

Review

Conceptualizing Forest Degradation

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Forest degradation is a global environmental issue, but its definition is problematic. Difficulties include choosing appropriate reference states, timescales, thresholds, and forest values. We dispense with many such ambiguities by interpreting forest degradation through the frame of ecological resilience, and with reference to forest dynamics. Specifically, we define forest degradation as a state of anthropogenically induced arrested succession, where ecological processes that underlie forest dynamics are diminished or severely constrained. Metrics of degradation might include those that reflect ecological processes shaping community dynamics, notably the regeneration of plant species. Arrested succession implies that management intervention is necessary to recover successional trajectories. Such a definition can be applied to any forest ecosystem, and can also be extended to other ecosystems.

The Degradation of Forests

One third of the population of the world is estimated to be affected by land degradation, which encompasses soil erosion, salinization, peatland and wetland drainage, as well as forest degradation [1]. In the tropics alone the total area of degraded forest has been estimated to be around 500 million hectares, in recognition of which emphasis has been placed on reducing further forest degradation [2,3]. Developing transparent and internationally harmonized forest policy and management responses relies on shared interpretations of ‘forest’, ‘deforestation’, and ‘degradation’ [3,4], as does the implementation of climate mitigation mechanisms, such as Reduced Emissions from Deforestation and Forest Degradation (REDD+) [5–8]. There are, however, many definitions of forest degradation, and their interpretations differ greatly [3,4,9,10] (Box 1).

We argue for an ecologically founded conceptual framework within which forest degradation can be described and understood [11], and on which operational definitions of forest degradation can be based. More specifically, degradation should be set in the context of an understanding of ecosystem processes that underlie forest dynamics, and which shape trajectories of recovery following disturbance [12–14]. The states and processes of forest change and recovery are, of course, relevant to the continued provision of forest goods, ecosystem services, and biodiversity conservation [15,16].

Problems in Defining Degradation

Forest degradation has been defined in more than 50 different ways [10], reflecting not only biophysical differences among forest formations but also different perceptions, objectives, and values. Forest degradation is generally considered to be a loss of some attribute, function, or service in response to disturbance (Box 1), where disturbance is defined as a discrete event in time that disrupts ecosystem composition, structure, or function, and brings about a change in resources, species interactions, or the physical environment. Indeed, the sustainable use of forests and forest resources is predicated on the assumption that exploited forests have

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Forest degradation results in biodiversity loss, greenhouse gas emissions, and diminution of ecosystem goods and services, but scientists, practitioners, and policy-makers are unable to agree a framework for defining degradation.

Forests are spatially and temporally dynamic, and this stymies the selection of appropriate reference states, timescales, and thresholds against which degradation might be determined.

Degradation is often defined as reduced capacity to provide goods and services. This definition takes little account of forest resilience – the ability of a system to reorganize and recover following disturbance.

Advances in describing and quantifying ecosystem functioning have been fundamental in understanding forest dynamics, and provide a promising framework by which degradation might be better understood and, ultimately, defined.

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Box 1. Degradation Dubiously Defined

Forest degradation is most often loosely defined as a loss of particular forest attributes: the Food and Agriculture Organization of the United Nations (FAO), for example, defines forest degradation as ‘the reduction of the capacity of a forest to provide goods and services’. Services might include biomass, carbon sequestration, water regulation, soil protection, and biodiversity conservation [11]. This very generic definition is often adapted to suit local management or policy contexts. The Intergovernmental Panel on Climate Change (IPCC), for example, defines forest degradation as ‘direct human-induced long-term loss...of at least Y% of forest carbon stocks...since [time] T’ [46]. Such a definition is limited in being determined by only a single variable presented in a binary format, and which is conditional on the assigned values of (in this case) carbon stock and time. Indonesia’s Forest Law lacks any legal definition of degradation at all, although a Ministry of Forestry report refers to forest degradation as ‘sustained, human-induced decrease in carbon stocks’ [75]. On this basis it has been estimated that two-thirds of the annual 6% decline of Indonesia’s forest timber stock from 1990–2005 is attributable to forest degradation [76]. Brazil’s National Environmental Policy Law (Política Nacional Do Meio Ambiente, Article 2) describes degradation as ‘...the resulting processes of the damages to the environment by which some of its properties are lost or reduced, such as the productive quality or capacity of environmental resources’. From this it is estimated that forest degradation is estimated to be responsible for 20% of greenhouse gas emissions in the Brazilian Amazon [77]. However, these statistics are not readily interpretable nor comparable because these definitions of degradation lack precision. Different national interpretations also stymie the development of coherent and harmonized international forest policies, which is a necessary precondition for comparable and transparent reporting of land use changes [4,10].

sufficient resilience to recover such attributes [17–20]. Interpreting degradation as a loss of attributes or functions, while intuitive, is not sufficiently precise to distinguish between the many states that forests can occupy. For example, forests recovering from natural disturbances, or secondary forests maturing on formerly cleared land, might be classified as degraded because their productivity or service provision is reduced relative to a ‘natural’ forest [21]. Neither does this approach accommodate non-equilibrium dynamics among multiple forest states, which might be driven by entirely natural disturbance processes. Moreover, such a vague interpretation runs the risk of being shaped by vested interests or political agendas that might have little bearing upon biophysical realities [3].

