Defining and defending Connell's intermediate disturbance hypothesis: A response to Fox

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Letter

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Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox

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In his recent Opinion article in *TREE*, Jeremy Fox [1] finds that evidence for the intermediate disturbance hypothesis (IDH) appears mixed and shows that some explanations linking disturbance to species coexistence are flawed. Based on this, he argues that we should abandon the IDH. Whereas we agree with his observations, we reject his conclusions. Fox's criticisms are misdirected because the ideas that he disputes are distinct from the authentic IDH. Although we acknowledge its vulnerability to misinterpretation and misrepresentation, Connell's IDH remains valid and useful.

Connell first presented the IDH in his review of mechanisms that might prevent competitive exclusion in complex sessile communities: tropical forests (trees) and coral reefs (corals) [2]. Connell identified that 'evidence comes from studies of ecological succession' and he took a Ugandan forest as his central illustration. The vegetation in this forest had been described as following a successional sequence where species richness rises during the colonizing stages and declines during late succession (Figure 1 in [2]).

Connell's reasoning addressed sessile communities, which have the trade-offs among species needed to drive a succession where low diversity is (or without disturbance would be) observed during late stages. In this context, the IDH seems self evident: sufficient disturbance facilitates establishment of early-stage (disturbance-dependent) species in late-stage formations and, thus, can increase diversity, whereas excessive disturbance is intolerable for some species and so will reduce diversity even in early-stage communities. Fox accepts that the competition–colonization trade-off theories provide 'a logically valid mechanism which can produce stable coexistence, and peaks in diversity at intermediate disturbance levels'. Thus, we all agree that the core concepts underlying Connell's IDH are sound.

Various aspects of Connell's IDH remain poorly defined. Disturbance and disturbance regimes are complex phenomena and species can persist in multiple ways (e.g., as long-lived seeds, in patches, or as post-disturbance residuals) [3]. Connell did not claim that the IDH addressed all these details, but offered it as a useful summary insight. We have previously described many challenges in evaluating and extending these ideas (e.g., [3,4]).

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Similar to most major theories, the IDH has precursors and relatives. These have sometimes been confused. Disturbance has numerous effects on diversity and competitive exclusion that lie outside the scope of Connell's IDH [5]. None of the mechanisms that Fox critiques reflect Connell's IDH, including both Huston's (non-successional) model and the more general mechanisms that link disturbance to rare species advantage [6]. (We note that Huston's model was considered distinct from Connell's IDH by both Connell and Huston [2,6].)

Empirical evaluations of the IDH, as Fox discusses, appear mixed (but we note 46% support in one recent summary [7]). As Fox acknowledges, we need to be critical about evaluating such results. We also note that a unimodal diversity pattern is not a universal prediction and that detection requires sufficient sampling of both the rising and falling sections of the curve. Connell's IDH does not claim that all stages in a succession are always present, neither did Connell claim his theory applied to mobile organisms (although both are interesting extensions). The IDH is simply one potential explanation when unimodal patterns are observed. In regions where successional states are synchronized, or sampling is conducted at the wrong scale, such patterns will be absent. IDH mechanisms can maintain species in the long term even where disturbance only appears to reduce diversity in the short term (Figure 3 in [3]).

Most ecologists accept that multiple mechanisms determine diversity patterns and species coexistence. In communities where late succession appears to be characterized by high diversity, other factors, such as density dependence, may prevent competitive exclusion. Nonetheless, even in these communities, disturbance contributes to diversity, although detection may be difficult [8].

As Fox notes, 'mechanisms should not be conflated'. Many have called for a clearer taxonomy of disturbance–diversity models [3,9,10]. By clarifying valid versus invalid mechanisms, Fox's arguments, although not his conclusions, support that position. Although not the only valid theory determining patterns of diversity and species coexistence, Connell's IDH has stimulated advances in theory and practical application and remains useful [9,11,12]. Rather than abandoning Connell's IDH, we advocate greater precision in its definition. Not all diversity–disturbance theories are correct, but neither are all of them the IDH.

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