In: Floreano, Dario and Nicoud, Jean-Daniel and Mondada, Francesco: *Advances in Artificial Life*, 119-128. Springer Verlag, Berlin, Heidelberg, 1999.

A Comparative Analysis of Biodiversity Measures

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Abstract The concept of biodiversity has received rapidly increasing interest in the biosciences during the last decade. Yet, it is unclear and disputed how biodiversity should be characterised and measured. We compared several biodiversity measures by applying them to data retrieved from the LindEvol-GA model of evolution. A series of LindEvol-GA runs with mutation ranges ranging from zero (producing no diversity) to one (producing maximal, but biologically meaningless, diversity) was analyzed with the measures to be compared. At intermediate mutation rates, biologically meaningful diversity can emerge.
We show that biodiversity measures can be classified according to the way in which they respond to these various types of diversity, and we discuss some implications of our observation for the design, choice, and application of biodiversity measures.

1 An approach to biodiversity

During the last ten years, the term "biodiversity" has become widely used in the biosciences [1, 2], including Artificial Life [3] as well as in the general public to refer to collections of biological entities which coexist in an intricately orchestrated, organismic fashion. But despite its widespread usage, there is no satisfactory scientific definition of biodiversity. In fact, quite a diversity of biodiversity definitions and measures have been proposed in the literature [4, 5, 6, 7, 8, 9], and some of them are not compatible.

Clearly, this problem is to some extent due to diverging concepts and objectives, which sometimes are political or economic in nature rather than scientific. However, even in the scientific domain, there are various sources of difficulties. Biodiversity is generally agreed to be a phenomenon occurring on multiple levels of biological organisation [2, 10, 11]. Unfortunately, biodiversity concepts that focus on different levels of biological organisation (e.g. molecular biology, morphology, ecology, evolutionary biology etc.) are sometimes difficult to reconcile.

Even on a given level of biological organisation, quantitative characterisation of biodiversity is not trivial. For example, simply counting species is a widely applied method for the quantification of biodiversity. However, while the number of species in a system is often suitable as an indicator of the system's biodiversity, it is possible to construct systems with equal numbers of species which nonetheless cannot be expected to be equal in biodiversity; e.g. a box containing thousand

different insect species would be considered to be less "biodiverse" than a box containing thousand species forming a small ecosystem of plants, microbes and some insects.

In response to this problem, biodiversity measures which take the evolutionary relations between species into account have been developed [7, 8, 12]. One may consider the contribution of distantly related species to biodiversity to be greater than the contribution of closely related species (e.g. [12]), or to define the conservation of evolutionary history to be the goal of biodiversity protection [6]. But according to such concepts, the bulk of biodiversity would reside within prokaryotes, because they diversified in evolution long before eukaryotes appeared. A tropical rain forest, the standard example for high biodiversity, might appear as a "monoculture" of two rather special groups of multicellular eukaryotes, namely animals and plants, from such a perspective.

Thus, both disregarding evolutionary depth as well as naively equating biodiversity with evolutionary depth fail to capture biodiversity adequately. The rainforest example implies that it is something like "the right mix" of degrees of evolutionary relatedness which characterises biodiversity. It therefore seems that biodiversity is a life phenomenon that emerges somewhere between order (close relatedness, complete identity in the limit) and chaos (distant relatedness, total unrelatedness in the limit). We therefore tested several biodiversity measures to see whether they show a maximum at some edge of chaos in an Artificial Life model of evolution.

All Artificial Life models of evolution are imperfect representations of biological evolution. Nonetheless, important aspects of biological evolution can be captured by models of evolution. Specifically, emergence of complex phenomena has been observed in many computer simulations. Therefore, Artificial Life models provide a suitable basis for investigating possible links between biodiversity and such emergent phenomena.