Some definitions focus on structural components of forests [22–24] while others adopt a functional approach [25], or one based on resources [26]. Confounding issues include how reference states should be constituted (if at all), and what are meaningful timeframes for forest recovery. Operational definitions usually focus on a limited number of elements that are rarely linked to processes of forest dynamics and recovery [8,10,27]. Such definitions provide few insights into the mechanistic processes that underlie functional degradation and, by extension, the trajectories of change and potential for recovery. Equally, vulnerabilities to non-linear responses or positive feedbacks are difficult to capture within such simple frameworks [12,28–32].

Many definitions idealize a reference state to which degraded forests are compared. This is often an undisturbed natural forest, or a forest with properties ‘normally associated with the natural forest type expected at that site’ [33]. This is unsatisfactory because it leaves open to interpretation what is meant by ‘normal’, ‘natural’, and ‘expected’. Forests are dynamic at multiple spatial and temporal scales. They respond to a wide range of natural and anthropogenic disturbances, and often include legacies of past disturbances of which we have little or no knowledge [34]. The concept of ‘pristine’ forest is hardly appropriate in an era of pervasive anthropogenic change [35] (Box 2). An alternative approach has been to specify the reference state in terms of the goal-orientated forest outcomes of a ‘sustainably managed forest’ [27]. This allows management outcomes to avoid the label of degradation even if a permanent change to forest state is incurred [4,36]. Its limitation is that it excludes non-managed forests that are nonetheless affected by human activities.

Degradation within the Context of Resilient Systems

We derive our concept of forest degradation from resilience theory and the analogy of basins of attraction [18]. A basin of attraction represents a range of ecosystem states that tend towards

Box 2. Anthropogenic Versus Natural Disturbances

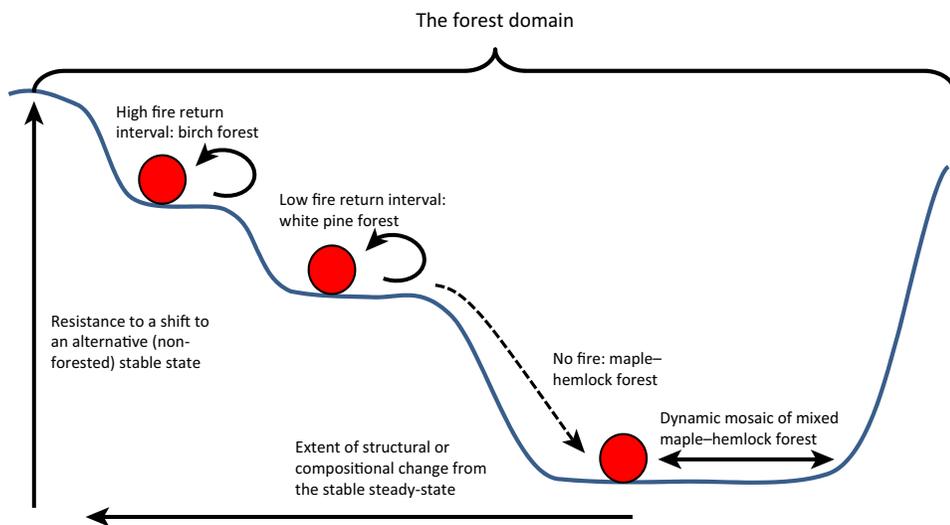
The crux in defining forest degradation lies in the distinction between anthropogenic and natural disturbances. Forests are dynamic, complex systems, constantly shifting in composition and forest formation in response to natural disturbance regimes and interactions among species expressed at local to regional scales [36]. Most ecologists therefore tend to exclude natural disturbances from those that could cause degradation [78]. However, the line between natural and anthropogenic disturbance is becoming increasingly blurred, and distinguishing between degradation, which implies some human intervention, from naturally disturbed forest, is no longer simple or even possible. Human disturbance legacies can be long-lived and difficult to distinguish from natural processes [79,80]. Global climate change, nitrogen deposition, and biotic mixing now influence forests across the entire planet [35]. Soil charcoal and pollen records have attributed increased fire frequency in temperate and boreal forests to changes in climate and human management [49]. Nonetheless, forest fires preceded major human influence, albeit at lower frequencies [35], and disentangling natural from anthropogenic drivers of forest fires is difficult. Furthermore, changes in forest properties resulting from natural and anthropogenic disturbances can be similar. Hurricanes and selective logging can both damage around 50% of a forest canopy, contributing to elevated fire risk through drying of fuel load. It is not obvious, in terms of forest change, whether these anthropogenic and natural disturbances should be treated differently. We suggest that, if it can be demonstrated, on balance of probability, that anthropogenic environmental changes have created the conditions by which natural disturbances cause non-reversible forest transitions, then we can apply the term degradation.

one, or often several, stable steady-states. A steady-state does not imply a static state, and indeed ecosystems are locally dynamic. Even in the absence of disturbance, local neighborhood effects, together with interactions among biotic and abiotic elements, will incur small-scale changes in forest composition and structure. Discrete disturbances, however, displace ecosystems from the stable steady-state to another state that lacks stability, meaning that without further disturbance the forest in its new state will tend to undergo changes that return it to the stable state through natural processes of succession. System displacement might be large or small, depending on the disturbance type, scale, intensity, and frequency. Resilience is the tendency for an ecosystem to return to its pre-disturbance stable state following disturbance [18,19]. If disturbances are too large, frequent, or novel, the ecosystem might be shifted to a state from which transitions back to the stable state are unlikely.

