Disturbing hypotheses in tropical forests

Douglas Sheil[1] **and David F.R.P. Burslem**[2]

[1]Center for International Forestry Research (CIFOR), P.O. Box 6596 JKPWB, Jakarta 10065, Indonesia
[2]Department of Plant and Soil Science, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, UK

The intermediate disturbance hypothesis (IDH) is a controversial explanation for the maintenance of tropical forest tree diversity, but empirical tests of it are rare. Two data-intensive evaluations have recently yielded contradictory outcomes: one for and one against the IDH. We propose that the explanation for these results lies in the subtleties of divergent interpretations and approaches, and in the different characteristics of the study sites. The apparent simplicity of the IDH is deceptive, because a range of distinct phenomena is involved, each of which can be defined and examined. Recent developments offer exciting opportunities for a deeper comprehension of how disturbance influences forest diversity.

Connell [1] summarized the intermediate disturbance hypothesis (IDH; Box 1)) as ‘the highest diversity of tropical rain forest trees should occur either at an intermediate stage in succession after a large disturbance or with smaller disturbances that are neither very frequent or infrequent; either represents an open non-equilibrium’. Does this help us to understand the maintenance of tropical forest tree diversity? Empirical evidence has been scarce, but two recent data-intensive studies reach contrasting conclusions. Hubbell *et al.* [2], working on Barro Colorado Island (BCI), Panama, examined treefall gaps within a 50-ha plot and noted that, although species densities increased in gaps, this reflected stem densities: species richness corrected for stem density was similar to that of the surrounding forest, and varied little with gap size. Molino and Sabatier [3], working in Paracou, French Guiana, quantified species richness (species per 40 stems sampled) in forest that had been logged unevenly ten years previously, and used the relative abundance of high light-requiring PIONEER (see Glossary) and HELIOPHILE species as a measure of past disturbance. They found that sapling richness peaked in quadrats with an intermediate representation of heliophiles. A similarly humped relationship was found when only unlogged forest quadrats were examined.

The studies reach different conclusions in spite of similarities in sample sizes and local climate (Table 1). The Paracou results support the IDH, because species richness shows a unimodal (rise and fall) pattern within the recorded range of disturbances. The authors of the BCI study imply that their results are not consistent with the IDH, because measured species richness appeared unrelated to implied disturbance. To explain these differences, we must examine the IDH (Box 1) and its application in tropical forests.

Disturbance and competitive exclusion in tropical forests

The role of the IDH in tropical forest has provoked several controversies. When evaluating the requirements and predictions of the IDH (Box 2) three topics are especially difficult: COMPETITIVE EXCLUSION, stand turnover, and the numbers of species benefiting from disturbance.

The IDH assumes that unhindered succession ultimately leads to dominance by a few species (Box 1). We thus expect to find low-diversity forests in undisturbed regions. The low-diversity MONODOMINANT forests that are scattered throughout the tropics can be interpreted in this manner [4]. An IDH-based rationale for the rarity of such forests would be that most sites are too disturbed [5]. Available information does indeed suggest that most forests are subject not only to small-scale local events, but also to occasional larger disturbances [6,7]. However, many other processes, unrelated to disturbance, have been hypothesized to prevent or slow competitive exclusion (e.g. [3,8]). Unfortunately, direct assessments in tropical forests are problematic, the experimental elimination of disturbances is unfeasible, and trends in long-lived tree communities remain open to alternative interpretations [9]. For us,

Glossary

Advanced regeneration: young trees (seedlings and saplings) that are not part of the forest canopy.
Competitive exclusion: the process by which increasing dominance by one or more species drives others to local extinction.
Dispersal limitation: suitable sites remain uncolonized because they are not reached by viable seeds.
Dosage effect: correlated with the abundance of parent plants.
Fugitive species: species vulnerable to competitive exclusion.
Gap-partitioning: the idea that gaps provide a range of conditions to which different species can be more or less specialized.
Heliophile: species requiring good illumination.
Life-history tradeoffs: the relation between two or more characters when variation in one implies variation in another. For example, seed number versus seed size. When constrained by limited energy, a plant might still evolve to give more small or fewer large seeds.
Monodominant: environment dominated by a single species.
Niche partitioning: different types or ranges of a resource can be most efficiently exploited and dominated by different organisms.
Pioneer: adapted to colonize vacant areas, usually good dispersers, requiring good illumination (species characteristic of early succession).

Corresponding author: Douglas Sheil (d.sheil@cgiar.org).

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Box 1. Introduction to the intermediate disturbance hypothesis

When organisms compete in a stable closed system, conventional wisdom suggests that superior competitors ultimately drive inferior competitors to extinction, and species number declines – a process called competitive exclusion. Connell [a] proposed the intermediate disturbance hypothesis (IDH) as an explanation of how species-rich tropical forests avoid competitive exclusion. Forest communities developing on vacant sites are viewed as evolving through a series of distinct states – a succession. Initially, the vegetation is dominated by colonizing species that are adapted to disperse well and can make use of abundant light and other resources, but which soon fail to establish in their own shade, and other more tolerant species then come to dominate. Finally, as increasingly shade-tolerant species edge out their predecessors, the series ends when the most effective competitors exclude any others. Therefore, in the absence of disturbance, species initially accumulate through succession (by dispersal and establishment) and are later lost through competition. Disturbance causes reversion of the community to younger successional states, in which species, previously excluded by competition, once again establish and grow.

