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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.

Padisák (1994) has reconsidered the question, and believes two of mine are the same: the 'Intermediate Disturbance Hypothesis' (IDH) and the 'Gradual Climate Change' mechanism (GCC).

The 'original' Intermediate Disturbance Hypothesis (IDH)

Padisák considers that I have a "misunderstanding of the original description of the IDH (Connell, 1978)". There is indeed confusion about the IDH, but I do not believe that it is mine.

The IDH concept can be traced to Hutchinson (1953) who wrote of a mechanism of coexistence in which catastrophic events created empty patches ('biotopes'). Before one species had time to exterminate its weaker competitors, a new, empty patch opened nearby. This resulted in a 'mixed population'. The essential elements of IDH are:

- there must be repeated local disturbance, creating bare (or partially bare) patches;
- disturbance must be frequent enough so that competitive exclusion does not occur over the whole area, yet not so frequent that most species are eliminated;
- the frequency of disturbance has to be seen in the context of generation time;

- there must be a trade-off between species' colonising ability and competitive ability (i.e. there must be distinct colonist and climax species). All these elements can be found in Hutchinson (1953), except the idea that there are few species when disturbance is too severe, which Hutchinson probably took for granted. Connell (1978) named this concept the 'Intermediate Disturbance Hypothesis' (IDH). His contribution was to assemble a list of mechanisms of coexistence, including IDH.

Within-patch and between-patch coexistence

Superficially, it would be possible understand the Intermediate Disturbance Hypothesis (IDH) as being based on within-patch coexistence, or on between-patch coexistence. There are different spatial scales involved in this contrast (cf. Petraitis, Lathan and Niesenbaum, 1989):

- disturbance patch (usually 'patch' below): a contiguous area in which the effect of a disturbance is uniform;
- disturbance area: the total area which is disturbed at one time;
- sampling area: the scale at which we sample, or at which we are considering the question: "How [is

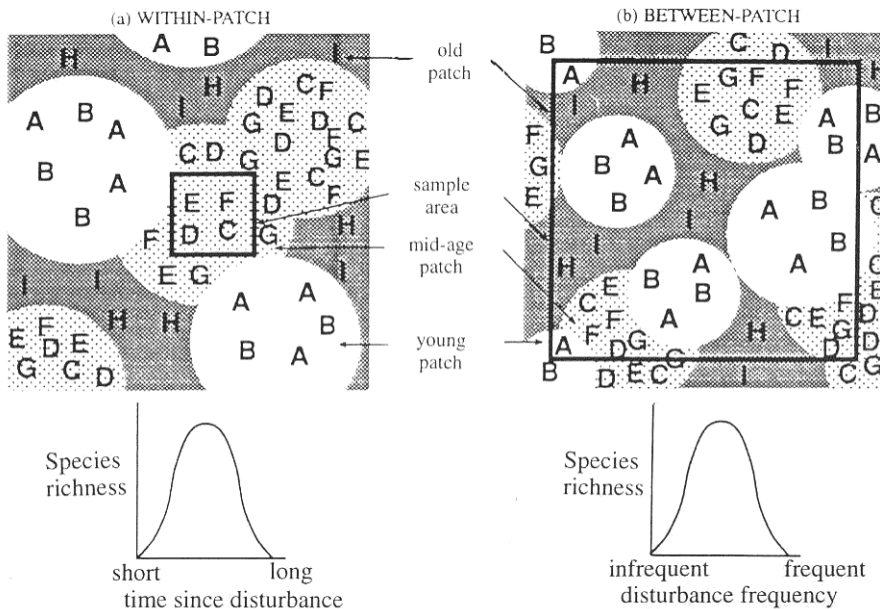


Figure 1: Within- and between-patch interpretations of the Intermediate Disturbance Hypothesis. In the maps, the letters represent species. (a) In the within-patch interpretation, the sampling area is small in relation to the disturbance patches; mid-age disturbance patches are the species-richest. (b) In the between-patch interpretation, the sampling area is large in relation to the disturbance patches, and therefore includes disturbance patches of different ages.

it] possible for a number of species to coexist ...” (Hutchinson, 1961);

- community extent: the spatial extent of the community.

Padisák says, apparently in criticism of Wilson’s (1990) use of a ‘sampling area’ of 10^3m^2 : “Several [communities] occupy square kilometres and others are restricted to square metres”. However, the community *extent* is not relevant, what is relevant is the relative sizes of the disturbance patch and the sampling area. If the disturbance patch is larger than the sampling area, we are considering within-patch mechanisms (Fig. 1a); if the disturbance-patch is smaller than the sampling area, we are examining mainly between-patch mechanisms (Fig. 1b). Which one we examine, depends on the scale at which we pose the Paradox, but I shall show below that only between-patch diversity can be the basis of the Intermediate Disturbance Hypothesis.

