

FORUM

IDENTIFICATION OF RELEVANT TIME-SCALES IN NON-EQUILIBRIUM COMMUNITY DYNAMICS: CONCLUSIONS FROM PHYTOPLANKTON SURVEYS

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This paper is a reflection on J.B. Wilson's (1990) publication which presents an attempt to understand the development of terrestrial plant communities of New Zealand against twelve different explanations of Hutchinson's Paradox. I make a rough comparison between terrestrial and planktonic communities; then I briefly review Hutchinson's Paradox and some of the later relevant phytoplankton results. I summarize the relevance of the IDH in phytoplankton dynamics, assessing its strengths and weaknesses; and finally, try to project our conclusions to terrestrial plant communities; this concerns chiefly the need for appropriate spatial and temporal scaling.

Keywords: scale; Intermediate Disturbance Hypothesis; community dynamics; paradox of the plankton; disturbance.

Introduction

Recently, Wilson (1990) tried to assess the importance of different mechanisms for species coexistence and their relevance in New Zealand plant communities. He tested twelve different explanations of Hutchinson's (1961) Paradox. One of the twelve explanations that Wilson considered and rejected as a mechanism of any importance is Connell's (1978) Intermediate Disturbance Hypothesis (IDH). The hypothesis states:

- 1) In the absence of disturbance (eternal steady state), competitive exclusion will reduce species diversity to minimal levels.
- 2) Under very intense disturbance only a few populations of pioneer species could establish themselves after each disturbance event. This would also lead to minimal diversity.

- 3) If disturbances are of intermediate frequency and/or intensity there will be repeated opportunities for the re-establishment of pioneer populations which would otherwise be outcompeted and the populations of the successful competitors could withstand the disturbance without completely taking over the community. Thus, a peak of diversity should be found at intermediate frequencies and intensities of disturbance.

As a phytoplankton ecologist I cannot completely share Wilson's interpretation of non-equilibrium explanations of the Paradox (briefly, 'there is never time for competitive exclusion to operate'; Wilson, 1990), although I agree with his general conclusion: non-equilibrium dynamics, and non-equilibrium models (IDH and the Gradual Climate Change Model, GCC) are of particular importance. I do not deal with density dependence nor with equilibrium concepts. In pelagic environments biomass can be thousands to hundreds of thousands times more dilute than on land (Cohen, 1994). Therefore, many of the density dependent mechanisms or equilibrium concepts are difficult to interpret in hydrobiology, although there are instances where they can be of prime importance.

Terrestrial and planktonic plant communities and their successions

The profound differences between terrestrial and planktonic vegetation are evident. Phytoplankton species are small (generally 10^{-2} - 10^{-7} m) and live short lives (10^4 - 10^7 s). Primary producers on land (especially in forests) are the biggest and longest living ones in their ecosystems. Plotting the generation time against the body size of

characteristic groups (plants, herbivores, other invertebrates, vertebrates), Cohen (1994; see Fig. 1) demonstrated the upside-down structure of marine food-webs as compared to terrestrial ones.

High diversity both in aquatic and terrestrial ecosystems can be explained by reference to internal and external mechanisms, and their heterogeneity through space or time. Traditionally, internal mechanisms are associated with terrestrial ecosystems while community changes in the open water are associated with external ones. These differences between the alternative explanations were justified through the overlap in the space and time scales of ocean physics and biology compared with separation between scales in most atmospheric systems (Steele, 1991). The basic assumption is that terrestrial populations exist in a 'white noise' atmosphere, whereas aquatic populations are embedded in a 'red noise' environment (Steele and Henderson, 1994).

Probably Elton (1927, pp. 59-60) was the first in modern ecology who assumed that uniform principles operate in sea and on land. Contemporary ecologists also stress that they 'assume that the laws of physics, chemistry and biology are the same in oceans and on continents' (Cohen, 1994); or that '...ecology' does not alter simply because its factual basis is assembled from observations on different systems' (Reynolds, *in press*).

