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The intermediate disturbance hypothesis should be abandoned

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A leading idea about how disturbances and other environmental fluctuations affect species diversity is the intermediate disturbance hypothesis (IDH). The IDH states that diversity of competing species is, or should be expected to be, maximized at intermediate frequencies and/or intensities of disturbance or environmental change. I argue that the IDH has been refuted on both empirical and theoretical grounds, and so should be abandoned. Empirical studies only rarely find the predicted humped diversity–disturbance relationship. Theoretically, the three major mechanisms thought to produce humped diversity–disturbance relationships are logically invalid and do not actually predict what they are thought to predict. Disturbances and other environmental fluctuations can affect diversity, but for different reasons than are commonly recognized.

The intermediate disturbance hypothesis

Environmental conditions fluctuate on all temporal scales. Sometimes these fluctuations take the form of disturbances, relatively discrete events (ranging from footfalls to hurricanes) that harm the affected organisms. A leading idea about how disturbances and other environmental fluctuations affect species diversity is the IDH. The IDH states that diversity of competing species is, or should be expected to be, maximized at intermediate frequencies and/or intensities of disturbance or environmental change [1–3]. The IDH features in numerous ecology textbooks [4–7]. The IDH also remains a popular research topic: Connell's original paper on the topic [1], which introduced the term 'IDH', has been cited over 1000 times just in the past five years according to ISI Web of Science.

Here I argue that the IDH should be abandoned. The IDH has been refuted on both empirical and theoretical grounds. I emphasize that I imply no criticism of the IDH's many supporters. The empirical flaws in the IDH have only been revealed through a gradual accumulation of evidence. The theoretical flaws, while very serious, are also subtle. Here I review empirical and theoretical refutations of the IDH. I emphasize clear, non-technical explication of key theoretical results, and crucial but little-recognized distinctions between different models. I suggest that the time is right for a new program of research on the effects of disturbance and environmental change on diversity, based on the rigorous foundation of recent theoretical results.

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Empirical refutation of the IDH

The empirical evidence on the IDH has been recently reviewed and so can be covered rather briefly [8,9]. Empirical studies rarely find the predicted peak in diversity at intermediate disturbance levels. A review of over 100 published diversity–disturbance relationships found that the predicted peak of diversity at intermediate disturbance levels rarely occurs ($< 20\%$ of studies; [8]). A more recent review reports the same result [9].

It could be argued that nature is more complicated than our oversimplified theories, so that other factors modify or obscure the predicted effect of disturbance on diversity, or prevent it from being detected. However, even tightly-controlled and highly-replicated microcosm and mesocosm experiments generally fail to find the predicted peak in diversity at intermediate disturbance or environmental fluctuation levels [10–14], or else find the predicted peak for reasons different than those commonly thought to underpin the IDH [13–18]. Further, insofar as the qualitative form of the diversity–disturbance relationship is determined by other variables, then humped diversity–disturbance relationships have no special empirical significance, being just one among many possibilities [13].

It is also possible that methodological artifacts skew empirical studies against the IDH. For instance, it is possible some empirical studies failed to support the IDH because they failed to sample a sufficient range of disturbance frequencies or intensities. But methodological artifacts can cut both ways. For instance, published empirical studies might overstate the frequency of humped diversity–disturbance relationships because researchers tend to look for such relationships only in systems where they think they are particularly likely to find them. The available empirical evidence does not allow quantitative assessment of different methodological biases, and so it is most appropriate to take the available evidence at face value.

It is interesting to note that other important hypotheses in community ecology have been treated with considerably more skepticism than the IDH, despite much better empirical track records. For instance, at various times the hypotheses of interspecific competition and trophic cascades have been highly controversial [19–22]. But most experimental tests for trophic cascades find trophic cascades, and most experimental tests for interspecific competition find interspecific competition [23,24]. The rarity of humped diversity–disturbance relationships has led to attempts to extend or refine the IDH (e.g., [9]), but critical reconsideration of the IDH seems in order.

