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Biodiversity measures revisited

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ABSTRACT

A few commonly used biodiversity measures such as the biodiversity index, the Kullback information measure and exergy are considered in order to check their capability to trace (and, potentially, to predict) negative changes in the community structure. We apply these measures to a model community of three competitive species and show that, in spite of the fact that all the species exhibit dynamically similar behavior, their contribution to the corresponding changes in the biodiversity measures is remarkably asymmetrical. While for two species the changes in their population sizes are strongly correlated/associated with the changes in the biodiversity measures, the information about the third species is virtually lost. In order to loosen the deterministic feedbacks between the species, we then include environmental noise and show that the results stay essentially the same.

1. Introduction

Loss of biodiversity in various ecosystems all over the world is currently considered as a major challenge for contemporary ecology (Tilman and Lehman, 2001; Thomas et al., 2004; Faith, 2005). There are several aspects of this problem. One of them is given by necessity to recognize the main threats for communities functioning and reasons for biodiversity loss; examples of such threats are given by biological invasions (Drake et al., 1989) and habitat fragmentation (Tilman et al., 1994). Other aspects are identification of effective environmental protection strategies and development of adequate approaches to environment rehabilitation. These and similar issues are apparently based on the assumption that sufficient and reliable information is available regarding the state of the community and its biodiversity. In its turn, it immediately brings forward the problems of effective monitoring and data assimilation in terms of appropriate biodiversity measures.

While considerable advances have been made in understanding the main mechanisms of biodiversity loss, the progress in biodiversity quantification has been much more meagre. There have been only a few different approaches to this issue. The first one is based on a direct counting of the species that go extinct as a result of ecosystem disturbances. The proportion that the extinct species makes of the total number of species in a given community is then used as a measure of biodiversity loss. Although proven to be useful in theoretical studies (cf. Tilman, 1994; Tilman et al., 1994; Loehle and Li, 1996; Solé et al., 2004), this approach leaves outside of its scope important information about species abundance. Being based on the ‘‘matter-of-fact’’ information whether a particular species is present or not, it does not allow for situations when a species is actually on the brink of extinction

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due to its small population size. Therefore, it does not make possible to reveal the tendency in the community evolution and in the corresponding biodiversity changes. Meanwhile, it seems obvious that adequate biodiversity measures must be able not only to diagnose negative changes but to do it at an early stage in order to give enough time for decision-making: once a species has gone extinct, it is too late to talk about its protection!

Alternatively, biodiversity measures are based on the idea that there must exist an optimal order in the biomass distribution between the species in a given community (Magurran, 1988). Although criteria of this optimality are not finally clear, it is often assumed (on the basis of ecosystems' thermodynamics and adopting some physical principles, cf. Jørgensen and Fath, 2004) that the optimal distribution (i.e., maximum biodiversity) is the homogeneous one. Considering for the sake of simplicity the case when an average body weight is approximately the same for individuals of different species, we immediately obtain that, at the optimal ecosystem's state, the abundances of all species must be equal. Any deviation from this marginal case would lead to a biodiversity loss. Correspondingly, the other marginal case is given by the situation when only one species persists and all others has gone extinct. A biodiversity index that possesses the necessary properties was first introduced by Margalef (1968):

$$S = -A\sum_{k=1}^{N} p_k \ln(p_k) \tag{1}$$

where N is the number of species in the community and A is a coefficient which can be chosen differently, and

$$p_k = n_k \left(\sum_{j=1}^{N} n_j\right)^{-1}. \tag{2}$$

Here n_k gives the population size of the kth species; thus, p_k is the probability of catching an individual of kth species in a random sampling. S reaches its maximum value, $S_{\max} = -A \ln N$, in case of the homogeneous biomass distribution, $p_1 = \ldots = p_N = 1/N$, and S falls to $S_{\min} = 0$ when only one species remains. Importantly, regarding the latter case, S can already fall to a very low value when other species are not yet extinct but their abundance is low.

Index S has been widely used both in theoretical and empirical studies, e.g., see Vinogradov and Shushkina (1987) and Solé et al. (2004). However, its actual predictive ability remains rather obscure. A question that is largely open is whether the biodiversity index is ‘‘statistically homogeneous'' in the sense that all species make equivalent contribution to its value and to the magnitude/direction of its changes in the course of community dynamics. In particular, it is not clear to what extent an increase/decrease in S may be correlated with changes in particular species, especially when the main feedbacks in the community are nonlinear and small variations in parameter values or population sizes may eventually result in dramatic changes in community structure.

These issues are addressed in the present paper by means of mathematical modeling and computer simulations. Specifically, we consider a model of a three competitive species community and show that, in spite of the fact that all the species exhibit similar dynamical behavior, only two of them have a significant correlation/association with S, while the impact of the third one is negligible. Also, we show that the impact of environmental stochasticity (modelled by means of inclusion of noise into the species growth rate) does not change this apparent asymmetry. In our search of an appropriate modification of the biodiversity index, we then consider two other relevant indices such as exergy and the Kullback measure of information (cf. Jørgensen and Fath, 2004) and show that the results stay essentially the same, although for certain parameter values exergy appears to be a somewhat better biodiversity measure.

2. Main equations and a paradigm

Our approach is as follows. We consider a model community of N interacting species described, at each moment of time t, by their population sizes, $n_1(t), \ldots, n_N(t)$. Correspondingly, at each moment the state of the community as a whole can be described by the biodiversity index S, cf. Eqs. (1) and (2). We assume that the population sizes can change with time as a result of inter- and intra-species interactions and/or parameter variation, and so does S. The question that we are primarily concerned with is whether the contribution of all species to the changes in the biodiversity index is of the same magnitude (provided that all species exhibit qualitatively similar dynamical behavior) or, on the contrary, there is any distinct asymmetry.

