

Biological theory and global change science

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Today the anthropogenic transformation of the biosphere is growing exponentially. This is accompanied by an equally rapid deterioration of environmental conditions favourable for humans on both local and global scales. The now well-established coupling of local and global processes raises issues associated with the role of ecological systems undisturbed by modern technological society in maintaining a life-compatible environment on Earth. As a consequence, the biological/ecological component of global change science is conspicuously expanding. It is therefore reasonable to expose to close scrutiny those theoretical biological principles that are employed in global change science, bearing in mind the potential large-scale practical implications of global change studies. The purpose of this brief article is to introduce the reader to such a critical re-examination of two biological principles, for the purpose of stimulating ongoing scientific dialogue on this issue.

There are two related theoretical principles that have been borrowed by global change science from biology and are now used to integrate biological factors into global change studies. These are the principles of “limitation” and “adaptation”. According to the limitation principle, productivity of biological systems is limited by the least available nutrients. For example, the productivity of agricultural systems can be elevated by introducing fertilisers that contain some particular chemical elements.

The adaptation principle refers to the proposition that biological species adapt genetically to changing environmental conditions. Any population is composed of individuals with different genetic composition (different genotypes). The genotypes allowing their carriers to produce the maximum number of offspring are by def-

inition the most fitted to the corresponding environment and enjoy the highest frequency in the population. When the environmental conditions change, different genotypes may appear to be most fitted and will dom-

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inate the population. If there are no genotypes fitted to a new environment, the population becomes extinct.

As well as the limitation principle, the adaptation principle has been verified in artificial, human-supported systems. During artificial selection, populations of natural

biological species are placed under human-created conditions where organisms with properties satisfying the corresponding human needs can be selected, while the wild-type organisms are artificially eliminated from the population. The possibility of artificial creation of new sorts of plants and breeds of animals is interpreted as empirical evidence proving the existence of genetic adaptation.

The two principles are extensively employed in various aspects of the global change research. For example, the “adaptation” principle underpins a fundamental strategy of conservation programs aimed at preserving the biological diversity of Earth under conditions of global change. Significant resources and scientific efforts are allocated to studying and preserving the genetic variability of the endangered species because this variability is assumed to be indispensable in giving the species the capacity to adapt to and survive in the continuously changing environment. The limitation principle is widely used in

the analysis of the global carbon budget – a central topic in global change studies. It is assumed that the oceanic biota does not react to the human-induced increase in concentrations of atmospheric and, consequently, dissolved carbon because its functioning is limited by nutrients other than carbon (nitrogen, phosphorus, iron etc.). As a result, the oceanic dissolved organic carbon pool is excluded from considerations of the global carbon cycle changes. On the contrary, the terrestrial biota, which is believed to be fertilised by the excessive carbon (limiting nutrient), is considered to be

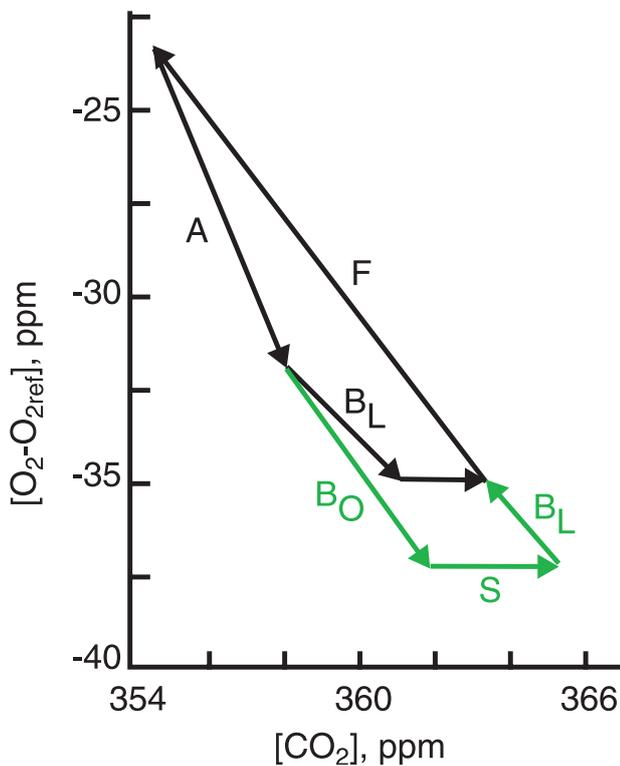


Figure 1. Possible different views on the global carbon cycle as dictated by acceptance/rejection of the limitation principle.