While succession theories for terrestrial habitats date back as early as the beginning of this century (Clements, 1916; Gleason, 1917, 1927), similar theories were lacking for phytoplankton for a long time. The few attempts (e.g., Pankin, 1945) at classifying algal associations have never received wide acceptance (see the review by Symoens, Kusel-Fetzmann and Descy, 1988). The first general concept of plankton succession, the so-called Plankton Ecology Group (PEG) Model, was developed during the 1980s (Sommer *et al.*, 1986).

Meantime, the "classical" succession theory underwent many changes (Pickett and McDonnell, 1989); most notably it embraced stochasticity (Drury and Nisbet, 1973; Czárán and Bartha, 1992). The Mosaic Cycle Theory of plant succession (Rimmert, 1991) questions the self-sustainability of the final state, consequently, the existence of a true climax in terrestrial plant communities. This statement is very important from the point of view of making connections between terrestrial and planktonic successions since it was a dogma that planktonic succession does not exist because climax vegetation can never develop (Whittaker, 1974).

Phytoplankton communities typically undergo significant changes within individual calendar years ('seasonal succession'). Seasonal succession of

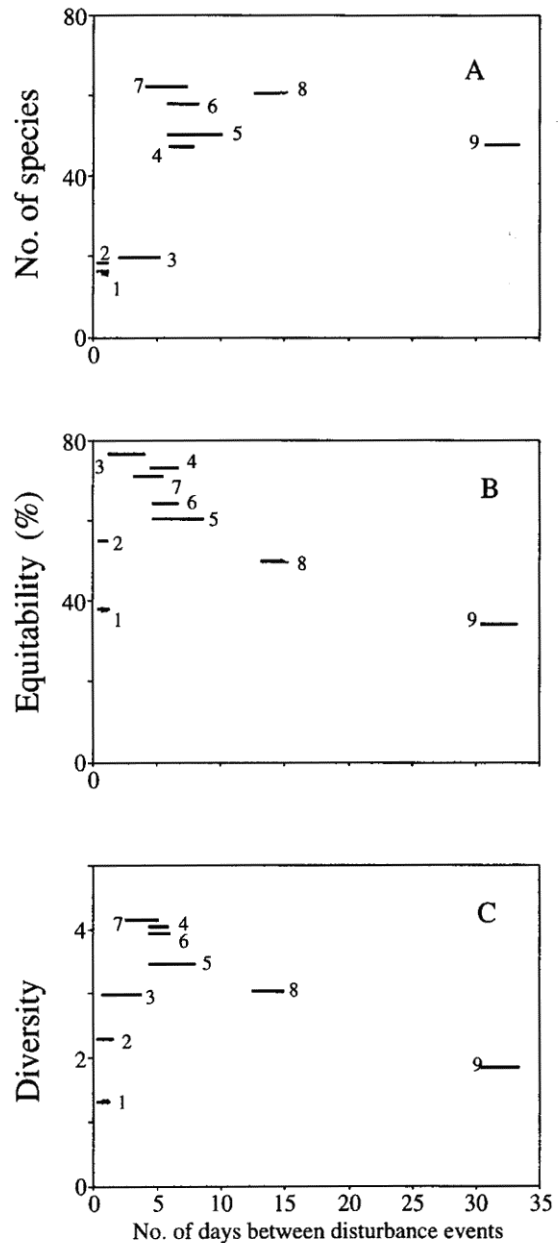


Figure 1: Arithmetical means of species number (A), equitability (B) and diversity (C) estimated by Shannon's function in different lakes and/or years based on 759 phytoplankton samples. See Padisák (1993) for details. Here, corresponding data sets are supplied with identical numbers. (Redrawn from Fig. 20 in Padisák, 1993, with permission of Kluwer Academic Press).

phytoplankton has more analogies with the succession of terrestrial vegetation than with its seasonal phenomena. Many generations are involved, and there are several quite predictable and distinct phases, etc. On the scale of generation times, periods of several months in plankton succession correspond to decades in grassland and centuries in forest succession. Under favorable physical conditions, the intrinsically transient nature of early and mid-successional phases as well as the self-sustainability of final stages can be shown. It is only the external cycle in climatic and hydrological conditions that forces plankton succession to restart each year (Sommer, 1991). In this way, the 'plankton year' is analogous to glacial and interglacial cycles.