2 LindEvol-GA runs with increasing mutation rates

For the investigation presented here, we used LindEvol-GA [13, 14], a computer model of the evolution of plant growth patterns. Plants in LindEvol-GA grow in a two-dimensional lattice world in which they compete for space and energy. After a vegetation period, a fitness value is assigned to each plant genome based on the amount of energy stored in the plant. Because the plants grow together in one lattice, this fitness value depends on the interactions of a plant with its neighbours. A new generation of genomes is constructed by removing some genomes from the population and creating an equal number of copies of genomes randomly drawn from the surviving part of the population. All genomes in the population are then mutated. The fraction of the population which is removed each generation is specified by a control parameter called the selection rate. The control parameter governing mutation in the runs presented here is the global replacement mutation rate, which is the probability with which the value of a

byte in a genome is replaced with a random value in one generation. Insertions and deletions were not used in the runs presented here.

At the start of each time step the effective mutation rate is set to the global mutation rate for all genomes. A plant may multiply or divide its individual effective mutation rate by 2 at the expense of one energy unit. Repeated modifications are possible. They reduce the fitness of the genome, but can increase the chance of accurate replication. Reduction of effective mutation rates can thus be an evolutionarily stable strategy which evolves in some runs with relatively high global mutation rates (see [15] for details).

We performed a series of LindEvol-GA runs in which the global replacement mutation rate rises from 0.0 to 1.0. From 0.0 to 0.4, a replacement mutation rate increment of 0.01 was used, larger increments were applied above 0.4. The selection rate was set to 0.5 in all runs. Mutation rate adaptation was enabled, and all other control parameters were chosen as in [15] as well. Since monoparental reproduction is used in our LindEvol-GA runs, the phylogenetic tree connecting all genomes can be recorded. Every ten time steps, this phylogenetic tree was used to compute the phylogeny-based biodiversity measures described below. The initial phase of each run, in which descendants of more than one of the randomly created genomes of the start population exist so that multiple unconnected phylogenetic trees are present, was excluded from this analysis.

Both extremes of the global mutation rate constitute neutral controls (cf. [16]): With no mutation, all genomes are identical after an initial phase, so the survivors are effectively drawn at random during selection. With maximal mutation, offspring are totally unrelated to their parents, therefore, achieving a high fitness value and surviving selection is again a pure chance event. Only with intermediate mutation rates, new genotypes and phenotypes which inherit information from their predecessors can arise, and thus, information which is biologically meaningful (with respect to the artificial biology of LindEvol) accumulates in the genomes. Assuming that biodiversity is constituted by collections of entities which are different in a biologically meaningful way, one thus expects that biodiversity measures should yield higher values for runs with intermediate mutation rates than for those with no or maximal mutation.

3 Biodiversity measures

Most measures which we tested in our analysis were proposed by Williams *et al.* [7]. These measures evaluate the topology of a rooted phylogenetic tree; the lengths of the edges in the tree are not taken into account. All measures are based on the following quantities:

- n is the number of terminal nodes in the phylogenetic tree.
- p_j is the number of nodes in the path from the terminal node j to the root node of the phylogenetic tree.
- s_{jk} is the number of nodes which are shared among the paths from node j to the root and from node k to the root.

– u_{jk} is the number of nodes which are on the path from node j to the root but not on the path from node k to the root.

On the basis of these quantities, WILLIAMS *et al.* define the following divergence measures:

$$\begin{aligned} d_{\mathrm{III}}(j,k) &:= s_{jk} \\ d_{\mathrm{IV}}(j,k) &:= u_{jk} + u_{kj} + 1 \\ d_{\mathrm{V}}(j,k) &:= \frac{u_{jk}+u_{kj}+1}{2s_{jk}+u_{jk}+u_{kj}} \\ d_{\mathrm{VI}}(j,k) &:= \frac{u_{jk}+u_{kj}}{s_{jk}} + 1 \end{aligned} \tag{1}$$

WILLIAMS *et al.* introduce four biodiversity measures which are derived from these divergence measures by

$$m_x := n \cdot \mathrm{mean}(d_x) \tag{2}$$

where x is III, IV, V and VI, respectively. Further measures used in [7] are the plain number of species ($m_{\mathrm{I}} := n$), root weight biodiversity, defined as

$$m_{\mathrm{II}} := \sum \frac{1}{p_j} \tag{3}$$

and finally, dispersion diversity, defined as

$$m_{\mathrm{VII}} := n \cdot (\mathrm{mean}(d_{\mathrm{IV}}) - \mathrm{std.dev.}(d_{\mathrm{IV}})) \tag{4}$$

The roman indices for these diversity measures were chosen to match those used in [7]. We determined measures II through VII for these phylogenetic trees.