Theoretical refutation of the IDH

Theoretical refutations of the IDH are less well-known than the empirical data and require more explication because of their technical nature. Theoretically, the IDH is based on three mechanisms which are thought to lead to maximum diversity at intermediate frequencies or intensities of disturbance or environmental change. All three are fundamentally flawed. They are all logically invalid, meaning that their assumptions do not imply the predictions they are thought to imply. Logically invalid hypotheses cannot hold in nature. It is possible for intermediate frequencies or intensities of disturbance or environmental change to maximize diversity – but not for any of these three reasons.

(i) Disturbance reduces species' densities, thereby weakening competition and preventing the competitive exclusion that would otherwise occur. Diversity peaks at intermediate disturbance levels because very frequent or intense disturbances eliminate disturbance-intolerant species, while rare or weak disturbances fail to prevent competitive exclusion.

Disturbances do reduce species' densities, thereby weakening competition. But disturbances also reduce the strength of competition needed for exclusion (see [25] for a general proof). Anything that reduces per-capita growth rate (e.g., disturbance, continuous sources of mortality, environmental 'harshness', predation, disease, and harvesting) also reduces the amount of competition (or any other growth-reducing factor) needed to push per-capita growth rate into negative territory [25]. The same point can be phrased in terms of densities rather than growth rates: any factor that reduces species' densities also reduces the amount of competition needed to reduce densities to zero. Violle *et al*. [12] provide an experimental demonstration of the proof of Chesson and Huntly [25]; their proof applies to all 'linear, additive' models (Box 1). Further, it can be shown that, in models outside of this class, coexistence is due to mechanisms other than simple weakening of competition via reduced species' densities [26–28].

Trade-offs between traits that confer high fitness when population densities are high and resources are scarce, and traits that confer high fitness when population densities are low and resources are abundant, can indeed promote competitive coexistence that would not occur in undisturbed environments ('gleaner–opportunist trade-off' [17]). However, as discussed below and in Boxes 2 and 3, such trade-offs generate disturbance-mediated coexistence via nonlinearities and nonadditivities, not because disturbances simply reduce species' densities [17,25–29].

(ii) Intermediate frequencies or intensities of disturbance interrupt competitive exclusion by temporarily reducing all species to low density, thereby allowing all species to subsequently increase and preventing the system from ever attaining equilibrium.

Connell [1] says that disturbances 'interrupt' and 'set back' the process of competitive exclusion, but perhaps the most influential treatment of this idea is that of Huston [30]. Huston [30] simulated a Lotka–Volterra competition model with periodic, density-independent mortality events. Inspection of the simulated population dynamics showed that, at intermediate frequencies of disturbance,

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Box 1. Competition in a linear, additive world

To understand how disturbances and environmental fluctuations can affect coexistence and diversity, it is useful to first consider a situation in which they cannot do so. As a simple example, consider a system in which two species compete for a single shared resource (see [25–28] for other examples and more general analysis). The per-capita growth rate of species i (i = 1, 2) depends linearly on resource levels with slope a_i, and on density-independent mortality m_i:

$$\frac{1}{N_i}\frac{dN_i}{dt} = a_i R - m_i \qquad \text{(I)}$$

In a constant environment, for species i to persist at equilibrium it must have a zero per-capita growth rate, which requires that equilibrium resource density R^* equal m_i/a_i. Unless the two species are ecologically identical, so that m_1/a_1 precisely equals m_2/a_2, the species with the lower m_i/a_i ratio will exclude the other ([49]; resource dynamics are left unspecified because they do not affect this conclusion).

Now imagine that per-capita mortality rates m_i fluctuate over time, for instance due to disturbances or environmental changes. This will cause species and resource abundances to fluctuate, and the average per-capita growth rate of species i will equal

$$\overline{\frac{1}{N_i}\frac{dN_i}{dt}} = a_i \overline{R} - \overline{m_i}, \qquad \text{(II)}$$

where overbars denote time averages. Unless the two competitors are ecologically identical and have precisely equal values of $\overline{m_i}/a_i$, the species with the lower value will competitively exclude the other by reducing $\overline{R}$ to a level so low that its competitor cannot replace itself on average $\left(\overline{\frac{1}{N_i}\frac{dN_i}{dt}} < 0\right)$. This is the same mechanism of competitive exclusion that occurs at equilibrium, with $\overline{m_i}$ values playing the same role as constant m_i values.