Considering the above, it appears quite paradoxical that while terrestrial ecologists are tending to share the Gleasonian view about plant community structure (Wilson, 1990: General conclusions, p. 31), phytoplankton ecologists discovered Clementsian elements in phytoplankton communities. Are phytoplankton assemblages more "Clementsian" than the terrestrial plant communities?

Hutchinson's Paradox

Natural lakes can be very rich in phytoplankton species. Many of the species are rather erratic in their appearance and abundance; others are more predictable but still very rare, when compared to the densities of the few dominant species (Padisák, 1992). The Competitive Exclusion Theory (Hardin, 1960) predicts that only as many species can coexist as there are limiting factors. Observation and theory contradict each other. Hutchinson (1961) termed the apparent contradiction between the number of species and the number of limiting resources the "Paradox of Plankton". In his original paper, Hutchinson suggested several possible explanations for his Paradox, including that the boundary conditions of competition change frequently enough to invert competitive hierarchies before exclusion occurs. It is widely accepted that the importance of the Paradox is not restricted to plankton communities (e.g., Grime, 1973).

Referring to time scales of disturbance, Reynolds (1988) translated the qualitative terms 'frequent', 'rare' and 'intermediate' of Connell's (1978) IDH to real time-intervals.

The Intermediate Disturbance Hypothesis and the phytoplankton

Before discussing whether or not IDH fits phytoplankton dynamics, it is essential to first answer

several general questions. What is disturbance? What is its origin? How is it identified? How do you measure it? The following discussion is mainly based on Padisák, Reynolds and Sommer (1993).

The nature and origin of disturbance

In his original paper, Connell (1978) considered disturbances primarily originating from internal processes (e.g., treefall gaps caused by the death of senescent trees). However, there is no *a priori* reason why disturbances of external origin should have different consequences on species diversity. The distinction between external and internal origin of disturbance is less important than the occurrence of disturbance *per se*. This empirical statement was later theoretically supported by Steele and Henderson (1994), who concluded, that 'the coupling between these different [biological and physical] scales, rather than the nature of the internal or external processes themselves, can provide a partial description, if not an explanation, of the diversity of patterns'.

Planktonologists tend to consider sustained thermal stratification as the 'undisturbed state' of a lake. However, permanent circulation can also create low disturbance status while a sudden stratification qualifies as disturbance (a terrestrial analogue may be to consider regular livestock grazing on a grassland or mowing the garden lawn as undisturbed states). For this reason Chorus and Schlag (1993) found it helpful to refer to 'Intermediate Quiescence'.

Definition of disturbance

Scientists using the term 'disturbance' rarely try to define it; exceptions are rare (Grime, 1979; Rykiel, 1985; Pickett *et al.*, 1989). Reynolds *et al.* (1993b) developed a working definition: "disturbances are primarily non-biotic, stochastic events that result in distinct and abrupt changes in the composition and which interfere with internally-driven progress towards self-organization and ecological equilibrium; such events are understood to operate through the medium of (e.g.) weather and the frequency scale of algal generation times". This definition, if applied to communities other than phytoplankton, can be easily reformulated; for example, biotic events may be stressed; weather can be replaced by seasonal cyclicality or different kinds of climatic fluctuations.

Disturbance does not exist *per se*. It is impossible to define it without involving the entity that is affected in the definition. There are both spatial and temporal aspects.

Temporal scaling

Individual analyses on phytoplankton structure *vs.* disturbance frequency supported Reynolds' (1988) scaling (Fig. 1c). Fig. 1a and 1b demonstrate that in accordance with Connell's theory, diversity is low at high frequencies of disturbance (because species' number becomes very limited), while at low disturbance frequencies low equitability diminishes diversity. The development of a near-equilibrium state may require 12-16 generations spanning 35-60 days in summer in the temperate regions. Diversity reaches a peak between the second to fourth generation (5-15 days).

Fig. 1c can be redrawn in a generalized form, using generation time as the units of the independent variable (Fig. 2). For the transformation of days into generation time, a net growth rate of doubling every 2.5 days was used. This figure shows a close agreement with Connell's (1978) original figure. Nevertheless, its asymmetry must not escape attention: the rate of change of diversity is much higher when disturbance occurs every 1-5 generations than less frequently.