In Connell's [a] scheme, this successional model links community richness with 'time since', 'frequency of', and 'size of disturbance' (Fig. I). Too much disturbance leads to the loss of late-successional species, whereas too little disturbance leads to exclusion of species adapted to colonizing younger sites. An intermediate disturbance regime enables coexistence.

What is disturbance?

Disturbance is usually considered as a rapid release or reallocation of 'community resources', but definitions do vary [b]. In Connell's [a] IDH, disturbance is defined as an event that regresses succession. However, combining all the factors that might regress succession within a single model of community diversity must be tempered by an appreciation of the very different processes, scales and impacts involved [b]. Some can selectively kill potential dominants (drought or windthrow), others open up new space (landslides or volcanic eruptions [c]), whereas some spatial processes (e.g. river meanders or dynamic forest edges [d,e]) also create colonization opportunities over large spatial and temporal scales. Biotic factors, such as disease and predation, are difficult to classify unambiguously. In extreme cases, natural enemies can modify local disturbance regimes by determining patterns of mortality and opening up space for colonization (e.g. defoliation of mangroves [c]), but the more subtle ways in which natural enemies act on individual species in relation to their density, and local conditions, can also play a role in preventing dominance in late-successional communities. Although such density effects are alluded to by Connell [f], they are not viewed as part of the IDH, because they do not rely on a succession–disturbance interpretation.

The multiple processes and scales involved mean that the IDH cannot be viewed as a single hypothesis without addressing numerous semantic and practical issues. Spatial scales were not directly examined in Connell's original brief account, although a later elaboration [f] emphasizes dispersal between areas at different successional stages. Timescales pose additional challenges. Most studies are forced to consider individual disturbance events, whereas communities are the products of the longer term disturbance regimes (e.g. [g,h]).

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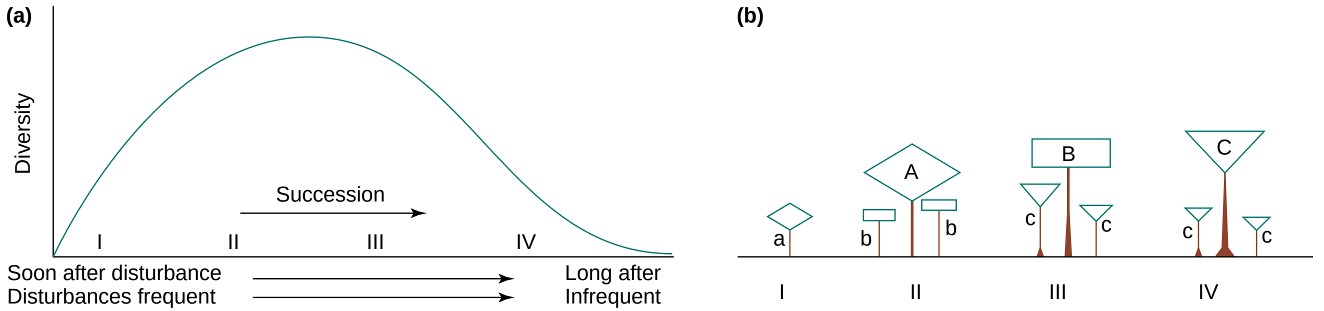

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Fig. I. The intermediate disturbance hypothesis. Connell [a] used one diagram (a) to link diversity with 'time since', 'frequency of', and 'size of' disturbances. The diagrammatic sequence of trees in (b) indicates the pattern of species replacement occurring in Eggeling's successional model of a Ugandan tropical forest [d] (and see Table 1, main text): 'In these colonizing stands the canopy was dominated by a few species (class A), but the juveniles (class B) were of different species. Adults of the class B species occur elsewhere as adults in mixed stands of many species. In these mixed stands, the juveniles were also mainly of different species (class C), those with even greater shade tolerance. Adults of class C occurred in other climax stands…in these stands, the understorey was composed mainly of juveniles of the canopy species'. Roman numbering denotes four stages in the sequence. Stage I is an addition to Connell's original diagram, because colonization involves only juveniles. Adapted, with permission, from Ref. [a].

the widespread occurrence of low diversity forests in close proximity to younger richer areas provides strong circumstantial support for competitive exclusion [4,5].