Fluctuations in m_i values cannot produce coexistence in this model. In particular, periodic disturbances that temporarily increase all m_i values, as in the model of Huston [30], will increase $\overline{m_i}$ values but will not produce coexistence. Environmental changes that alternately cause $m_1 > m_2$, and $m_1 < m_2$ will cause competitive dominance to alternate as assumed by Hutchinson [2], but will not produce coexistence, no matter what the frequency of environmental change relative to the rate of competitive exclusion.

The reason fluctuations in per-capita mortality rates cannot produce coexistence is because this is a linear, additive model. Equation (II) looks exactly like equation (I), just with some parameters and variables replaced by their time averages. Fluctuations around these averages simply cancel out, so that long-term average per-capita growth rates depend only on average values of fluctuating parameters and variables.

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all the competitors increased after each disturbance – a steady state equilibrium was never attained, and competitive exclusion was slowed. Huston [30] concluded that intermediate disturbance frequencies slow competitive exclusion by temporarily interrupting the approach to equilibrium, although without actually producing stable coexistence. He also noted that very frequent disturbances actually increased the rate of competitive exclusion, a result he attributed to frequent disturbances not allowing species with low intrinsic rates of increase sufficient time to recover between disturbances.

These conclusions are incorrect, but the reason is rather subtle. Adding disturbances (here, density-independent mortality events) to a disturbance-free model changes two features of the model, not one. Adding disturbance prevents the model from reaching a steady state equilibrium. But less obviously, adding disturbance also changes the long-term average mortality rate. The correct 'control

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Box 2. Coexistence in a nonadditive world

One way for temporal variation to promote coexistence is if average per-capita growth rates depend nonadditively on temporal variation. I illustrate this with a simple modification of the competition model from Box 1 (see [25–28] for other examples and more general analysis).

Instead of allowing per-capita mortality rates to vary over time, as in Box 1, allow a_i values to vary over time, for any reason. This will cause species' growth rates, and thus densities, to fluctuate, leading in turn to fluctuations in resource density R. When a_i and R fluctuate, the average per-capita growth rate of species i becomes

$$\overline{\frac{1}{N_i}\frac{dN_i}{dt}} = \left(\overline{a_i}\right)\left(\overline{R}\right) + \mathrm{cov}\left(a_i, R\right) - m_i \qquad (I)$$

where overbars denote time averages and cov is the population (not sample) covariance. Equation (I) follows directly from the definition of the arithmetic mean of the product of two variables. Covariance is a simple example of nonadditivity (see [27,28] for discussion of 'nonadditivity'). This provides the potential for a nonadditivity-based coexistence mechanism known as the 'storage effect' [27,28]. One species may be the superior competitor on average [i.e., have a higher value of $\left(\overline{a_i}\right)\left(\overline{R}\right) - m_i$] but suffer from negative, or less positive, a_i-R covariance [i.e., grow worst (low a_i) during times when R is high]. The other species may be the inferior competitor on average but benefit from more positive a_i-R covariance.

The 'flip-flop competition' model of Klausmeier [50] provides an example. In this model, the environment alternates between longer periods in which $a_1 > a_2$, thereby favoring species 1, and shorter periods in which the reverse is the case. R fluctuates over time, increasing after environmental change reduces the growth rate of the previously dominant species, and then decreasing to a low level as the new dominant increases. R is thus lower on average during the lengthy periods when species 1 is favored, causing cov(a_1,R) < 0. By contrast, species 2 grows best during the short periods when R is high on average, cov(a_2,R) > 0. Species 1 can increase when rare by virtue of its superiority on average, while species 2 can increase when rare by virtue of its superiority on average, while species 2 can increase when rare because the rarer it becomes, the more positive the a_2-R covariance becomes. This model makes some of the same predictions as that of Hutchinson [2], for instance that intermediate frequencies of environmental change will promote coexistence most strongly, but does so for completely different reasons. Intermediate frequencies of environmental change promote coexistence not because they match the timescale of competitive exclusion, but because they generate resource dynamics that lead to appropriate patterns of covariation between a_i and R.

