The Ecology and Conservation of Seasonally Dry Forests in Asia

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The Role of Disturbance in Seasonally Dry Tropical Forest Landscapes

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*D*isturbance can be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). This definition requires that the spatial and temporal scales of the system and disturbance be determined. Disturbances are typically characterized by their size, spatial distribution, frequency or return time, predictability, and magnitude (which includes both intensity and severity; White and Pickett 1985). These disturbance attributes set the parameters for the suite of species, both plant and animal, that can persist within a given system. As such, an understanding of seasonally dry tropical forests in Asia requires an understanding of disturbance within the region. However, disturbances are relatively poorly understood in dry topical forests, partly because of the weak seasonality in temperature and high tree species diversity of these forests relative to most forest systems of the world (Huete et al. 2008).

Miles et al. (2006) report that there are about 1,048,700 km² of dry tropical forest worldwide and that only 3 percent of this land is in conservation status. In other words, 97 percent of the world's seasonally dry tropical forest is at risk of human disturbance. About half of this forest occurs in South America, where most of the conservation lands are located. Satellite imagery based on MODIS (Moderate Resolution Imaging Spectroradiometer) data shows that only about 3.8 percent of the world's dry tropical forests are in Australia and Southeast Asia (Miles et al. 2006). The susceptibility of these forests to human disturbances is of great concern and is largely unstudied. Because natural disturbance regimes shape the ecosystem structure and are in many ways integral to these forest systems, it is critical to know how natural disturbance affects dry forest in order to understand the effects of human activities on these forests. Even basic information about disturbances in dry tropical forests is only recently available. Therefore this chapter brings together much of the available information from dry tropical forest throughout the world with the goal of developing an understanding of the role of disturbance in Asian dry forests.

Most ecologists now recognize that disturbances, rather than being catastrophic agents of destruction, are a normal, perhaps even an integral, part of long-term system

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dynamics (Weatherhead 1986; Lugo et al. 2006; Imbert and Portecop 2008). The composition, structure, organization, and developmental and trophic dynamics of most forest systems are the products of disturbances (Denslow 1980; Leach and Givnish 1996; Lugo and Scatena 1996; Wootton et al. 1996; Werneck and Franceschinelli 2004; Kennard and Putz 2005; Otterstrom et al. 2006; Chazdon et al. 2007; Urquiza-Haas et al. 2007; Alvarez-Yepiz et al. 2008; Arredondo-Leon et al. 2008; Sahu et al. 2008; Mehta et al. 2008a, 2008b; Poorter et al. 2008; Anitha et al. 2009; Sapkota et al. 2009; Zimmer and P. Baker 2009). For example, Anitha et al. (2009) compared forest composition for two disturbances in the Anaikatty Hills of Western Ghats, where the low disturbance was from past logging followed by cutting and illicit felling and grazing and the high disturbance was due to human presence, past logging, and fuelwood collection. They found higher species richness and Shannon-Wiener diversity index for the low-disturbance forest (98 and 3.9, respectively) compared to the high-disturbance stand (45 and 2.71, respectively) as well as significant differences in mean basal area of trees, density of seedlings, number of species, density and diversity of shrubs, and number of species and diversity of herbs.

Some ecological systems contain species that have evolved in response to disturbances. Adaptations typical of dry tropical forest plants are drought tolerance, seed dispersal mechanisms, and the ability to sprout subsequent to disturbance (see Kozlowski and Pallardy 2002; Otterstrom et al. 2006). In contrast, Farwig et al. (2008) found evidence that human disturbance in Kakamega Forest of western Kenya has significantly reduced allelic richness and heterozygosity, increased inbreeding, and slightly reduced gene flow in *Prunus africana* in the past century.

DISTURBANCE SCALE, DISTRIBUTION, FREQUENCY, AND MAGNITUDE

The scale of disturbance can vary from those disturbances larger than typical management activities (e.g., large-scale fires or hurricanes) to those at the microscale (e.g., collection of firewood in a locale). Martini et al. (2008) studied patterns of tree mortality and damage in an old-growth, semi-deciduous seasonal forest at the Caetetus Ecological Station, southeastern Brazil. Of the 743 disturbance events recorded, 650 involved the demise of entire trees (33 percent uprooted, 28 percent dead-standing, 26.5 percent snapped, 10.5 percent inclined, and 2 percent complex events) while 93 involved only parts of trees (60.2 percent branch-falls and 39.8 percent stem-fall from multi-stemmed trees). The most abundant trees in the area experienced much resprouting, suggesting that this ability increases the competitive potential of these species, especially in forests with high disturbance rates.