We use this framework to interpret forest dynamics and degradation. The basin of attraction comprises a suite of forested states (although forest definitions can themselves be contentious [4]) which, in the absence of disturbance, tend towards one stable state, or several temporally-stable but non-equilibrium states. This implies that ecological processes integral to forest dynamics and resilience remain intact. Disturbances are a natural reality of any ecosystem (Box 2), and thus forest states are never static but shift around the basin (Figure 1). The position occupied by the ecosystem within the basin topography describes two attributes: horizontal distance from the lowest point represents dissimilarity from the most stable state, and height above the lowest point reflects vulnerability to switching to an alternative (non-forested) ecosystem state. The cold temperate forests of northeastern USA, for example, might comprise stands of birch, white pine, or mixed stands of maple and hemlock, depending on the frequency and severity of fire (Figure 1). These states are stable given particular fire return intervals, but if fire frequency (or intensity) changes then one forest type shifts to another [37,38]. Without disturbance, the forest tends towards maple and hemlock, which, by virtue of a less-flammable leaf litter, reduces the likelihood of further fire. Neither birch, white pine, nor maple/hemlock stands are degraded because they exist in non-equilibrium states shaped by the disturbance regime. In this sense, there is no particular reference state because all states are equally valid as natural ecosystem states. There is, in other words, no arrested succession.

Loss of Resilience

We define forest degradation as human-induced loss of resilience which prevents natural recovery to the pre-disturbance state. States of degradation can be illustrated by locally-stable states that lie within the realm of the larger basin (Figure 2). Within these smaller basins ecological processes act to return the ecosystem to the local basin of attraction (hence preventing a return

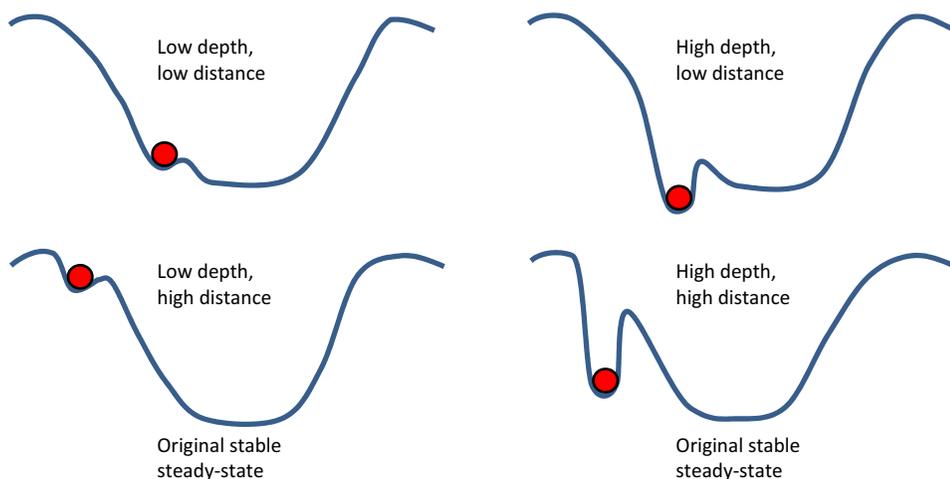


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Figure 1. Shifts Among Successional Stages Driven Purely by Natural Phenomena and Processes. None of these states can be considered as degraded because, in the absence of perturbations, they would each tend towards the most stable state. Note that the stable steady-state is a more or less broad basin encompassing multiple forest states that constantly shift in response to ecosystem interactions.

to the larger basin), implying arrested succession (Figure 2). Escaping these ‘sub-basins’ can only be achieved through human intervention, or by sufficient subsequent natural disturbance. Ecosystems at these locations are forested (i.e., they remain within the larger basin) but, being locally stable, the natural process of recovery is arrested, and time alone cannot return the system to its pre-disturbance state.

In Uganda, for example, cleared forest often becomes dominated by the native shrub *Acanthus pubescens*, after which there is little opportunity for tree regeneration [39]. Tree seedlings initially



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Figure 2. Representations of Types of Degradation. The extent of ecosystem compositional and structural change is reflected by the horizontal distance from the original stable state. The effort required to return the degraded state to a trajectory of recovery towards the original stable state is reflected by the depth of the local basin.

thrive in *Acanthus*-dominated clearings, but are smothered by periodic collapses of the shrub. Elephants feed on *Acanthus*, and in so doing flatten the foliage, further smothering tree seedlings. Elephants also open up new forest areas that are rapidly invaded by *Acanthus*. In the absence of elephants *Acanthus* thickets will eventually be replaced by trees, but in the foreseeable future the only means to escape this positive feedback, which arrests forest succession, is through continued human clearance of thickets until trees attain sufficient height to shade out *Acanthus*. A similar situation affects the humid forests of Madagascar which, after logging, are often invaded by the non-native tree *Psidium cattleianum*. In Ranomafana National Park, monospecific *Psidium* stands have persisted for 150 years after logging [40]. In this example the initial discrete disturbance, logging, facilitates invasion of *Psidium*, a chronic environmental change. Without human intervention there is little likelihood of forest recovering its earlier species richness and composition.

Modifying the basin of attraction to include our concept of degradation as arrested succession identifies two elements of degradation (Figure 2). First, the distance of the local basin of attraction from the main stable state represents the extent of compositional or structural change from the non-degraded state. Second, the depth of the locally-stable basin reflects the extent to which the ecosystem state is bound to this new state, and the amount of external intervention needed to restore the system to its original recovery trajectory. Degradation reflects the combination of these two measures. Thus a state can be variously degraded depending on the extent of departure from the undisturbed state, and also on the effort required to escape from the new locally-stable state back to the original trajectory towards recovery. A highly degraded state is where values of both the distance and depth of the local basin of attraction are large (Figure 2).

