



The Disturbing History of Intermediate Disturbance

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The disturbing history of intermediate disturbance

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'A person who is not interested in the growth and flux of ideas is probably not interested in the life of the mind. A ... scientist working in an advancing field of research should certainly try to identify the origin and growth of current opinion.'

Medawar (1979)

A recent review introduced the idea of intermediate disturbance thus: 'One of the best-known consequences of disturbance is reduction in the proportionate abundance of competitively dominant species, as in Connell's (1978) 'intermediate disturbance hypothesis'. Connell proposed that too little disturbance leads to low diversity through competitive exclusion, and too much disturbance eliminates species incapable of rapid re-colonization' (Hoopes and Harrison 1998: 146). They go on to claim that 'Intermediate disturbance has become perhaps one of the best-accepted principles in ecology'. This is a significant complement, given the trouble ecology has experienced in identifying general principles of potentially predictive use (McIntosh 1995). This identification of the intermediate disturbance hypothesis with Connell's 1978 paper is shared by nearly all ecology textbooks (e.g. Ricklefs 1990, Colinvaux 1993, Brewer 1994 and Krebs 1994), the partial exception to this being Begon et al. (1996) who credit Connell but then write 'see also the earlier account by Horn 1975'. If the idea is indeed 'one of the best-accepted principles in ecology' then surely its real history is of some interest and should replace the pseudo-history given in the textbooks.

Many current textbooks when describing the idea of intermediate disturbance make use of a graph similar to Fig. 1. Rudwick (1992) has stressed the importance of illustration in the history of science rather than just using textual analysis. In this respect this 'hump-backed' graph is very useful as it makes explicit the

authors' ideas on the relationship between diversity and disturbance. Connell (1978) presents such a graph (his Fig. 1) as does Horn (1975: 209). In his legend for this figure Horn wrote 'Note that intermediate disturbances produce higher diversity than either very high or very low levels' (Horn 1975: 209). A very clear statement of the intermediate disturbance hypothesis three years before the paper the textbooks cite as its origin. This graph has an even longer history. In his paper on 'Competitive exclusion in herbaceous vegetation' Grime (1973a) produced a graph (his Fig. 2) showing the characteristic hump-backed relationship between 'species density' (i.e. species richness per unit area) and both 'environmental stress' and 'intensity of management' (defined as 'intensity of grazing, mowing etc.' i.e. disturbance). Grime (1973a: 345) pointed out that Odum (1963) had previously observed that 'the greatest diversity occurs in the moderate or middle range of a

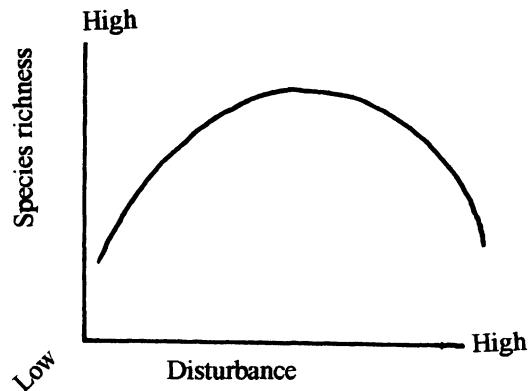


Fig. 1. A generalised version of the hump-backed graphical model of the intermediate disturbance hypothesis.

physical gradient' but cites no prior source for the similar relationship with disturbance. Grime (1973a) provides the earliest graph linking disturbance and species richness that I am aware off, five years before Connell. He reprinted this graphical model in a paper in the *Journal of Environmental Management* published in the same year as the *Nature* paper (Grime 1973b). In a later book Grime (1979: 163) provided a more generalised version of this graph calling it the 'hump-backed model'. If this characteristically shaped graph is taken as central to the intermediate disturbance hypothesis then it should be Grime rather than Connell who is cited as its originator.

It will come as no surprise to anyone with an interest in the history of science that the intermediate disturbance hypothesis does not emerge fully formed during the 1970's without any prior history. Scientific ideas seldom appear 'from nowhere' without a history of earlier related ideas. A classic illustration of this are the attempts at theories of evolution and selection prior to Darwin (Mayr 1982, Bowler 1989). During the 1960's several now classic papers (e.g. Connell 1961, Paine 1966) showed that disturbance due to predation in marine communities could lead to increased species coexistence. Indeed Horn (1975) suggested that the model of intermediate disturbance he outlined in his Fig. 1 'provides a conceptual basis for Paine's original contention that predation allows a successional patch-work to replace a community dominated by mussels'.

Related ideas can be traced back to at least the 1940's (e.g. Eggeling 1947, Watt 1947, Tansley 1949). A good example is Tansley's (1949: 140) suggestion that the diversity of plants in a grassland may be related to grazing; e.g. 'intensively grazed' or 'undergrazed' areas (cf. Grime 1973a discussed above). In his well known 1978 paper Connell compared his version of the hump-backed graph with Eggeling's (1947) data on succession in the Budongo forest, Uganda.

To summarise; by the 1940's the idea was current that disturbance was in some way important in controlling species richness in succession. During the 1960's classic studies showed that disturbance through predation could effect the coexistence of species. This led to a full statement of the intermediate disturbance hypothesis (complete with hump-backed graphical model) first by Grime (1973a), then Horn (1975) and finally Connell (1978). Why then does the modern literature almost always cite Connell as the origin of this idea?

When the first publication of an idea is ignored by the literature in favour of a later description of essentially the same idea, then it is often the case that the first version was in an obscure publication and/or failed to fully develop the idea. Examples include Patrick Matthew's ideas on natural selection (Mayr 1982) or the independent anticipation of equilibrium island biogeography by K. W. Dammerman and E. G. Munroe in the late 1940's (Wilkinson 1993). Clearly this was not

the case with intermediate disturbance. All three contenders published a full explanation, complete with graphical model, in highly visible publications. Grime in *Nature*, Horn in the proceedings of a major conference dedicated to the memory of Robert MacArthur and Connell in *Science*. Given this I find it disturbing that the modern literature gives an erroneous view of the origin of this idea. Part of the problem could be that Connell (1978) did not cite a source for the idea (I assume he considered it to be an idea in such common currency in the late 1970's that it did not require a citation). This means that a naive reader of Connell's paper would assume it was an idea novel to the author. As a contributor to the Robert MacArthur memorial volume, Connell is likely to have been aware of the work of Horn even if unaware of Grime's study. Once an idea gets repeated in a few textbooks it can easily become 'a well known fact' however wrong it may be (e.g. Gould 1991: chapter 10). Perhaps this is what has happened with the widespread citation of Connell (1978) as the origin of the intermediate disturbance hypothesis.

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