Box 3. Coexistence in a nonlinear world

A second way for temporal fluctuations to create stable coexistence is if average per-capita growth rates depend nonlinearly on fluctuations rather than linearly. For instance, as a mathematically-simple illustration, imagine that the dynamics of species 1 are described by equation (I) in Box 1, while the growth of species 2 depends linearly on R and R^2, meaning it depends nonlinearly on R:

$$\frac{1}{N_2}\frac{dN_2}{dt} = a_2(R + R^2) - m_2. \qquad (I)$$

If R varies over time for any reason, the average per-capita growth rate of species 2 will equal

$$\overline{\frac{1}{N_2}\frac{dN_2}{dt}} = a_2\left[\overline{R} + \overline{R}^2 + \mathrm{var}\left(R\right)\right] - m_i, \qquad (II)$$

where overbars denote time averages and var(R) is the (population) variance in R. Equation (II) follows directly from the definition of the arithmetic mean of the square of a variable. Now both species can coexist, because the average per-capita growth rate of species 2 depends not just on the mean resource density $\overline{R}$, but also on the variance around the mean. This temporal variability acts like a second 'resource', which only species 2 can 'consume'. Variability in R does not affect species 1 because species 1's growth rate is a linear function of R and so has a time average of $a_1\overline{R} - m_1$. A trade-off between growth rate under average conditions, and growth rate as a function of the variance around average conditions, can allow multiple competitors to stably coexist. This coexistence mechanism is known as 'relative nonlinearity', because it depends on inter-specific differences in the nonlinearity of species' per-capita growth rates as a function of shared limiting factors [26,28,51].

Very few studies have attempted to test for coexistence via relative nonlinearity in nature. This is an important gap in empirical work, because key prerequisites for coexistence via relative nonlinearity are common. Desert shrubs provide one example of nonlinear growth functions like equation (I): recruitment and survival are disproportionately high in wet years, so that per-capita growth rate is an increasing, accelerating function of water availability [48]. Further, per-capita growth rate of 'opportunistic' shrub species varies more nonlinearly with water availability than does the per-capita growth rate of drought-tolerant species [48].

Other nonlinear growth functions are possible. For instance, a predator with a type II functional response will have a per-capita growth rate that is a nonlinear, decelerating (saturating) function of prey density, so that coexistence of competing predators could be mediated by a trade-off between growth rate at average prey densities and insensitivity to variability in prey density [51].

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treatment' for the simulated 'experiment' of Huston [30] is not the disturbance-free model. The correct 'control treatment' is a model with continuous mortality at the same long-term average rate as the model with disturbance. As can be proven analytically, fluctuations in the model of Huston [30] (and in other 'linear additive' models) are irrelevant to slowing competitive exclusion ([25], Figure 1 and Box 1). Intermediate frequencies of disturbance slow competitive exclusion by increasing the long-term average mortality rate, thereby reducing the difference in average growth rate between competitively superior and inferior species (Figure 2). It is the difference in average growth rate between competitively superior and inferior species that determines the rate of competitive exclusion. Intermediate long-term average mortality rates in this model are an 'equalizing' mechanism, but not a 'stabilizing' mechanism, because they slow competitive exclusion but do not help rare species to 'bounce back' [28]. Put another way, raising per-capita mortality rates to intermediate levels (whether via periodic disturbances or constant, continuous mortality) changes the equilibrium

from one that is approached quickly to one that is approached more slowly (Figure 2). High frequencies of disturbance raise the long-term average mortality rate to high levels, which in the model of Huston [30] both changes the identity of the dominant competitor, and leads to rapid exclusion. High disturbance frequencies lead to rapid exclusion because they produce a large difference in average per-capita growth rate between species with high intrinsic rates of increase, and their slower-growing competitors (Figure 2). Fluctuations in mortality in the model of Huston [30] cause visually obvious fluctuations in species' abundances, but do not affect coexistence. This is a crucial point, because long-term average conditions, and fluctuations around the average, can vary independently of one another in nature. It is important to distinguish effects of changes in the average from effects of changes in variability around the average.