In order to describe it quantitatively, we introduce the correlation coefficients between each of the species and the biodiversity index, $\varrho(n_k, S)$, $k = 1, \ldots, N$, where $\varrho(X, Y)$ is given by the following equation:

$$\varrho(X, Y) = \frac{\mathrm{cov}(X, Y)}{\sqrt{\mathrm{cov}(X, Y)\mathrm{cov}(Y, Y)}}. \tag{3}$$

Here cov(X, Y) is the covariance, which is calculated as

$$\mathrm{cov}(X, Y) = M([X - M(X)][Y - M(Y)]) \tag{4}$$

where $M(X)$ denotes the mean value of variable X.

For the purposes of this study, it is not important to distinguish between correlation and anticorrelation; the point of interest is to what degree the changes in given biodiversity measure ‘‘feel'' the changes in species abundance. Thus, we quantify the *association* between different dynamical variables by the absolute value of the corresponding correlation coefficient. For convenience, which we call it the association coefficient:

$$q(X, Y) = |\varrho(X, Y)|. \tag{5}$$

We expect that an adequate biodiversity measure should have approximately the same degree of association with each of the species.

A particular model determining the behavior of the population sizes can be different allowing for the great variety of possible ecological situations and existing modeling approaches. In this paper, we consider the case when the variables $n_1(t), \ldots, n_N(t)$ describe a community of N competitive species and arise as a solution of the following system:

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = \varepsilon_i\left(1 - \sum_{j=1}^{N} a_{ij} n_j\right) n_i, \qquad i = 1, \ldots, N \tag{6}$$

(cf. Hofbauer and Sigmund, 1988; Kot, 2001) where ε_i is the intrinsic per capita growth rate of the ith species and a_{ij} is the competition coefficient between species i and j.

Note that in the model (1–6) the number N of species can be different: although the biodiversity index S was originally introduced in order to describe many-species communities, to the best of our knowledge there is no any formal restrictions on N. Thus, for modeling purposes we can consider the cases when N is not necessarily large. Moreover, robustness of S as biodiversity measure in few-species model communities can perhaps be regarded as a necessary condition for its robustness in more complicated situations. Also, while for a large N the system (6) is unlikely to be treated analytically, which makes its properties obscure and its dynamics poorly understood, for a small N dependence of the system's properties (such as existence and stability of equilibrium states, existence of limit cycles, etc.) on parameter values is readily revealed.

As an illustrative example of our approach, we consider a community of two competitive species:

$$\frac{dn_1}{dt} = \varepsilon_1(1 - a_{11}n_1 - a_{12}n_2)n_1, \tag{7}$$

$$\frac{dn_2}{dt} = \varepsilon_2(1 - a_{21}n_1 - a_{22}n_2)n_2. \tag{8}$$

In order to make the model somewhat more ecologically realistic, we assume that it incorporates environmental stochasticity. Specifically, we assume that ε_1 and ε_2 are not constant parameters but depends on time in a random manner, i.e.,

$$\varepsilon_1(t) = \varepsilon_1[1 + \xi_1(t)], \qquad \varepsilon_2(t) = \varepsilon_2[1 + \xi_2(t)] \tag{9}$$

where ε_1 and ε_2 are the mean values and ξ_1, ξ_2 are stochastic variables describing a white Gaussian noise. In numerical calculations below, at each time step the values of ξ_1 and ξ_2 are generated as normally distributed random numbers with zero mean and the standard deviation σ.

Without noise, i.e., for $\varepsilon_1(t) \equiv \varepsilon_1 = \text{const}$, $\varepsilon_2(t) \equiv \varepsilon_2 = \text{const}$, the system (7)–(8) is known to have a few equilibrium states in the biologically meaningful domain $n_1 \geq 0$, $n_2 \geq 0$. Namely, they are the "no species" state $E_0 = (0, 0)$, the "first species only" state $E_1 = (\varepsilon_1/a_{11}, 0)$, the "second species only" state $E_2 = (0, \varepsilon_2/a_{22})$ and, depending on parameter values, also the coexistence state $E = (n_1, n_2)$ where n_1 and n_2 are expressed via the parameters; for more details see Kot (2001). The system, having started from an initial condition, gradually approaches a stable equilibrium state. Apparently, during the process of system's relaxation, the species composition changes. That results in the corresponding change in the biodiversity index.

Details of the system's dynamics depend not only on parameter values but also on the initial conditions. Here we consider the case when both E_1 and E_2 are stable while the coexistence state E exists and is unstable; it readily seen that it takes place when $\varepsilon_1/a_{11} > \varepsilon_2/a_{21}$ and $\varepsilon_2/a_{22} > \varepsilon_1/a_{12}$. In this case, it depends on the initial condition which equilibrium state the system approaches. For a hypothetical parameter set $\varepsilon_1 = \varepsilon_2 = a_{11} = a_{22} = 1$, $a_{12} = 1.1$, $a_{21} = 1.2$ and the initial conditions $n_{10} = 0.1$, $n_{20} = 0.19$, the population sizes versus time in the no-noise case are shown in Fig. 1a. After a certain transient stage, the system gradually approaches the state E_1. Biodiversity index versus time is shown in Fig. 1c. Here and below, we let $A = 1/\ln N$ so that S is bounded between 0 and 1. Thus, S remains on the order of unity at the early stage of the system's dynamics (reaching its theoretical maximum $S = 1$ when the population sizes are equal) and tends to zero in the large-time limit as a result of the second species' extinction.

Next, we calculate the association coefficients q according to (3)–(5). It appears that both of them are close to unity; specifically, we obtain that $q(n_1, S) = q(n_2, S) = 0.93$. This result is hardly surprising taking into account that the system (7)–(8) is purely deterministic and contains only two components.

Interestingly, although introduction of noise can change the system's dynamics significantly, it does not destroy the high degree of association between S and each of n_1 and n_2. Fig. 1b shows the population sizes versus time for the same parameter set as above and 20% noise ($\sigma = 0.2$). The impact of noise disturbs the attraction basins so that starting from the same initial conditions the system now relaxates to the other equilibrium state E_2. The behavior of the biodiversity index, however, remains qualitatively similar to the no-noise case, cf. Fig. 1c and d. Also, the association coefficients changes only slightly compared to the previous case; the calculated values are $q(n_1, S) = 0.97$ and $q(n_2, S) = 0.92$.

