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Natural Disturbance in Forest Environments

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Introduction

Disturbance in plant communities has been defined as consisting of ‘the mechanisms which limit the plant biomass by causing its partial or total destruction.’ In forests, disturbance arises from the agencies of tree damage or death. At small spatial scales, individual trees die standing or fall over, but in both cases a gap in the canopy is created and this initiates a successional process known as the forest growth cycle. The agencies of natural disturbance at larger spatial scales include windstorms, fire, and landslides and these factors vary in their impacts on forests and the ensuing mechanisms

of forest recovery. Natural disturbance regimes in forests are important because they impact on tree population dynamics, the relative abundance of different species and functional groups, the biomass and carbon content of vegetation, and interactions with other components of the biotic community. Community ecologists have highlighted the importance of disturbance among mechanisms proposed for the maintenance of tree species richness, particularly in species-rich tropical forest communities.

Small-Scale Disturbance: Gap Phase Dynamics

Small-scale natural disturbances are an inherent component of all plant communities because plants have a finite lifespan. In forests, the size of the individual tree at the time of its death and the mode of death determine the scale of the disturbance created. The death of individual small understory trees and shrubs that live their entire life in the shade, and of the suppressed juveniles of canopy trees, may have limited impact on forest stand structure. However, the death of canopy-level or emergent trees has significant potential for localized modifications of canopy structure, resource availability, and microclimates. Some large trees die standing, perhaps following lightning strike or the synergistic effects of old age and wood decay fungi. Many trees lose large branches or parts of their crown long before the entire tree has died, and these events may lead to partial opening of the canopy and to some damage of surrounding smaller trees and other plants. However, the threshold for a natural disturbance event is usually regarded as the death of an individual large canopy or emergent tree, which results in the creation of a hole through all layers of the forest down to 2 m above the ground surface (a canopy gap). The size of a canopy gap varies according to the height of the tree that died, its architecture (height : canopy width), and its neighborhood. The fall of a large tree will inevitably lead to damage or death of surrounding trees, particularly if their crowns are connected by lianas. Thus canopy gaps arising from small-scale tree death can vary from a lower limit of 25–50 m² up to about 1000 m² for a large multiple tree-fall gap. Gaps can be further divided into zones influenced by the fallen crown (crown zone), the bole (bole zone), and the site where the fallen tree had been rooted (root zone). In addition, when trees fall over, particularly during severe windstorms, they frequently create an elevated mound of consolidated soil and roots known as a tip-up mound and an associated pit with exposed subsoil on its base and sides. Microclimatic conditions and availability of

some resources for plant growth are known to vary between zones within a gap and on tip-up mounds. This variation within canopy gaps and between gaps of different size is thought to be one factor contributing to the maintenance of tree species richness in forests.

Changes in Microclimate and Resource Availability Following Gap Creation

Solar radiation reaching the forest floor increases following creation of a canopy gap because canopy leaves absorb a high proportion of radiation that falls within the range of wavelengths absorbed by photosynthetic pigments (440–770 nm) and reflect radiation of all wavelengths. Thus the proportion of total irradiance that reaches the forest floor increases from about 1% beneath a mature closed canopy site to 10–25% in the centers of large canopy gaps. Solar radiation is important because it affects directly other aspects of the aerial microclimate, it contributes to modifications to the belowground environment, and it impacts on plant growth and development in gaps both directly (via photosynthesis) and indirectly (for example via temperature-mediated effects).

Measurements have demonstrated that canopy gaps have higher mean and maximum air and ground surface temperatures, lower mean relative humidity, and greater wind speeds than sites beneath a closed forest canopy. This combination of conditions drives greater evaporation from exposed surface soils and thus a reduced water content at the top of the soil profile. Water availability lower down the soil profile, however, varies according to the density of live fine roots that survive gap creation, and can be either greater or no different to conditions beneath closed canopy forest.