Within-patch mechanisms

If we interpret the Intermediate Disturbance Hypothesis (IDH) as a within-patch mechanism for indefinite species coexistence, the mechanism is that patches of mid-age are more species-rich (Fig. 1a). However:

- This is not a situation where the Paradox of the Plankton applies. The Paradox refers to long-term coexistence; by definition the existence of patches of mid age is limited.
- We cannot apply the concept of intermediate frequency of disturbance to one patch. A single patch does not have a frequency of disturbance, only a time since last disturbance.
- Whilst it is possible (but not proven) that patches of mid age are more species-rich, this is not a mechanism of coexistence, any more than is the usually greater-than-one richness of young and old patches. If we are suggesting that all the species can coexist permanently within a mid-age patch, we have to invoke one of the other 11 mechanisms to explain why, for example, the Equal chance hypothesis (mechanism 3).

We can explain that the species can coexist temporarily in a mid-age patch, until the patch ages, by which time a new patch appears, but still the species have to persist over the whole population of patches, and the problem arises, as it arose in the first place, that one species must have a higher population growth rate (metapopulation growth rate in this case), and so will oust the others.

To say that seeds immigrated from other types of patch (Palmer, 1994), is to invoke a different mechanism of coexistence - the Spatial Mass Effect (mechanism 8). To say that there is a mixture of

pioneer species that are disappearing, mid-successional species, and climax species that are arriving (Palmer, 1994) is close to Gradual Climate Change (mechanism 4), and anyway is not a recipe for indefinite coexistence.

IDH as a within-patch process can be an explanation of why some areas are more species-rich than others (Palmer, 1994), but it cannot be an explanation of indefinite coexistence (i.e. a solution to the ‘Paradox of the Plankton’).

Between-patch mechanisms

If we interpret IDH as a between-patch mechanism, we mean that at any time some disturbance patches within the sampling area will be in the early stages of colonisation, some in mid succession, and perhaps some at equilibrium ‘climax’ (Fig. 1b). The coexistence therefore comes *between* patches: some species are in one type of patch, some in another. This is the “mixed population” of Hutchinson (1953), or the “patch dynamics” of later workers (Pickett, 1980).

Apparently, Padisák does not realise the significance of patch dynamics for IDH. The dependence of IDH on patch dynamics has been pointed out by many authors (e.g. Pickett, 1980; Shmida and Ellner, 1984; McGowan and Walker, 1985; Bengtsson, Fagerström and Rydin, 1994), though several statements of IDH have failed to specify the exact process.

Rejmánek (1984) modelled the process and showed that robust coexistence depended on the existence of patch dynamics, and on a colonising-*versus* competitive-ability trade-off (e.g., Fig. 2).

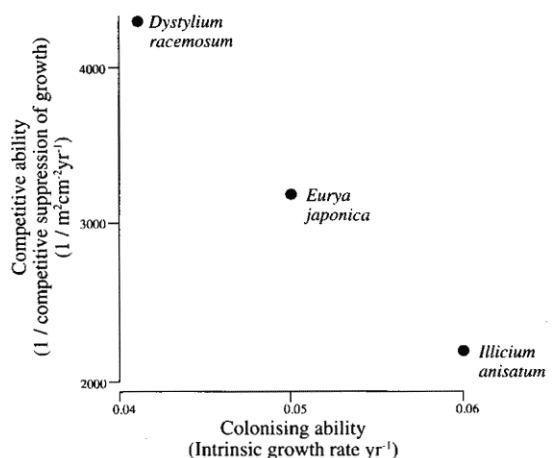


Figure 2: The trade-off between colonising ability and competitive ability in the data of Kohyama (1993).

This coexistence was explicitly between disturbance patches. Similarly, Hastings (1980) and Abugov (1982) used patch-based models of IDH; in these cases disturbance occurred in patches so small they were occupied by single species or species-types. Petraitis *et al.* (1989) examined disturbance-mediated coexistence in detail, and concluded that IDH would not operate unless there were both patch disturbance and a trade-off between colonising- and competitive-ability, again confirming the suggestion of Hutchinson (1953). Thus, in order to explain the Paradox of the Plankton the IDH has to be based on patch dynamics.

The patch-dynamics of IDH are probably the underlying mechanism of some other explanations of the Paradox of the Plankton. For example, Chesson and Pantastico-Caldas (1994) interpreted the model of Kohyama (1993) as a new mechanism of coexistence. However, Kohyama's model was of patch disturbance, and the necessary trade-off between colonising-ability (seen in intrinsic growth rate) and competitive-ability (seen in resistance to competitive suppression of growth) was present between the three species used to parameterise the model (Fig. 1a). It is possible to explain the major coexistence results obtained by Kohyama (1993) by the operation of the IDH mechanism, without resorting to a new 'forest architecture' mechanism.

IDH v. the Gradual Climate Change mechanism

Padisák has failed to see the difference between the IDH and the Gradual Climate Change mechanism (GCC), and questions whether there be any.