An alternative approach to measuring biodiversity was proposed by NEE and MAY [6], who suggested to use the length of a phylogenetic tree as a biodiversity measure. The tree length is defined as the sum of the lengths of all edges in the phylogenetic tree. Evidently, this measure differs from those developed by WILLIAMS *et al.* in that edge lengths are taken into account. Edge lengths in the trees retrieved from LindEvol-GA simulations are given in generations.

As a third approach, we used distance distribution complexity (DDC) [13] as a biodiversity measure. DDC is defined as the shannon entropy of the distribution of (discrete or discretized) distance values. In [13], the edit distance between genomes was used for DDC calculation. In this paper, we also calculate DDC on the basis of phylogenetic distances. The phylogenetic distance of two terminal nodes is defined as the sum of the lengths of the edges on the path connecting these nodes. This distance is computed from the trees retrieved from the LindEvol-GA runs. We denote edit distance based DDC by C_{edit} and phylogenetic distance based DDC by C_{phyl}.

Finally, we also combined the concepts of WILLIAMS *et al.* and edit distance into two new measures. One is a combination of mean distance diversity (equation 2) and edit distance:

$$m_e = n \cdot \mathrm{mean}(\text{edit distance}) \tag{5}$$

while the other one was constructed from the distance dispersion approach (equation 4) and edit distance:

$$m_{edisp} := n \cdot (\text{mean(edit distance)} - \text{std.dev.(edit distance)}) \quad (6)$$

4 Results

Fig. 1 shows the time averages of all biodiversity measures which are based on the evaluation of the phylogenetic trees retrieved from the runs. Quite strikingly, none of these measures exhibits any significant response to the global mutation rate[1]. This is true for the measures which operate on tree topology only (measures II to VII) as well as for those which take edge length into account (tree length and C_{phyl}).

The results from the measures which are based on genetic distances (i.e. the edit distance between genomes) are shown in Fig. 2. The number of different genomes is also included as an approximation to the number of species, which is often used to quantify biodiversity. In strong contrast to the graphs in Fig. 1, the quantities shown in Fig. 2 all are pronouncedly correlated to the global mutation rate.

There are two runs (those with global mutation rates of 0.18 and 0.37) which deviate very significantly from the general trends in the graphs shown in Fig. 2. In these runs, mutation rate adaptation evolves. For the global mutation rate 0.18, this effect is strongest. Data from this run are shown in Fig. 3. Shortly after time step 1000, a pronounced transition to mutation rate adaptation is indicated by a sharp drop of the average mutation modification exponent. This transition has marked effects on average fitness, C_{edit} and m_e (left panel of Fig. 3). On the other hand, no sign of this transition is visible in the time series of various phylogeny-based diversity measures (right panel).

Given the expectation that biodiversity measures should respond to randomization, these observations provide a strong indication that biodiversity can be measured much more adequately on the basis of genetic distances (or other pairwise distances) than on the basis of evaluating phylogenetic trees. While it cannot be ruled out that other phylogeny-based measures would exhibit a significant response to the mutation rate, it is clear that none of the measures we tested does so.

In Fig. 2, two modes of response to mutation rate can clearly be distinguished: While the number of different genomes, m_e and m_{edist} rise monotonically with the mutation rate, C_{edit} steeply rises from 0 in the run without mutation to a maximum at low nonzero mutation rates and decays with further growth of the mutation rate, as described before [13]. Thus, mean edit distance (equation 5) turns out to be a traditional complexity measure (cf. [17]), like the number of different genomes. The example of C_{edit} illustrates, however, that genetic distances are also suitable for calculating alternative complexity measures.

[1] The variation seen in mean tree length (Fig. 1g) is mainly correlated to the number of trees that were analyzed, which varies as the initial phase in which multiple independent phylogenies may have different lengths in different runs.

