

FORUM

SPATIOTEMPORAL SCALES OF NON-EQUILIBRIUM COMMUNITY DYNAMICS: A METHODOLOGICAL CHALLENGE

Summary: The Intermediate Disturbance Hypothesis [IDH] and the Gradual Climate Change Hypothesis [GCC] offer intuitively appealing, verbal non-equilibrium explanations to species coexistence in competitive communities, but so far they lack a solid theoretical background and a proper experimental methodology. To make them testable and comparable on a solid methodological basis, they should be formulated as well-defined non-equilibrium community dynamical models. We suggest that this is possible, if explicit assumptions on the spatiotemporal structure of the environment and the pattern-generating mechanisms of the species assemblage in question are given. In the framework of a non-spatial population dynamical model we show that disturbance and climate change effects can be safely distinguished, and the “intermediate” level of external effects leading to maximum community diversity can be quantified. Based on the information statistical analysis of field data and simulation results, we explain why it is necessary to consider simultaneously the spatiotemporal patterns of the vegetation, the abiotic environment and the disturbances in order to predict the consequences of external effects regarding community diversity.

Introduction

Non-equilibrium mechanisms are considered to be hopeful candidates for explaining the diversity of coexistent species in many different communities. The Intermediate Disturbance Hypothesis [IDH] and the Gradual Climate Change Hypothesis [GCC] (Connell 1978, Wilson 1990) are two characteristic examples for such non-equilibrium approaches. These hypotheses have induced a vigorous debate in the Forum section of *New Zealand Journal of Ecology* recently (Wilson, 1990; Padisák, 1994; Wilson, 1994; Reynolds, 1995; Collins and Glenn, 1997). The actual topic of the debate is the role of environmental disturbances and gradual milieu change in maintaining the diversity of terrestrial and aquatic systems, along with arguments about some of the related methodological problems of theory and empirical work. Contributors clarified the criteria to distinguish between the two concepts; however, they disagreed on the related relevant temporal and spatial scales.

Although the heuristic value of IDH and GCC is obvious, we think that, in their present form, they should not be used as working hypotheses, because they are poorly specified. Both hypotheses assume

mechanisms that prevent competitive exclusion either by the increased mortality of the competitive superiors [IDH] or by the permanent rearrangement of the competitive dominance hierarchy [GCC]. Very strong disturbances and extreme environmental changes result in communities of low diversity. Low-level (infrequent, low intensity or small spatial scale) occurrences of these mechanisms cannot prevent competitive exclusions and also lead to low diversity. The trivial expectation, common in both hypotheses, is that there should be some ‘intermediate level’ of these mechanisms that would produce the highest diversity. However, the present versions of IDH and GCC are unable to define, specify, and measure “intermediacy”.

All previous contributors emphasized that population parameters (generation time, growth rates, competitive abilities) and community parameters (successional states) together with the parameters of disturbance regime or environmental fluctuations are important to predict diversity. However, neither have clear quantitative predictions been formulated nor have clear methodological recipes been proposed to define what to measure and at which scales.

In this paper, similarly to Collins and Glenn (1997), we will focus on IDH, but we believe that our points are more general and most of them are also applicable to GCC. We disagree with Collins and Glenn (1997), who, accepting the present historical status, regard IDH only as a 'general conceptual framework' instead of a suitable working hypothesis. In order to improve the currently weak verbal concepts of non-equilibrium mechanisms, we suggest to develop a clear operational methodology that explicitly considers the patterns of coexisting populations, the patterns of the environment, and the related scales. Specifically:

- (1) We stress the importance of building explicit models to test non-equilibrium hypotheses. As an example, we demonstrate that a quantitative solution does exist for IDH even in the frame of a non-spatial model. The spatial patchiness of the community and the environment is not a prerequisite for IDH to work.
- (2) However, the majority of plant communities are patchy, and thus non-spatial models are irrelevant and spatial constraints should be considered explicitly. An appropriate spatial scaling is necessary to quantify diversity, environmental variability, and their interactions.
- (3) We propose a new, pattern-based operational definition of IDH, and suggest that a similar definition of GCC is possible. We show two examples that prove the interaction of disturbance and vegetation patterns.
- (4) We urge that scale-sensitive pattern-analytical methods are required to make non-equilibrium hypotheses operational in future field studies.