After a tree dies its tissues decompose and contribute to fluxes of carbon and nutrients from plant biomass into microbial biomass and soil compartments. Leaves are the most readily decomposable aboveground plant tissues because they have the highest concentrations of nutrients and the lowest concentrations of lignin and fiber. Therefore the crown zone of canopy gaps receives the highest quantities of dead organic material and a transient increase in available nutrients in soil has been detected. Organic matter decomposition rates are enhanced by the relatively high temperatures in gaps, and the lower density of live roots in soil results in reduced competition for nutrients. Woody material decomposes much more slowly than leaves, particularly the bole and other material of large dimension. In tropical forests, termites and other components of

the soil mesofauna initiate and hasten the process of wood decomposition, although it is common to observe large boles surviving semi-intact long after the gap created by the fall of the tree has closed over the fallen bole.

Forest Regeneration in Gaps

The changes in microclimate and resource availability that are induced by gap creation contribute to the mechanisms of forest regeneration, which describes the processes of recovery following disturbance. Regeneration proceeds via processes of both sexual and vegetative modes of reproduction. It is initiated by the germination of seeds, which either emerge from the buried soil seed bank or arrive in the gap after it has been created, or by the release of seedlings and saplings that were present at the time of gap creation (advanced regeneration). In addition, saplings and small trees of some species that are damaged during gap creation have the capacity to produce epicormic resprouts that grow rapidly in height and can contribute significantly to the regenerating tree community. Gap creation also stimulates enhanced growth of tree canopies surrounding the opening, which contributes to canopy closure and influences the development of vegetation growing up in the gap.

Some trees possess mechanisms that increase the likelihood that they germinate and grow rapidly in response to the environmental conditions that are stimulated by gap creation. Some of the species that adopt this strategy are termed 'pioneers' because they represent a distinctive functional group among all forest floras and share a suite of life-history characteristics that predisposes them to establish and grow in canopy gaps. Species of birch (*Betula* spp.) are characteristic pioneers of the cool temperate deciduous forests of Western Europe and North America, while *Cecropia* (neotropics), *Musanga* (tropical Africa), and *Macaranga* (tropical Southeast Asia) are the classic genera of pioneers in lowland tropical evergreen rainforests. All forest floras possess pioneer species, but their abundance and richness vary according to the characteristic disturbance regime manifested at a particular site.

Many (but not all) pioneer species possess seeds that are small and widely dispersed by animals or wind. Small seeds have few resources with which to grow a shoot and therefore cannot establish when deeply buried beneath soil or litter. For this reason, many species have evolved photoblastic germination, that is, they only germinate when the seeds are illuminated by light rich in wavelengths in the far-red

range of the electromagnetic spectrum (centered on 720 nm) relative to wavelengths in the red light range (centered on 660 nm). Thus species with photoblastic germination are described as being responsive to the red to far-red ratio of light. The function of this response is to prevent germination when the seed is located in an inappropriate microsite for successful emergence (i.e., buried beneath a layer of soil or litter), or establishment (i.e., beneath a closed forest canopy).

Photoblastic germination in pioneers is concentrated among species with the smallest seeds (e.g., in neotropical pioneers, seeds with a fresh mass <1.5 mg). However, pioneer species with larger seeds have evolved alternative mechanisms to target germination in well-lit canopy gap sites, such as germination in response to an increased magnitude of diel temperature fluctuation. Surface soil temperature rises higher during the day in canopy gaps than beneath a closed forest canopy and at night falls either to the same or to a lower minimum value because of enhanced radiative cooling. Thus the magnitude of diel temperature fluctuation is an index of canopy gap size and a number of species have been shown to germinate poorly in the absence of a fluctuating temperature regime. One example from semideciduous tropical forest in Panama is provided by balsa (*Ochroma pyramidale*).

Germination in gaps is important for pioneer tree species because they lack an ability to survive and grow in the shaded conditions of the forest understory. For example, their photosynthetic physiology is adapted to rapid carbon assimilation at high light rather than persistence for long periods in the shade. To achieve this, they produce short-lived leaves containing high concentrations of nitrogen (required for the enzymes involved in photosynthesis) that tend to be poorly defended against herbivores and pathogens. In addition, the high respiration rates required to maintain the enzymatic machinery involved in photosynthesis and carbon assimilation precludes long-term survival of pioneers in the shade.