It should be mentioned that, contrary to the deterministic case, in the presence of stochasticity the system's dynamics is not uniquely defined. For every new simulation run, the actual plots of $n_1(t)$ and $n_2(t)$ will be somewhat different from the ones shown in Fig. 1b. (In particular, it may happen that the system actually relaxates to the state E_1, not to E_2.) Correspondingly, dependence of the biodiversity index on time can be slightly different as well. Importantly, however, the value of the correlation coefficients remains essentially the same up to only small variations.

3. Three-species system

The system of two competitive species considered in the previous section is of course far too simple to enable us to make any ecologically sound conclusion regarding the biodiversity index robustness. As a next step, in this section we consider a model consisting of three species, i.e., system (6) for $N = 3$. In spite of the fact that only one equation is added, the behavior of the model now becomes much more complicated. Depending on parameters, the system can have as much as eight equilibrium states and even a limit cycle (cf. Petrovskii et al., 2001), although it has been proved that it cannot exhibit chaotic dynamics.

In order to avoid unnecessary complexity, here we consider the case of special relation between the system's parameters:

$$\frac{dn_1}{dt} = \varepsilon_1(1 - n_1 - \alpha n_2 - \beta n_3)n_1, \tag{10}$$

$$\frac{dn_2}{dt} = \varepsilon_2(1 - \beta n_1 - n_2 - \gamma n_3)n_2, \tag{11}$$

$$\frac{dn_3}{dt} = \varepsilon_3(1 - \gamma n_1 - \beta n_2 - n_3)n_3 \tag{12}$$

where we have assumed for convenience that the species population sizes are scaled by the corresponding carrying capacities so that $a_{11} = a_{22} = a_{33} = 1$.

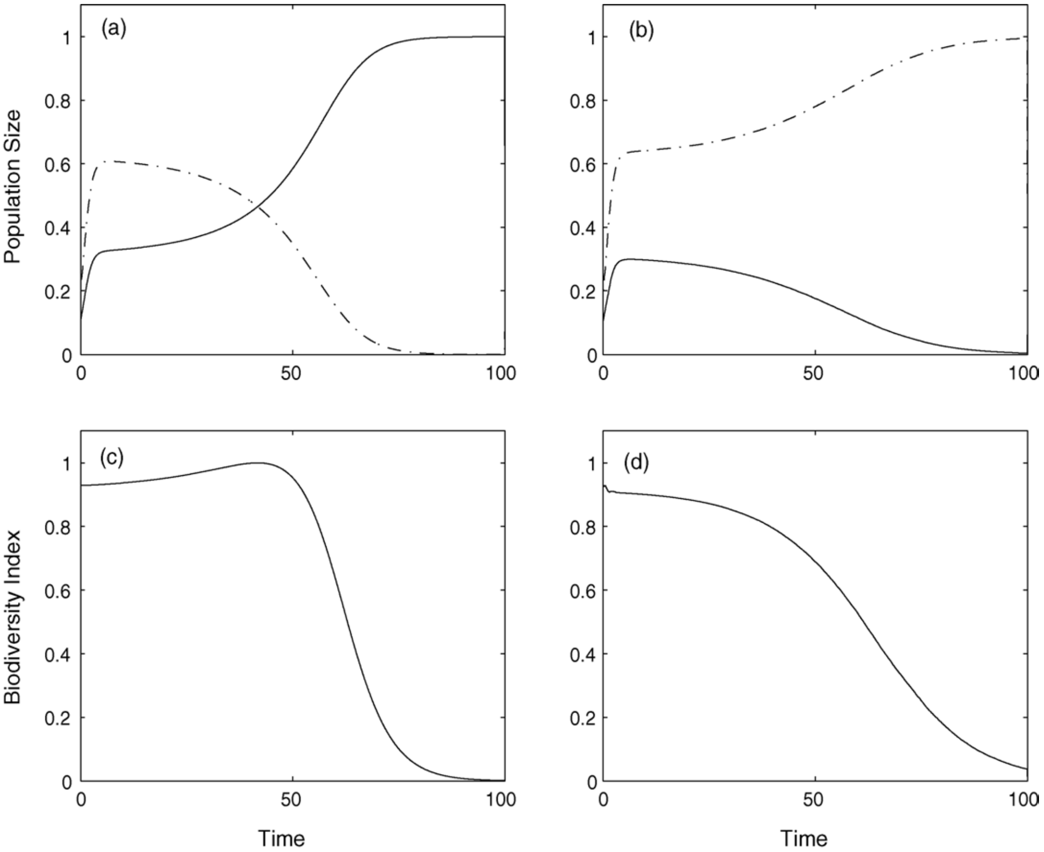

Fig. 1 – Dynamics of the two competitive species system in (a and c) the absence of noise and (b and d) for 20% environmental noise. In (a) and (b), solid curves and dashed-and-dotted curves show species 1 and 2, respectively. Parameters are: $\varepsilon_1 = \varepsilon_2 = 1$, $a_{11} = a_{22} = 1$, $a_{12} = 1.1$, $a_{21} = 1.2$ and $\Delta t = 0.1$.

As well as above, our goal is to reveal whether the degree of association of all species with the value of the biodiversity index S is the same. In order to avoid the impact of transients caused by the initial conditions, we will focus on the large-time asymptotics when the system's dynamics takes place along a stable manifold.