One difficulty with applying the IDH to forests is the relationship between internal tree-fall dynamics and external drivers of disturbance (e.g. storms, fire and drought). Connell [1,10] only discusses treefalls caused by external drivers in his account of the IDH. Tree death

Table 1. Characteristics of three tropical forest studies that address the IDH

Study location	**Budongo, Uganda (1° 43′N 31° 30′E, 1000 m)**	**Paracou, French Guiana (5° 2′N, 53° 0′W, 40 m)**	**BCI, Panama (9° 5′N, 79° 45′W, 120–160 m)**
Rainfall (mm yr^{1}); length of dry season (mths)	1500; 3–4	2500–4000; 3–4	2550; 3–4
pH_{H_2O} of soil at 0–15 cm[a–c]	5.6–5.9	4.2–4.6	6.0–6.2
Vegetation type	Closed-canopy semi-deciduous forest	Closed-canopy semi-deciduous forest	Closed-canopy semi-deciduous forest
Population minimum stem diameter (cm)	10	2	1
Sample scheme	Ten 1.4-ha plots placed to show variation in >100 km^2 (assumed successional sequence)	Ten 20 × 250 m transects within a 300-ha area: three in primary, seven in logged forest	Single plot
Total sample area (ha)	14	4.56[d]	50
Unit of analysis	Complete plots	20 × 20 m quadrats	20 × 20 m quadrats
Total stems	6127	$>17\,000$	$>300\,000$
Total species	149	546	314
Diversity measure	Species per plot	Species per 40 stems	Count of species divided by count of stems[e]
Measure of disturbance	None	Percentage of heliophilic stems per quadrat	Area of canopy <5 m tall (in 5 × 5 m grid square, annual 1983–1996)
Implied disturbance	None	Logging and natural tree fall gaps	Natural tree fall gaps
Main analysis	Richness versus implied succession	Diversity versus disturbance	Diversity of stems in two-year-old gaps (by size) versus nongaps
IDH expectation	Unimodal pattern	Unimodal pattern	Gaps richer[f]
Supports IDH?	Yes	Yes	No

Refs [1–3], respectively.

[a] C. Walaga, MSc Thesis, Makerere University, 1993.

[b] Ref. [49].

[c] Ref. [31].

[d] Excluded 8.8% as swampy or flooded areas.

[e] Chazdon *et al.*[19] point out that Hubbell *et al.*'s [2] measure of diversity (species per quadrat divided by stem count) is biased, because it is not independent of stem density. Molino and Sabatier [3] use a more satisfactory rarefaction technique to report species per 40 stems.

[f] This is the interpretation of the study's authors, not our own view.

and gap creation occur at all stages of forest succession and provide opportunities for the regeneration of colonizing species. If the net impact of such turnover was sufficient to counteract local competitive exclusion, low-diversity stands could not develop; yet the existence of large-scale self-maintaining low-diversity forest is among the best evidence that we have for the IDH, suggesting a possible paradox. It might be that monodominant forest species support an inherently low-intensity disturbance regime. The dense timber and broad buttresses of many such dominants enables them to die standing with little 'turnover impact' on the surrounding forest (D. Sheil, pers. obs.). Intrinsic gap processes remain an important component of community dynamics, but, in our view, the violent histories of many tropical forests [7] imply that external drivers will prove crucial in our understanding of differences between areas.

Various studies have shown that hurricanes [11], silvicultural treatment [9,12] and logging [3,13] can all raise sampled tree diversity. However, the number of species maintained is less certain. For example, in hurricane-impacted forests, the increase in species richness following storm damage is primarily due to a short-lived pulse of a few fast-growing pioneer species [14]. Longer term observations generally note the relative similarity of pre- and post-storm communities, with little ongoing successional change that might account for the coexistence of most species present [15]. Hurricane zone forests might be a special case as, in spite of major damage, forest recovery for most species occurs from vegetative regrowth and from regeneration present before the storm [16]. Although pioneer species are clearly maintained by suitable disturbance regimes, the extent to which the IDH can account for the persistence of most tree species remains unknown.

Redefining the IDH

Molino and Sabatier [3] suggest that the differences between their study and the results from BCI [2] arise from their different approaches to gaps and the background disturbance regimes. Here, we consider these suggestions and explain why, in our view, the BCI study is not an evaluation of the IDH.

Measuring disturbance

There is no simple indicator of rainforest disturbance. A direct measure of the changes in the quantity and quality of light, other resources and microclimate through space and time is unrealistic [17,18]. Field studies require indirect measures of disturbance. Hubbell *et al.* [2] used canopy height, but the biological meaning of this measurement is uncertain. Molino and Sabatier [3] used the percentage of heliophilic stems (and local basal area), a biological measure that has a definite successional interpretation, as required for the IDH (but that does suffer analytical pitfalls: Fig. 1).

Within or among gaps?

Both studies addressed finer spatial and temporal scales than did Connell's original example (Table 1, Fig. 2). Hubbell *et al.* [2] evaluated the IDH using small-area 'per gap' estimates of species richness and showed that these

Box 2. IDH axioms and predictions

The intermediate disturbance hypothesis (IDH) can be viewed as a means to explain species coexistence, and to predict how local and broader scale diversity is related to disturbance history. The model has *a priori* requirements (axioms), which, in terms of falsification, can be considered predictions. These are:

- Starting with colonization of empty habitat and continuing without disturbance, vegetation follows a recognizable successional sequence.
- In the succession, diversity initially rises, but ultimately declines through competitive domination by a few species.
- Disturbance causes regression to previous successional states (depending on intensity).