Anthropogenically driven species loss is represented in this framework as a shift in the vertical and horizontal positions of the stable state. Extirpation of species is a permanent change in forest composition from which recovery to the original state is not possible, but, if this incurs no functional changes, then vulnerability to switching to a non-forested state remains low (Figure 3A). If forest functionality and resilience remain unaffected, the forest is not degraded. Instead, we suggest referring to such forests as impoverished (although impoverished forests can also be degraded). Nevertheless, continued species loss, or the loss of functionally-important species, might increase vulnerability to subsequent disturbances that shift the system to another alternative stable state (Figure 3B). This might describe the ‘empty-forest syndrome’, where extirpation of large mammals has knock-on effects on plant composition through diminished seed dispersal and herbivory [41], and increased seed predation by small mammals [42,43].

More difficult to track is degradation in response to chronic environmental changes driven by anthropogenic effects. Gradual climate change might underpin non-recoverable ecosystem changes. Increasing frequency of drought, for example, increases mortality among pinyon pines (*Pinus edulis*) in pinyon–juniper woodland of southwestern USA [44]. This is causing dramatic changes in the structure and diversity of these woodlands, particularly because around 1000 other species are associated with pinyon pine. These include bird seed dispersers and ectomycorrhizal fungi, both essential for the regeneration of pinyon pine, and without which recovery of the woodland might prove difficult [44].

Another form of degradation is when the forest retains the same state but becomes more vulnerable to disturbance [45]. This is represented figuratively by a basin of attraction that has the same overall shape except that it is shallower, and the threshold for shifting to an alternative state is lower relative to the former state (Figure 4). Such degradation is both cryptic and chronic because there might be no obvious change in ecosystem species composition, nor any obvious way for the forest to return to its previous pre-disturbance state because that state no longer

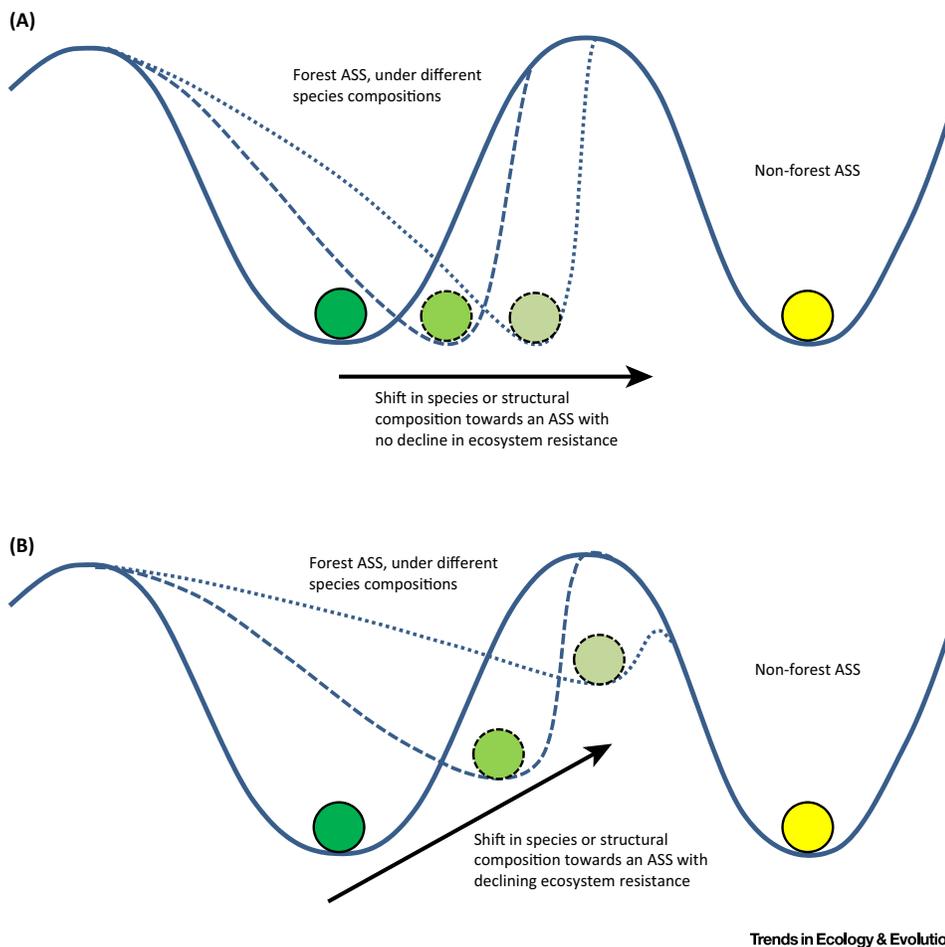
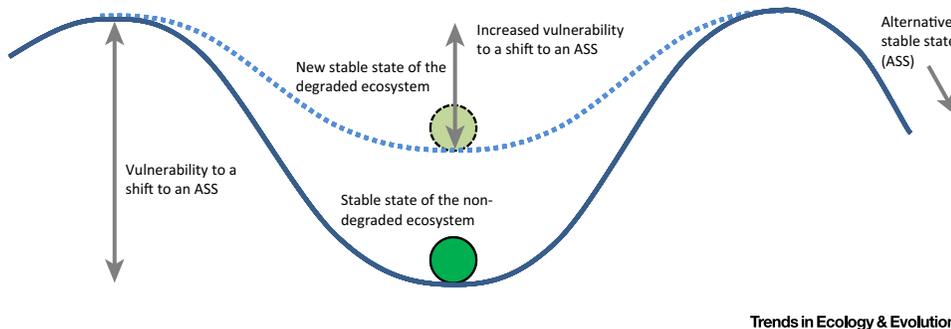