We begin with the case when all coefficients in (10)–(12) are constant parameters, i.e., they are not affected by noise. The case $\alpha = \gamma$ corresponds to a so-called cyclic competition which has been studied in much detail (May and Leonard, 1975; Hofbauer and Sigmund, 1988). It was shown that, under additional constraints

$$\alpha = \gamma \quad \text{and} \quad \alpha + \beta > 2, \qquad \alpha > 1 > \beta, \tag{13}$$

the system (10)–(12) possesses five stationary states. Namely, they are the "no species" state (0, 0, 0) and three "one species only" states (1, 0, 0), (0, 1, 0) and (0, 0, 1). The no-species state is always an unstable node and the one-species-only states are saddle-points. There is also one coexistence equilibrium state (n_1, n_2, n_3), the stationary value of the species concentrations being the solution to the following system:

$$n_1 + \alpha n_2 + \beta n_3 = 1, \qquad \beta n_1 + n_2 + \gamma n_3 = 1, \qquad \gamma n_1 + \beta n_2 + n_3 = 1. \tag{14}$$

It is readily seen that, under constraints (13), the coexistence steady state is always a saddle-point. The only attractor in the phase space is a heteroclinic cycle consisting of the three one-species-only states and the orbits connecting these states (May and Leonard, 1975). Apparently, it means that the system (10–12) is not permanent.

The properties of the system (10)–(12) change significantly when $\alpha \neq \gamma$. In case det $(a_{ij}) > 0$ (where (a_{ij}) is the matrix of the system, cf. (6)), a criterion of the system permanence is

$$(\gamma - 1)^2(\alpha - 1) < (1 - \beta)^3, \tag{15}$$

which evidently could not be satisfied under constraints (13).

Since under condition det $(a_{ij}) > 0$ the solutions of the system are uniformly bounded, a stable limit cycle can appear when the co-existence state (n_1, n_2, n_3) is unstable. One particular set of parameters corresponding to existence of a stable limit cycle was found to be as follows: $\alpha = 1.08$, $\beta = 0.8$, $\gamma = 1.24$, $\varepsilon_1 = \varepsilon_2 = 1.0$, $\varepsilon_3 = 5.0$. The population sizes versus time for these parameter values and the corresponding changes in the biodiversity index are shown in Fig. 2a and b, respectively. It should be mentioned that the system is rather sensitive to a variation of parameter values and the parameter range where the limit cycle exists is rather narrow. For convenience, below we will refer to the above parameter set as the "reference point" (meaning a point in the parameter space).

The type of the large-time system's asymptotical behavior which seems to be the most appropriate for the purposes of our study is oscillations along the stable limit cycle. In

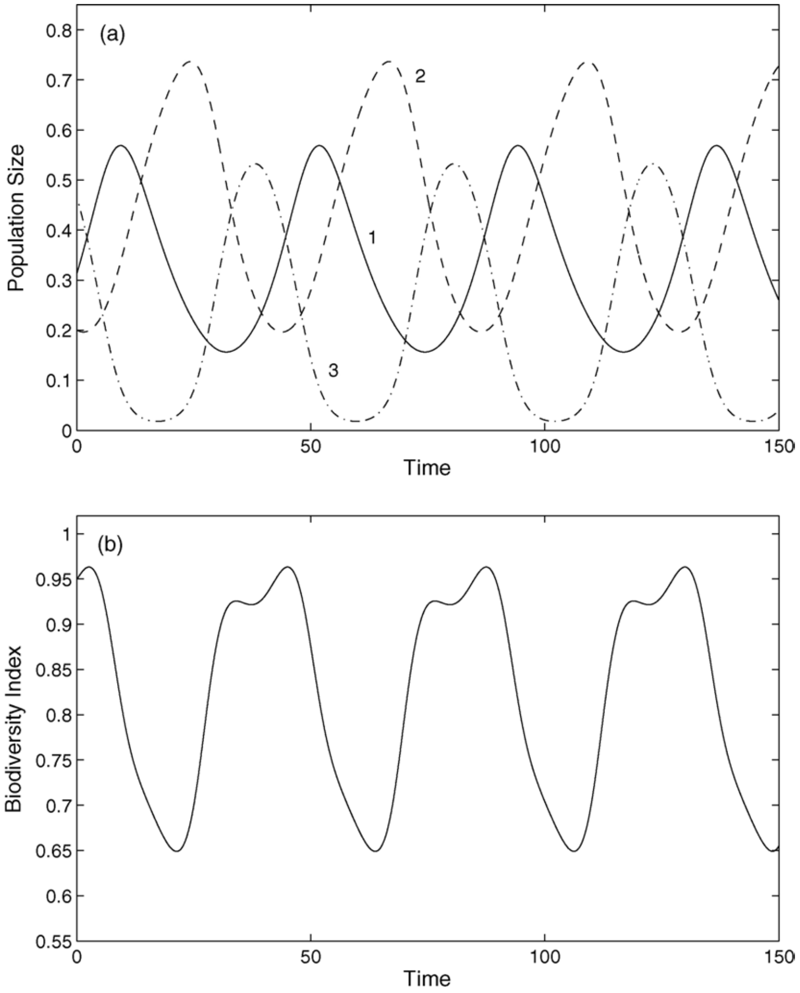

Fig. 2 – (a) Oscillatory dynamics of the three competitive species system, curves 1, 2 and 3 for species 1, 2 and 3, respectively; (b) corresponding changes in the biodiversity index S. Parameters are: $\varepsilon_1 = \varepsilon_2 = 1$, $\varepsilon_3 = 5$, $\alpha = 1.08$, $\beta = 0.8$, $\gamma = 1.24$ and $\Delta t = 0.05$.

consistence with our approach, our next step is to calculate the correlation coefficients between the population sizes and the biodiversity index at the "reference point, " cf. Fig. 2. They are found to be $q(n_1, S) = 0.17$, $q(n_2, S) = 0.83$ and $q(n_3, S) = 0.88$. Contrary to the two-species case, now we obtain that only the dynamics of species 2 and 3 are strongly associated with the changes in biodiversity index. Thus, while changes in S can be used to follow (and, potentially, to predict) the changes in the population sizes of species 2 and 3, the biodiversity index provides only very little information about species 1.