The trade-off between survival in shade and growth response at high light is resolved in different ways by different tree species, so that a continuum of response to heterogeneity in light conditions will exist among any group of coexisting species. This shade-tolerance continuum has important consequences for the changes in community structure that occur during tree regeneration in gaps. As described above, pioneer species are well represented among the community of seedlings that establish early following gap creation, particularly in large gaps or the centers of small gaps. However, over time species

with more shade-tolerant seedlings will become established beneath the developing canopy of the early-colonizing pioneers. The shade-tolerant species grow more slowly in height than the pioneers, but they survive for longer. Therefore as the cohort of pioneers matures and dies their canopies begin to receive more light and their growth rates increase. Ultimately, the saplings and pole-sized trees of these attain dominance in the gap, and the forest growth cycle is said to be in the 'building phase.' The cycle is closed by the growth of poles to canopy trees and the recreation of forest understory light and microclimatic conditions in the former gap site.

Importance of Chance Effects

The description of forest regeneration provided above implies that the changes that take place after small-scale disturbance are entirely deterministic, such that disturbances of a similar scale in sites sharing the same species pool would proceed through a predictable sequence to an end point that is identical in terms of species composition and structure to its status prior to the death of the original canopy tree. However, it must be recognized that this description is an oversimplified caricature of many highly complex processes that collectively reduce the predictability of forest regeneration pathways in a particular site. For example, it is highly unlikely that all species that have the ecological potential for regeneration in any particular site will actually get there, because of constraints on dispersal.

Forest Growth Cycle

The processes of tree death and regeneration described above are intrinsic to all natural forest communities. They provide examples of internal secondary successions that arise because of the uneven-aged structure of most natural forest communities. The heterogeneous nature of forest composition and history creates a mosaic of patches at different stages in the forest growth cycle. Experienced foresters and ecologists have attempted to map the distribution of patches at different stages using species composition and forest structure as indicators of patch status, although these efforts are inherently limited by the low degree of spatial coverage relative to inherent spatial heterogeneity. However, in one well-replicated study of a semideciduous forest in Panama, approximately 0.1% of the ground surface area was covered by canopy gaps (defined as contiguous areas of at least 25 m² in which the height of the canopy is <5 m).

Large-Scale Disturbances

In addition to the small-scale internal dynamics inherent to all forests, most forests also show evidence of perturbation by agencies operating over larger spatial and temporal scales. These factors can be divided into those that destroy all vegetation and *in situ* sources of regeneration (such as landslides, volcanoes, and earthquakes), and those that do not (for example, windstorms, lightning strikes, drought, and fire). This distinction is important because loss or burial of seeds and stumps means that forest recovery can occur only via a primary succession. By contrast, those factors that leave components of the vegetation or a buried soil seed bank intact will undergo secondary succession and a more rapid recovery of structure and floristic composition. There is a third category of disturbance factor that arises from gradual processes occurring over longer time-scales, such as climate change and plate tectonics. Although these processes might fall under some definitions of disturbance, their impacts extend over such long intervals that short-term effects on community biomass (as opposed to species composition) are likely to be minimal.

Disturbances that Result in Primary Succession

Landslides occur wherever steeply dissected terrain occurs in a wet climate. They occur most often after earthquakes or periods of very heavy rainfall, and are therefore most frequent in mountainous, tectonically active regions of the world. In New Guinea, for example, 8–16% of the land surface area is affected by landslides per century. Landslides often result in the exposure of nutrient-poor subsoils and parent rock at the surface and plant recolonization of these sites tends to be limited by the low nutrient status and instability of the soil. The plant community that re-establishes may differ in composition from the surrounding vegetation for a long period because of the slow pace of succession on these substrates. Studies of forest regeneration on landslides in the Caribbean have suggested that old landslides provide a habitat for some species that do not occur elsewhere in the surrounding forest matrix.