Given this system (however vague and statistical the operational definitions) the IDH predicts, for single events:

- Disturbance leads to reduction in local diversity for systems in early (diversity climbing) successional stages.
- Disturbance of appropriate (low enough) intensity, in late (diversity falling) successional stages can lead to an increase in local diversity.

Over longer periods, and at scales larger than the disturbance events themselves:

- As in Box 1, Fig. I, the richness maintained in any given area should show a unimodal relation to intensity of disturbances (when applied at constant frequency).
- As in Box 1, Fig. I, the richness in any given area should show a unimodal relation to frequency of disturbances.
- The system maintains more total species when the disturbance regime enables the maintenance of diverse successional stages.

The original formulation lacked explicit spatial predictions, but implied a truism, from which spatial models can be developed, that is:

- Fugitive species can be maintained if they have adequate chances to disperse from areas where persistence is impossible (in the longer term) to new areas where they can complete their life cycle. In general:
- Species can be lost locally if disturbances are too severe, too often, or too synchronized, or if competitive exclusion is enabled through long-term lack of disturbances.

were similar in gaps and closed forest. Commentators have requested an alternative analysis with observations pooled among gaps [19,20]. Hubbell declined, and explained that differences between gap communities were due to limited dispersal, an explanation that he views as distinct to the IDH [19,20]. We view dispersal (in the context of tradeoffs) as a clear component of a spatial implementation of the 'between-patch' IDH (Box 3).

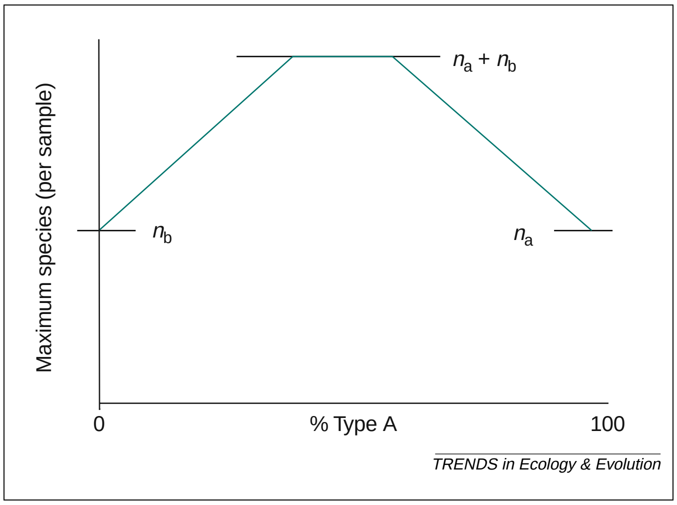

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Fig. 1. The humped null-model problem: the maximum possible counts of species in samples of a population comprising two groups A and B with n_a and n_b species respectively, plotted against the proportion of type A in the sample. We can create such a relationship: (1) list all the species in a community and allocate each at random to group A or B, (2) take samples of a fixed number of individuals and, for each, plot species number versus the proportion of class A individuals (we assume for this illustration that the number of individuals per sample is larger than $n_a + n_b$). When A is 100%, the maximum species number is n_a; when $A = 0\%$ ($B = 100\%$) the maximum possible species number is n_b. Yet the highest species number in one sample is $n_a + n_b$, which occurs with a near complete mix of A and B species. As the species-group allocation was random, this result has no ecological significance in spite of the resulting rise and fall pattern. Mean samples from mixed populations also behave in a similar unimodal fashion: higher counts are more likely when species groups are mixed. Thus, the null model for such analyses is not a straight line, but a humped unimodal shape [48]. Is the relationship seen in the Paracou study [3] merely a reflection of this artefact? Molino and Sabatier have used randomized species to group allocation to develop the appropriate null relationship [48], however, this null curve is significantly less humped than the real pattern using the ecologically constructed guilds from Paracou [3] and the IDH interpretation survives the test [48].

Or across ages?

Although Connell's original formulation of the IDH lacked an explicit spatial structure, he later argued that many species could be maintained when a forest contains a variety of successional stages and species are able to flow between patches [10]. Local enrichment in recent disturbances (gaps) is not required, but enrichment occurs at larger scales that include multiple successional states [21]. A suitable analysis would consider the degree to which post-disturbance sites: (1) include species that occur only in such areas; and (2) enable the establishment of species that might persist in the older (nongap) forest but would not be present without past disturbance events. Neither Hubbell *et al.* [2] nor Molino and Sabatier [3] address such aspects. Even on BCI, gaps enrich forest at the broader community level by maintaining a set of strict heliophile pioneers that are intolerant of shaded areas [22,23].