Indeed, a closer look at Fig. 2 immediately reveals that the position of the hollows in the plot of $S(t)$ nearly coincides, up to a small shift, with that of $n_3(t)$ and with the position of the humps in the plot of $n_2(t)$. Apparently, this is what is implied by a strong association between S and n_2, n_3 (with correlation between S and n_3 and anticorrelation between S and n_2). On the contrary, there is no any visual association between the plots of $S(t)$ and $n_1(t)$.

The next step is to check how the association coefficients change with parameter values. For that purpose, we choose γ as a controlling parameter and keep the value of all others fixed. Variations of γ are considered in the range where the system's dynamics remains oscillatory. A convenient range is found to be between 1.239 and 1.27, see Fig. 3. For $\gamma \leq 1.238$ the limit cycle does not exist (the coexistence state is stable) and for $\gamma > 1.27$ the system eventually becomes degenerated because the cycle's amplitude increases significantly and it approaches very closely to the phase space boundary and to the "one species only" states.

Dependence of the association coefficients on γ is shown in Fig. 4a where squares stand for species 1, diamonds for species 2 and triangles for species 3. Covariances are calculated for a triple oscillation period. It is readily seen that $q(n_2, S)$ and $q(n_3, S)$ tend to decrease with an increase in γ, although their value always remains a few times higher than $q(n_1, S)$.

We then check how these results can be modified under the impact of noise. For this purpose, in the system (10)–(12) the constant coefficients ε_i are now changed to

$$\varepsilon_i(t) = \varepsilon_i[1 + \xi_i(t)], \qquad i = 1, 2, 3, \tag{16}$$

where $\xi_{1,2,3}$ correspond to a white Gaussian noise, cf. the lines below Eqs. (9). Fig. 4b shows the association coefficients versus

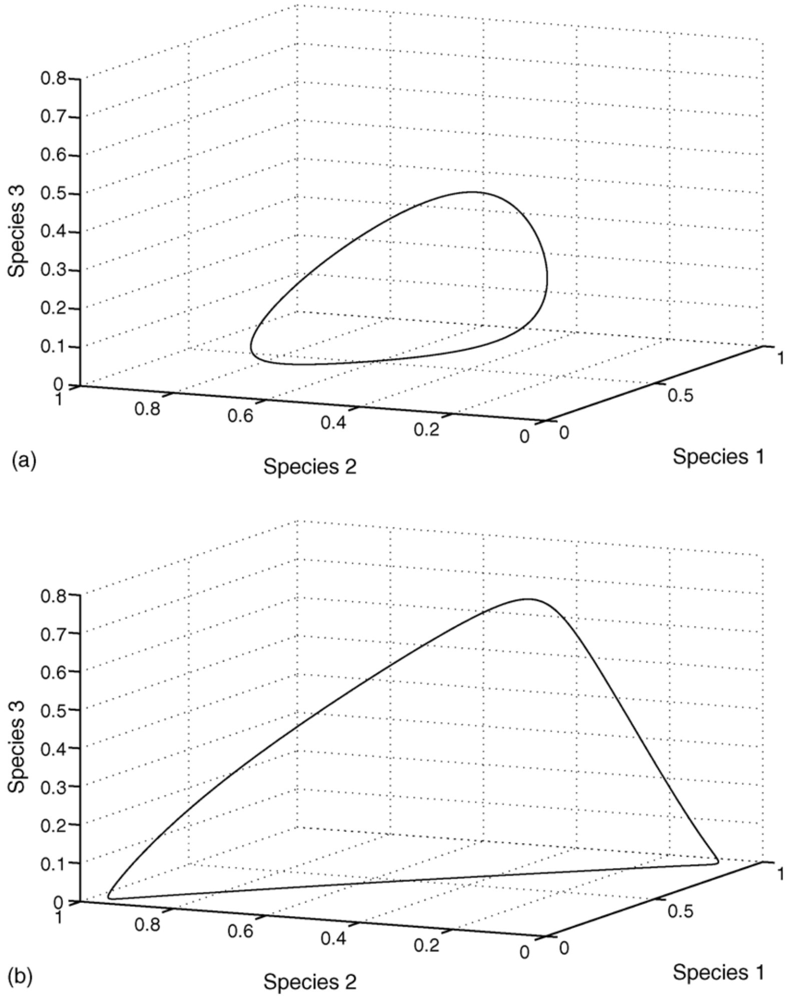

Fig. 3 – Limit cycle in the phase space of the three competitive species system for: (a) $\gamma = 1.24$ and (b) $\gamma = 1.27$, other parameters the same as in Fig. 2.

γcalculated for 20% noise. Interestingly, their values appear to be only very slightly affected by stochasticity and their values stays practically the same as in the no-noise case, species 2 and 3 showing much stronger association with S than species 1.

4. Alternative biodiversity measures

The results of the previous section lead to a conclusion that the biodiversity index S, cf. (1), may not always be capable of providing reliable information regarding the tendency in changes of the species abundance. That makes a reason for a search of alternative biodiversity measures. At least two such values can be immediately found in the relevant literature (e.g., see Jørgensen and Fath, 2004). One of them is called the Kullback information measure (Kullback, 1959):

$$K = \sum_{k=1}^{N} p_k \ln\left(\frac{p_k}{p_{k0}}\right) \tag{17}$$

where the probabilities p_k of different states of the system are defined as above, see (2), and p_{k0} are the probabilities in the state of "thermodynamical equilibrium." Contrary to physical systems, for ecosystems the state of thermodynamical equilibrium is vaguely defined; thus, tentatively, we will identify it with the steady coexistence state. Correspondingly, $p_{k0} = n_k/(n_1 + n_2 + n_3)$.