Vectors indicate the three-year (1991-1994) changes in carbon and oxygen content in the major global reservoirs: A — atmosphere, F — fossil fuel, BL — land biota, S — dissolved inorganic carbon of the ocean, BO — oceanic biota (dissolved organic carbon). Vector slopes are determined from the stoichiometric ratios $a \downarrow O_2/CO_2$ for the land biota ($a = 1.10 \pm 0.05$), oceanic biota ($a = 1.30 \pm 0.03$, Redfield ratio) and fossil fuel ($a = 1.38 \pm 0.04$), and by direct measurements for the atmosphere ($a = 2.2 \pm 0.2$, Keeling et al. 1996).

Black vectors: Global carbon cycle as predicted by the limitation principle (from Keeling et al. 1996): the oceanic biota vector BO is missing, the land biota BL becomes a large net sink of carbon.

Green vectors: Global carbon cycle if one accounts for possible reaction of the oceanic biota (from Gorshkov and Makarieva, 1998): the oceanic biota ensures a considerable sink of carbon, the land biota represents a net source of carbon to the atmosphere in accordance with direct measurements of carbon flows from cultivated lands. (The inorganic carbon sink S was determined from $^{13}C/^{12}C$ data under the assumption that the rate of inorganic carbon uptake by the ocean grows proportionally to the relative increment of atmospheric CO_2 .)

the critical carbon sink in terms of the contemporary greenhouse problem, see Figure 1.

As already noted, the validity of these two principles in accounting for biological systems has been tested on examples of organisms artificially extracted from their natural ecological niches. Moreover, they were tested using time periods not exceeding the average human life-span. For example, the limiting principle predicts a short-term increase in productivity of a fertilised plant, but says nothing about the processes of soil erosion and the general instability of cultivated biological systems where such fertilisation is widely used. These negative effects take a longer time to become apparent and are caused by complex interactions among various organisms rather than by processes in the fertilised plant

itself. Similarly, global change processes are impacted by ecological communities rather than by individual organisms and until very recently have been

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characterised by a longer time scale (e.g. the anthropogenic perturbation of the atmospheric composition is more than hundred years old). Nevertheless, following recognition in the scientific community of the need to incorporate biology into global change studies, we suggest that

the two principles noted above have been uncritically adopted without any detailed analysis of their applicability to describing the long-term behaviour of natural ecological communities.

In the meantime, the independent development of both empirical and theoretical global change research has outlined the possibility of a different approach to the problem of biota-environment interactions, where the natural biota is largely responsible for formation and maintenance of a life-compatible environment on the planet. Functioning of natural ecological communities compensates all external environmental disturbances, stabilising the environment in a certain optimum state. (Information needed for such regulation should be then coded in the genomes of biological species that form the ecological community.) It fol-

lows that anthropogenic transformation of natural genetic programs of species in the course of artificial selection, as well as direct anthropogenic disturbance of natural ecological communities, disable the proposed mechanism of biotic regulation.

It is easy to see that if the biotic regulation of the environment is in action, the “adaptation” and “limitation” principles cannot be valid for describing the natural biota.

First, if the biota forms and maintains its environment, there cannot be any nutrients that would limit its functioning. The very notion of limitation becomes meaningless. Second, species cannot adapt genetically to environmental changes, because if the biotic regulation of the environment exists, their reaction to environmental change should be compensatory (not adaptive). In other words, the species do not change themselves, but return the environment to its (pre-perturbation) initial state.

If species changed genetically and became adapted to a new environment, there would be no need for them to return the environment to its previous state. Similarly, if there existed nutrients limiting functioning of the biota, this would mean that biotic regulation of the environment is impossible. This is because the “limitation” principle implies an absence of biotic reaction to changes in non-limiting nutrients (as per the above example with the oceanic biota).