Short timescales

Hubbell *et al.* [2] imply that local diversity should peak before 'gap forest' is old enough to be considered 'nongap

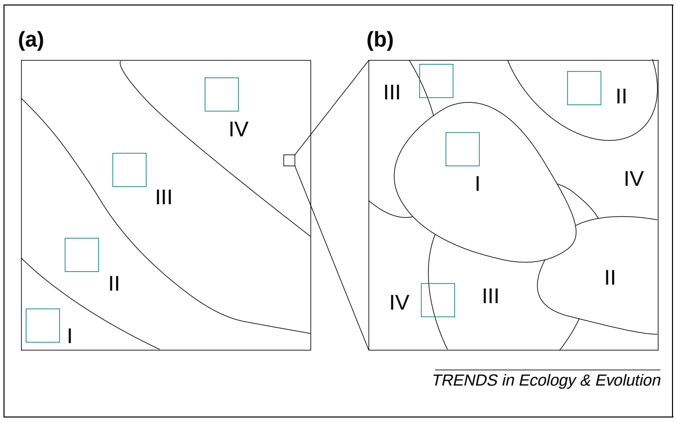

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Fig. 2. Comparing scales of assessment in stands and gaps. In Connell's original example (a), the forest undergoing succession results in various vegetation types I–IV (Box 1), which form a continuum with a core of older forest (IV) grading into younger forest (I). Squares represent the samples being compared. In both Hubbell *et al.*'s [2] and Molino and Sabatier's [3] interpretations (b), these ideas are applied at the scale of individual treefall gaps within 'mature' forest. A single tree gap is now treated as a distinct community.

Box 3. Coexistence in time and space

The central premise of the intermediate disturbance hypothesis (IDH) has stood the test of time. Numerous analytical- and simulation-based models, in which two or more species possess different colonization abilities and tolerance to competition, show that coexistence is possible only with an appropriate disturbance regime. Such models, in which each species occupies a unique point on a defined competition–dispersal tradeoff continuum, do not set any upper limit to the number of species that can coexist [a].

Patches and persistence

There is more than one mechanism by which disturbance can facilitate species coexistence. 'Within-patch' and 'between-patch' models illustrate the mechanisms involved [b,c]. Within-patch models consider a homogeneous closed system in which space is not explicitly considered: competitive exclusion is prevented when the disturbance regime provides intermittent opportunities for the recruitment of species at all points along the life-history spectrum, from late-successional competitors to early-successional colonizers. Species with low tolerance of competition, which would be eliminated without disturbance (fugitive species) can endure periods of severe competition in a dormant (seeds) or durable (seedling bank or long-lived adults) life stage, a mechanism that is sometimes referred to as temporal niche sharing (see Box Glossary) or the storage effect [d]. Intuitively, the storage effect should have most significance for long-lived organisms with overlapping generations, such as forest trees, because rare opportunities for recruitment can be sufficient to maintain populations. Few analyses have, however, incorporated species life-stage characteristics, such as time to reproductive maturity. When such factors are considered, the storage effect remains a potentially powerful means to avoid competitive exclusion (S. Dewi, PhD Thesis, Australian National University, Canberra, Australia, 1997).

Between patches and spatial structure

Between-patch models include dispersal. Fugitive species might be eliminated in any given patch by local competition, but with local disturbances, recolonization can occur from patches that are at earlier successional stages [c]. Connell [e] emphasized such an 'open systems' perspective for the operation of the IDH in tropical forests. There is however, an important caveat once fully spatial models are considered: poor dispersal by dominant species can itself slow exclusion, as it might take many generations to reach and win all the potential sites, even in the absence of disturbance. If fugitive species are highly mobile by comparison, they can take advantage of very limited opportunities in both space and time [c]. Observations are required to clarify the scale and influence of these mechanisms in tropical forest.

Dispersal in forests

Seed-trapping studies have estimated median dispersal distances between 0.8 and 83.1 m for 14 pioneer species on Barro Colorado Island (BCI), the overall results implying that mobility is highly localized [f]. However, such observations might underestimate the significance of occasional long-distance dispersal events. Much of the variance in seedling community composition remains unexplained by dispersal distances [f]. A comparison of seedling and local adult communities at Gunung Palung, Kalimantan, Indonesia [g] a forest that has a more intact fauna than does BCI, implied that 68% of species and 46% of individuals in the seedling community must have been actively dispersed ($\geq$17 m). Such high rates of active dispersal effectively eliminate dispersal limitation as a mechanism slowing competitive exclusion at this site[g].

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Box Glossary

Storage effect: a species persists, in spite of the presence of superior competitors, because of an unstable environment that enables occasional release from competition.
Temporal niche sharing: species coexist in the same space and use the same resources but avoid direct competition in some periods through unsynchronized life-history schedules.

forest'. This is the 'IDH prediction' that Hubbell *et al.* falsify. Their account focuses on a two-year gap age and the ultimate threshold for separating gaps from nongaps appears to be reached 13 years after gap creation. These are very short intervals in forest succession, and continued observation might find that species accumulation occurs over longer periods.

