Tropical forest recovery:
legacies of human impact and natural disturbances

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Abstract

Land-use history interacts with natural forces to influence the severity of disturbance events and the rate and nature of recovery processes in tropical forests. Although we are far from an integrated view of forest recovery processes, some generalizations can be made. Recovery of forest structure and composition is relatively rapid following disturbances that primarily impact forest canopies, such as hurricanes. Recovery is considerably slower following disturbances that heavily impact soils as well as aboveground vegetation, such as bulldozing, heavy or long-term grazing, and severe fires, often with long-lasting effects on species composition. The landscape matrix plays a critical role in local recovery processes. Proximity of disturbed areas to remnant forest patches promotes more rapid recovery, which depends heavily on seed dispersal. Recovery of aboveground biomass is constrained by soil fertility and texture across regions as well as across soil types within a region. Restoration of soil fertility may be a prerequisite for forest recovery on sites with severely degraded soils. Despite evidence of rapid forest recovery following large-scale deforestation, many degraded areas of today's tropics will require human assistance to recover forest structure, species composition, and species interactions typical of mature tropical forests.

Key words: disturbance, land-use history, landscape matrix, recovery, soil fertility, tropical forests

"Primeval tropical rain forest, undisturbed and stable, 'since the dawn of time' is a myth. Instability of varying extents occurs on several time-scales. The recovery to a steady-state is likely to take several centuries and is perhaps never achieved in many places."

TC Whitmore (1991, p. 73)

Introduction

Tropical forests, like all of earth's ecosystems, are subject to a wide range of disturbances of variable duration, intensity, and frequency. In their review of major disturbances in tropical rain forests, Whitmore & Burslem (1998) emphasized the pervasive nature of both natural and human disturbances in tropical forests. They suggest that contemporary human activity affecting tropical forests should be viewed in the context of the panoply of natural disturbance events and the dynamism that characterizes tropical forest systems. In 2000, an estimated 60% of the world's tropical forest was classified as degraded forest, including secondary forests, degraded primary forests and degraded forest land (ITTO 2002). Human disturbance in tropical forests is not simply a phenomenon

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of the colonial and modern eras, but dates back to early human occupation in tropical regions (Denevan 1976; Bayliss-Smith & Feacham 1977; Sanford et al. 1985; Gómez-Pompa & Kaus 1990; Fairhead & Leach 1998). Vast areas of forests widely considered to be primary or virgin are, in fact, late secondary forest (Aubreville 1938; Budowski 1970; Bush & Colinvaux 1990, 1994). The Okomu Forest Reserve in southwest Nigeria was considered to be primary forest by Richards (1939), but later studies by Jones (1955, 1956) revealed extensive charcoal and pottery deposits and a tree population structure reflecting second-growth vegetation. Recent studies now provide evidence that the mahogany forests of Okomu can be traced back to a period soon after 700 years ago, following a period of intensive human use (White & Oates 1999). Archaeological remains and charcoal fragments lie beneath much of the rain forest in Africa and the New World tropics (Sanford et al. 1985; White & Oates 1999). Extensive forests in the Yucatan peninsula in México are now recognized as secondary, once managed by Mayans for food and fibre (Gómez-Pompa et al. 1987). Even the forest of the 50-ha plot on Barro Colorado Island, considered by many ecologists to represent an example of 'mature forest' structure and composition, is still recovering from human impacts that occurred over 300 years ago, and resulted in the establishment of emergent, long-lived pioneer tree species (Knight 1975). Species of pioneers and light-demanding trees have been declining there since the plot was established (Condit et al. 1998), a trend consistent with expectation in an old secondary forest (Sheil & Burslem 2003).

The human legacy of historical land-use interacts with natural forces to influence recovery processes (Goldammer 1992; Zimmerman et al. 1994; Foster et al. 1999; Thompson et al. 2002). Through effects on species composition and forest structure, anthropogenic disturbance can determine landscape patterns of damage due to disturbances such as hurricanes and fires. I focus here on recovery processes in tropical rain forests, emphasizing studies of forest recovery following human disturbances. Several excellent reviews of secondary forest succession provide much background for this topic (Brown & Lugo 1990; Corlett 1995; Finegan 1996; Guariguata & Ostertag 2001; de Jong et al. 2001). In this review I integrate results from studies of secondary succession on abandoned farmland and in slash-and-burn fallows with studies of forest responses to a wide range of disturbances, including hurricanes, floods, logging, and fires. I address the following three questions: (1) Are there predictable aspects of forest recovery processes following anthropogenic and natural disturbances? (2) Do different ecological processes change at different rates? (3) Can stand-level recovery processes be used to predict landscape level changes in ecosystem function and species composition? I focus here on recovery of vegetation. Recovery of animal populations following human disturbances is the topic of a recent review by Dunn (in press).

Paradigms of forest recovery

The disturbance/recovery mosaic

The 'disturbance/recovery' paradigm has been gradually replacing the 'stability/fragility' paradigm for tropical forest ecology (Whitmore 1991; Waide & Lugo 1992; Lugo 1995; Hartshorn & Whitmore 1999). Abolishing the myth of virginity in tropical forests (Whitmore 1991; Clark 1996) requires that the notions of climax and stability must be replaced with a model of flux and dynamism. If all tropical forests have experienced at least some levels of disturbance, which is now a widely accepted view, then it follows that all tropical forests are also in various stages of recovery. The situation is highly complex due to simultaneous disturbance and recovery processes acting at multiple temporal and spatial scales. Adding further to this complexity is the fact that some recovery processes, such as aboveground biomass accumulation, can occur within decades while others, such as species composition, occur over centuries (Guariguata & Ostertag 2001). Despite a century of opportunities for dispersal and the presence of contiguous mature forest, secondary forest in Singapore contained only 40–60% of the original number of species per plot (Turner et al. 1997).

Ecologists have long recognized that disturbances and recovery processes overlap in both spatial and temporal dimensions (Watt 1947). Consider a patch of remnant tabonuco forest (dominated by *Dacryodes excelsa*) at Luquillo Experimental Forest in eastern Puerto Rico. Within this stand, natural disturbances due to tree-falls, hurricanes, landslides (Guariguata 1990; Lugo & Scatena 1995), and anthropogenetic disturbances such as selective logging (Foster et al. 1999) create a complex spatial disturbance mosaic (Thompson et al. 2002). Yet this stand is part of a regional matrix of agricultural lands and former agricultural lands now in various stages of successional regrowth (Thomlinson et al. 1996). A multifaceted mosaic of current and historic disturbance composes the backdrop for a comprehensive understanding of disturbance and recovery in tropical forests.