(iii) If, due to fluctuating environmental conditions, the identity of the dominant competitor changes on an intermediate timescale, no one species will ever have time to
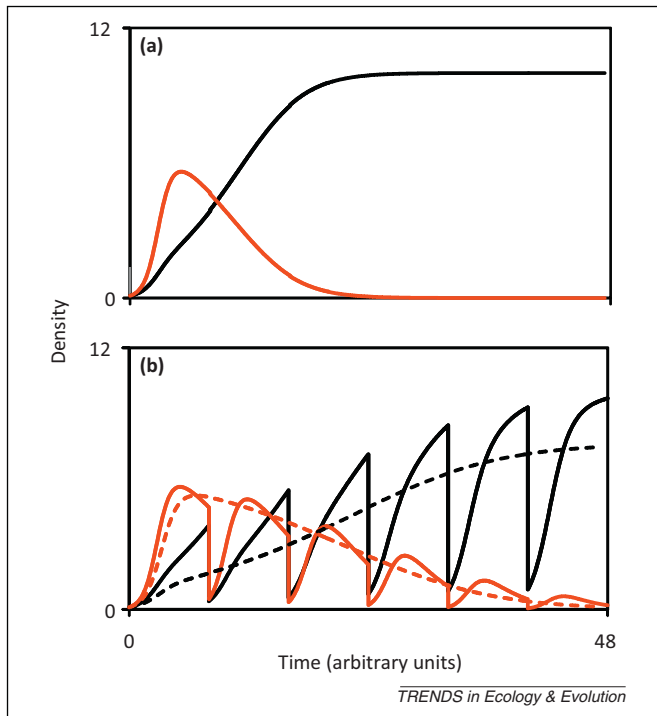
Figure 1. **(a)** Population dynamics of two species competing according to the Lotka–Volterra model. The winning species (black) has the higher *K*, the losing species (red) has the higher *r*, and both competition coefficients equal 1. **(b)** As (a), but with the addition of periodic disturbances that kill 90% of all individuals (unbroken lines), or with the addition of continuous, density-independent mortality at a constant rate (broken lines). The addition of constant per-capita mortality at an appropriately chosen rate has the same effect on long-term population dynamics as does the addition of periodic mortality events. This illustrates that disturbance in the model of Huston [30] slows exclusion by increasing the average mortality rate, not by 'interrupting' competitive exclusion.

Figure 2. Illustration of how changes in long-term average mortality rate affect the rate of competitive exclusion in the model of Huston [30]. Unbroken lines show per-capita growth rates of two competitors growing according to the Lotka–Volterra competition equations with both competition coefficients equal to 1. There is no difference between intra- and inter-specific competition, so the per-capita growth rates of both species decline linearly with increasing total density of both species. The two species exhibit a trade-off between high *r* (species 1) and high *K* (species 2). In the absence of additional mortality, species 2 excludes species 1 because it can maintain a zero per-capita growth rate at a higher total density than can species 1. The exclusion is rapid because when species 2 is at equilibrium, species 1 has a very negative per-capita growth rate, as indicated by the rightmost double-headed arrow. Adding density-independent mortality at an intermediate rate slows competitive exclusion by reducing the difference in per-capita growth rate between species 2 and 1, as indicated by the middle double-headed arrow. Adding a high rate of mortality reverses the competitive outcome, and leads to more rapid exclusion than in the case of intermediate mortality, as indicated by the leftmost double-headed arrow.

exclude the others and all will coexist. Overly-slow fluctuations will allow exclusion to take place before conditions change. Species will average across overly-fast fluctuations, and whichever species competes best on average will exclude the others.