Small gaps

Most of the gaps in the BCI study were small (894 out of 1284 gaps were <50 m^2, this is 70% of gaps and 37% of gap area [2]): will these regress succession? Simulations of the maximum potential duration of direct radiation arriving at ground level indicate that the centre of square gaps of 25 and 50 m^2 on BCI would receive no direct radiation, except as short duration sunflecks (assuming a site on flat ground with a mean canopy height of 30 m: http://www.abdn.ac.uk/pss/elec.hti). Generalizations are risky, but it appears that even well-lit gaps are rapidly filled by shade-tolerant seedlings that existed before gap formation [24,25] or by resprouts[26], resulting in little direct impact on composition and diversity. Thus, typical tree-fall gaps do not appear to involve the successional changes required by the IDH.

Gap partitioning or the IDH?

Hubbell *et al.* [2] equate the IDH with a gap-partitioning theory in which life-history tradeoffs favour different species in different gap sizes [25]. However, gap size is not the only factor that matters. Location within a gap, gap shape, orientation, aspect and time of creation might all influence the seed dispersal, survival, germination and persistence probabilities that determine local regeneration [25]. Seedlings, and resprouts of stems already present at the time of the disturbance, often take advantage of gaps, reducing the significance of any post-disturbance recruitment from seeds. Both gap heterogeneity and the predetermined nature of gap filling advanced

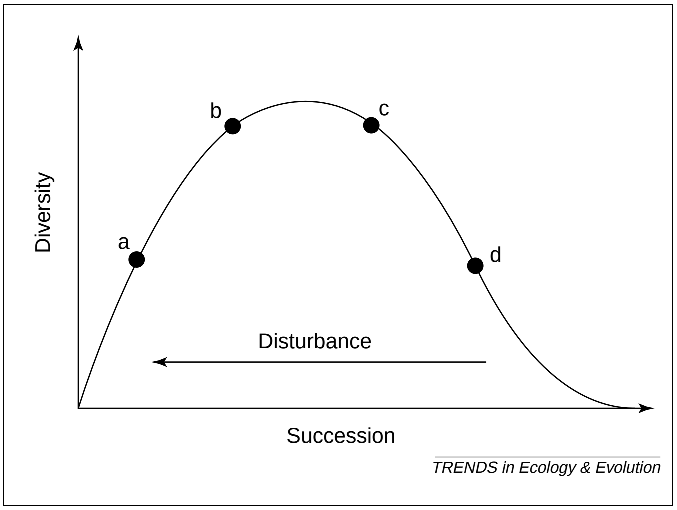

Fig. 3. The species decline paradox. Stages along an idealized IDH curve are labelled, a–d. In the absence of disturbance, any point on the curve moves to the right over time. A suitable disturbance can cause the community to revert from any stage to any earlier stage. Enrichment follows some of these transitions (e.g. if d reverts to b or c). However, many transitions do not yield such short-term enrichment (d to a, c to a or to b, and b to a) even though species number might slowly climb subsequently. Knowledge of the overall successional pattern enables us to understand that all these disturbance events help prevent an ultimate decline in diversity to points beyond d, which would occur if there were no disturbances. An adequately severe event at BCI might involve a transition such as b to a, showing a net decline in local richness, although the IDH tells us that species richness should subsequently rise. Indeed, asynchronous phasing of the disturbance cycles (e.g. the coexistence of some areas in state a, whilst others are in state d) also contributes to broader scale species maintenance. Paradoxically, many disturbances have a short-term negative impact on species richness yet prevent competitive exclusion and maintain broader scale diversity.

REGENERATION helps explain why gap size has low explanatory power as a predictor of post-disturbance species richness [24]. To us, gap-partitioning theory is distinct from the IDH. A theory that relates nonsuccessional gap heterogeneity with NICHE PARTITIONING among species complements rather than includes the IDH as a potential explanation for species coexistence.

In spite of our concerns about the BCI study, the Paracou researchers used similarly small quadrats (Table 1), and found an IDH-related pattern after only ten years. Site differences provide an explanation.

The disturbing history of BCI

In many tropical forests, the larger canopy species do not regenerate in the same locations in which the adults occur [27]. Such patterns are integral to the successional changes required by the IDH (Box 1, Fig. Ib). Hubbell and colleagues have argued previously that an explanation of this kind is needed to account for the presence of long-lived pioneer species found only as large diameter stems on BCI [28]. They suggest that 'there were small clearings 600–800 years ago where the plot is now; this is clearly within the life span of a giant *Ceiba* or *Anacardium*…Another reasonable possibility is that these species do occasionally recruit following large-scale natural disturbances…' [28, p. 507]. Disturbance would also explain the forest-wide abundance of pioneer and light-demanding species at BCI that 'have been in steady decline since the plot began'. If the current community indeed reflects a recovery following past disturbances, the impact of further disturbances will be affected. The observation that the gap vegetation on BCI is initially less rich than that of older forest [19] is consistent with the IDH view that any disturbance will reduce local richness if the forest is still in the early, species-accumulating stage (Fig. 3).