The interplay between disturbance and recovery has several critical implications for ecological studies in tropical rain forests. First, current studies of forest

dynamics must be interpreted in the context of historical patterns of human impacts as well as natural disturbance events (Foster et al. 1997, 1999). Second, because of the overlay of different disturbance events (including anthropogenic disturbance), we may not be able to identify clearly the nature of vegetation response to particular disturbance regimes, even if we have access to paleoecological data and historical information on land use and disturbance events. For example, the species composition and canopy structure of the tabonuco forest in Luquillo Experimental Forest reflects species-specific responses to wind damage as well as to land-use history and subsequent recovery (Foster et al. 1999). Similar controversies revolve around the extent to which tropical forest expansion following long-term savannization in northern tropical Australia is due to reduction of Aboriginal-induced fire or to recovery following other human impacts (Ash 1988; Harrington & Sanderson 1994; Bowman 2000). Finally, the role of individual species responses in ecosystem recovery may reflect interactions of site history with species growth requirements. Growth of *Guarea guidonia* (Meliaceae) responds rapidly and markedly to increased soil nitrogen availability (Pascarella et al. 2000). This species occurs commonly in mature forest and also dominates successional stands in abandoned coffee and cacao plantations in several regions of Puerto Rico and the Dominican Republic (Zimmerman et al. 1995; Rivera et al. 2000; Pascarella et al. 2000). In coffee plantations, use of the nitrogen fixing legume *Inga vera* as a shade tree species for over 30 years has led to increased soil nitrogen availability (Rivera & Aide 1998).

A comparative framework for disturbance and recovery: beyond secondary and primary succession

Forest recovery is often viewed in a traditional context of primary versus secondary succession. Recovery following landslides, volcanic eruptions, and annual flooding follows a process of primary succession, where soils are removed or buried, leaving substrate free of organic matter available for colonization (Walker 1999). In contrast, recovery following windstorms, hurricanes or cyclones, lightning, fire, or biotic disturbances (herbivore or pathogen attack) follows a course of secondary succession (Whitmore & Burslem 1998). Recovery following human impacts can follow either processes, depending on the extent of soil degradation and remnant vegetation. The concept of patch dynamics applies strongly to forest recovery processes (Pickett & White 1985), and facilitates extension of the traditional successional dichotomy to a continuum-based approach. Recovery following large-scale disturbances often follows a patch-dynamics model,

with significant spatial heterogeneity in disturbance producing a spatial mosaic of post-disturbance vegetation (Turner et al. 1998). Spatial mosaics are particularly prominent following cyclones, fires, and mechanized logging (de Foresta 1984; Grove et al. 2000). This spatial mosaic can include patches with little or no residual vegetation or soil organic horizon adjacent to patches with substantial residual vegetation and organic matter.

Turner et al. (1998) emphasized that a key distinction in recovery processes is the presence or absence of residuals, defined as individual organisms or their propagules that survive a disturbance event. They suggest, following Franklin et al. (1985) and del Moral & Bliss (1993), that primary succession differs from secondary succession in the absence of residuals and propose that the abundance of residuals surviving a disturbance be used as a measure of disturbance intensity, apart from the effect of soil development. Here, I adopt this suggestion and examine recovery processes in the context of three continuous axes: (1) abundance of residuals (living individuals or seed bank), (2) spatial extent, and (3) the frequency of disturbances. Spatial extent can be viewed as a measure of the distance from seed sources for colonization. A similar approach was advocated by Waide & Lugo (1992).

Metrics of forest recovery: structure, composition, and ecological interactions

This disturbance/recovery framework provides us with a method for comparing forest recovery following a wide range of disturbances, including human impacts. An essential component to this comparison, however, is the choice of variables used to measure recovery. Many studies (including most of the studies described here) focus on structural measures of recovery, such as basal area, aboveground biomass, tree height, or stem density, as these most directly apply to measures of ecosystem function. These structural characteristics often show rapid, easily measurable changes following disturbance. Other studies have examined changes in canopy structure, the frequency and size of canopy gaps, and light availability during forest recovery (Yavitt et al. 1995; Nicotra et al. 1999; Denslow & Guzman 2000). Soil nutrient and carbon stocks and nutrient cycling components can also be used as measures of recovery of ecosystem functions (Reiners et al. 1994; Silver et al. 1996; Hughes et al. 2002). Multivariate approaches are frequently used to examine patterns of species composition across stands differing in land-use history, soils, and elevation (Aide et al. 1996; Foster et al. 1999; Pascarella et al. 2000). Stands are often compared in terms of species density (number of species per unit area), species richness (number of

species per common number of individuals measured), evenness, or species diversity (using Shannon or Simpson diversity indices). These comparisons can be problematic if effects of stem density are confounded with effects of species richness (Gotelli & Colwell 2001) or if sample plots are small and poorly replicated. Rarefaction techniques should be used to assess recovery of species richness following disturbances (Guariguata et al. 1997; Cannon et al. 1998; Webb & Peralta 1998; Vandermeer et al. 2000; Molino & Sabatier 2001). Alternatively, estimates of species richness based on multiple samples can be used to compare sites (Chazdon et al. 1998; Boucher et al. 2001). Several studies have examined recovery of particular species, with a focus on tree population structure and overall changes in abundance (Knight 1975; Milton et al. 1994; Condit et al. 1998; Sheil 1999). Measures of forest recovery can also track changes in economic value, and in the abundance and richness of species used for non-timber products as forests recover from disturbances (Salick et al. 1995; Chazdon & Coe 1999).

Although trees and soils are usually the focus of forest ecology and management studies, forest recovery is often associated with changes in the distribution and abundance of different life forms, and functional groups (Condit et al. 1996; Denslow 1996). Recovery has recently been examined in herbaceous communities, lianas, and non-vascular epiphytes (Turner et al. 1996; Romero 1999; Costa & Magnusson 2002; Schnitzer & Bongers 2002). Recovery of species interactions is another metric that should be more widely used (Dirzo & Miranda 1991). Legacies of phylogeny and land-use history strongly influence the distribution of reproductive traits (sexual system, pollination syndromes, and seed dispersal modes) within and among tropical forests (Chazdon et al., in press). Logging has also been shown to impact pollination and reproductive biology of rain forest tree species (Curran et al. 1999; Ghazoul & McLeish 2001).

The role of residual vegetation in forest recovery

Remnant vegetation plays a critical role in forest recovery, promoting rapid increases in species richness, tree density and aboveground biomass (Guariguata & Ostertag 2001). Shrubs and trees in pastures and abandoned fields attract birds that deposit or regurgitate seeds while perched (Guevara et al. 1986; Viera et al. 1994; Galindo-Gonzalez et al. 2000; Slocum & Horvitz 2000). Even if trees are severely damaged, as occurs during hurricanes or logging, many species have the capacity to resprout. Following Hurricane Joan, which hit south-eastern Nicaragua in 1988, only 27% of the trees remained standing and 18% had leaves in the study areas of Yih et al. (1991), but by Feburary of

1989, most of the trees had resprouted and 77% of the trees had leaves. Of the 79 species found, all but two had some resprouting individuals. Extensive resprouting encouraged regeneration of species present in the pre-existing mature forest, rather than favouring dominance of early-successional shrub and tree species (Vandermeer et al. 1995, 2000; Yih et al. 1991). Following Hurricane Hugo in Puerto Rico in 1989, the first 5 years of recovery were characterized by the re-leafing of surviving trees as well as establishment of early-successional plants (Scatena et al. 1996). During this interval, 75–92% of the nutrient uptake was retained in aboveground vegetation, and aboveground biomass reached 86% of the pre-hurricane value (Scatena et al. 1996). The predominance of sprouting as a mechanism of forest recovery following hurricane damage led to rapid recovery of tree species composition in Jamaican forests (Bellingham et al. 1994).