Figure 3. Representations of Shifts in Ecosystem Species Composition Through Extirpation of Species. Return to the original state is not possible because extinct species are not recoverable. Nonetheless, the new ecosystem stable state might retain high resistance (A), or have reduced resistance (B), to further perturbation that would cause a wholesale change to a non-forested condition. The situations illustrated in (A) represent compositional shift (perhaps impoverishment) but not degradation, while the states shown in (B) are degraded on account of lost ecosystem resistance. Abbreviation: ASS, alternative stable state.

exists. In Atlantic forest remnants in Brazil, for example, successful palm regeneration depends on dispersal of the large palm seeds by frugivorous birds with wide gapes [45]. Hunting and forest fragmentation have decimated the populations of such birds. Palms in defaunated fragments have consequently evolved smaller seeds, allowing dispersal by the smaller birds that persist. Although smaller seeds have a higher chance of dispersal, they are, however, more vulnerable to desiccation, which is particularly problematic in fragmented forests [45]. In consequence, vulnerability to recruitment failure due to drought is higher now than before fragmentation.

Temporal Considerations

Forests are dynamic resilient systems capable of recovering pre-disturbance states given sufficient time [36]. The Intergovernmental Panel on Climate Change (IPCC) definition of forest degradation introduces the notion of timescale as a loss of a state ‘persisting for X years or more’ [46]. The selected timescale is mostly defined by management objectives rather than by system properties. Assigning appropriate timescales can thus be approached from two perspectives: land management and natural forest dynamics. In the former, management goals frame



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Figure 4. Increasing Vulnerability to a Transition to an Alternative Stable State (ASS), Represented by a Shallower Basin of Attraction. This can occur without loss of species composition or structure, and hence no horizontal shift in the basin is displayed.

appropriate timescales, typically on the order of several decades. The timeframe remains subjective in that it is negotiated within the frame of utilitarian objectives rather than being determined by natural processes.

Our interpretation of degradation seeks to avoid the ambiguities that time-limited recovery might impose. Indeed, we specifically exclude any time-delimited outcome from our degradation concept, and a strict interpretation of our definition of degradation implies that succession is permanently arrested. In biology nothing is ever permanent, and hence a more pragmatic interpretation is that degradation implies arrested succession for the foreseeable future. Even a slowed recovery response, provided that it is detectable, cannot be classified as degradation under our framework. The recovery response might be reflected by metrics characterizing the community of seedlings and saplings, which convey information on the direction and rates of plant regeneration. This approach removes ambiguities associated with contestable timescales. It also accommodates different rates of recovery among forest systems. For example, in subalpine forests of the Southern Rocky Mountains seedling establishment after a blowdown, followed by salvage logging and a large fire that removed nearby seed sources, took longer than areas where some localized seed sources were left unscathed [47]. In both situations there was nothing to prevent forest recovery because seed dispersal and establishment processes remained functional, and therefore we argue that it is more consistent to say that forest resilience (interpreted as the rate of recovery) has been diminished but not lost, and the recovering forest is not degraded. The forest is only degraded if seed dispersal is completely disrupted by, for example, the extirpation of some important seed-dispersing agents, in which case recovery is not possible without intervention by, for example, reintroducing the lost dispersal agent.

Slowed recovery might, however, increase exposure to further disturbances while already in a vulnerable state. This might incur cumulative and even synergistic ecosystem changes that lead to a state of degradation. In this case, forests are more vulnerable to degradation, but are not degraded. Amazonian forests readily recover from fire provided that they are not subject to subsequent fires, but the first fire incurs positive feedbacks in future fire susceptibility by increasing fuel load and altering the microclimate [48,49]. Disturbance that alters ecosystem states could therefore be a first and necessary, but not sufficient, step towards a state of degradation, while slowed recovery that exposes forests to subsequent disturbances could increase the probability of future degradation [50].

Operationalizing Forest Degradation

To be of useful practical utility, our concept must be operationalizable. Earlier proposed metrics for assessing degradation commonly refer to states of forest attributes which are related to

reference conditions, and only convey information on processes insofar as they are measured repeatedly over time [27]. Such metrics include stocks of biomass and non-timber forest products, forest fragmentation, abundance of species and functional species groups, tree species composition, alien invasive species, fire frequency and extent, soil erosion, and water flows. A limitation of this approach (apart from the need for repeated measurements) is that it is often difficult to characterize consistent changes in, for example, biomass or species compositions with succession [51,52]. Moreover, while forest transitional pathways often converge [53], they can also be unpredictable and divergent [37,38,52]. Thus the designation of particular reference states might misconstrue the reality of complex natural dynamics.

Instead of focusing on forest states, we favor metrics that convey information about the functional processes that underlie forest dynamics, namely, those related to regeneration processes (resprouting, seed production, seedling number and diversity, seed bank), and population size structure (as a proxy for age structure) (e.g., [47,54]). Biotic interactions that determine the direction and rate of forest transitions (e.g., pollination and seed dispersal) could provide an early indicator of ecosystem health [55], but assessing such processes directly is not easy. It is more straightforward and informative to measure the outcomes of these processes rather than the processes themselves. Such outcomes might include the number of resprouting woody plants, seed availability within soil seed banks, seedling abundances and a continuous age structure for common species, and other elements that embody the processes of forest transition and recovery. A lack of progeny of common species, be it within seed banks or among seedlings and saplings, implies a failure of regeneration processes, and hence of species and community recovery. These metrics encapsulate the process-oriented approach without requiring repeated measurement. Neither do these measures require comparison to a reference value because elements of regeneration are either present, and the forest is recovering, or they are absent and recovery of species common to that forest is disrupted.