The temporal scaling of community dynamics

In contrast to the intuitive expectation of Wilson (1994) who says that IDH can only be based on patch dynamics, first we demonstrate that spatial aspects are not in fact necessary to consider for IDH to be operationalized. Given a non-spatial model of community dynamics, a convenient temporal scaling of population and disturbance parameters is enough to find a specific temporal "disturbance regime" at which extinction is much slower than in the corresponding equilibrium situation. In a seminal paper driving the attention of ecologists to the importance of non-equilibrium mechanisms in maintaining diversity, Huston (1979) studied Lotka-Volterra competition models, where the spatial processes were not considered explicitly. The effect of disturbance event was to reduce all population densities to a certain fraction of their original values.

Disturbances were aspecific in the sense that the densities were cut to the same fraction $1/I$ for all the species; disturbance events were repeated with a frequency f . Assuming that competitive capabilities and reproductive rates are in trade-off, there is an interval of the parameter space where exclusion time is maximal, thus diversity is maintained for the longest time. Huston (1979) established qualitative relations between disturbance frequencies and exclusion times for different dynamical parameters, but he did not quantify what "intermediate" means.

Padisák (1994) suggested generation time as an adequate scaling parameter. Here we show that a few additional scaling parameters are also necessary to determine the range of maximum diversity within these simple non-spatial systems. We apply Huston's (1979) Lotka-Volterra models, specifying the parameter range where disturbances are considered "intermediate". This model offers solid and testable hypotheses for future field experiments.

Clearly, if disturbances are too frequent and/or too intense, then the fastest reproducing species quickly excludes all others. We show that the general condition for this to happen is

$$2f \log(I)/(r_i+r_j) \geq 1$$

to hold for every possible (i,j) species pair, in which r_i is the intrinsic rate of increase for population i .

This inequality defines "strong" disturbance for the non-equilibrium model. Rare and/or weak disturbance allows only the equilibrium competitor to survive; weaker species are quickly outcompeted. If the equilibrium system is such that all but the dominant species die out, the definition of "weak" disturbance is

$$2f \log(I)/\lambda_i \leq \partial(K_d, r_{df}) < 1,$$

where $\lambda_i = |r_i - a_{id} K_d|$ is the estimated speed of exclusion for species i , K_d is the carrying capacity of the dominant, a_{id} is the competitive effect of the dominant species and $\partial(K_d, r_{df})$ is a joint constant composed of the parameters of the model.

Under "weak" disturbance, the behaviour of the system is very similar to that of the equilibrium model. We can say that *the system is disturbed at an "intermediate" level if none of these inequalities hold*. A two-species Lotka-Volterra system (Fig. 1.) shows that exclusion times increase steeply within the parameter range where disturbance is "intermediate".

Quantification of the "intermediate disturbance" is thus rather straightforward in an extended classical population dynamical framework – but how would one represent "global climatic change"? According to the verbal definition of Wilson (1994),

Hutchinson's (1961) qualitative scaling rationale seems most appropriate, assuming that environmental variation affects the dynamical parameters (growth rates, carrying capacities, and competition coefficients) of the equilibrium model. In other words, the corresponding system of differential equations is not autonomous. In this sense the difference of IDH and GCC is easy to identify, at least in the classical (non-spatial) modelling framework: IDH assumes that it is the state variable (density) vector that is directly affected by external disturbances, whereas GCC postulates that it is the vector of model parameters that is directly driven by environmental variation, and population densities change accordingly. Collins and Glenn (1997), similarly to Wilson (1994), distinguished IDH and GCC on the basis of the temporal pattern of environmental fluctuations. Disturbance is associated with discrete and abrupt changes in the environment, whereas GCC is gradual. We argue that this distinction is scaled arbitrarily and we concur with Padisák (1994) that environmental variation should be scaled according to the responses of the organisms. From our definition it is clear that the same physical pattern of environmental fluctuation can be disturbance for some species, if they respond with increased mortality, but it can be a Gradual Climate Change (i.e., stress) for the others, if they respond with changing their performance.

Defining spatial scales is not even possible in classical Lotka-Volterra systems, but a temporal scaling of disturbance parameters is applicable. The range of "intermediate disturbance" is quite easy to define in non-equilibrium versions of the classical approach, thus IDH and GCC can be made operational in systems which conform to these assumptions.