Many tree and shrub species from wet and dry tropical forests are capable of resprouting (Paciorek et al. 2000). In recently cut and cleared dry forests of Central America, stem coppicing and root sprouting rapidly restore the number of species on a given site (Ewel 1977; Murphy & Lugo 1986). Sprouting from cut stumps is a common regeneration mode after forest cutting in the San Carlos region of Venezuela (Uhl et al. 1981). Burning after cutting, however, killed sprouts and also significantly reduced the seed bank, limiting regeneration to seeds that survived the burning and seedlings from seeds newly dispersed into the area following burning (Uhl et al. 1981). Tree sprouts contribute strongly to regenerating vegetation following slash-and-burn agriculture in eastern Paraguay (Kammesheidt 1998). Over 59% of the small stems (1.0–4.9 cm dbh) in young regrowth stands (2–5 years old) originated from sprouts. This figure decreased to 31% in older stands (10–15 years old).

Residual vegetation can also take form as living seeds stored in the soil. As land-use intensity increases, the importance of seedling recruitment from the seed bank decreases (Guariguata & Ostertag 2001). An experimental study in Chiapas, México, showed that in secondary forest seedlings of early-successional tree species were recruited primarily from the seed rain, while in mature forest and abandoned pasture areas, the seed rain and seed bank contributed equally to seedling recruitment (Benitez-Malvido et al. 2001). Early pioneer seedling communities in artificially created gaps in 70-yr-old secondary forest in Panama strongly reflected the soil seed bank composition (Dalling & Hubbell 2002). The composition and abundance of seeds stored in the soil reflects site history as well as features of neighboring vegetation (Saulei & Swaine 1988; Quintana-Ascencio et al. 1996). The abundance of seeds in the soil seed bank is substantial-

ly higher in second-growth forests compared to old-growth forests in north-eastern Costa Rica (Dupuy & Chazdon 1998). The soil seed banks of secondary forests that have been historically surrounded by mature forests show a higher fraction of tree species and a lower fraction of weedy herbaceous species (Dalling & Denslow 1998). Herbaceous early-successional species of grasses and sedges initially dominated the soil seed bank in newly cleared areas of forest in Papua, New Guinea, but declined markedly in abundance after 2–3 years, whilst seeds of pioneer trees and shrubs gradually increased in abundance (Saulei & Swaine 1988).

Tropical forest recovery following large, infrequent forest disturbances

Large, infrequent disturbances, such as hurricanes, floods, volcanoes, and fire, have strong impacts on forest landscapes (Fig. 1; Foster et al. 1998; Turner et al.

1998). The impacts of these disturbances are strongly influenced by the pre-disturbance vegetation as well as by topographic exposure. Following these large-scale disturbances, surviving individuals or 'residuals' determine much of the initial pattern of succession (Turner et al. 1998). Everham & Brokaw (1996) describe four paths of recovery from catastrophic wind disturbance: (1) regrowth (sprouting of surviving trees), (2) recruitment of early-successional species, (3) rapid growth of subcanopy trees, and (4) repression (invasion of herbaceous growth). The actual route of recovery will depend on the severity of damage in conjunction with a variety of abiotic and biotic factors, including previous land-use history (Zimmerman et al. 1995; Everham & Brokaw 1996). A few studies have examined long-term recovery processes following hurricanes or cyclones. In lower montane forests of Puerto Rico, stem density, species number, and the rate of biomass accumulation reached a maximum 15 years after hurricanes (Weaver 2002). After 50 years of recovery, most

Fig. 1. Recovery of canopy damage following Hurricane Rona at the Australian Canopy Crane Research Facility near Cape Tribulation, Queensland, Australia. Three years after the cyclone passed, prolific vine and liana growth drapes over damaged tree trunks and crowns. The black palm *(Normanbya normanbyi)* recruits in large canopy gaps created by tree falls and damaged crowns.

of the secondary species that established following the disturbance had disappeared, and the rate of biomass accumulation had reached a plateau (Weaver 2002).

Vandermeer et al. (2000) examined patterns of species accumulation over a 10-yr period following the impact of Hurricane Joan on the Caribbean coast of Nicaragua in 1988. Within each 0.1–0.15 ha plot studied in the hurricane-damaged area, species richness increased 2–3-fold over the 10-yr study period. Hurricane-damaged areas, when compared with undamaged areas, also showed higher species accumulation with increasing number of individuals. Vandermeer et al. (2000) proposed that large storms, such as Hurricane Joan, may lead to increased species diversity because pioneer species are unable to saturate the disturbed area, allowing many other species to colonize and establish. This pattern is predicted by the intermediate disturbance hypothesis (Connell 1978). As noted above, forest recovery in hurricane-damaged areas was dominated by resprouting of residual trees, leading to a rapid recovery of species composition. Few pioneer species were present in the seed bank or as seedlings in the prehurricane forest. Eight years after the hurricane, proportions of stems that were pioneers ranged from 0.09–0.16 (Vandermeer et al. 2000).

Studies of forest recovery following cyclones on Kolombangara in the Solomon Islands provide further evidence that the effects of cyclones on species composition can be short-lived (Burslem et al. 2000). Over a 30-yr period (1964–1994), mean stem density and basal area of the twelve most common big tree species were significantly auto-correlated. Moreover, no substantial change in relative abundance of these species was observed over time, despite the impact of four cyclones that caused massive canopy damage between 1967 and 1990 (Burslem et al. 2000). Thus, the rank hierarchy of abundant tree species remained intact. Studies in Sri Lanka, Puerto Rico, and Jamaica all suggest that tropical windstorms have relatively little long-term impact on forests, despite extensive short-term damage (Dittus 1985; Walker 1991; Bellingham & Tanner 1995). In all of these cases, recovery was dominated by vegetative regrowth and recruitment of seedlings from advance regeneration, rather than by development of pioneer vegetation.

Studies in Hawaii following Hurricane Iniki in 1992 suggested that soil nutrient supply can influence rates of damage and recovery (Herbert et al. 1999). Experimental phosphorus addition led to increased leaf area index and aboveground net primary productivity in *Metrosideros polymorpha* forests at 1134 m elevation on Kauai, Hawaii. Following the passage of the hurricane, absolute and fractional reductions in leaf area index were significantly greater for the added-phosphorus treatments (Herbert et al. 1999). But after 2 years of recovery, diameter growth increments in the added phosphorus treatments had returned to prehurricane rates and were greater than those in treatments lacking phosphorus fertilization. Therefore, fertilization with the limiting nutrient, phosphorus, decreased resistance to structural damage, but increased the rate of recovery, supporting the hypothesis of Holling (1973) that resistance and resilience of ecosystems are inversely related (Herbert et al. 1999).

