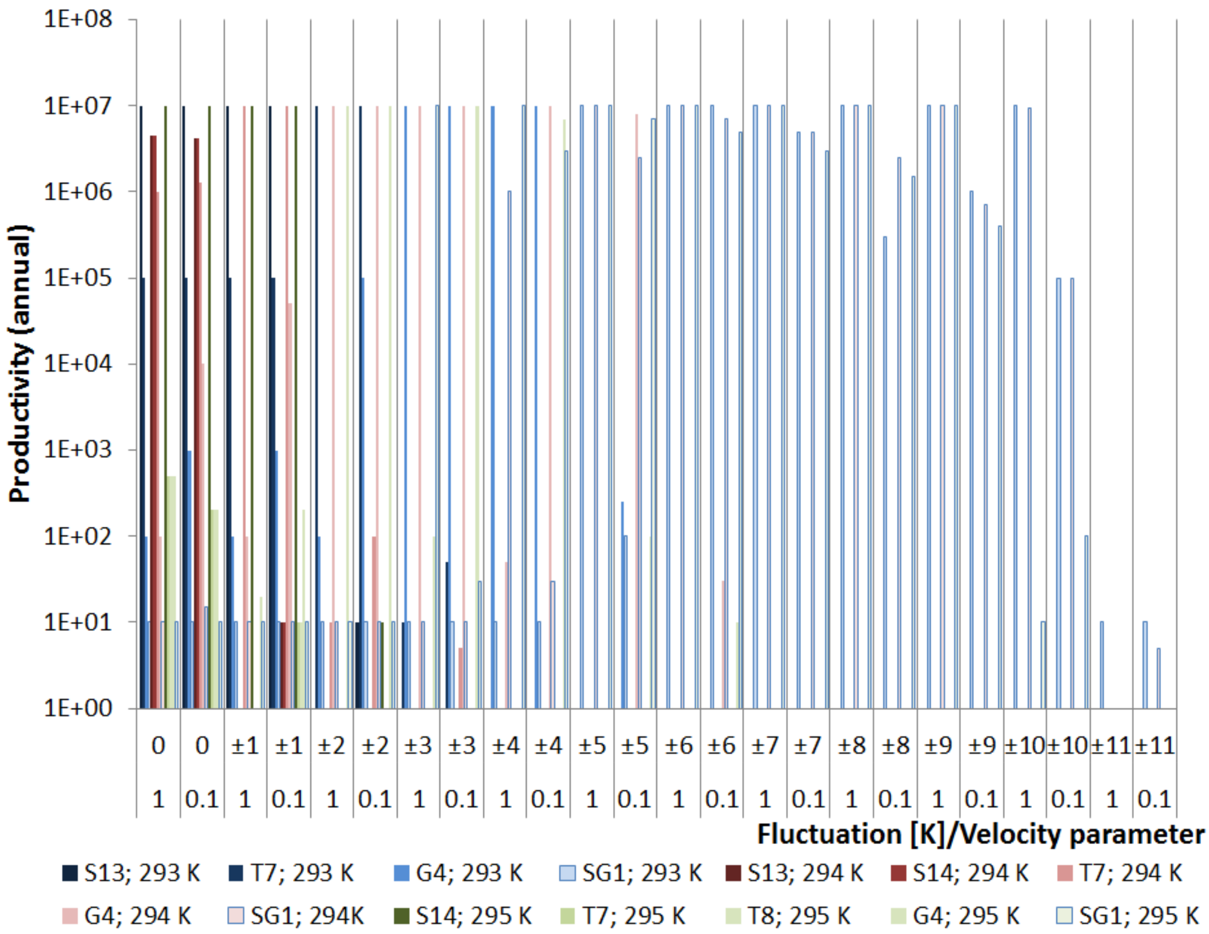

Fig. 10. Annual maximum number of specimens of the species on constant temperature with different velocity parameters (logarithmic representation) (Drégelyi-Kiss & Hufnagel, 2010)

5. Conclusion

The theoretical freshwater algae community reacts on the effect of temperature impulse in different ways depending on the magnitude of the impulse (1K-100K). If the ecosystem is affected by small or medium temperature impulses, then the composition of the evolving equilibrium state is differs from what could be expected. 1K impulse in temperature does not change the composition of the ecosystem in cases of 293K and 295K base-temperatures. So the specialists, as S13 and S14 are the strongest species during the competition. In 294K in case of 1K impulse the S14 specialist extruded the other species in the competition. In 294 K temperature (which is not an optimum value for the reproduction in either species) the given small or medium impulse results that the specialist wins the competition which has optimum closer to the temperature evolved during the impulse. Under small or medium temperature impulse the evolved new equilibrium differs significantly from the status before.

If the ecosystem being in equilibrium state at constant temperature is affected by 2K temperature step the productivity of specialists decreases fast, and the transient genre becomes the winner during the competition. In case of TEGMa the balance exists through 25 years but there is a slow exchange in species during the years under TEGMb simulations. This point out that the generalists, which are able to spread well, could exploit the changing habitat conditions (Dukes & Mooney, 1999). To analyse the results of the unit step function it is found that the composition of the ecosystem determines the diversity of the evolving new balance.

If the temperature changes linearly and slowly in time, then there is a competition between the specialists and the transient species during the days of simulation. The largest diversity values can be observed when the species has just exchanged with each other. Such a thing was observed by Sanford (1999), who examined the ecological system of starfish and shellfish with in-field and lab experiments. To analyse the results of the unit step function it is found that the composition of the ecosystem determines the diversity of the evolving new balance.

Increasing the daily fluctuation the community tries to adapt to its environment and many genre compete for the environmental elements with large number of specimens. In case of large noise the diversity is large and the annual total number of specimens is low, because a few genres could adapt to the environmental conditions. It is stated that the specialists reproducing in narrow temperature interval are dominant species in case of constant or slowly changing temperature pattern but these species disappear under small fluctuation in the temperature. As a result it is found, that species with narrow adaptation ability disappear, species with wide adaptation ability become dominant and the biodiversity decreases. The results of the simulations show that the way towards the equilibrium is different in cases of various disturbances. The composition of the ecosystem in equilibrium at a given time affects the evolved new equilibrium under disturbances.

The strategic model, so-called "TEGM" was adapted to field data (tactical model). The "tactical model" is a simulation model fitted to the observed temperature data set (Sipkay et al. 2009). The tactical models could be beneficial if the general functioning of ecosystems is in the focus.

6. Acknowledgement

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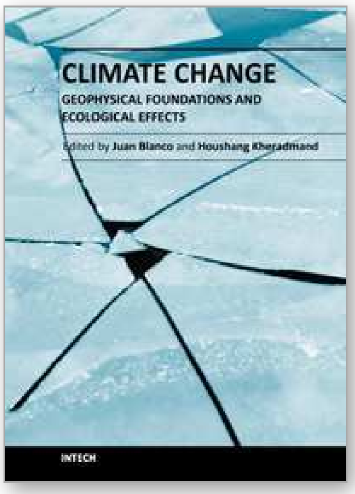

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