We refer primarily to common plant groups because almost all ecological systems are disproportionately dominated (in number and biomass) by a relatively small number of species or families. This is also true of tropical forests. Mature canopies of Southeast Asian forests are, for example, dominated by the Dipterocarpaceae, and within this family several common species can be identified for different forest regions. Focusing attention on the regeneration of these species could convey much information on forest dynamics without requiring major investment in time or resources. Rapid methods for ecosystem function assessment are being proposed and developed [56], and these provide fertile ideas that could be adapted as metrics of degradation referring to aspects of ecosystem function underpinning forest recovery.

A reduction in temporal dynamics, which is central to our definition of forest degradation, also implies reduced spatial heterogeneity. Spatial heterogeneity is a common feature of dynamic forest landscapes, which typically comprise a shifting mosaic of mature and regenerating patches of various sizes and compositions, as dictated by neighborhood effects, dispersal processes, biotic and abiotic interactions, and disturbance regimes across multiple scales [21,57–60]. Constrained temporal dynamics reduces spatial heterogeneity by limiting the diversity of response trajectories. Invasive species, for example, tend to homogenize forest environments by obstructing natural regeneration processes, thereby reducing both local diversity and community turnover [61–64]. Excessive hunting of seed-dispersing mammals can similarly limit the dispersal of large-seeded trees, causing loss of tree species diversity and a reduction in the range of seed types [65–70]. We propose that the extent of spatial heterogeneity in forest structure and composition might serve as another degradation metric that can be applied at larger scales and evaluated using remote-sensing technologies [71]. The rapid development of more sophisticated remote-sensing capabilities is providing opportunities to also evaluate landscape heterogeneity in plant form and function including, for example, variation

in leaf chemistry [72]. Understanding and quantifying the links among spatial and temporal heterogeneity remains challenging, at least insofar as developing a degradation metric. Nonetheless, this would provide a valuable area for future research that would enable a better understanding of forest dynamics in the context of anthropogenic change, and particularly with reference to accommodating external impacts on forests (often resulting from human decisions) with the internal biological dynamics of the forests.

Concluding Remarks

Given continued tropical forest losses, and increasing forest exploitation globally, the state of remaining forests is becoming increasingly important. Despite this, there is no agreed definition of forest degradation, without which it is difficult to quantify or respond to forest degradation. Conceptualizing degradation through an ecosystem resilience lens recognizes that forests are dynamic and complex ecosystems that, following disturbance, have self-organized ecological processes of recovery to pre-disturbance states. Our definition of degradation is a state of arrested succession, to be set in contrast to natural systems that undergo constant transitions subject to both neighborhood effects and natural disturbances. The corollary of this is that a forest is not degraded provided that it retains dynamics that facilitate recovery to former steady-states. Once in a state of arrested succession, external intervention is required to recover successional trajectories, for which decision-making and management processes may be involved and complex [73,74]. Our framework provides an ecologically grounded foundation for the development of ecologically-relevant operational metrics of forest degradation that focus on trajectories of change rather than on system states at any point in time. The approach also avoids comparison to particular 'reference states' which are inherently problematic in view of the multiple natural states that forests might shift between. It is not without problems, however, because in many cases we simply do not yet understand the range of natural ecosystem states and the dynamics that underlie shifts between them. This is not a conceptual limitation, but rather a lack of knowledge of forest processes which can be overcome with research (see Outstanding Questions).

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References

1. UNEP (2007) *Global Environment Outlook GEO4: Environment for Development*, United Nations Environment Programme
2. ITTO (2012) *Annual Review and Assessment of the World Tropical Timber Situation 2012*, International Timber Trade Organisation
3. Putz, F.E. and Romero, C. (2014) Futures of tropical forests (sensu lato). *Biotropica* 46, 495–505
4. Sasaki, N. and Putz, F.E. (2009) Critical need for new definitions of 'forest' and 'forest degradation' in global climate change agreements. *Conserv. Lett.* 2, 226–232
5. Olander, L.P. *et al.* (2008) Reference scenarios for deforestation and forest degradation in support of REDD: a review of data and methods. *Environ. Res. Lett.* 3, 025011
6. Murdiyasar, D. *et al.* (2008) How do we measure and monitor forest degradation? In *Moving Ahead with REDD* (Angelsen, A., ed.), pp. 99–105, CIFOR
7. Vargas, R. *et al.* (2013) Quantification of forest degradation and belowground carbon dynamics: ongoing challenges for monitoring, reporting and verification activities for REDD. *Carbon Manage.* 4, 579–582
8. Morales-Barquero, L. *et al.* (2014) Operationalizing the definition of forest degradation for REDD+, with application to Mexico. *Forests* 5, 1653–1681
9. Schoene, D. *et al.* (2007) *Definitional Issues Related to Reducing Emissions From Deforestation in Developing Countries*. FAO *Forests and Climate Change Working Paper 5*, Food and Agriculture Organisation of the United Nations
10. Simula, M. (2009) *Towards Defining Forest Degradation: Comparative Analysis of Existing Definitions*, Food and Agriculture Organisation of the United Nations
11. FAO (2011) *Assessing Forest Degradation: Towards the Development of Globally Applicable Guidelines*. *Forest Resources Assessment Working Paper 177*, Food and Agriculture Organization of the United Nations
12. Mori, A.S. (2011) Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. *J. Appl. Ecol.* 48, 280–292
13. Snell, R.S. *et al.* (2014) Using dynamic vegetation models to simulate plant range shifts. *Ecography* 37, 1184–1197
14. Christensen, N.L. (2014) An historical perspective on forest succession and its relevance to ecosystem restoration and conservation practice in North America. *For. Ecol. Manage.* 330, 312–322
15. Foley, J.A. *et al.* (2007) Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Front. Ecol. Environ.* 5, 25–32
16. Thrush, S.F. *et al.* (2009) Forecasting the limits of resilience: integrating empirical research with theory. *Proc. Biol. Sci.* 276, 3209–3217