[Although in Wilson (1990) I followed Connell in naming it the 'Gradual *Climate* Change' mechanism, I made it clear that it applied to any environmental factor.] Many others have made a distinction between IDH and GCC (e.g., Connell, 1978; Shmida and Ellner, 1984; Silvertown, 1987; Crawley, 1986). I am sure it would be possible to find intermediate cases between IDH and GCC. However, the two mechanisms are different in several ways. I listed (Wilson, 1990):

- a. "There is premature death of plants (not just failure to reproduce". Padisák questions this, saying that "In plankton, intermediate disturbance acts through modifying growth and loss rates", thus changing the definition of disturbance so that it means environmental change.
- b. "typically all species are killed". Padisák asks "If all species are killed, then how can the community regenerate at all?". This demonstrates that Padisák has not realised that IDH is based on patch dynamics (Fig. 1b), and

that recolonisation can occur from other patches, probably of similar age.

- c. "the disturbance is sudden". This is a component of most definitions of disturbance, so surely not controversial. Padisák comments that the definition of 'sudden' depends on the organisation of the system, but it was one of Padisák's major points that the timescale of disturbance should be expressed relative to the generation time of the organisms involved. Her own definition of disturbance uses 'abrupt', so she can hardly complain when I use 'sudden' in mine.
- d. Of course, that the effect is temporary does not mean that the disturbance will not recur.

Padisák also remarks that "both IDH and GCC need the *de facto* presence of a species' pool ...". Earlier (Padisák, 1992), she made this criticism of Wilson (1990) more explicit: "If there is an insufficient pool of storage species in New Zealand (as it is has been argued against IDH), then how can GCC ... operate?". Leaving aside what 'storage species' might be, I wrote: "It has been suggested that N.Z. has a deficit of early-successional species". Early successional species are found, under IDH, after a disturbance; they are not usually found in GCC. This illustrates Padisák's confusion between IDH and GCC.

What Padisák is doing here is to change the definition of IDH, making it identical to GCC, and then complaining that the two are the same.

IDH and phytoplankton communities

There seems to be some vagueness about IDH amongst phytoplankton ecologists. For example, Sommer *et al.* (1993) explain the operation of IDH as: "there will be repeated opportunities for the re-establishment of pioneer populations". Is this patch dynamics or not?

The misunderstanding seems to occur because of insufficient allowance for the time scale relevant to organisms with a short generation time. This results in what is really environmental ('climate') change, for the species involved, being seen as disturbance. Padisák admits that the timescale is different between planktonic and terrestrial communities; she says "the 'planktonic year' is analogous to glacial and interglacial cycles". This suggests a plankton:terrestrial difference in timescale in the order of 1 : 100000.

It is not clear that disturbance is occurring at all in the plankton communities to which Padisák, and the various authors in Padisák, Reynolds and Sommer (1993), refer. Many of the examples given by Reynolds, Padisák and Sommer (1993) are really

environmental change: carbon limitation, fluctuation in nutrient supply (Olrik and Nauwerck, 1993), and periods of strong winds lasting several days (Holzmann, 1993). Reynolds *et al.* (1993) give examples (sudden storm, flash flood, heavy rainfall) that look superficially like disturbances until we consider time scaling. Storms and floods would last say 1 hour to 48 hours. Using Padišák's time scaling of 1:100000, this translates to a terrestrial equivalent of 12 to 600 years, similar to timescale of terrestrial climate change. I do not believe that Padišák has made a case that disturbance even occurs in phytoplankton communities. Because the generation time is so short, most environmental impacts on plankton are, to use Padišák's own arguments on time scaling, more like environmental changes.

Moreover, for IDH to operate, it must be *patch* disturbance. Because phytoplankton organisms are so small, the 10³m² that Wilson (1990) used for terrestrial communities must translate to less than 10 cm x 10 cm for the plankton. Few or none of the examples of disturbance given by Reynolds *et al.* (1993) would operate on this scale. How can heavy rainfall affect only a patch 10 cm x 10 cm? Surely an event like a storm or flood would tend to sweep away the water, and the community with it. I cannot understand the concept of patch disturbance when the community and its substrate are swept away *in toto*.

The misunderstanding of IDH by the participants in the Baja (Hungary) symposium (Padišák *et al.*, 1993) can be traced to the pre-conference guidance (Sommer *et al.*, 1993). It described the IDH in terms of "fluctuations in resource availability", and defined disturbance as "any event that interrupts the approach towards the eventual exclusion". It failed to mention that the IDH model is based on patch dynamics. These descriptions effectively redefine IDH as being GCC, and it is therefore unsurprising that many of the participants described environmental changes as if they were examples of IDH.

I do not believe that Padišák and co-workers have made a case that the Intermediate Disturbance Hypothesis has any applicability to the plankton. Connell (1978) specifically excluded communities such as the plankton when he discussed IDH. Perhaps he was wise. Other mechanisms of coexistence must explain the Paradox of the Plankton for the plankton.

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