Fig. 5 shows the values of the association coefficients between the population sizes and K (squares for $q(n_1, K)$, diamonds for $q(n_2, K)$, and triangles for $q(n_3, K)$) in the no-noise case and for 20% environmental noise, see Fig. 5a and b, respectively. As well as for the biodiversity index, the noise does not bring much changes to the degree of association. On the whole, the information measure appears to be even less appropriate than S: although for γ being around 1.24 all three association coefficients are on the same order, their value appears to be quite small. That means that K is not capable to catch the tendency in population sizes' changes for any of the species constituting the community. For γ being 1.25 or larger, the situation is similar to what was observed for the biodiversity index, i.e., much of the information about the dynamics of species 1 is lost.

Another alternative value often used in theoretical studies is exergy:

$$E = -\tilde{A} \sum_{k=1}^{N} n_k \ln\left(\frac{n_k}{n_{k0}}\right). \tag{18}$$

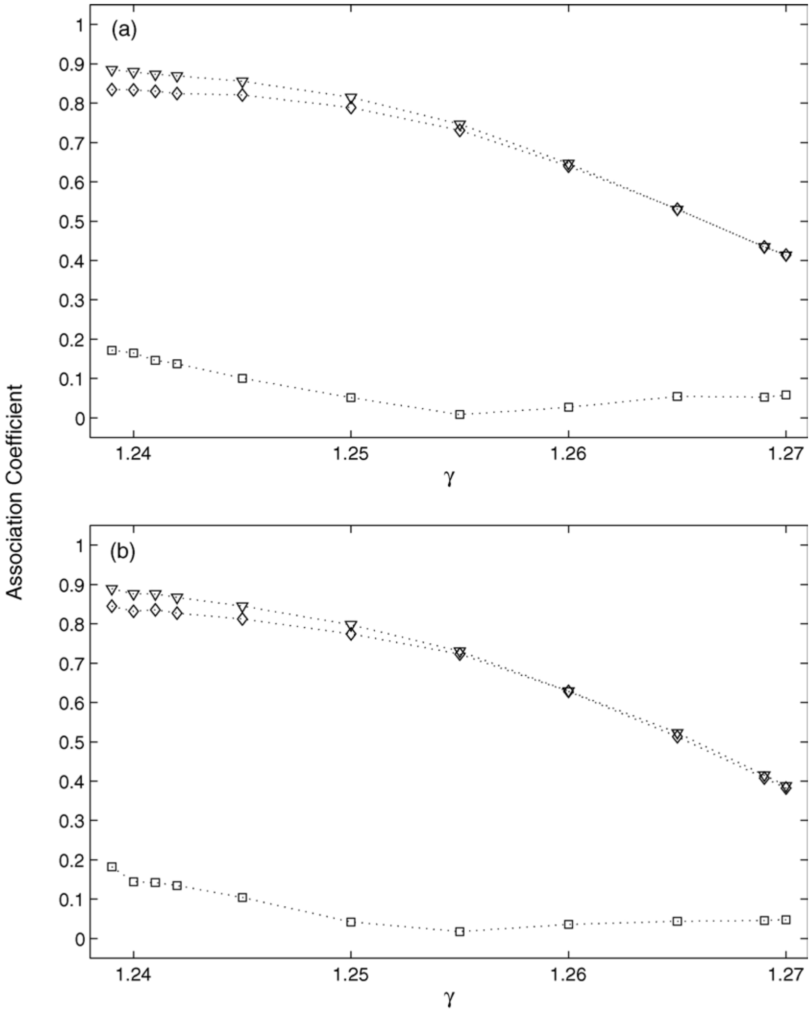

Fig. 4 – Association coefficients between the biodiversity index S and the population sizes in the three competitive species system (squares for $q(n_1, S)$, diamonds for $q(n_2, S)$ and triangles for $q(n_3, S)$) for: (a) no noise and (b) 20% environmental noise.

Note that, unlike to S and K, exergy is expressed via the original state variables, not via probabilities. Here, again, n_{k0} is the concentration of the kth system's component in thermodynamical equilibrium which we will treat as the steady coexistence state; thus, $n_{k0} = n_k$, $k = 1, 2, 3$. In real systems, the coefficient $\tilde{A}$ should be expressed through some thermodynamical values; since here we are more concerned with the changes in E and their association with the corresponding changes in species' abundance rather than with its exact value, we assume $\tilde{A} = 1$.

Fig. 6a and b show the association coefficients $q(n1, E)$ (squares), $q(n2, E)$ (diamonds) and $q(n3, E)$ (triangles) for no noise and 20% noise, respectively. As above, noise does not change the degree of association. Interestingly, although coefficients' dependence on γ appears to be somewhat more complicated than it was observed for S and K (with all three coefficients falling in turn to very small values), in a certain parameter range (e.g., for $\gamma \approx 1.24$) the degree of association between exergy and each of the species appears to be on the same order. That may indicate that, intrinsically, exergy is a more relevant biodiversity measure than the standard biodiversity index S and the information measure K.

5. Concluding remarks

In this paper, we have revisited a few commonly used biodiversity measures such as biodiversity index S, exergy E and information measure K in order to check whether they adequately reflect the changes that take place in a given community in the course of its dynamics. Our main attention was focused on a three competitive species system. We have shown that, in spite of the fact that dynamical behavior is similar for all species (i.e., periodical oscillations along a stable limit cycle), their contribution to the value of the biodiversity measures is in most cases remarkably asymmetrical. Introduction of environmental stochasticity into the model, although potentially capable to change the system's dynamics significantly (cf. Fig. 1a and b), does not bring any changes to the degree of association between the biodiversity measures and the system's components.