Outstanding Questions

How can we resolve novel disturbance regimes derived from interactions between anthropogenic and natural disturbances?

Can internal processes that drive ecosystem dynamics be coupled with external drivers of change?

How do we quantify the influence of the surrounding landscape mosaic on forest recovery processes, both in terms of promoting and obstructing recovery?

How can degradation be defined at multiple spatial scales given the spatial heterogeneity of forest recovery processes?

How can we accommodate slow and chronic environmental change within a resilience-based degradation framework?

How should an ecologically based framework for forest degradation be implemented for ecosystem management while taking social and economic values into account?

What range of metrics will best represent ecosystem dynamics?

How can metrics be practically applied for rapid assessment of forest degradation as a state of arrested succession?

To what extent does spatial heterogeneity at multiple scales reflect ecosystem dynamics and processes of forest recovery?

How should the provision of goods and services be aligned to an ecologically derived and functionally based conceptualization of forest degradation?

How acceptable is an ecologically derived definition of degradation, relying on processes of recovery rather than delivery of goods and services, to the wider social and policy environment?

How do we move towards a general theory of natural forest dynamics?

17. Attiwill, P.M. (1994) The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manage.* 63, 247–300
18. Holling, C.S. (1973) Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23
19. Folke, C. *et al.* (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* 35, 557–581
20. Peterson, G. *et al.* (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1, 6–18
21. Chazdon, R. (2014) *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*, University of Chicago Press
22. Nieuwenhuis, M. (2000) *Terminology of Forest Management*, International Union of Forest Research Organizations
23. Bai, Z.G. *et al.* (2008) Proxy global assessment of land degradation. *Soil Use Manage.* 24, 223–234
24. Liu, J. *et al.* (2001) Ecological degradation in protected areas: the case for Wolong Nature Reserve for Giant Pandas. *Science* 292, 98–101
25. Blaser, J. *et al.* (2011) *Status of Tropical Forest Management 2011. ITTO Technical Series No 38*, International Tropical Timber Organization
26. Klooster, D. (1999) Community-based forestry in Mexico: can it reverse processes of degradation? *Land Degradation Dev.* 10, 365–381
27. Thompson, I.D. *et al.* (2013) An operational framework for defining and monitoring forest degradation. *Ecol. Soc.* 18, 20
28. Liu, J.G. *et al.* (2007) Complexity of coupled human and natural systems. *Science* 317, 1513–1516
29. Hughes, J.S. *et al.* (2015) Effects of forest spatial structure on insect outbreaks: insights from a host-parasitoid model. *Am. Nat.* 185, E130–E152
30. Mueller, D. *et al.* (2014) Regime shifts limit the predictability of land-system change. *Global Environ. Change Hum. Policy Dimens.* 28, 75–83
31. Ratajczak, Z. *et al.* (2014) Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. *J. Ecol.* 102, 1374–1385
32. Moore, S.A. *et al.* (2009) Diversity in current ecological thinking: implications for environmental management. *Environ. Manage.* 43, 17–27
33. ITTO (2009) *Guidelines for the Conservation and Sustainable Use of Biodiversity in Tropical Timber Production Forests. ITTO Policy Development Series No 17*, The World Conservation Union (IUCN) and International Tropical Timber Organization (ITTO)
34. Baker, P.J. *et al.* (2005) Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecol. Monogr.* 75, 317–343
35. Malhi, Y. *et al.* (2014) Tropical forests in the Anthropocene. *Annu. Rev. Environ. Res.* 39, 125–159
36. Messier, C. *et al.*, eds (2013) *Managing Forests as Complex Adaptive Systems*, Routledge
37. Frelich, L.E. and Reich, P.B. (1995) Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecol. Monogr.* 65, 325–346
38. Frelich, L.E. and Reich, P.B. (1995) Neighborhood effects, disturbance, and succession in forests of the Western Great Lakes region. *Ecoscience* 2, 148–158
39. Paul, J.R. *et al.* (2004) Arrested succession in logging gaps: is tree seedling growth and survival limiting? *Afr. J. Ecol.* 42, 245–251
40. Brown, K.A. and Gurevitch, J. (2004) Long-term impacts of logging on forest diversity in Madagascar. *Proc. Natl. Acad. Sci. U.S.A.* 101, 6045–6049
41. Wright, S.J. (2003) The myriad consequences of hunting for vertebrates and plants in tropical forests. *Perspect. Plant Ecol. Evol. Syst.* 6, 73–86
42. Effiom, E.O. *et al.* (2013) Bushmeat hunting changes regeneration of African rainforests. *Proc. Biol. Sci.* 280, 20130246
43. Nunez-Iturri, G. and Howe, H.F. (2007) Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica* 39, 348–354
44. Mueller, R.C. *et al.* (2005) Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *J. Ecol.* 93, 1085–1093
45. Galetti, M. *et al.* (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340, 1086–1090
46. Penman, J. *et al.*, eds (2003) *Good Practice Guidance for Land Use, Land-Use Change and Forestry*, IPCC National Greenhouse Gas Inventories Programme
47. Buma, B. and Wessman, C.A. (2011) Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2, 64
48. Cochrane, M.A. and Schulze, M.D. (1999) Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica* 31, 2–16
49. Adams, M.A. (2013) Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. *For. Ecol. Manage.* 294, 250–261
50. Gerwing, J.J. (2002) Degradation of forests through logging and fire in the eastern Brazilian Amazon. *For. Ecol. Manage.* 157, 131–141
51. Marin-Spiotta, E. and Sharma, S. (2013) Carbon storage in successional and plantation forest soils: a tropical analysis. *Glob. Ecol. Biogeogr.* 22, 105–117
52. Norden, N. *et al.* (2015) Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc. Natl. Acad. Sci. U.S.A.* 112, 8013–8018
53. Norden, N. *et al.* (2009) Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecol. Lett.* 12, 385–394
54. Johnstone, J.F. *et al.* (2010) A sensitive slope: estimating landscape patterns of forest resilience in a changing climate. *Ecosphere* 1, 14
55. Valiente-Banuet, A. *et al.* (2015) Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307
56. Meyer, S.T. *et al.* (2015) Towards a standardized Rapid Ecosystem Function Assessment (REFA). *Trends Ecol. Evol.* 30, 390–397
57. Turner, M.G. (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849
58. Frelich, L.E. and Reich, P.B. (1999) Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems* 2, 151–166
59. Metz, M.R. *et al.* (2008) Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. *J. Trop. Ecol.* 24, 9–18
60. Norden, N. *et al.* (2007) Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. *J. Ecol.* 95, 507–516
61. Kueffer, C. *et al.* (2010) Managing successional trajectories in alien-dominated, novel ecosystems by facilitating seedling regeneration: a case study. *Biol. Conserv.* 143, 1792–1802
62. Ramaswami, G. and Sukumar, R. (2011) Woody plant seedling distribution under invasive *Lantana camara* thickets in a dry-forest plot in Mudumalai, southern India. *J. Trop. Ecol.* 27, 365–373
63. Sundaram, B. and Hiremath, A.J. (2012) *Lantana camara* invasion in a heterogeneous landscape: patterns of spread and correlation with changes in native vegetation. *Biol. Invasions* 14, 1127–1141
64. Prasad, A.E. (2012) Landscape-scale relationships between the exotic invasive shrub *Lantana camara* and native plants in a tropical deciduous forest in southern India. *J. Trop. Ecol.* 28, 55–64
65. Peres, C.A. *et al.* (2003) Demographic threats to the sustainability of Brazil nut exploitation. *Science* 302, 2112–2114
66. Galetti, M. *et al.* (2006) Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Bot. J. Linnean Soc.* 151, 141–149
67. McConkey, K.R. and Drake, D.R. (2006) Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* 87, 271–276