This is Hutchinson's [2] solution to the 'paradox of the plankton', the apparent coexistence of dozens of species of planktonic algae in apparently-homogeneous lakes in which only a few resources and other factors could ever possibly be limiting (called the 'gradual change' hypothesis in [1]). Hutchinson [2] deserves great credit for emphasizing the difficulty of solving the paradox of the plankton solely with coexistence mechanisms that operate at steady state equilibrium. But his nonequilibrium coexistence mechanism has a subtle but fundamental flaw.

Varying the relative timescales of environmental fluctuation and competitive exclusion is neither sufficient nor necessary, on its own, to affect long-term competitive outcomes (Box 1). In ecology, Chesson and Huntly [25] provide a proof of this point, but it has long been recognized in evolutionary biology (e.g., [31–33]). If, as assumed by Hutchinson [2], environmental fluctuations do nothing but change the relative fitness of different species, then whichever species is favored on average (highest geometric mean per-capita growth rate) will eventually exclude the others, no matter what the frequency of environmental change ([31]; Figure 3a). The rate of exclusion is governed by differences in average fitness and is slowest when those
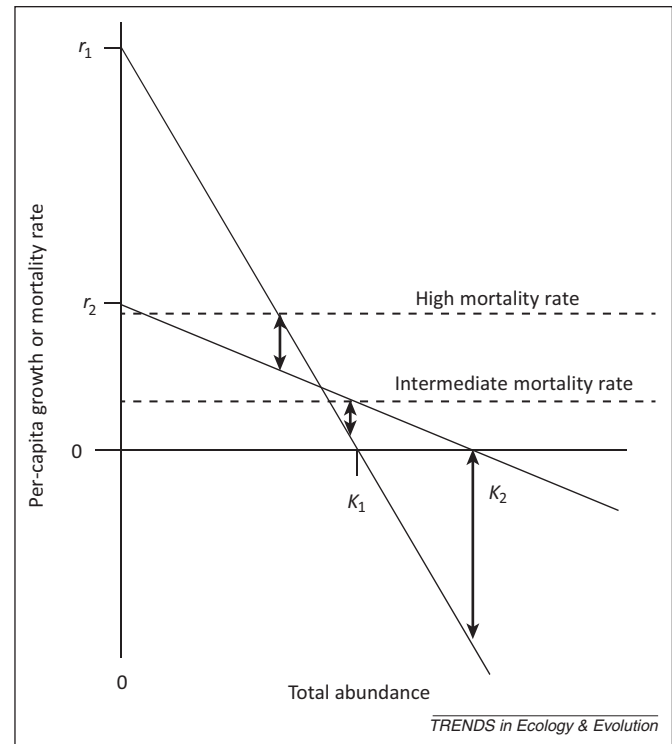
differences are small (Figure 3b). Importantly, constant conditions that slightly favor one species over another lead to exactly the same long-term outcome as fluctuating conditions that favor one species slightly more often than another (Figure 3b).