The Spatial scaling of vegetation patterns

Although we have seen that spatial aspects are not necessary to consider for IDH to work in a mathematical model, most biological facts show that they are indispensable to incorporate in any realistic approach. Basic assumptions of classical non-spatial models, such as those of Lotka-Volterra systems, are unrealistic for plant communities (Czárán and Bartha, 1992; Czárán, in press). One of the more unrealistic classical postulates is that each individual of a community interacts with all the others, which means that mass-action type interaction terms can be legitimately applied in ordinary differential equations. The spatial variability of local species combinations, however, is an inherent feature of vegetation (Greig-Smith, 1979), and it has a

profound effect on community dynamics (Czárán and Bartha, 1989; Etter and Caswell, 1993; Durrett and Levin, 1994; Tilman, 1994; Lavorel and Chesson, 1995), which should not be omitted in models.

In non-spatial models, due to the homogeneity assumptions, the number of species and the species/abundance diversity are appropriate indicators of diversity and coexistence relationships. However, in real plant communities these diversity parameters are inappropriate from two reasons. First, they depend on the study area or volume considered (Arrhenius, 1921), that makes these estimates inherently arbitrary (Wilson, 1990). Second, because of the local variability of species combinations, a coarse resolution estimate of species richness does not inform about the details of how species interact and coexist at finer scales.

Having recognized this frustrating scaling problem, Juhász-Nagy (1967, 1984, 1993) developed a new methodology based on information statistics for describing coexistence relations in plant communities). His major innovation was to work with the diversity of observed (realized) species combinations estimated across a range of spatial resolutions (i.e., in samples recorded with a series of different sampling unit sizes):

$$\hat{H}_j(A, B, \dots, S) = - \sum_{k=1}^z p_{kj} \log p_{kj}$$

where p_{kj} is the probability of the k th species combination in the sample of sampling unit size j , and $z=2^s$ is the number of possible species combinations of s species.

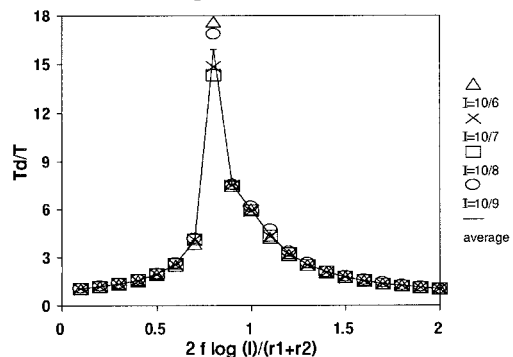


Fig.1. The relative exclusion time, T_d/T , of the competitively subordinated species as a function of $2f \log(I)/(r_1+r_2)$, a relative disturbance measure, in a 2-species system. Two dimensionless scaling variables are compared: the strength of disturbance determined by its frequency (f), its intensity (I) and the growth parameters of the two species (r_1 and r_2), and the effect of it on the system characterised by the ratio of exclusion time in the disturbed (T_d) and the undisturbed (T) case. $r_1=2.5$ and $r_2=2.0$ are fixed.

This new type of diversity, called 'compositional diversity', refers to the spatial variability of within-community local coexistence of species. If spatial autocorrelation exists between individuals and if spatial association exists between species, then the field estimates of compositional diversity will differ from random expectation. The difference, called 'overall association' can be interpreted as an estimate of the total spatial dependence among species combinations. Similar to other spatial statistics, e.g., the variance of species number/quadrat (Wilson *et al.*, 1987), these models plotted against quadrat size follow maximal curves (Juhász-Nagy and Podani, 1983). However, in Wilson's approach, if two quadrats have the same number of species, they are taken as identical, while in Juhász-Nagy's approach all quadrats with different species lists are distinguished. Distinct species combinations refer to the patches within the communities, therefore the Juhász-Nagy models give a detailed description of the within-community patchwork. This new method reveals that the natural complexity of within-community patchwork is deep, usually one or two magnitudes greater than the number of patch types artificially distinguished in field studies testing hypotheses of species coexistence (Fig.2.). A series of case studies (e.g. Juhász-Nagy and Podani, 1983; Szollát and Bartha, 1991; Podani *et al.*, 1993; Tóthmérész 1994; Bartha *et al.*, 1995) demonstrated that (1) the spatial scales where the Juhász-Nagy models reach their maxima are different according to the type and dynamical state of communities, and (2) the models adequately characterize the patterns studied.