It should be mentioned that, in the system (10–12), there is no any distinct hierarchical structure, which would make this asymmetry expectable and easily understandable. While for given parameter values ($\varepsilon_1 = \varepsilon_2 = 1.0$, $\varepsilon_3 = 5.0$) the third species can perhaps be regarded as a more successful competitor, the

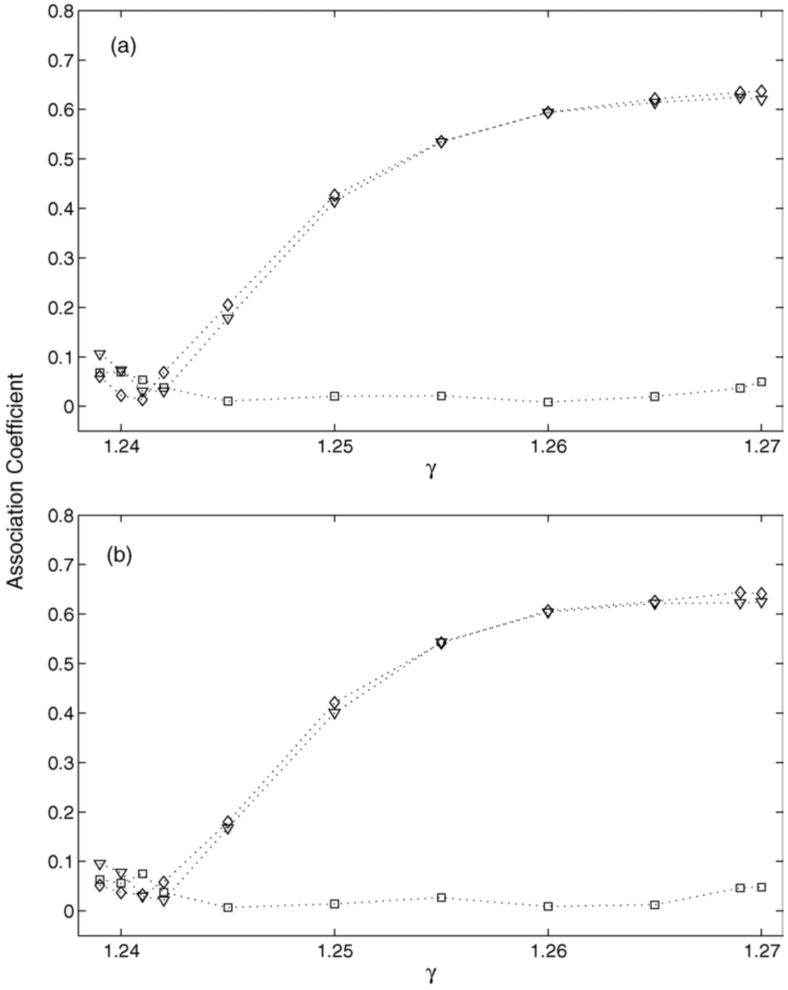

Fig. 5 – Association coefficients between the information measure *K* and the population sizes in the three competitive species system (squares for $q(n_1, K)$, diamonds for $q(n_2, K)$ and triangles for $q(n_3, K)$) for: (a) no noise and (b) 20% environmental noise.

first and second species are pretty equal. Moreover, since $\alpha < \gamma$, the competition press is actually lower on the first species than on the second species. Thus, from the point of hierarchy, it is the second species that is likely to become a junior member; yet its contribution to the properties of the system as a whole (quantified by S) is remarkably higher.

In our study, we have used a relatively simple model. Naturally, it leaves open the question about the properties of biodiversity measures in more complicated systems containing a larger number of species. We want to emphasize, however, that, from a theoretical stand-point, there is no any formal restriction on the use of S (or E, or K) in terms of the number of species, especially, when stochasticity/noise is taken into account. Clearly, a biodiversity measure, which is robust in a many-species community can be expected to remain robust in a few species community as well.

There have been two distinctly different philosophies in ecological studies during the last few decades. One of them is based on the idea of *analysis*, i.e., when an ecosystem is, in some sense, decomposed into its parts and the focus of research is on some specific species and/or on the interactions between particular species, e.g., see Hofbauer and Sigmund (1988), and Nisbet and Gurney (1982). The alternative approach, however, is based on *synthesis* and can be called ‘‘holistic’’ because it focuses on the ecosystem as a whole (Jørgensen and Mejer, 1979; Li, 1986, 2000; Li and Müller, 1995) rather than on its separate parts.

There have been many explicit and implicit attempts to find a reasonable compromise between these two apparently converse approaches. One of them is based on biodiversity indices; such an approach is used in order to describe the community as a whole but also involve information about the dynamics/abundance of particular species. It should be mentioned here that, originally, the biodiversity index S was adapted from physics: up to a constant coefficient, Eq. (1) coincides with the Boltzmann–Shennon entropy which is widely used in statistical physics and thermodynamics (Ebeling, 1993). The other two measures considered in this paper, i.e., E and K, although provide a certain extension of the original quantity, still have essentially the same functional structure. The question thus arises about the limits of similarity between a physical system and an ecological community. During recent years, there has been a growing tendency to treat ecosystems from thermodynamical/statistical physics point of view as well