It is true that environmental fluctuations that change the identity of the dominant competitor give each species an opportunity to grow. In a constant environment, inferior competitors never get such an opportunity. But a change in environmental conditions that creates an opportunity for one competitor necessarily creates the opposite of an opportunity for the previously favored competitor. Evolutionary biologists recognize this by distinguishing 'opportunities in space' from 'obligations in time' [33]. Spatial environmental variation creates an opportunity for species to avoid unfavorable environmental conditions; each can persist in the location where it is the best competitor. But temporal environmental variation imposes obligations: in order to persist in the long run, a species must be able to grow and compete sufficiently well under all the conditions it will experience. Boxes 2 and 3 explain two ways in which species can coexist by 'meeting' or 'avoiding' the 'obligations' imposed
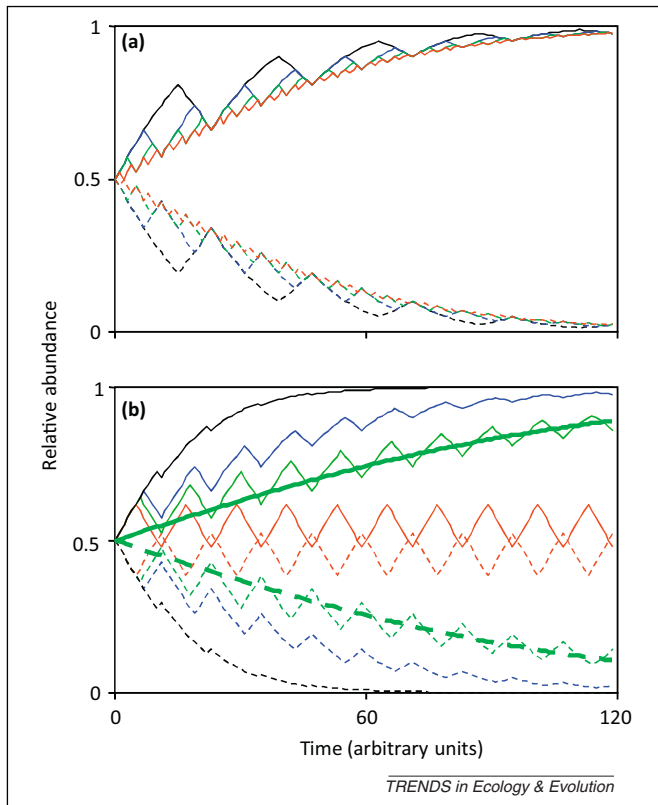
Figure 3. **(a)** Dynamics of relative abundance of two competing species (broken and unbroken lines) for different frequencies of environmental change (different colors). The environment alternates between a state in which species 1 (broken line) has relative fitness of 1 and species 2 has relative fitness of 0.9, and a state in which relative fitnesses are reversed. Species 1 is favored 2/3 of the time in every case, and so the rate of exclusion is the same in every case. **(b)** As (a), but now different colored lines indicate scenarios in which species 1 is favored different fractions of the time, ranging from 11/12 of the time (black lines) to 1/2 the time (red lines). The rate of exclusion slows as species 1 is favored less often, and when each species is favored 1/2 the time they coexist via neutrally-stable oscillations around their initial relative abundances. The boldfaced green lines show dynamics for a scenario in which species 1 is slightly favored at all times, so that it has the same fitness advantage on average as when it is favored 7/12 of the time (thin green lines).

by temporal variation, neither of which applies to the linear world assumed by Hutchinson [2].

Summary of theoretical refutations

It is essential to recognize that these three theoretical mechanisms are logically invalid, and so should be abandoned. This may seem like an overly strong conclusion. After all, are not all theoretical models false in some way? Yes – but crucially, not by being logically invalid. Wimsatt [34] classified the many different ways in which theoretical models can be false while remaining useful to empirical investigations. All of these ways of being 'usefully false' involve false assumptions. Rarely if ever will any theoretical assumption be literally and exactly true. More typically, an assumption might be only approximately true, or true in some circumstances but false in others, or false but unimportant because changing it would not greatly change the model's behavior. But to be useful, the predictions of a model must follow logically from its assumptions. Any 'prediction' which is not logically implied by a model's assumptions is not actually a prediction of the model at all. Data supporting or falsifying that 'prediction' therefore

have no implications for the truth or falsehood of the (logically unconnected) assumptions. The theoretical assumptions underpinning the IDH are empirically unproblematic. Disturbances can weaken competition, perturbations can interrupt progress towards equilibrium, and fluctuating conditions can alter the identity of the competitively-dominant species. But these assumptions do not imply the consequences (predictions) they are widely believed to imply.

What about competition–colonization trade-offs?