Applicability of IDH to phytoplankton changes

The previous section demonstrates that the IDH is an appropriate theory to understand many events in the seasonal succession of phytoplankton. However, it is difficult to ignore the weaknesses of the concept.

Several of the case studies did not detect an effect on phytoplankton diversity of a supposed disturbance. For example, in a Finnish lake, community structure tended toward a late-summer

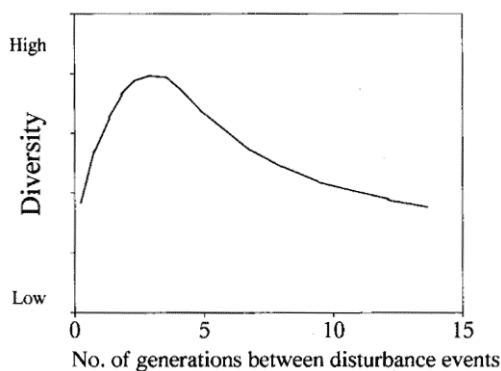


Figure 2: The smoothed diversity-disturbance relationship in phytoplankton using the data of Fig. 1c and transforming days to generation time on the x-axis (see text).

complexity independently of the imposed disturbance patterns (Eloranta, 1993).

The regular periodic events in the plankton (significant changes in the grazing pressure at the onset of the clear-water phase, autumnal cooling) are followed by significant changes in community structure and diversity. Thus, the relative importance of intermediate time scale disturbances has its own seasonality: it is increasingly important in periods in which competition among phytoplankton species is increasing.

It is difficult, if not impossible, to apply the IDH in highly flushed systems or in environments characterized by extremes of acidity, alkalinity, turbidity, etc.

In spite of the difficulties (or as a consequence of them) that arise when we try to quantify 'disturbance' (see below), numerous case-studies (Jacobsen and Simonsen, 1993; Olrik and Nauwerck, 1993; Reynolds, 1993) demonstrated that the effect of disturbance depends upon the perception of the structure of the ecological system concerned. In general, the earlier in the succession a given stimulus is imposed, the greater and more immediate is the compositional response. Advanced phases appear to be less sensitive to external disturbances.

Another controversial feature of the IDH is that it not only maintains species richness in an ecosystem, but, as a mechanism, it requires its *de facto* existence. If equilibrial species (K-strategists) are absent, alternative early successional colonists replace each other, even if the circumstances are appropriate for a progress towards an 'equilibrial species' dominated community (Padisák, 1993).

Diversity and disturbance, despite the demonstrable connection (Figs. 1c, 2), are only indirectly linked through the hierarchical structure of the ecosystem. By quantifying the biotic response (diversity) rather than the stimulus (disturbance), the problem of commensurability is circumvented. However, it is replaced by a danger of circular reasoning in that the strength of the disturbance is the strength of the biotic response (Sommer, 1993). This is why Juhász-Nagy (1993) stated: 'IDH is still too weak for a proof or disproof... in its present form, [and] is not suitable either for verification or falsification'.

Possible consequences for higher plant communities

Wilson (1990) considered many of the possible sources of disturbance described by other authors as occurring on a 'too large' spatial and/or a 'too long' time scale. He considered only snow break and

freeze-thaw soil heave in alpine zones and treefall-gaps to occur on the 'required scales'. According to his opinion, Gradual Climate Change (GCC) was the most likely factor for maintaining diversity in New Zealand.

I cannot completely share Wilson's interpretation of the non-equilibrium explanations of the Paradox, although concerning the final conclusion I agree with him: non-equilibrium dynamics, and non-equilibrium models are of particular importance. Wilson's (in my opinion) misinterpretation is driven from several sources, most notably from insufficient scaling and a misunderstanding of the original description of the IDH (Connell, 1978).

The spatial scale

Wilson takes extreme care to quantify the spatial scale, and he uses a value of 10^3 m^2 (0.1 ha) as the limit of the within community (alpha) diversity. Consequently, he excludes most of the possible case studies that would support IDH (listed under 15-17 in Table 1 in Wilson, 1990), because they do not occur on this required scale.