Wilson (1994) pointed out that instead of the

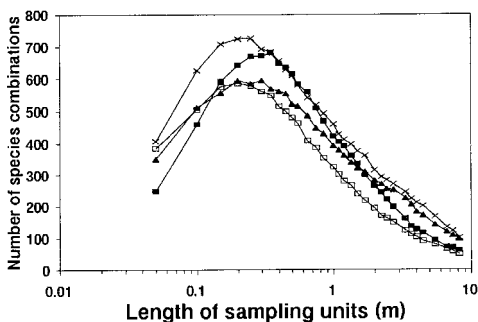


Fig.2. *Within-patch complexity of coexistence exemplified with grassland communities. (Estimated from transects of 1024 contiguous 5x5cm sampling units. Recalculated from Szollát and Bartha, 1991; Bartha *et al.*, 1995; Hochstrasser, 1995; and unpublished data.)* \square open sand steppe. \blacksquare open dolomite grassland. \times closed loess grassland; \blacktriangle upland tallgrass prairie.

community extent, the relative sizes of the disturbance patch (a contiguous area within which the effect of a disturbance is uniform) and the sampling area (the scale at which we sample) are relevant in disturbance-induced non-equilibrium community dynamics. Because the scale of the sampling area is artificial, we suggest that *the relative sizes of disturbance patch and the characteristic maximum area of the community* (where the within-community heterogeneity is maximal) are eminently relevant. It can be expected that the area within which the compositional diversity is maximal, is an important natural threshold, because if disturbance patches are smaller than this maximum area, then individuals of abundant species have a disproportionately high probability to be killed. The rare species will be favored by this scale of disturbance. If rare species are favoured, diversity will increase. Another aspect is the recolonization after disturbance events. If the scale of disturbed patches is in the magnitude of the maximum heterogeneity area of the community, bare patches will be recolonized the most diverse way. This again, will increase diversity.

Interaction between disturbance patterns and the spatial pattern of the disturbed vegetation

The verbal explanations of the IDH suggest that communities can be considered as asynchronous mosaics of disturbance patches in different stages of post-disturbance succession. Disturbance-patch is defined as "a contiguous area in which the effect of disturbance is uniform" (Pickett and White, 1985; Petraitis *et al.*, 1989; c.f. Wilson, 1994). This definition implies that (1) disturbance can be uniform over an area, (2) this area is detectable, and (3) the finer-scale pattern of vegetation within a disturbance patch is irrelevant or negligible for the dynamics of vegetation. Most of the field studies testing IDH were based on these assumptions.

However, we do not know of any field study which directly tested these assumptions. If disturbance does not completely destroy the vegetation, this definition is difficult to apply in the field. In our opinion, the controversy of whether IDH is a 'between-' or 'within-patch' phenomena (see Wilson, 1994; Collins and Glenn, 1997) originated in the non-operational definition of disturbance-patch, and the related scaling problems.

We report here a field study to demonstrate that fine-scale vegetation patterns interact with larger scale physical disturbances. Based on this result, we give a better operational definition of disturbance. Finally, we show, using simulation methods, how

fine-scale vegetation patterns are relevant in non-equilibrium dynamics.

To test the relationship between fine-scale pattern of vegetation and the larger scale patterns of disturbances, we sampled the spatial pattern of tallgrass prairie vegetation along a disturbance gradient of increasing frequency of fire. The vegetation data was analyzed by the methods of Juhász-Nagy (1967, 1984, 1993). The experiment was the same cited by Collins and Glenn (1997). The management units, several hectares each, had the same uniform vegetation before the experiment started (Hulbert, 1978). Therefore, the differences we found in vegetation patterns of different management units along the disturbance gradient should be attributed to the temporal pattern of spatially uniform physical disturbances alone. Fig. 3. shows that *within a disturbance patch, the fine-scale spatial patterns are obviously affected by disturbance frequency*: compositional diversity seems to follow a weak maximum trend, and spatial associations vanish as the frequency of fires increases. The maximum trend of compositional diversity can be regarded as a spatiotemporal manifestation of IDH; the decrease in the strength of local associations demonstrates that *even spatially uniform disturbances can induce the spatial restructuring of vegetation*.