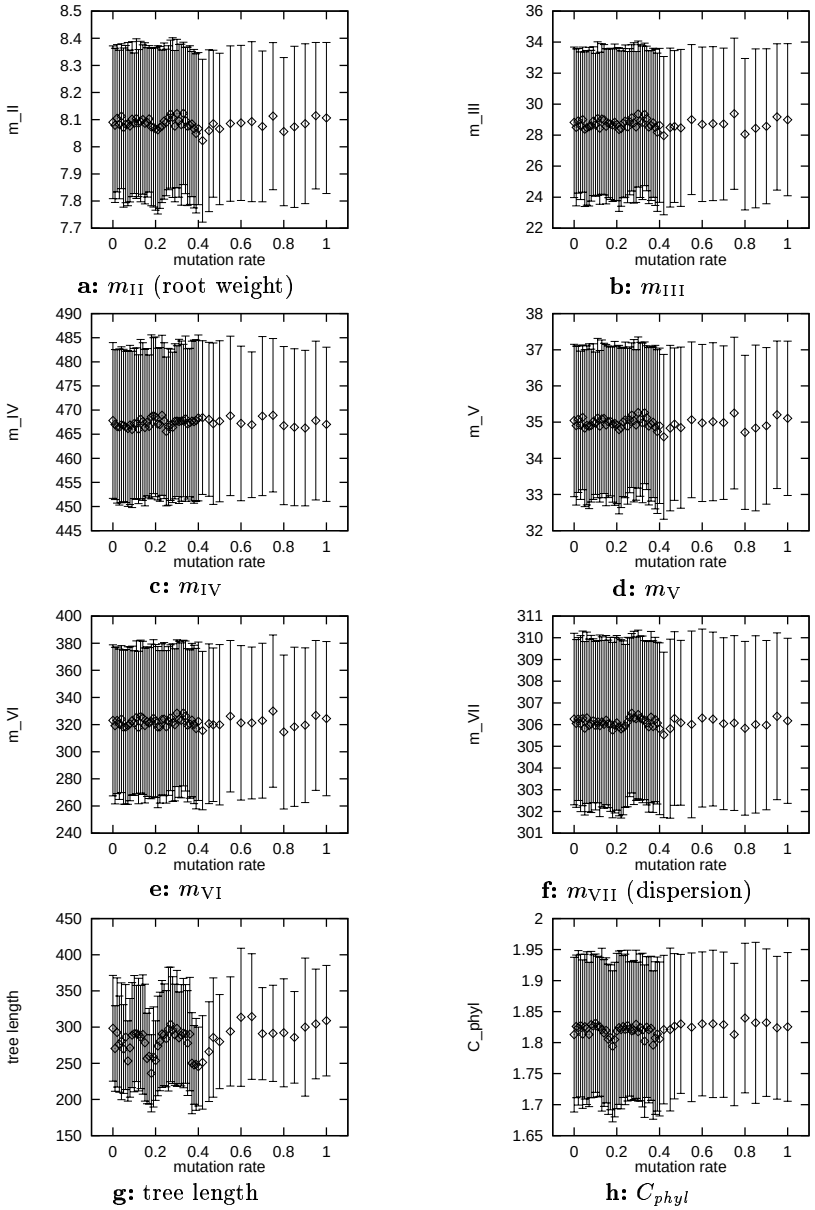
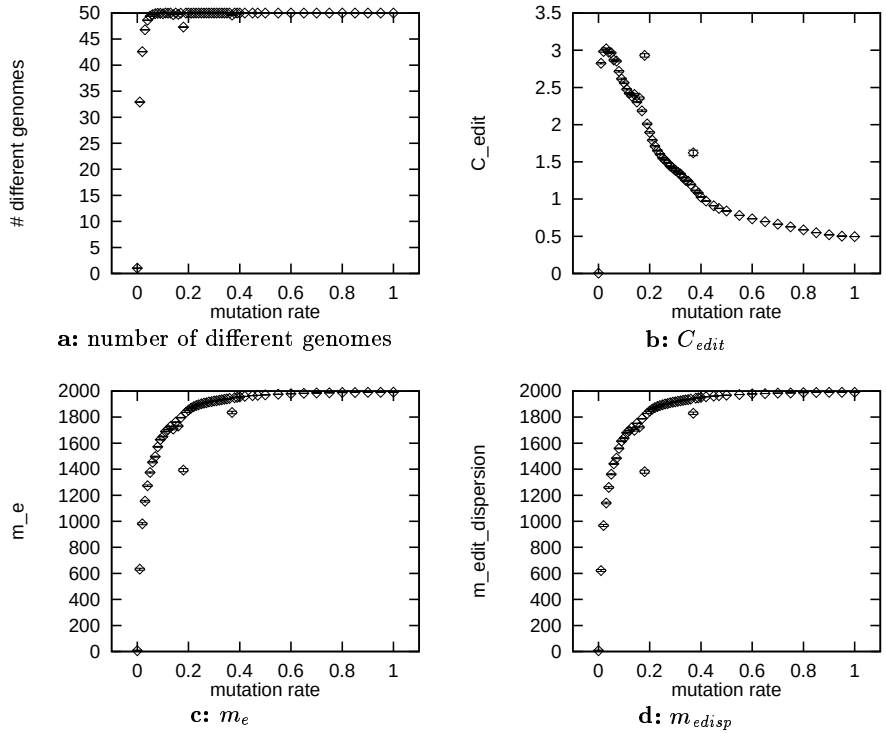