My question is: does not the appropriate spatial scale depend on the spatial extension of communities? Several of them occupy square kilometers and others are restricted to square meters. Why apply 0.1 ha for each of them? Probably Wilson also recognized the trap of the uniformly fixed patch-size when writing about the need of documentation on the spatial scale of both disturbances and vegetational response.

A plankton analogue can be the description of horizontal patchiness in a large lake ($10^4 - 10^5$ ha) and a small pond ($10^{-2} - 10^{-1}$ ha). If the small pond is dominated by flagellates that can swim with a speed of some m day^{-1} , most of the horizontal patchiness can be explained by growth and migration. The explanation of patchiness in a large lake requires comparison of the growth rate of organisms within the patch to the eroding effect of horizontal water currents (Reynolds *et al.*, 1993a). Vertical heterogeneity in plankton is analogous to the vertical stratification of terrestrial plant communities even if the organisms can move freely from one stratum to another.

The temporal scale

While Wilson is very accurate (even if too rigid) in quantifying the spatial scale, I could not trace a similar effort in quantifying the time-scale.

As it was clearly demonstrated by plankton ecologists, the generation time is the unit for judging what 'short', 'long' and 'intermediate' are

(Fig. 2). Without quantifying it, it is impossible to define disturbance frequency. In forests, the unit can be the characteristic renewal time. The exact length of the unit will be different for forests, grasslands, etc.; consequently the 'required' intermediate frequency of disturbance will also be different.

Ács and Kiss (1993) faced a similar problem when they tried to apply the IDH to periphytic algal communities. Their 'intermediary time' was about twice as long as suggested in Sommer *et al.* (1993, Appendix).

I should mention here that Whittaker (1974) was in principle right when he started to classify different formations (communities) according to how the length of their life cycles related to environmental fluctuations. Then he came to the (wrong) conclusion that a climax state in plankton can never be achieved (permanent aclimax) because life cycles of planktonic organisms are too short compared to environmental fluctuations. He missed the point that the periodicity of environmental fluctuation does not equal the periodicity of seasons. As a consequence of short generation times, plankton communities are responsive to meteorological variability. The 'weather' experienced by terrestrial vegetation is the 'climate' perceived by phytoplankton (Sommer *et al.*, 1993).

The 'required' frequency and the frequency of climatic cycles

Wilson concludes that the GCC is probably the major explanation of the Paradox in New Zealand.

Larger climatic cycles are usually understood to alter in a frequency measured in centuries. These hundreds of years in climatic cycles divided by a supposed forest renewal time of 100-200 years ('Even 1000 years is within a generation or two for some species'; Wilson, 1991, p. 18) provide a number of 2-8, just the required frequency for disturbance to be classified as 'intermediate'. Smaller mesoclimatic cycles (dry and wet periods) can appear on a scale of decades, an appropriate intermediate scale for grasslands, where the renewal time is probably shorter. Superimposing all these environmental cycles/events, and bearing in mind that it was necessary to complete the IDH theory with features of the GCC (necessity for a species pool, see *The storage effect*, below), I cannot see any essential difference between the IDH and the GCC. This opinion is supported by the recent modeling results of Steele and Henderson (1994) according to whom 'climate change can have impacts at scales less than centuries, so that the white noise paradigm for the atmosphere may no longer be useful'.

The intensity and the immediacy of disturbance

Wilson lists the differences between IDH and GCC in four points (p. 25): ...“(a) there is premature death of plants (not just failure to regenerate); (b) ‘typically all species are killed’; (c) the disturbance is sudden; and (d) the effect is a temporary one, with eventual restoration of the original species composition of a patch.” Let’s consider these four points one by one.

(a) Premature death of plants

Maturity (therefore prematurity, like senescence; c.f. Sommer, 1991) is difficult to observe in planktonic algae because when an algal cell is ‘mature’ enough it simply divides providing characteristically two or four organisms not much different in size. In plankton, intermediate disturbance acts through modifying growth and loss rates, thus maintaining diversity.

Premature death is not necessary at all. Imagine the following scenario: during consecutive dry years (unidirectionally changing conditions), some dominant species grow more quickly than others. When this is replaced by a different competitive arena (for example, a spell of wet years), the relative growth speed of these same species flips over - now other species grow better, and can increase their relative biomass. None of the wet/dry dominants would die, diversity yet could be maintained. I think that the failure to grow/decline with a constant speed is essential in the IDH, on land as well as in the water.