Fires also cause widespread damage to tropical forests, particularly in areas with strong seasonal dry periods (Whitmore 1985). ENSO-related droughts create the potential for large-scale forest fires in tropical wet forests as well (Nepstad et al. 1999). Charcoal deposits in soils beneath tropical moist forests throughout the tropics indicate that these forests can and do recover from fires (Goldammer & Seibert 1990), but few studies have examined recovery processes over more than a decade. In Amazonian moist evergreen forests, most trees resprout and survive fires of low intensity (Uhl & Jordan 1984), whereas repeated burning eliminates nearly all resprouted trees (Uhl & Kauffman 1990). Smaller trees are far more likely than large trees to be killed by a burn (Hall & Swaine 1976; Holdsworth & Uhl 1997). Typically, a single burn will kill nearly 40% of the trees of <10 cm dbh, but will reduce living biomass by as little as 10% because few large trees are affected (Cochrane & Schulze 1999).

Fires are now recognized as historic elements of the disturbance regime in many tropical regions (Sanford et al. 1985; Goldammer & Seibert 1990). In Sabah, Borneo the prospects for recovery of approximate prefire forest structure appeared to be good for unlogged forest sites burned by a relatively low-intensity fire (Woods 1989). Recovery of plant cover was rapid after fire, and little exposed soil remained after three months. In contrast to results from studies in the Neotropics, most species appeared to have a low ability to coppice from basal shoots after fire (Woods 1989). Few seedlings and saplings survived the burning, but newly recruited pioneer trees provided sufficient canopy to inhibit invasion of grasses or woody creepers. Recovery of dipterocarp forest from the 1982–1983 fires in Borneo requires more than several decades, and biomass recovery to the level of unburned primary forests could take up to 60 years (Mori 2000). Unfortunately, forests that burned in 1982–1983 only had 15 years to regrow before the fires of 1997–1998 destroyed the recovering vegetation.

In East Kalimantan tree density recovered 15 years after the burning of a lowland dipterocarp forest, but

tree species richness remained lower than in unburned forest (Slik et al. 2002). After 8 years of succession following a severe fire in south-western Sabah, Borneo, total aboveground biomass recovered 24% of the pre-fire biomass (Nykvist 1996). Pioneer trees, such as *Macaranga* species, dominated the site, but a few primary tree species were also establishing due to seed dispersal from undamaged areas nearby. Forest recovery from burning, as with post-agricultural succession, strongly depends on initial colonization of the site by pioneer trees (Whitmore 1983). Furthermore, the establishment of late-successional trees depends strongly upon the presence of remnant forests in the immediate area (Hawthorne 1990).

Tropical river basins are associated with dynamic floodplains, creating forests in a continual state of primary succession (Salo et al. 1986; Nelson 1994). Meander loops of the Río Manu create sandbars that undergo colonization (Foster et al. 1986). Successional forests recovering from floodplain formations cover 12% of the Peruvian lowland forest, as assessed using satellite imagery (Salo et al. 1986). Terborgh & Petren (1991) estimated that over 300 years are required to reach the species composition of mature floodplain forests in these areas. Zones undergoing primary succession are embedded in a matrix of continuous forest cover, promoting rapid colonization through seed dispersal (Terborgh et al. 1996). The successional matrix

created by river dynamics is thought to promote high beta diversity in western Amazonia (Salo et al. 1986).

Legacies of human impact

Forest recovery following abandonment of agriculture

Features of post-agricultural succession are well described in other reviews (Brown & Lugo 1990; Finegan 1996; Guariguata & Ostertag 2001), so I will not elaborate on these studies here. Early studies of vegetation dynamics following forest clearing emphasized the first 5–10 years of regrowth (Wyatt-Smith 1955; Williams et al. 1969; Swaine & Hall 1983). Most of our knowledge of post-agricultural succession in sites older than 10–15 years since abandonment is based on chronosequence studies rather than on long-term studies in monitored study plots. Detailed long-term studies are essential for a mechanistic understanding of recovery processes (Redondo et al. 2001). Aside from the problems associated with studies based on space-for-time substitution (Pickett 1987), sites that are abandoned early are usually the most marginal for agricultural use (Birdsey & Weaver 1987). Thus, there may well be important biotic and abiotic factors that interact strongly with age since abandonment to influence successional processes. In the Cayey mountains of

Fig. 2. Active pastures, riparian forest strips, isolated pasture trees and forest fragments of old-growth and second-growth compose a complex landscape matrix throughout northeastern Costa Rica.

Puerto Rico, higher elevation pastures were abandoned earlier than lowland sites, confounding independent effects of elevation and time since abandonment (Pascarella et al. 2000).

Abandonment of farmland during the past 30–50 years in many tropical regions has permitted an assessment of the effects of land-use and time since abandonment on aspects of forest recovery. Several clear patterns have emerged. Rates of recovery are accelerated if prior land-use intensity was low, if recovering areas are relatively small, if soils are fertile, and if there are remnant forest areas nearby (Fig. 2; Guariguata & Ostertag 2001). Pastures that have been subjected to overgrazing, repeated weeding and burning over long periods (>10 years) or have been bulldozed have slow recovery or no recovery. If use is light, recovery proceeds rapidly. In a study of 13 abandoned pastures in eastern Amazonia, sites on pasture for <8 years were repopulated with trees within a few years of abandonment (Uhl et al. 1988). In these pastures, sprouting was an important means of regeneration; more than half of the 171 tree species identified in abandoned pastures had the ability to resprout. Nepstad et al. (1996) found that prolonged use of pastures decreased the number of sprouting roots and reduced the number of tree seeds in the soil. In the humid tropical region of Los Tuxtlas, México, recovery of aboveground biomass in eleven post-agricultural sites ranging from 6 months to 50 years since abandonment was inversely related to number of years of land use prior to abandonment, but was not correlated with forest age (Hughes et al. 1999).