Figure1. Biodiversity measures calculated on the basis of phylogenetic trees. The time averages computed over the entire runs are shown as a function of the global replacement mutation rate setting used in the run. Error bars indicate standard deviations.



a: number of different genomes **b:** C_{edit} **c:** m_e **d:** m_{edisp}

Figure2. Number of different genomes and biodiversity measures calculated on the basis of genetic distances. Error bars indicate standard deviations (very narrow in these graphs).

5 Conclusions

As a result of our investigation, biodiversity measures can be classified into three types, according to their response to increasing mutation rates:

1. Measures which are insensitive to randomization.
2. Measures which monotonously grow with increasing mutation rates.
3. Measures which yield low values at extremely low and high mutation rates, and elevated values in between.

While the second and the third type are well known in Artificial Life [18, 19] and in complex systems, the first type comes as a surprise and raises some questions. One question is: Why do the evolutionary transitions not leave any traces in the phylogeny-based measures? Our answer to this question is that the bare phylogeny is not an useful source of information about biodiversity, at least in LindEvol-GA. A phylogeny arises even in the control runs, where no diversity is generated (zero mutation control) or no biologically meaningful diversity

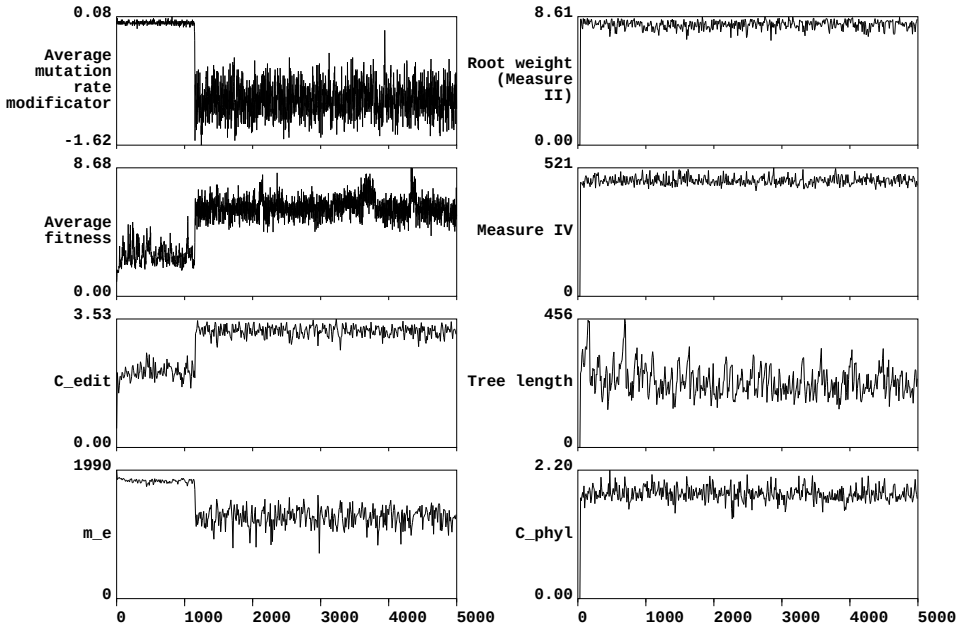
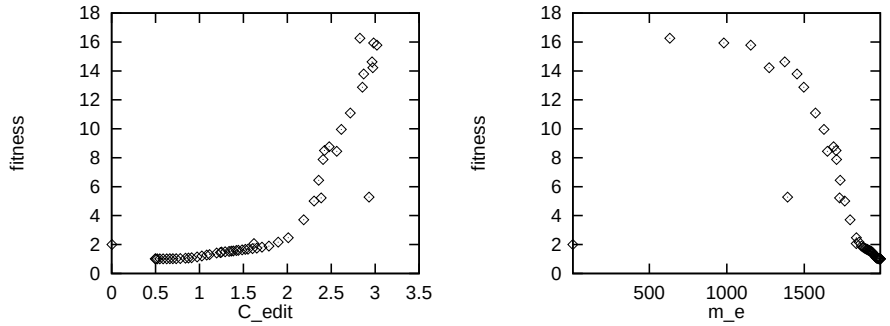