(b) All species are killed

There must be a misunderstanding here that results in problems of logic. If all species are killed then how can the community regenerate at all? Or should we exclude on this basis all the disturbance sources (for example, treefall-gaps) that obviously do not kill every species? Possibly Wilson formulated this point more sharply than he really meant.

As follows from points (a) and (b), Wilson thinks that a disturbance event must be severe. In his original paper, Connell (1978, p. 1303) says that “Diversity is higher when disturbances are at intermediate intensities”. The question of intensity of disturbance received much less attention (even in Connell’s original paper) than its frequency. This, taking into account the serious difficulties with commensurability, is not a surprise. In rivers, where water discharge is the ultimate disturbance factor, both plankton and periphyton show that it is not so much the intensity of the physical force that is critical for the development of ecological structure - it is the frequency with which it is applied (Reynolds *et al.*, 1993b). Disturbance events are

certainly not catastrophes that kill entire population of species.

(c) The disturbance is sudden

As it was discussed above, and more intensively in Reynolds *et al.* (1993b) the classification of disturbance (slight/strong, sudden/gradual, etc.) depends upon the organization of the system it is imposed on. In this respect, it is very problematic to say anything general about graduality or immediacy. The problem is closely connected with the theoretical weaknesses of the IDH. Therefore, I do not find this criterion a good separator between IDH and GCC.

(d) The effect is temporary

The effect is not a temporary one; it is temporally recurrent. Otherwise it is meaningless to speak about intermediacy.

The storage effect

I completely agree with Wilson that the ‘importance of disturbance, especially in New Zealand, would be less than elsewhere if there really is a paucity of pioneers and an ability of some climax species to act also as pioneers’. A similar phenomenon was observed in plankton when, in the absence of K-strategists, alternative early successional phases replaced each other even if the circumstances were appropriate for a progress towards an ‘equilibrium species’ dominated community (Padisák, 1993). I have to point out that both IDH and GCC need the *de facto* presence of a species’ pool; otherwise both mechanisms are ineffectual.

Summarizing my comments on the above points claiming to be separating criteria between IDH and GCC and involving the spatial scale problem and the storage effect, I have to conclude that there is no difference left: either the two mechanisms are only one, or our present knowledge is insufficient to reliably separate them.

Final remarks

I am convinced that even if plankton ecologists modified Connell’s original theory, the essence of the hypothesis remains. The conclusions and projections can be understood as small steps to generalize the concept and this can help to eliminate the present weaknesses (Juhász-Nagy, 1993) of the IDH: ‘in spite of unresolved weaknesses, the concept of intermediate disturbance remains too useful in its potential to reject’ (Reynolds *et al.*, 1993b).

It is increasingly recognized that human activity results in global changes, such as increasing

UV radiation, acidification, etc. The global importance of non-equilibrium dynamics is increasing. If the IDH, *sensu* Wilson, is able to work 'only' in forest gaps, it is enough reason to qualify it as one of the most important concepts describing vegetation dynamics. Finally, its interesting to note that terrestrial and phytoplankton ecologists came independently to a very similar conclusion: intermediate timescale disturbances result in greater and more immediate compositional responses in early stages of succession.

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THE 'INTERMEDIATE DISTURBANCE HYPOTHESIS' OF SPECIES COEXISTENCE IS BASED ON PATCH DYNAMICS

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The 'Intermediate Disturbance Hypothesis' (IDH) is one mechanism suggested to explain indefinite species coexistence. Hutchinson's original concept of the IDH was of a mechanism based on patch dynamics, and logical consideration shows that IDH works only if interpreted this way. Dependence on patch dynamics distinguishes IDH from Gradual Climate Change (GCC), though they are distinct also in terms of premature death of individuals,

species selectivity, and the suddenness and transience of the perturbation. The application of the concepts of 'disturbance' and of IDH to phytoplankton communities is questioned.

Introduction

In 1990, I tried to work out how many distinct mechanisms there were that could permit indefinite species coexistence (Wilson, 1990). I found twelve.