Definition of disturbance

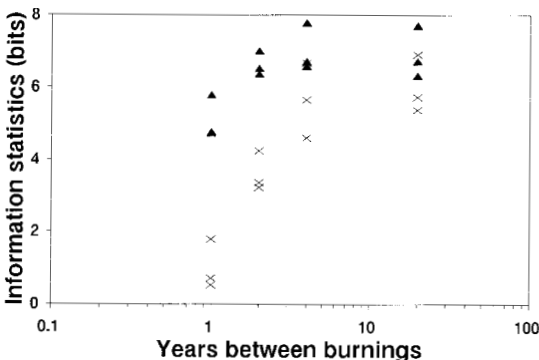


Fig. 3. *Fine-scale pattern transformations within disturbance patches in tallgrass prairie vegetation along an experimental disturbance gradient. Each treatment was sampled by 3 transects of 512 contiguous 5x5 cm sampling units (data from Bartha, unpublished). ▲ maximum compositional diversity. × maximum overall association of species*

The results presented on Fig. 3. imply the necessity to distinguish between the physical agent of disturbance (i.e., the burning), and the effect, the resulting biological disturbance (the pattern of dead individuals). Clearly, the pattern of dead individuals depends on the pre-disturbance pattern of the vegetation. This is what Padisák (1994) stresses: “Disturbance does not exist per se. It is impossible to define it without involving the entity that is affected.... There are both spatial and temporal aspects...”.

Therefore, we propose that disturbance should be defined as a *multi-species, spatiotemporal pattern of mortality of non-competitive origin*. This pattern-based definition is general, yet sufficiently operational because both the spatio-temporal pattern of dead and surviving individuals can be detected and analysed by appropriate spatial statistical techniques. In this way we can generate a clear rationale for field measurements and data analysis.

We argue that we should distinguish:

- the physical disturbance agent (e.g. fire) that can be measured by physical methods and
- the effect, the ‘disturbance’. It is important to realise that the same physical disturbance agent can cause different ‘biological disturbance’ (for example, the effect of the same hurricane will be different in a forest vs. a prairie). This latter can only be measured through the resulting effect, the mortality pattern. This mortality pattern is superimposed on the mortality pattern resulting from the competitive interactions. If the original, pre-disturbance pattern has fine-scale spatial constraints, this needs to be taken into account when measuring the effect of disturbance, too. The usual time-related pattern as well as the spatial pattern has to be analysed.

Dependence of the realized disturbance effect on the pattern of vegetation

We demonstrate our approach on a simulated community. For this demonstration, we used a spatially-explicit, individual-based Monte Carlo competition model to generate multispecies community patterns. (For more details about the model and applications see Czárán and Bartha, 1989; Czárán, 1993). Simulated plant communities consisted of 10 species, both annuals and perennials, with trade-offs between their competitive abilities and reproductive capacities. Two types of communities were generated. One with an additional trade-off assumed between the competitive and the dispersal abilities of the species, i.e., the dispersal capacity of strong competitors was weak and vice

versa. Very limited dispersal produced a patchy vegetation, even in the absence of disturbance. In the other community type, dispersal limitation was released, so that the spatial pattern of the community was random at all times. The simulated community processes were in all cases disturbed with spatially contagious and temporally cyclical mortality events, in a series of increasing disturbance frequencies. The spatiotemporal patterns of living and dead individuals were sampled and analysed in accordance with the methodological instruction implied in the definition of disturbance above. The information statistical technique of Juhász-Nagy (1984, 1993) was applied to measure compositional diversity at the characteristic (maximal) points of the spatial scale.

Conforming to the expectation of IDH, the maximal compositional diversity appeared at an intermediate disturbance frequency (Fig.4.). The disturbance frequency that produced the highest diversity was, however, different for the two types of vegetation, illustrating the dependence of the effect of disturbance on the pattern of vegetation. The rate of species extinction is slower when dispersal is limited, thus the corresponding patchy vegetation requires less frequent disturbance to maximise compositional diversity. We see a clear correlation between the compositional diversity of living and dead vegetation, but the response of mortality patterns was stronger to the changing frequency of physical disturbances than the response in the pattern of living vegetation.

Our results showed that there was a correlation between the patchiness of vegetation and the frequency of disturbance that produced the highest

diversity: the spatial pattern of vegetation imposed constraints on its dynamics. Logically, we should measure these constraints with appropriate spatial statistics, and their effects should be taken into account in our hypotheses. The traditional, hypothesis of IDH is weak because it is unable to distinguish between the two simulated cases presented here (Fig.4.a.): it cannot explain why the *more patchy vegetation had its highest diversity at less frequent disturbances*. We suggest to improve IDH in the future with coupling temporal and spatial scaling, i.e., coupling the measurement of dynamical parameters with the measurement of the related spatial patterns.