What might have caused past disturbance on BCI? Drought, fire, lightning and destructive wind storms all occur, but anthropogenic effects are our primary suspects. Extensive human use of the now forested regions of lowland Panama before the post-Spanish depopulation, c. 300–400 years ago, is well documented (e.g. [29,30]). Half of BCI was disturbed up to 150 years ago, and the older forest was probably cultivated until c. 600 years ago [28]. The forest is only a few tree generations old, and we believe it is still undergoing succession.

Soils

The relatively nutrient-rich soils of lowland central Panama would have been attractive to shifting cultivators. The surface soils of BCI have a relatively high pH, and plant-available nutrient concentrations are also relatively high [31], whereas those at Paracou are similar to the more acidic and nutrient-poor soils that underlie much of the Guiana Shield and most lowland tropical forests [32]. The richer soils of BCI might also explain the high stand turnover and exceptional growth rates of trees >1 cm stem diameter [33]. The role of soil fertility in controlling the rate of competitive exclusion is uncertain, and can be argued either way. Faster growth might be expected to speed up stand dynamics and therefore hasten competitive exclusion. However, rich soils might promote the growth and survival of nutrient- and light-demanding species relative to light-limited slow-growing species. If so, nutrient-rich soils might enable nutrient-demanding pioneers to complete their life cycles more rapidly in comparison to background stand dynamics and, in this way, gain an advantage that might slow ultimate exclusion. Soil fertility and past disturbances might explain why fast-growing heliophiles are so plentiful on BCI.

In the context of regional patterns

Similar to Paracou in French Guiana, much of the forest in neighbouring Guyana has relatively nutrient-poor soils. Ter Steege and Hammond [34] examined patterns in tree communities across Guyana and found that the more-diverse tree communities were associated with mean species characteristics that were indicative of pioneers (low wood density, small seeds and effective dispersal), whereas the low-diversity communities were characterized by dense-timbered, slow-growing, more competition-tolerant species. They inferred that regional patterns of plot-level species richness were in a mature successional decline, as implied by the right-hand side of the IDH curve (Fig. 3), with low rates of disturbance associated with low diversity. Paracou also appears to be in this 'declining-species' state (beyond c in Fig. 3) which would mean that small-scale disturbance would lead to a consistent increase in local diversity.

Isolation

BCI became an island when the Panama Canal was completed in 1914, and such recent isolation from surrounding forests has ecological implications for forest regeneration. The composition and structure of the mammal and bird communities have changed: experimental studies have demonstrated lower seedling damage from animals and higher seed predation of four large-seeded tree species, such as *Gustavia superba* and *Virola nobilis*, on BCI relative to mainland sites with an intact fauna [35]. Altered herbivory patterns influence tree survival and reproduction and forest composition [36]. The determinants of regeneration on BCI might not be typical for tropical forests.

Future supremacy

Would we observe a trend towards competitive exclusion on BCI if the forest was left undisturbed for long enough? Perhaps. *Prioria copaifera* is a candidate species for attaining dominance in lowland central Panama. Similar to other caesalpinoid legumes that form monodominant lowland tropical forests, *P. copaifera* has a tendency to form dense aggregations. Although often considered a swamp species, it can attain high local densities on well drained sites, including parts of the BCI 50-ha plot [37]. Within the plot, the mortality rate of *P. copaifera* is much lower than that for the forest as a whole, and its abundance has increased consistently (by 6% in only eight years [37]).

Practical relevance

Many of the tropical rainforests of the world are influenced by human disturbance. Does consideration of the IDH provide any practical insights? Damage, such as that caused by industrial logging and silvicultural treatments, can cause a rise in species richness [9,12,13], but theory and evidence suggest that cosmopolitan species benefit at the expense of old-growth vegetation. It is the late-successional species, those that grow slowly, reproduce late and are poorly dispersed, that suffer in response to chronic disturbance and that need conservation. These specialists of undisturbed habitats are also the species lost in simulated habitat fragmentation [38] and are the taxa in which the highest levels of local endemism are expected [34]. One recent study in peninsular Malaysia has indicated that rarer species with restricted distributions become disproportionately rarer in areas harvested for timber [39]. Maintaining undisturbed old-growth forest should be considered an important conservation goal. There is, in addition, an increasing awareness of the role that chronic disturbance can play in enabling invasion by weedy species [40]. The proximity of disturbance also has impacts on community structure, because vegetation is susceptible to invasion by weedy species via a DOSAGE EFFECT [41]. Crucially, as implied by the IDH, species are not equivalent, and species counts need not represent any inherent conservation value [42].