Virtually all studies of post-agricultural recovery of tropical forests indicate that recovery of forest structure, soil nutrient stocks, and species richness is far more rapid than recovery of species composition. Zou et al. (1995) found that tree basal area and annual litter fall rates were similar for a 50-yr old secondary forest and an adjacent mature tabonuco forest in the Luquillo Mountains of Puerto Rico, but leaf litter had significantly higher nitrogen concentrations in the younger forest, reflecting domination by the fast-growing, early-successional species *Casearia arborea* and *Cecropia schreberiana*. Slow recovery of species composition in secondary forests is often attributed to inadequate dispersal of late-successional species (Whitmore 1991; Gorchov et al. 1993; Ingle 2003). Many large-seeded species that persist in remnant forests in Puerto Rico (*Dacryodes escelsa, Prestoea montana, Manilkara bidentata*, and *Sloanea barteria*) are rare or absent in secondary forests in the same regions (Aide et al. 2000; Pascarella et al. 2000). Corlett (1991, 1992) and Turner et al. (1997) report similar findings on the island of Singapore, where large-seeded species characteristic of primary forests occur only

in a few protected remnant forest areas. In 15–20-yr old secondary forests of the north-eastern lowlands of Costa Rica, basal area reached similar levels to values observed in old-growth forests of the region, but tree species richness remained substantially lower in second-growth forests (Guariguata et al. 1997). Similarity values between secondary and old-growth stands were higher for saplings than for trees (Guariguata et al. 1997).

Forest recovery following shifting cultivation

Small-scale shifting cultivation, also known as slash-and-burn agriculture, is generally associated with the most rapid rates of forest recovery compared with more intensive and extensive types of agriculture (Guariguata & Ostertag 2001). The early establishment of pioneer tree species (short- and long-lived) is a critical aspect of rapid recovery. These fast-growing species appear to function as critical nutrient and carbon sinks that drive the successional process forward (Uhl et al. 1982; Uhl 1987; Brown & Lugo 1990). In most cases, pioneer species establish abundantly in abandoned pastures and cultivated fields, but the particular species that colonize will depend upon soil fertility, drainage, and compaction, presence or absence of a seed bank, and peripheral remnant vegetation.

In West Kalimantan, Indonesia, biomass accumulation is rapid following long-fallow shifting cultivation, with a mean accumulation rate of 5.4 Mg ha^{-1} yr^{-1} over the first 40 years (Lawrence 1998). A fallow period 106 years would be required to achieve biomass within 10% of mature forest values (Lawrence 1998). Levels of soil phosphorus increased with each shifting cultivation cycle through the first 100–120 years (Lawrence & Schlesinger 2001). With stand age held relatively constant, the number of shifting cultivation cycles showed no significant effect on total biomass or total biomass increment. Across a wide range of forest ages, biomass increments declined with age and increased in inherent soil fertility (Lawrence 1998).

Even when succession proceeds relatively quickly during fallow periods, studies across a range of soil types suggest that it is unlikely that species composition will reach pre-disturbance levels within a period of less than 200 years, particularly in low fertility soils (Saldarriaga et al. 1988). Riswan et al. (1985) concluded that re-establishment of primary forest species following slash-and-burn agriculture in mixed dipterocarp forest would require between 150 and 500 years. The dominance of pioneer species during initial phases of post-agricultural recovery stands in striking contrast to the dominance of residual vegetation in certain types of natural disturbances described earlier. Although pioneer tree establishment sets the course for

secondary succession, this course is inevitably slower and less predictable than recovery following canopy disturbance during hurricanes.

Studies of succession following shifting cultivation in dry tropical forests suggest similar rates of recovery of aboveground biomass compared with those found in more humid forests. Following shifting cultivation of maize in the Southern Yucatan Peninsula of Mexico, where mean annual rainfall ranges from 900–1400 mm yr^{-1}, recovery of total aboveground biomass was estimated to take a minimum of 40–60 years and a maximum of 95 years (Read & Lawrence 2003). Previous human disturbances, including cultivation history and logging activity may significantly constrain recovery of forest biomass across this region more than effects of variation in annual rainfall (Read & Lawrence 2003). These estimates compare well with those of Hughes et al. (1999) for the humid region of Los Tuxtlas (4000 mm annual rainfall); they projected a 73-yr recovery period. In southern Yucatan, litter production and forest floor biomass recovered significantly faster than aboveground biomass; young stands only 2–5 years after abandonment produced 70% of the fine litter mass of mature forest, but only 15% of the aboveground biomass (Lawrence & Foster 2002).

Effects of agricultural land-use and soil fertility on forest recovery

A recent chronosequence study documents strong effects of land-use and soil fertility on recovery of forest structure and species composition in forests along the east coast of Puerto Rico (Chinea 2002). Sites on alluvial substrate attained greater basal area than sites on plutonic or volcanic substrate, but had approximately twice as high a percentage of exotic species. Bulldozed sites had significantly reduced species diversity and a higher percentage of exotic species than non-bulldozed sites (Chinea 2002). Site age was the best predictor of species richness and diversity, but distance to older forest at the time of abandonment added significantly to explained variability, underscoring the critical importance of seed dispersal for colonization. In the Cayey mountains of southwestern Puerto Rico, Pascarella et al. (2000) sampled secondary forests ranging from 4–80 years old in abandoned pastures, abandoned coffee plantations and old-growth forest sites on two soil types. After 25–30 years, basal area and species richness were similar to those found at old-growth forest sites, but species composition remained distinct. Exotic species had higher importance values in young forests (4–13 years) on former pasture and in abandoned coffee plantations. Abandoned pastures and coffee plantations differed in species composition,

as has also been shown in chronosequence studies in the Luquillo Mountains of Puerto Rico (Zimmerman et al. 1995). Some studies show slower rates of recovery in abandoned pastures compared to abandoned crop cultivation (Aide et al. 1995; Steininger 2000), while others do not indicate a consistent difference (Zarin et al. 2001). Recruitment of native woody species in abandoned coffee and cacao plantations may be inhibited by the existing forest structure, leading to a slower rate of accumulation of species richness (Rivera & Aide 1998; Pascarella et al. 2000; Rivera et al. 2000).

Soil fertility and texture strongly affect rates of recovery from anthropogenic disturbance. An extensive survey by Moran et al. (2000) compared rates of successional forest recovery across five regions of the Amazon basin. Inter-regional differences in rates of forest regrowth (average stand height) were best explained by differences in soil fertility, whereas variation within regions was best explained by land-use type (traditional shifting cultivation, agroforestry, mechanized agriculture, or cattle ranching). In secondary forests on alfisols, soil fertility increases as sites rapidly accumulate biomass; on ultisols and oxisols, slow accumulation of aboveground biomass cannot compensate for nutrient losses due to leaching (Lu et al. 2002). In a global comparison including tropical and temperate secondary forests, Johnson et al. (2000) showed that aboveground biomass accumulation on nutrient-poor sandy soils is lower than on non-sandy soils. A regional test of this finding using data for 85 plots at eight sites across the Brazilian Amazon showed that soil texture is a critical correlate of post-agricultural rates of aboveground biomass accumulation (Zarin et al. 2001). Both soil fertility and soil moisture tend to covary with soil texture (Johnson et al. 2000).

