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]).

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.

References

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The intermediate disturbance hypothesis is broadly defined, substantive issues are key: a reply to Sheil and Burslem

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I appreciate Sheil and Burslem's thoughtful comments [1] on my opinion piece [2] arguing for abandonment of the intermediate disturbance hypothesis (IDH). I am gratified that they agree with my substantive criticisms of several ideas relating disturbance and species diversity. They argue, however, that those criticisms are directed at ideas that, although related to the IDH, are not actually the IDH as Connell [3] defined it. They argue that the IDH, properly and precisely defined, remains a valid hypothesis.

As Sheil and Burslem [1] acknowledge, the proper definition of the IDH has been much debated. Wilkinson [4] noted that although Connell [3] coined the term 'IDH', earlier writers proposed very similar ideas. Wilkinson [4] argued that Connell [3] should not be considered the original source of the IDH. Connell [3] himself recognized the close connections between his ideas and those of others. He referred to the model of Huston [5] as 'an extension of the intermediate disturbance hypothesis', saying it 'should be true, other things being equal', although he questioned the applicability of Huston's [5] model to tropical rain forests or coral reefs. Huston [5] characterized Connell's [3] IDH as capturing 'half' of his own model, and cited Connell [3] repeatedly as a source of empirical evidence and theoretical ideas supporting his model. Notably, Huston [5] described Connell's [3] IDH as 'simply population reductions which prevent competitive equilibrium', a rather different description than that of Sheil and Burslem [1], and an illustration of the difficulty of precisely characterizing a purely verbal model such as Connell's [3]. In a major review of the empirical literature, Mackey and Currie [6] cited Connell [3], Huston [5], and several other authors as sources for the

IDH. All of the ideas discussed in my paper are ones which have been widely taken to be part of the IDH, or so closely related as to make it natural to consider them together with the IDH, for instance in textbooks (e.g., [7]).

Even if Connell [3] is interpreted as proposing competition–colonization trade-offs, it is far from 'self-evident' whether, and how, competition–colonization trade-offs or other successional mechanisms can maintain diversity [8–10]. Many different mathematical models have been proposed, differing greatly in their assumptions and predictions, including their predictions about whether intermediate disturbance maximizes diversity [8–12]. Sheil and Burslem [1] see recent mathematical theory as extending and developing the ideas of Connell [3]. But, given the important differences among recent mathematical models in their assumptions and predictions, and the fact that not all recent models predict maximum diversity at intermediate disturbance, it is not clear to me that it is useful to group all of these models under the label 'IDH', even if all can be regarded as ultimately tracing back to Connell [3].

My own greatest concern is that future empirical studies of disturbance and diversity be placed on theoretically-firm foundations. There is no disagreement here as to what those foundations are. In my view it would be unfortunate if debate over the definition of the IDH were to distract from agreement on substantive matters. Given that, in practice, many researchers and textbooks have not adopted Sheil and Burslem's [1] narrow definition of the IDH, and given the ambiguity inherent in Connell's [3] verbal statement of the IDH, there is a risk that arguments to retain the term 'IDH' will be misunderstood as arguments to retain invalid ideas about how

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