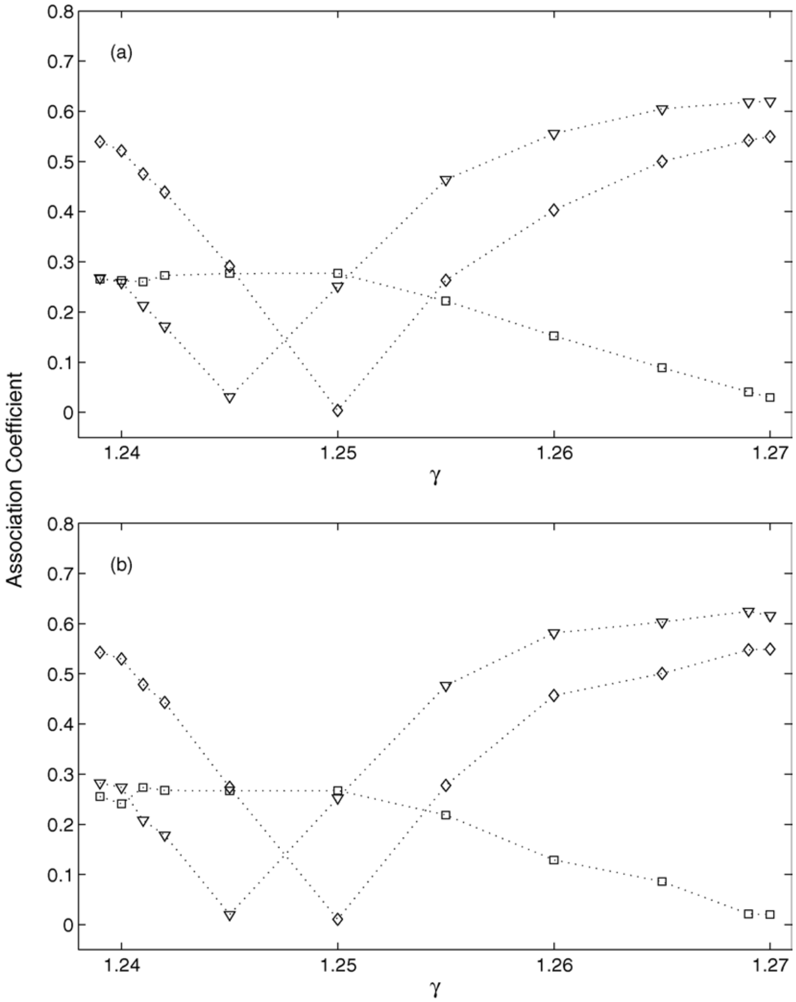

Fig. 6 – Association coefficients between exergy *E* and the population sizes in the three competitive species system (squares for $q(n_1, E)$, diamonds for $q(n_2, E)$ and triangles for $q(n_3, E)$) for: (a) no noise and (b) 20% environmental noise.

as to bring corresponding tools for their study and analysis (cf. Li and Charnov, 2001; Li, 2002; Kolasa and Li, 2003; Jørgensen and Fath, 2004; Maurer, 2005). Although it is quite obvious that some basic principles such as mass and energy conservation must be true in an ecosystem as well as in any other system, application of more specific principles is much less evident. Our results indicate that this approach may have hidden pitfalls and should be applied with care.

In this paper, we were more concerned with revealing the problem rather than with giving it a full and exhaustive consideration. The next stages of the study should extend our results on systems with larger number of species and on system with a larger degree of stochasticity (e.g., described by time-discrete equations), and probably also allow for spatial dimensions. These tasks will become a focus of the future work.

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REFERENCES

Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M., Williamson, M. (Eds.), 1989. Biological Invasions: A Global Perspective. John Wiley, Chichester.
Ebeling, W., 1993. Entropy and information in processes of self-organization: uncertainty and predictability. Physica A 194, 563–575.
Faith, D.P., 2005. Global biodiversity assessment: integrating global and local values and human dimensions. Global Environ. Change A 15, 5–8.
Hofbauer, J., Sigmund, K., 1988. The Theory of Evolution and Dynamical Systems. Cambridge University Press, Cambridge UK.
Jørgensen, S.E., Mejer, H., 1979. A Holistic approach to ecological modelling. Ecol. Modell. 7, 169–189.
Jørgensen, S.E., Fath, B.D., 2004. Application of thermodynamical principles in ecology. Ecol. Complexity 1, 267–280.

Kolasa, J., Li, B.-L., 2003. Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability. Proc. R. Soc. Lond. B 270 (Suppl.), S198–S201.

Kot, M., 2001. Elements of Mathematical Ecology. Cambridge Univeristy Press, Cambridge, UK.

Kullback, S., 1959. Information Theory and Statistics. John Wiley & Sons, New York.

Li, B.-L., 1986. Pansystems analysis: a new approach to ecosystem modelling. Ecol. Modell. 32, 227–236.

Li, B.-L., 2000. Why is the holistic approach becoming so important in landscape ecology? Landscape Urban Plan. 50, 27–41.

Li, B.-L., 2002. A theoretical framework of ecological phase transitions for characterizing tree-grass dynamics. Acta Biotheoretica 50 (3), 141–154.

Li, B.-L., Charnov, E.L., 2001. Diversity-stability relationships revisited: scaling rules for biological communities near equilibrium. Ecol. Modell. 140, 247–254.

Li, B.-L., Müller, F., 1995. Application of the pansystem entropy concept to hierarchical ecosystem analysis. Adv. Sys. Sci. Appl. 1, 13–18.

Loehle, C., Li, B.-L., 1996. Habitat destruction and the extinction debt revisited. Ecol. Appl. 6, 784–789.

Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Chapman and Hall, London.

Margalef, R., 1968. Perspectives in Ecological Theory. Chicago University Press, Chicago.

Maurer, B.A., 2005. Statistical mechanics of complex ecological aggregates. Ecol. Complexity 2, 71–85.

May, R.M., Leonard, W., 1975. Nonlinear aspects of competition between three species. SIAM J. Appl. Math. 29, 243–252.

Nisbet, R.M., Gurney, W.S.C., 1982. Modelling Fluctuating Populations. Wiley, Chichester.

Petrovskii, S.V., Kawasaki, K., Takasu, F., Shigesada, N., 2001. Diffusive waves, dynamical stabilization and spatio-temporal chaos in a community of three competitive species. Jpn. J. Ind. Appl. Math. 18, 459–481.

Solé, R.V., Alonso, D., Saldaña, J., 2004. Habitat fragmention and biodiversity collapse in neutral communities. Ecol. Complexity 1, 65–75.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2–16.

Tilman, D., Lehman, C., 2001. Human-caused environmental change: impacts on plant diversity and evolution. Proc. Natl. Acad. Sci. U.S.A. 98, 5433–5440.

Tilman, D., May, R.M., Lehman, C.L., Novak, M.A., 1994. Habitat destruction and extinction debt. Nature 371, 65–66.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J., Asher, J., Fox, R., Clarke, R.T., Lawton, J.H., 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303, 1879–1881.

Vinogradov, M.E., Shushkina, E.A., 1987. Functioning of Plankton Pelagic Communities in Ocean. Nauka, Moscow, [In Russian].