Active volcanoes have the potential to destroy forests over a large area by the direct effects of lava and ashfall and indirect effects caused by tsunamis and changes to atmospheric conditions. For example, the 1883 and subsequent eruptions of Krakatau, in the Sunda Straits between Java and Sumatra, are still evident in the contemporary flora of the Krakatau island group, which is dominated by a small group of well-dispersed tree species. Differences in the species composition of the islands in the Krakatau archipe-

lago demonstrate the vagaries of chance colonization events and the patchy effects of historic and contemporary volcanic activity. The long-distance effects of the eruption of Krakatau are also illustrated by impacts on forest structure and composition on Ujong Kulon, west Java, located 70 km from the island group.

Rivers that migrate across the landscape on decadal timescales can cause disturbance to natural forest communities and stimulate primary successions on newly deposited substrates. In the Amazon floodplain of Peru, rivers can move by as much as 180 m during the annual floods, with resultant dramatic impacts on forest structure and composition. The communities that develop on land exposed by lateral river movement are initially species-poor and dominated by early-successional pioneers, but these forests are gradually replaced by richer communities that are more similar to the surrounding matrix of terra firme forest. It is sometimes possible to identify zonation in forest structure and composition that reflects species accumulation over time and the nature of the underlying substrate as the river moves across the landscape.

Disturbances that Result in Secondary Succession or Recovery

Cyclones and hurricanes impact forests in two belts between 10° and 20° either side of the equator, although their frequency and intensity vary greatly. Severe windstorms also occur occasionally at higher and lower latitudes. Typhoons also have localized impacts on forests in their path and occur over a broad range of latitudes. In the Caribbean, forests are impacted by hurricanes once every 15–20 years on average, and the forests are, therefore, permanently in a state of recovery. Severe windstorms cause trees to be snapped, uprooted, and defoliated, but only a minority is actually killed instantaneously. Studies in the Solomon Islands and the Caribbean have shown in both cases that about 7% of trees were killed outright by severe windstorms, although a larger number were damaged. Recovery occurs by a combination of resprouting of surviving damaged stems, release of seedlings that had been previously growing in the shaded forest understory, and germination of pioneer species in response to canopy opening. The pioneer trees soon grow up, reproduce, and die, so that within a relatively short period the species composition of the forest community may differ little from that of the forest that existed prior to the storm. There are three caveats that must be considered in response to this statement. First, if a second or subsequent disturbance intervenes before

recovery is complete, the structure and composition of the forest may become permanently affected, particularly if the windstorm is followed by fire. Second, forests that contain a mixture of species or species groups that are differentially susceptible to wind (e.g., susceptible conifers vs. tolerant angiosperms) may exhibit a higher dominance of the tolerant group after a severe windstorm, particularly in areas where severe windstorms are relatively infrequent. Third, forests that are most frequently impacted by severe windstorms may develop a modified structure, such as a low and even stature (as in the forests of the eastern Sierra Madre mountains of Luzon, Philippines), or an open structure with a low density of large trees and many lianas (for example in east-facing slopes of the north Queensland rainforests).

Windstorms and volcanic activity may be associated with lightning strikes that can cause death of trees in large numbers. Even if only one tree is struck by lightning, others surrounding it can be damaged or killed if they are connected by lianas or roots. In New Guinea, mangrove forests may have patches of up to 50 m in diameter in which all trees have been killed by lightning strike, and *Nothofagus* forests may possess circular holes with a similar origin.

Lightning strike may also give rise to natural fires that impact much beyond the original source of ignition. Fires are a natural and inherent component of the disturbance regime in most natural forests, including those in the wet tropics that were formerly considered not to burn. However, recent evidence derived from dating of charcoal fragments extracted from soil profiles in tropical rainforest areas of South America and Africa have demonstrated a history of recurrent fires on millennial timescales even in sites that are currently very wet. Fires are an even more important feature of the disturbance regime for dry tropical forests and woodland, Mediterranean vegetation, and boreal forest, for which frequent and intense fires may be an important component of ecosystem functioning. The importance of fires in these forests is demonstrated by the occurrence of species that are either tolerant of fire, or possess mechanisms that facilitate their regeneration after fire. Fire tolerance is conferred by shielding living tissue beneath a thick bark or in underground storage organs, while regeneration after fire is enhanced by fruit or seed structures that are stimulated by high temperatures. Although fires have the potential to destroy living plant tissues, they can also have an important role in releasing nutrients from recalcitrant pools in the ecosystem and reducing species dominance. These effects depend on the intensity,

timing, and frequency of fire and interactions with other disturbance agents.