Forest recovery following logging

Logging disturbances in tropical forests vary widely in their impact on forest structure and composition. At one extreme, low-intensity, polycyclic, selective logging is thought to mimic closely natural disturbances due to canopy gap formation, forming the basis for sustainable forest management practices (Hartshorn 1995). On the other hand, clear-cutting removes essentially all forest cover, paving the way to secondary forest succession through resprouting and pioneer seedling establishment as in post-agricultural succession. As with other disturbances that involve tree damage, spatial heterogeneity in canopy removal is high, leading to patches of greater and lesser damage (Molino & Sabatier 2001). In addition, soil damage due to skid trails and logging roads causes highly patchy pat-

terns of soil disturbance and light availability. Guariguata & Dupuy (1997) and Dickinson et al. (2000) documented small-scale recovery patterns associated with this heterogeneity, particularly the effect of skid trails. The actual impacts of logging and the pathways for subsequent recovery, however, have more to do with the aftermath of logging than with the actual disturbance created by timber harvesting itself. It is now well known that recently logged forests are highly susceptible to burning (Hawthorne 1990; Holdsworth & Uhl 1997; Nepstad et al. 1999; Dennis et al. 2001; Siegert et al. 2001), to further degradation, or to conversion to agriculture (Kartawinata et al. 2001; de Jong et al. 2001). Because of these later impacts, it has been difficult to study recovery processes in logged forests.

Indonesia has an estimated 23 million ha of post-extraction secondary forest (Kartawinata et al. 2001). In a small number of ecological studies the recovery of tree species richness and density after logging have been followed in stands with no subsequent disturbance. Commercial logging operations in a 60,000 ha concession along the Sungai Matan River, West Kalimantan, Indonesia removed 43% of the total stand basal area and opened up 45% of the canopy (Cannon et al. 1998). Within 1 year of logging, density and species number for trees >20 cm dbh in 0.1-ha plots were reduced 41% and 31%, respectively, compared to pre-logging conditions. Eight years after logging, tree densities were still lower in logged forest, but the number of species per 50 sampled individuals was higher than in unlogged forest. Cannon et al. (1998) proposed that the reduction in dominance of commercial species following selective logging permitted an increased number of species among the individuals of small-tree recruits, thus mitigating effects of reduced density on species-area relations. In lowland dipterocarp forest of East Kalimantan, the number of trees, tree species richness and Fisher's alpha (a measure of species-richness) reached pre-disturbance levels after approximately 15 years (Slik et al. 2002). Another study in East Kalimantan showed a rapid recovery of tree mortality 4 years after logging (Sist & Nguyen-The 2002). In areas where more than 15% of the tree basal area was removed, pioneer species regeneration became limiting to growth and establishment of dipterocarps. Not all logged areas of Indonesia show good recovery from logging, however. Sites on white sand soil ('kerangas' heath forest) recover particularly slowly, due to low soil fertility (Kartawinata et al. 2001).

Studies in other regions present mixed results on the rate of recovery of forest structure and species richness after logging. One long-term study is based on forest inventory data from 1924 to 1999 in a logged area of Central Guyana (ter Steege et al. 2002). Over 75 years

there was little change in overall species composition or the proportion of functional groups in the tree community, although populations of the targeted species, *Chlorocardium rodiei* (Greenheart), declined by 63%. Moreover, tree diversity did not change detectably during this period (ter Steege et al. 2002). Effects of logging of moist evergreen forest in the Western Ghats (South India) were still noticeable 10–15 years after harvest (Pelissier et al. 1998). The mortality rates of trees with a dbh of 40 cm or greater were still higher, and the diameter increments of emergent and upper canopy trees were still stimulated by 50% compared to trees in unlogged forest. In forests of Kibale National Park, Uganda, reduced sapling density and reduced tree growth rates were observed 25 years after heavy logging, a possible effect of concentrated elephant activity (Chapman & Chapman 1997). However, density and species-richness of seedlings did not differ between logged and unlogged forests. The stimulation of tree growth immediately after logging can be rather short-lived. In Tapajos National Forest in the Brazilian Amazon, logging stimulated growth for only 3 years; by 13 years, growth rates were similar to those in unlogged forest and basal area recovered to 75% of the unlogged forest levels (Silva et al. 1995). Ten years after commercial logging in forests of French Guiana tree species richness increased at intermediate levels of canopy disturbance (Molino & Sabatier 2001).

Measures taken to reduce logging impacts in Sabah, Malaysia have been shown to accelerate recovery of forest structure and species composition (Pinard & Putz 1996; Pinard et al. 2000). One year after logging, conventional and reduced-impact logging areas contained biomass equivalent to 44% and 67%, respectively, of pre-logging levels (Pinard & Putz 1996). In Brazilian forests, reduced-impact logging through pre-cutting of lianas has been shown to significantly reduce liana proliferation in logging gaps after 6 years (Gerwing & Uhl 2002). Reduced-impact logging can also reduce the risk of fire subsequent to logging (Holdsworth & Uhl 1997).

Challenges for forest recovery

Multiple and overlapping disturbances

Forests are often faced with multiple, overlapping disturbances. Cyclones interact with other disturbances to influence damage and recovery processes (Grove et al. 2000). When a cyclone hit the coast of the Daintree lowlands in northeastern Australia in 1999 (Fig. 1), the most severely impacted site was an old-growth stand, whereas the least impacted site was a logged stand. Underlying topography may also have influ-

enced these impacts (Grove et al. 2000). Fires that follow cyclones in tropical monsoon forests can have devastating effects. Bowman et al. (1999) contend that combined effects of cyclone damage and subsequent severe fire have caused contraction of monsoon rain forest boundaries in Australia.

Effects of prior land use and human impacts, such as logging, strongly influence responses to large-scale disturbances. Differences in forest composition across Kolombangara, Solomon Islands, are more likely a reflection of differential anthropogenic disturbance linked to settlement patterns than to differential cyclone impacts (Burslem et al. 2000). Similarly in Puerto Rico, Zimmerman et al. (1995) found that legacies of land-use history were more long lasting than hurricane impacts.

Trees damaged by logging suffered higher rates of mortality after drought and fire than undamaged trees. The rate of mortality of trees in unlogged forest is generally lower in corresponding size class than in logged forests. Selective logging greatly increases susceptibility of forests to fire (Uhl & Kauffman 1990). Cochrane et al. (1999) showed that previously burned forests were also much more likely to burn than were unburned forests. Burned forests are often adjacent to fire-maintained pasture and agriculture plots and are frequently exposed to ignition sources (Uhl & Buschbacher 1985). Invading grasses and weedy vines add to a highly combustible fuel load. Fires in highly degraded areas are significantly more severe in all respects. Recurrent fires have potential to totally eradicate trees from the landscape (Hawthorne 1990). Nepstad et al. (2001) describe three positive feedback loops that drive expansion of forest fires in Amazonia: (1) fire can directly promote drought by reducing rainfall; (2) fire increases susceptibility of forests to recurrent burning; and (3) fires destroy agricultural and forestry systems, discouraging farmers from investing in land-management activities that are vulnerable to fire.