In case of the GCC, similar arguments about the importance of spatial relationships are relevant. Performances of individuals are spatially variable (Hara 1988) and spatial variability of individual performances have a stabilizing effect on plant species coexistence (Hara 1993). Therefore these spatial patterns cannot be omitted when GCC is tested. We propose that the Gradual Climate Change Hypothesis should also be redefined and studied in a spatially-explicit way.

The 'pattern to pattern' approach

For historical reasons, non-equilibrium mechanisms were first studied in the framework of non-spatial population dynamical models (Huston, 1979). Classical field experiments were designed to test the predictions of these (Sousa, 1979a,b; Armesto and Pickett 1985; Collins *et al.*, 1995), mostly using non-spatial statistical methods. Recent

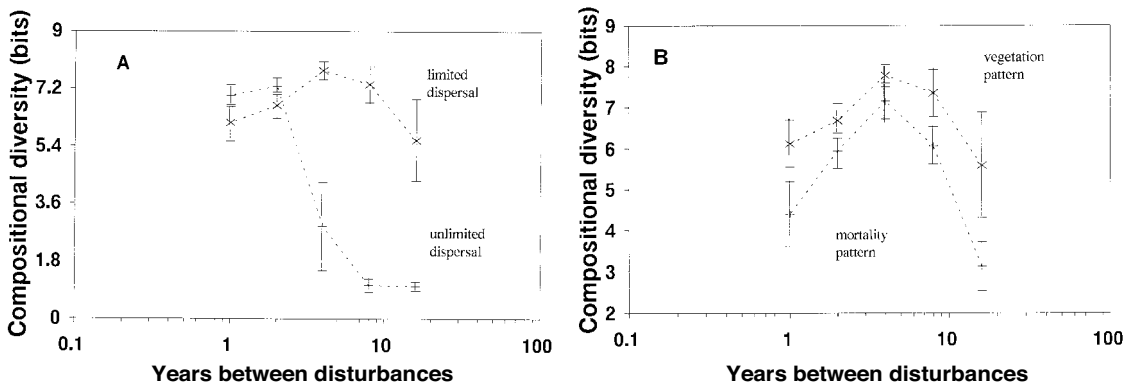


Fig.4. Simulated transformations of compositional diversity along a disturbance frequency gradient. A, Responses of communities with limited and with random (unlimited) dispersal. B, The survival and the mortality response of the community with limited dispersal.

population and community dynamical models clarified the importance of spatial structure in relation to persistence and coexistence issues (Czárán and Bartha, 1992; Etter and Caswell, 1993; Lavorel and Chesson, 1995; Czárán, in press), but field ecology seems to lag behind theory in this respect.

For reasons explained above, we think that any field study aiming to provide evidence for the existence and the relevance of a particular mechanism in maintaining community diversity - such as IDH or GCC - is wasted without an experimental design sensitive to the spatial and temporal scales of community dynamics. The importance of spatiotemporal patterns in the dynamics of natural communities had been recognized as long as 50 years ago (Watt (1947), but this has had little impact on actual field sampling designs. Since vegetation is a spatiotemporal phenomenon adapted to and perturbed by the spatiotemporal patterns of the environment, the time is more than ripe to reconsider our field sampling methodology in Watt's spirit.

Therefore we think that a sensible and operational program should start by exploring characteristic spatial and temporal scales from field patterns of (1) populations, (2) environmental variables and (3) disturbances, with the help of scale-sensitive statistics. The information thus obtained can be used as the input parameters of an appropriate spatiotemporal model, in order to assess the contribution of a certain mechanism to species coexistence. This way the relations of the scales of all the relevant patterns could also be discussed on a solid methodological basis and unnecessary misunderstandings stemming from confusing terminology could be avoided.

The real paradox of the Paradox of the Plankton is a methodological one: we try to describe the complex reality with simplex models. The heuristic appeal of IDH and GCC tempts us to search for simple explanations applying to diverse field situations from aquatic to terrestrial communities. We are tempted by an explanation that is devoid of complications unavoidable in scaling problems and the inherent complexity of ecological entities. Yet, it seems to us that these complications simply cannot - and should not - be ignored if we seek to move beyond heuristics to prediction and comprehension.

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