Figure3. Time series of various quantities observed with a global mutation rate of 0.18.

emerges (maximum mutation control). Phylogenies that emerge by evolution which is governed by biological semantics either are not signficiantly different from random phylogenies, or the biodiversity measures we tested fail to respond to such differences. In contrast to this, signatures of the evolution of biologically meaningful information, i.e. of biosemiosis [20], can readily be detected in the genetic distances between the genomes in LindEvol-GA. It may thus turn out that phylogenetic diversity, as quantified by the measures we investigated, is less suitable as an index for biodiversity than genetic diversity.

While the phylogeny based measures have not produced significantly different values for random and biologically meaningful phylogenies from LindEvol-GA, these measures did yield reasonable results in other contexts. Certainly, it is possible that these measures may detect aspects of biodiversity which cannot be modelled by LindEvol-GA. Another explanation, however, is that there is a qualitative difference between the LindEvol-GA data and the other data with which the measures were tested. Usually, phylogenies are reconstructed based on differences in genes or other biologically meaningful properties. These signatures of biological meaning may be partially preserved during reconstruction, and the measures may respond to this information. In contrast to this, we extracted phylogenies from LindEvol-GA independently of differences in genomes or phenotypes, thereby eliminating the information which is relevant for biodiversity. According to this line of reasoning, measurement biodiversity should be based



a: C_{edit} vs. mean fitness **b:** m_e vs. mean fitness

Figure4. Scatter plots showing the correlation of C_{edit} with mean fitnes and the mean number of used genes.

on biological distance data directly; the construction of a phylogeny from these data may be an unnecessary step that obscures the biodiversity signal.

Finally, a question that also remains is whether measures of the second or of the third type are more adequate for characterising biodiversity. We think that the scatter plots shown in Fig. 4 provide a clue that type 3 measures may capture the essential aspects of biodiversity better than type 2 measures. The semantics of LindEvol-GA define that achieving high fitness values is meaningful in that this maximises the chances for successful reproduction. High mean fitness values therefore indicate successful accumulation of information which is meaningful in LindEvol-GA's artificial biology. Fig. 4a shows that there is a pronounced monotonous positive correlation between C_{edit} and mean fitness, while Fig. 4b reveals that the highest values of m_e occur in runs where mean fitness is low. From Fig. 2c, it can be concluded that the low fitness values are due to high mutation rates which prevent the accumulation of significant amounts of biologically meaningful information.

Regarding future directions, we intend to include more diversity measures and to use additional Artificial Life models. We argue that correlations to aspects of biosemiosis should be considered when new biodiversity measures are designed. Assessing such correlations is notoriously difficult for non-artificial systems, but the accumulation of molecular data may open new possibilities. For example, progress in genomics may soon allow to analyse the correlation between numbers of active genes and biodiversity measures, as shown for LindEvol-GA data and C_{edit} in [13]. Molecular data may thus provide a basis for further characterising and understanding biodiversity.

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