Landscape-level recovery

Most of the studies describing forest recovery processes involve comparisons among individual study areas on the spatial scale of less than a hectare to several hectares. Although many studies are conducted in the context of particular landscapes and regions (Moran et al. 2000), few studies have actually monitored forest recovery at the landscape scale. One of the best-documented examples of landscape-level recovery is the increase in forest cover in Luquillo Experimental Forest, Puerto Rico. Between 1936 and 1988, forest cover increased from 15 to 54% (Thomlinson et al. 1996). Three factors influenced the rate of land-cover change

in this region. Regeneration of forest was greatest within 100 m of forest islands and riparian zones. Areas that showed the highest percentage of areas increasing in forest cover were close to the experimental forest boundary, at higher elevations, and close to dense forest remnants present in 1936 (Thompson et al. 1986). Decreasing intensity of agricultural activity led to increasing rates of forest recovery. A recent study of forest recovery in Babeldaob in the Republic of Palau also shows that established forest is critical for facilitation of forest recovery across the landscape (Endress & Chinea 2001). Between 1947 and 1976, upland forest cover increased from 72% to 83% across the landscape. Most recovery occurred through expansion of previously established forest patches. Anthropogenic grasslands dating from pre-colonial times have not regenerated back to forests, however, suggesting that dense herbaceous cover may have impeded tree regeneration (Endress & Chinea 2001).

Fire plays a major role in controlling rain forest boundaries in Australian landscapes (Bowman 2000). Altered fire regimes following interruptions to Aboriginal land management have resulted in substantial changes in the range and demographic structure of rain forest and open wet sclerophyll forest. In the wet tropics of NE Australia, expansion of rain forest into open (wet sclerophyll) forest has been attributed to a reduction in aboriginal fire (Ash 1988; Unwin et al. 1988; but see Hill et al. 2001). Between 1943 and 1992, rain forest had expanded into 70% of tall *Eucalyptus grandis* open forests and 57% of mixed-species tall eucalypt open forest in three study areas (Harrington & Sanderson 1994). Hill et al. (2000) found that expansion of rain forest into open forest since 1945 represents recovery following extensive rain forest destruction associated with sugar cane cultivation in the first 70 years of European occupation.

Recovery from anthropogenic versus natural disturbances

Janzen (1990) listed several ways in which succession of abandoned field and pastures differ from recovery of natural disturbances, such as canopy gaps. The dispersal of fauna is likely to be substantially altered by human occupation and extensive periods of land use. Seed predators may be more common in altered habitats. Wind-dispersed species may dominate numerically over animal-dispersed species in abandoned clearings, particularly in dry forest zones. Seed rain from neighboring vegetation may favor species that did not originally occur on the cleared site. Finally, there is less predictability and more serendipity in the process of old-field colonization compared to gap dynamics. And when species are deliberately planted to restore condi-

tions within a clearing, the selection process involves human decision making rather than an evolutionary process.

Few studies have directly compared forest recovery following anthropogenic and natural disturbances within the same region and time period. Boucher et al. (2001) compared 5-yr old forests undergoing post-agricultural succession with forests recovering from Hurricane Joan in two sites in south-eastern Nicaragua. Species composition closely follows the history of land use. Six post-hurricane forests clustered together, and the two post-agriculture forests clustered together. Moreover, post-hurricane forests were more similar to pre-hurricane forests than to the post-agriculture forests. Basal area and stem density did not differ between the two land-use histories or between the two sites (Boucher et al. 2001). Species of high importance in the post-hurricane succession were not found in the post-agricultural sites, but they were common in the pre-hurricane forests. These findings may, in part, reflect the young age of post-agricultural areas studied. For example, some of the species noted for their absence in the post-agricultural sites in southeastern Nicaragua, *Cupania glabra*, *Inga thibaudiana* and *Vochysia ferruginea*, do commonly occur in older (>12 years) post-agriculture secondary forests in northeastern Costa Rica (Redondo et al. 2001). Because post-agricultural forests have greater dominance by fewer species, their species-richness and evenness are low, especially for tree size classes (Guariguata et al. 1997; Boucher et al. 2001). Species richness of woody saplings and seedlings, however, can recover rapidly (within 15–20 years) in post-agricultural secondary forests that are close to mature forest areas (Guariguata et al. 1997; Chazdon et al. 1998).

Aide et al. (1995) found that recovery in abandoned pastures of the Luquillo Mountains in Puerto Rico was slower in comparison with recovery following other types of human and natural disturbance. The successional trajectory in pastures was different in comparison to recovery from natural disturbances in the nearby Luquillo Mountains, and species that commonly colonize gaps in mature forests, such as *Cecropia schreberiana* (Cecropiaceae) and *Ochroma pyramidale* (Bombaceae) were not important colonizers in abandoned pastures. These differences could be due to high compaction of soils in abandoned pastures, resulting in poor infiltration, greater runoff, and increased erosion. Alternatively, these differences could also reflect the absence of these species in the seed bank of pasture soils. In Amazonia, as well as other regions, highly degraded tropical pastures impose many obstacles to tree colonization, as described in detail by Nepstad et al. (1996). The dense growth of grasses and ferns can also inhibit the establishment of trees in abandoned pastures (Aide et al. 1995), although fern thickets can also significantly impede tree regeneration on landslides (Walker 1994).

Seed dispersal is often a major limitation to tree recruitment following human disturbances (Turner et al. 1997; Holl 1999; Wijdeven & Kuzee 2000). Within a 25-ha clearing created by tree harvesting for paper pulp in French Guiana, Toriola et al. (1998) examined changes in species diversity from the periphery to the center of the plot. Mean values of the Shannon-Wiener index differed significantly between distance classes and decreased toward the center of the clearing (200 m from the plot edge), demonstrating a strong effect of proximity to seed sources.

When recovery fails: the need for restoration

There are limits to recovery in tropical forests. Following abandonment of agricultural land on degraded, infertile soils with no residual vegetation and no local sources of seed dispersal, forest recovery fails to initiate within the expected time frame of 5–10 years. Forest recovery following logging can also fail due to insufficient seedling regeneration of commercially exploited species (Guariguata & Pinard 1998). Recovery of native vegetation can fail if exotic species become competitively or numerically superior (Vitousek et al. 1997; Horvitz et al. 1998; Denslow et al. 2001). Repeated cycles of burning can reduce tropical forests to savannas (Swaine et al. 1997).

Uncontrolled livestock grazing, logging, fuel wood collection, erosion, unsustainable agricultural practices, and fires cause significant degradation of tropical forests and woodlands. Recent estimates indicate that degraded forest land covers 350 million ha of tropical Asia, America, and Africa, with an additional 500 million ha of degraded primary forest and secondary forest (ITTO 2002). Restoration efforts are needed to recover at least some of the functions and diversity of heavily degraded tropical forests. Restoration approaches vary widely in cost and intervention, depending on goals and expectations for particular recovery projects. The most popular approach to forest restoration is based on establishment of tree plantations, usually composed of single-species, to increase site fertility and catalyze the process of native forest succession (Fig. 3; Parrotta 1992; Lamb et al. 1997; Parrotta et al. 1997; Holl et al. 2000; Montagnini 2001). Shading by plantation species suppresses grasses and ferns that may impede initial tree colonization (Otsamo 2000; Ashton et al. 2001). Rapidly-growing tree species, particularly nitrogen-fixing legumes, can increase organic matter in the soil, prevent erosion, and enhance nutrient cycling (Montagnini & Sancho 1994).