Severe fires may be associated with periods of low rainfall, either naturally because they are concentrated in the dry season, or at supra-annual scales because they follow climatic droughts. Droughts may themselves directly increase rates of tree mortality, particularly when they occur in forests that are not normally associated with water shortage. For tropical rainforests, there is evidence that large trees are relatively more likely to be killed during a drought than small trees, and that droughts contribute to increased susceptibility to disturbance by fire. Both drought and fire are therefore more common in years when the El Niño-Southern Oscillation (ENSO) phenomenon is impacting global climates. In one or more regions of the world, severe ENSO events may be associated with increased rates of forest perturbation from either drought, fire, flooding, windstorms, lightning, landslides, or combinations of these factors. As a dramatic illustration of this phenomenon the 1982/83 ENSO caused a reduction to one-third of average rainfall across some parts of Southeast Asia and destruction of 3 millions ha of rainforest in Borneo by drought and fire. In Panama, the same ENSO event caused increased mortality rates of 70% of woody plant species represented as individuals ≥ 1 cm diameter at breast height on a large forest plot, from about 2% year⁻¹ in a nondrought period to about 3% year⁻¹ in the interval spanning the ENSO-related drought. This 50% increase in mortality rate has been associated with dramatic changes in species composition on the plot, because not all species were affected equally.

Conclusions

This discussion has demonstrated that disturbance to natural forests varies greatly in scale and effect in different forest types and for different disturbance agencies, such that robust generalizations are difficult to construct. A disturbance regime has components describing the intensity, frequency, and extent of its effects, although these are rarely quantified. These properties are important because they may influence emergent properties of the forest community, such as species composition and tree diversity. For example Connell's intermediate disturbance hypothesis, relates the intensity, frequency, or timing of disturbance to community diversity and has recently been tested in forests (*see Biodiversity: Plant Diversity in Forests*). Although disturbance and its impacts are difficult to quantify, the evidence from historical and ecological analyses of forest

communities is highlighting the importance of natural disturbance regimes to forest community structure and ecosystem functioning. It is self-evident that all forests experience the small-scale disturbances associated with individual tree death and mortality. However, it is now clear that most well-studied forests also exhibit the imprint of one or more of the large-scale disturbance factors discussed above. This consideration highlights the importance of disturbance history in any attempt to understand contemporary forest ecology.

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Biological Impacts of Deforestation and Fragmentation

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Introduction

In addition to housing the majority of the planet's biodiversity, forest ecosystems are the basis for trillions of dollars in global revenue. They are homes to indigenous groups, sources of food, medicines, and raw materials for industry, and they provide opportunities for recreation and tourism. They are also being logged, cleared, or otherwise altered by humans at alarming rates. Consequently, understanding the physical and biological consequences of deforestation has become one of the leading areas of research in forest ecology.

This review aims to describe the physical and biological consequences of deforestation on four levels of ecosystem organization: individuals, populations, communities, and ecosystems. In addition, I will also highlight some of the major gaps in our understanding of how fragmented forests function.

Physical Consequences of Deforestation

Habitat Loss and Insularization

The most dramatic and immediately obvious consequence of deforestation is the loss of native habitat in newly cleared areas. However not all deforestation results in the denuded landscapes one typically associates with clear-cut logging or industrial cattle ranching. In many cases deforestation proceeds unevenly, leaving behind a patchwork of forest fragments that are isolated at varying degrees from one another. These fragments of forest are embedded in an intervening habitat, referred to as the 'matrix habitat,' whose use varies in intensity from regenerating forest, to cattle pasture, to human settlements. The study of the physical and biological consequences of this now widespread phenomenon, known as habitat fragmentation, has become one of the principal areas of research in conservation biology. While these consequences can vary substantially by location and forest type, some general patterns have begun to emerge. As a result, we now have a greater understanding not only of how individual species are influenced by fragmentation, but also of what some of the consequences of