Some authors suggest a different rationale for the IDH: diversity may peak at intermediate disturbance levels because of a trade-off between competitive ability and colonizing ability (e.g., [1,35–37]). On this view, disturbances clear patches, which are first colonized by competitively-inferior species, which have time to reproduce and send out colonists to other newly-disturbed patches before competitively superior species arrive and exclude them. Infrequent disturbances fail to clear patches fast enough to support the competitively-inferior species, while overly-frequent disturbances wipe out the competitively superior species faster than they can colonize. This is a logically valid mechanism which can produce stable coexistence, and peaks in diversity at intermediate disturbance levels [35–37]. However, it is important to recognize four points. First, this logically valid mechanism should not be conflated with the logically invalid ones discussed above, although it often is (e.g., [1]). Second, some competition–colonization trade-off models are actually equilibrium models, in which patches transition between different states (empty, or occupied by different species) at constant, continuous rates and the proportion of patches in each state reaches a stable equilibrium (e.g., [36,37]). This is precisely analogous to how, in a population at equilibrium, births and deaths occur continuously and balance one another out, and so is an equilibrium rather than a nonequilibrium coexistence mechanism. Third, while other competition–colonization trade-off models do produce coexistence based on spatio-temporal fluctuations in patch states and other relevant variables, in these models, stable coexistence depends on nonlinearities and nonadditivities, not on the three logically invalid mechanisms discussed above [29,35,38,39]. Fourth, while competition–colonization trade-off models can predict peaks in diversity at intermediate disturbance levels, they often do not do so, and so do not support the IDH as a general hypothesis [13,39].

So how can disturbance and fluctuating environments actually promote stable coexistence?

Stably coexisting species must exhibit bounded population growth, also known as negative frequency dependence or stabilizing mechanisms: they must exhibit a sufficiently-strong tendency, on average, to increase when rare and decline when common, thereby keeping their abundances within bounds [27,28,40]. Bounded growth is necessary to ensure that species will replace themselves on average, and so exhibit no long-term trend in abundance [26]. Conversely, if species have no tendency on average to 'bounce back' from rarity, then they are doomed to decline to extinction [28,40]. For instance, in Figure 1 the species

being excluded exhibits brief transient growth after each disturbance – but this is followed by a more substantial decline, so that this species ends each inter-disturbance interval rarer than it was at the end of the previous interval, meaning that it fails to increase when rare on average and to replace itself on average. None of the three theoretical mechanisms discussed above creates any tendency on average for rare species to 'bounce back'. Disturbances and environmental fluctuations cause per-capita growth rates to fluctuate – but they generate stable long-term coexistence if and only if the fluctuations they generate act as stabilizing mechanisms [28], causing sufficient negative frequency dependence such that population growth is bounded and species increase when rare on average. This can occur only when average per-capita growth rates are nonlinear and/or nonadditive functions of fluctuating variables [25–29,38,39] (Boxes 2 and 3).

Coexistence-promoting nonlinearities and nonadditivities are not mere theoretical curiosities; they likely are common in nature [28]. For instance, [41] showed how environmental fluctuations combine with a trade-off between growth capacity and low-resource tolerance to promote stable coexistence in desert annuals via nonadditivity. Nonadditivity combined with environmental fluctuations also has been implicated in stable coexistence of perennial grasses, tropical trees, zooplankton, desert, shrubs and coral reef fish [42–48].

Abandoning flawed theoretical ideas about how disturbance and environmental fluctuations affect diversity would not leave ecologists without theoretical guidance. Indeed, theoretical ecologists have an increasingly well-developed understanding of diversity–disturbance relationships. Notably, recent models predict various diversity–disturbance relationships, including both humped and non-humped relationships [39]. These models therefore have the potential to explain the wide range of diversity–disturbance relationships seen in nature, and the rarity of humped relationships [8]. Rather than the rarity of humped diversity–disturbance relationships being a puzzle which needs to be solved by extensions or modifications of the IDH [9], it may simply be the expected consequence of nonlinearities and nonadditivities.

While recent models based on nonlinearities and non-additivities are more complex and less intuitive than the models on which the IDH was based, this is because recent models incorporate the biological complexities that actually drive ecological responses to disturbance and environmental change. Such complexity makes these models realistic, and facilitates empirical testing. The time is ripe for ecologists to abandon the IDH, and embark on a new research program testing the assumptions and predictions of logically valid models of diversity and coexistence in fluctuating environments. In nature, what frequencies and intensities of disturbance and environmental change actually promote coexistence via nonlinearities and nonadditivities?

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