Fig. 3. A 7-yr old plantation of the native commercial tree species *Vochysia guatemalensis* (Vochysiaceae) on former pasture land in northeastern Costa Rica. Landowners can obtain tax credits for establishment and maintenance of plantations of selected native and exotic tree species. Plantations have the potential to restore soil fertility and biodiversity, as well as providing sources of high-quality timber.

Plantation trees also serve a critical function in attracting seed-dispersing birds and bats to restoration areas (Parrotta 1995; Wunderle 1997; Holl et al. 2000). The species used in plantations are often exotic species that are widely available, with well-studied silvicultural characteristics, and readily established nursery stocks. Native species are becoming increasingly popular, as silvicultural and nursery techniques develop (Fig. 3). Lugo et al. (1993) showed that the number of native understory species in plantations increased over a 30-yr period at a constant rate, regardless of whether plantation species were native or exotic. After 50 years, understory species richness of a plantation of mahogany (*Swietenia macrophylla*, Meliaceae) in Luquillo Experimental Forest in Puerto Rico approached that of secondary forests of similar age under the same edaphic and climatic conditions (Lugo 1991).

Experimental studies are urgently needed to determine the best management practices to promote differ-ent recovery processes and to compare the effects of different tree species or species mixtures. Government incentives are a critical component of restoration efforts, especially if the management goal is to promote natural development of diverse secondary forest rather than to promote single-species plantations for harvesting (Castro et al. 2000). Incentives for protection of environmental services in forests and for reforestation are the cornerstone of Costa Rica's sustainable development strategy.

Conclusion: prospects for forest recovery in the face of human disturbance

We are far from an integrated view of forest recovery processes, yet some generalizations are beginning to emerge. Are there predictable aspects of forest recovery processes following anthropogenic and natural dis-

turbances? – One clear message is that severe disturbances that impact canopies, such as large-scale wind disturbances, often have relatively short-lived effects on forest structure and species composition. In contrast, disturbances that impact soils as well as aboveground vegetation, such as bulldozers, skidders, heavy grazing, and fires significantly slow down the rate of forest structural recovery and can have long-lasting effects on species composition. In extreme cases, intervention may be needed to restore species composition and soil fertility.

A second prediction that applies equally well to human and natural disturbances is that proximity of disturbed areas to remnant forest patches promotes more rapid recovery, particularly in species composition. The landscape matrix plays a critical role in local recovery processes (Fig. 2). A patch of bare soil or an area of heavily disturbed forest embedded in a matrix of structurally and compositionally intact forest has significantly improved options for recovery than a similar area surrounded by a matrix of agricultural land or heavily degraded forest. A third prediction is that the rate of successional recovery is constrained by soil fertility and texture across regions as well as across soil types within a region. Restoration of soil fertility may be a prerequisite for forest recovery on sites with severely degraded soils.

Do different ecological processes change at different rates? – Recovery of soil fertility is closely linked with recovery of aboveground biomass. In contrast, changes in species composition occur independently of changes in structural variables, and show far more long-lasting legacies of disturbance. At the landscape level, mature forests exhibit small-scale spatial heterogeneity in edaphic features, forest structure and species composition (Clark et al. 1996, 1999), so there is every reason to expect regenerating forests to develop heterogeneous spatial patterns over time. Yet studies of secondary forest regeneration are generally conducted in very small plots, so the larger-scale patterns are often missed. Herrera & Finegan (1997) document localized effects of soil fertility and topography on patterns of dominance of tree species in a secondary forest in Costa Rica. To assess adequately the changes in species composition in regenerating stands, we need to adopt rigorous sampling and analysis approaches that enable appropriate comparisons with heterogeneous mature forest areas (Vandermeer et al. 2000; Gotelli & Colwell 2001).

Can stand-level recovery processes be used to predict landscape level changes in ecosystem function and species composition? – Conditions that constrain stand-level recovery processes, such as low soil fertility, also appear to constrain landscape-level patterns, suggesting that we may be able to predict landscape-level rates of recovery, particularly for assessments of aboveground biomass (Moorcroft et al. 2001). Landscape-level patterns of species composition are far more challenging to scale-up from stand-level patterns, however, due to patchiness of species distributions, unpredictable distributions of rare species, turnover of species richness along gradients, and the presence of biodiversity 'refugia' within landscapes (Palmer & Dixon 1990). These questions deserve far more concentrated research efforts.

The distinction between anthropogenic and natural disturbances is very blurred. Increasingly, we are witnessing inextricable linkages between anthropogenic and natural disturbances. Forest recovery processes are therefore also inextricably linked. Droughts caused by ENSO events encourage the spread of fire from cultivated land into forests. Damage resulting from cyclones can be greater in plantations than in secondary forests of the same age (Fu et al. 1996). The tendency has been to consider natural disturbances as 'healthy' for the ecosystem, with a high potential for complete and rapid recovery. In contrast, disturbances due to human actions are generally considered 'detrimental' for forests, potentially resulting in deflected successions or altered successional pathways. More often than not, however, human and natural disturbances interact in complex ways to influence disturbance intensity and recovery processes.

Human interference can have positive impacts on many aspects of recovery and can also mitigate against effects of subsequent disturbance. Examples are the establishment of fire-breaks to prevent runaway forest fires (Nepstad et al. 2001), application of reduced-impact logging techniques (Davis 2000), and restoration of abandoned farmland to establish wildlife corridors and re-establish forests (Janzen 1988; Lamb et al. 1997; Kaiser 2001). We should feel encouraged by the realization that extensive areas of forests in Mesoamerica have seemingly recovered from widespread human intervention thousands to hundreds of years ago (Bush & Colinvaux 1994; Gómez-Pompa & Kaus 1999). Yet, as Bush & Colinvaux (1994) caution, "The prolonged existence and abrupt demise of the ancient cultivators of Darien show us that rain forest can survive sustained disturbance, but only when the disturbance is so constrained that massive local extinctions of rain forest species are prevented."

Today's forests face new and more recurrent threats than ever before. Between 1990 and 2000, 10 million ha of regenerating forest were documented in the world's tropics compared to 142 million ha of forest conversion to non-forest land use (FAO 2001). Thus, for every hectare of naturally recovering forest in the tropics, 14.2 hectares of forest are being destroyed. Hopefully this balance will shift in the coming decade.

Many degraded areas are in need of deliberate management to speed recovery. Humans need to develop partnerships with forests to ensure a future world with diverse tropical forests that conserve biodiversity while providing essential ecosystem services and products. Thus, our future is inexorably bound to the future recovery of tropical forests.

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