Conclusions

Natural treefall gaps, defined by low canopy areas, do not yield short-term gap-scale increases in tree species richness at BCI [2], although observations in Paracou suggest that localized disturbances can raise local community richness [3]. We have argued that both observations are consistent with the IDH, the difference relates to the successional status of the sites, and the methods employed by the researchers.

Hubbell and his colleagues working on BCI have inspired numerous advances in tropical forest ecology and, in spite of our concerns, their recent study [2] might not be an exception. It provides a valuable description of some gap processes, and the observations of DISPERSAL LIMITATION are important. Nonetheless, we conclude that the forest on BCI might be too disturbed to provide a convincing test of the IDH as an enriching process at any scale. Indeed, we go further and suggest that the rich soils, abundance of pioneers and recent isolation of BCI from the mainland set it apart from tropical lowland forests more generally. We remain convinced that tree-fall gaps do contribute to important aspects of stand behaviour, but believe that larger scale longer term processes have played a major role in moulding the current richness and behaviour of tree communities on BCI.

The IDH is an elegant but oversimplified representation of a complex knot of concepts: that many events and processes can both augment and erode diversity through various linked processes at a range of scales. The least satisfactory aspects of this simplification are: (1) the assumed predictability of the successional process; (2) the need to better reflect spatial structure in communities and disturbance regime; and (3) ambiguity concerning both appropriate measures; and (4) scales of assessment. Modern hypotheses that consider succession need to reflect the more conditional, stochastic and spatially explicit processes that feature in recent efforts to account for community change [18,43,44]. A deeper understanding requires attention to scale, landscape-pattern, history, species pool and the many processes that together influence forest communities [17,44,45]. However, in elegantly capturing fundamental concepts, we believe that the IDH is still relevant in most tropical forest locations, even BCI: not as the sole explanation of tree diversity, but as a significant one.

New directions

We foresee many opportunities to clarify how disturbance influences species richness in tropical forests, especially at larger scales, building on theoretical advances and simulations (e.g. Box 4). Recent approaches to assessing the consequences of disturbance and temporal changes through guild ratios [3], species characters [34] and recruitment variation as inferred from stem size distributions [46] require further investigation, and would be applicable across a variety of scales. These approaches also justify the expansion of local networks of forest dynamics plots to larger scales, and into species-poor monodominant tropical forests to examine whether competitive exclusion is the exception rather than the rule. The use of large-scale experimental disturbance regimes, or their analogues, such as the logging in Paracou, offers opportunities for investigating local enrichment and loss in controlled systems. In addition, dispersal needs broader evaluation for its role in regulating succession and exclusion, in maintaining FUGITIVE SPECIES, and in spatial pattern relationships and the interplay between pattern, phenology and chance. New tools offer an array of

Box 4. Forests and disturbance: other directions

The intermediate disturbance hypothesis (IDH) is not the only source of concepts with which to gauge the relation between tree diversity and disturbance. Hubbell's [a] neutral model is successful in explaining several aspects of community structure, even though the assumption of the model of species equivalence prohibits successional processes. Such results imply that differential responses to disturbance are not required to explain common patterns of relative species abundances. They also reveal that dispersal limitation can greatly reduce the speed of competitive exclusion over large regions among equal species, to suggest timescales that might be adequate for an evolutionary equilibrium between extinction and speciation rates [a]. However, Hubbell's model cannot explain community patterns where succession is an obvious determinant (e.g. [b]). Chave *et al.* [c] have shown the potential for unification through models similar to Hubbell's, but which do reflect interspecific competition–colonization tradeoffs. Simulations reveal realistic community-level patterns and enable successional phenomena[c].

Although Hubbell's results provide a counterbalance to previous niche theories, most theorists agree that some species differentiation will arise in evolving systems, especially in the context of variable conditions [d]. In his 'strategy space model', Loehle [e] suggests how multiple life-history traits enable tree coexistence when disturbance patterns fluctuate in space and time. Loehle proposes that multiple tradeoffs, among shade tolerance, height, capacity for vegetative reproduction and dispersal distances (he also suggests 'nutrient capture strategies', age of reproduction and crown architecture) would be selected for in response to temporal, spatial and intensity aspects of disturbance. Quantification of these tradeoffs and predictions of species number has not yet been attempted for tropical forests, although Loehle argues that tree diversity patterns are likely to be determined principally by the disturbance regime, combined with forest stature and latitude [e].

Evidence for species differentiation includes life-history tradeoffs in seed germination behaviour, seed size and seedling growth, community phenology and seedling persistence, tree architecture and allometry, and habitat occupancy [f]. A broad review of empirical evidence has concluded that the pioneer–nonpioneer continuum, together with maximum size, summarizes much of the associated variance in tropical tree life histories, which implies an important role for disturbance in the evolution of these taxa [f].

Advances in both analytical and computational approaches have clarified the roles of spatial pattern and limited dispersal as a basis for alternative competitive strategies [g,h]. Spatial and temporal patterns are now major concerns in our understanding of tropical forest behaviours.

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possibilities for examining dispersal in individually mapped communities such as exist in several tropical forest locations [47].

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