On the other hand, within the biotic regulation approach it is possible to offer a different interpretation of evidence that is commonly interpreted to sup-

port the “adaptation” and “limitation” principles. When an additional amount of a certain nutrient is introduced into an ecosystem, it leads to increased productivity of the corresponding ecological community, which is considered as an experimental proof of the limitation principle. However, an alternative explanation is possible, namely, that the increased productivity represents the biota’s stabilising response to the disturbance of the optimum nutrient concentration. By increasing

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its productivity, the biota is able to return the nutrient concentration in the environment to the optimum in the shortest possible time, storing the excessive nutrient amounts in the form of additionally synthesised inactive compounds. Which of the two explanations is true can be discerned by a long-term continuation of the experiment. If it is indeed limitation of primary productivity by the respective nutrient, then the community will keep the increased productivity for a long time, given that the corresponding nutrient is continuously supplied. No environmental degradation is to be expected. If, on the contrary, it is a stabilising reaction of the community, then, if the perturbation is artificially supported for a long time despite the community’s efforts, the stabilising potential of the community may be exhausted and the commu-

nity may degrade together with its environment. An analogy of such a long-term experiment can be found in agriculture. Primary productivity in modern agricultural systems is currently sustained by continuous increase in supply of fertilisers and is accompanied by continuous degradation of environmental conditions, e.g. soil erosion, which is in agreement with the second explanation of the observed phenomena.

Empirical evidence interpreted in favour of the “adaptation” principle can be summarised as follows: changes in environmental conditions bring about changes in the genetic and morphological properties of individuals. However, appearance of new genetic variants in an altered environment may be a consequence of erosion (i.e. decay) of the normal genetic program of the species rather than acquisition of some new properties. Under natural environmental conditions such erosion is prevented by natural selection, which effectively “monitors” a great variety of morphological properties in individuals. In artificial or significantly distorted environments only a few basic morphological properties of individuals are “monitored”, namely those directly related to viability and artificially selected qualities. Thus, genetic defects may accumulate up to the lethal threshold. Such a process will be manifested as changes in the genetic composition of the population but will have nothing to do with a stable state of adaptation to a new environment. In accordance with this view, the majority of artificially selected plants and animals are characterised by lower fitness (e.g.

lower resistance to infections) than their wild-type progenitors.

Given the extent to which the "adaptation" and "limitation" principles influence global change science, issues associated with whether or not they are scientifically valid is of more than academic interest. As noted above, the extension of the limitation principle to the whole oceanic biota became the sole ground for the exclusion of the latter from the global carbon budget. If one accepts that the oceanic biotic response may be more diverse and complicated than predicted by the limitation principle, it is possible to obtain quite a different picture of the modern global carbon cycle, see Figure 1. For example, the stabilising reaction of the oceanic biota to the anthropogenic disturbance of the atmospheric composition may take the form of changed proportions in production of long-lived and short-lived biomatter, the overall productivity remaining unchanged. If more long-lived biomatter is produced, one may expect to find a significant organic carbon sink in the ocean. Its magnitude can be deduced from the available data on atmospheric O_2/N_2 ratio change and the known stoichiometric C/O

ratios in the biotas of land and ocean as well as in the fossil fuel. As one can see from Fig. 1, such a consideration makes it possible to account for the modern global carbon budget without assuming the existence of a substantial carbon sink on land. Such a sink can hardly be assigned to the terrestrial biota. The latter is significantly transformed by humans, while it is well-known that the exploited lands add carbon to the atmosphere, mostly due to deforestation and soil erosion.

During the course of human history the biological sciences have been predominantly applied to solving the tasks of feeding humans and their medical treatment, while their application to global environmental problems is a more recent phenomenon. We think that the issues raised here are sufficient to suggest that the various scientific paradigms and theories upon which the multidisciplinary endeavour of global change science is based need to be critically evaluated and tested – even if for no other reason than they are being applied in a novel context. The scientific community must foster the fearless re-examination of cherished modes of

thinking should they prove inadequate in meeting the environmental challenges we currently face.

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More discussion at:
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