68. Beaune, D. *et al.* (2013) Seed dispersal strategies and the threat of defaunation in a Congo forest. *Biodivers. Conserv.* 22, 225–238
69. Beaune, D. *et al.* (2013) Doom of the elephant-dependent trees in a Congo tropical forest. *For. Ecol. Manage.* 295, 109–117
70. Haurez, B. *et al.* (2013) Impacts of logging and hunting on western lowland gorilla (*Gorilla gorilla gorilla*) populations and consequences for forest regeneration. A review. *Biotechnologie Agronomie Soc. Environ.* 17, 364–372
71. Asner, G.P. *et al.* (2003) Scale dependence of biophysical structure in deforested areas bordering the Tapajo's National Forest, Central Amazon. *Remote Sensing Environ.* 87, 507–520
72. Cho, M.A. *et al.* (2013) Assessing the effects of subtropical forest fragmentation on leaf nitrogen distribution using remote sensing data. *Landscape Ecol.* 28, 1479–1491
73. Hobbs, R.J. *et al.* (2014) Managing the whole landscape: historical, hybrid, and novel ecosystems. *Front. Ecol. Environ.* 12, 557–564
74. Chazdon, R.L. (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320, 1458–1460
75. MoFOR (2008) *Consolidation Report: Reducing Emissions from Deforestation and Forest Degradation In Indonesia*, Ministry of Forestry, Republic of Indonesia
76. Marklund, L.G. and Schoene, D. (2006) *Global Assessment of Growing Stock, Biomass and Carbon stock. Forest Resources Assessment Programme Working Paper 106/E*, Food and Agriculture Organisation of the United Nations
77. Asner, G.P. *et al.* (2005) Selective logging in the Brazilian Amazon. *Science* 310, 480–482
78. Hunter, M. (1996) Benchmarks for managing ecosystems: are human activities natural? *Conserv. Biol.* 10, 695–697
79. Josefsson, T. *et al.* (2009) Long-term human impact and vegetation changes in a boreal forest reserve: implications for the use of protected areas as ecological references. *Ecosystems* 12, 1017–1036
80. van Gemerden, B.S. *et al.* (2003) The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *J. Biogeogr.* 30, 1381–1390