Sapkota et al. (2009) found that the spatial distribution, advanced regeneration, and stand structure of *Shorea robusta*–dominated forests in five seasonally dry deciduous sal forests in the Nawalparansi district of Nepal were influenced by disturbance intensity. The most disturbed forest plots had less tree species richness in the more-disturbed plots, greater density of saplings (trees with less than 1.5 cm diameter at breast height [dbh]), and no significant difference in stem basal area. The overall stand

density changed quadratically across the disturbance gradient, with moderate disturbance intensity not only ensuring high stand density but also enhancing the advanced regeneration of socioeconomically important tree species and affecting their dispersion patterns. The study recorded 67 tree species in the forest plots, with 41 species in the least disturbed forests and only 10 species in the most heavily disturbed forests. Ten species varied in their dispersion patterns across the disturbance gradient, and yet most of the socioeconomically important tree species considered had little or no regeneration in both the least and most heavily disturbed forests. In addition, select species had unique responses to disturbance ranging from "tolerant" (*Shorea robusta*, *Lagerstroemia parviflora*, and *Symplocos* spp.) to "sensitive" (*Trewia nudiflora*, *Adina cardifolia*, and *Terminalia alata*).

Sahu et al. (2008) also documented that tree density, diversity, and structure at forty-two sites in the Achanakmar-Amarkantak Biosphere Reserve of central India responded to anthropogenic disturbance. The number of species and indices of species diversity were positively associated with copicing and also with total disturbance (which included foot trails and dung piles as evidence of livestock grazing).

Even though epiphytic assemblages are a notable part of these ecosystems, existing information on how epiphytes are affected by different degrees of human disturbance, and what drives their recovery, is limited or region-specific. Yet a recent study by Werner and Gradstein (2009) in northern Ecuador focused on how sensitive these plants, especially bryophytes, are to changes in relative humidity, which are often associated with disturbance events. They found that the density of bryophytes species was significantly lower in edge habitat and on isolated trees than in closed forest, in contrast to species of vascular epiphytes, which did not change between habitat types.

The intensity of disturbances can be large enough to set the system back to an earlier stage in its developmental sequence or to initiate a different seral pathway. However, very intense disturbances are rare (Turner et al. 1997). Other disturbances may be so small in intensity, or common in time or space (or both), that some managers may consider them to be a part of the natural functioning of the system (see Werner and Gradstein 2009).

Disturbance magnitude has two attributes: intensity, which refers to the physical force of the event on a per area basis, and severity, which refers to the impact on an organism, community, or ecosystem. Severity measures the extent to which the pre-disturbance vegetation is damaged and ecosystem properties are disrupted. Vegetation at a site will often reestablish more slowly after a severe disturbance than after a mild disturbance (Turner et al. 1998). Human activities, the landscape context, and site fertility typically greatly influence vegetation reestablishment after a disturbance to dry topical forests (as Velazquez and Gomez-Sal [2008] documented subsequent to a landslide in Nicaragua). However, severity can also be measured as an effect on ecosystem function. A disturbance may affect soil properties and long-term nutrient dynamics. In one such case, Bormann and Likens (1979) found that a severe disturbance resulted in such substantial erosion and nutrient losses that the ecosystem might require decades to recover its key properties.

Both spatial and temporal regimes of disturbances can vary greatly (Tilman 1989), and direct measurement of the effects of broad-scale disturbances on these forests are

quite difficult and rarely done (but see P. Baker et al., 2005). Yet Vieira and de Carvalho (2008) found that high genetic diversity of *Protium spruceanum* correlates with the diversity of the forest fragments that occurs in the vegetation corridors that connect small remnants of undisturbed primary forest in the Lavras landscape in Brazil. Furthermore, evidence of recent bottlenecks by anthropogenic disturbance was also detected in these fragments. Thus Vieira and de Carvalho found high levels of gene diversity in the vegetation corridors and absence of any inbreeding. Given that they also found bottlenecks in landscape patterns, these corridors provide a high potential for in situ genetic conservation and for seed collection destined to restore degraded areas. These results suggest that landscape management strategies should both create new vegetation corridors and manage the protection of existing ones.

TYPES OF DISTURBANCE

Fire

The frequency, size, intensity, seasonality, and type of fires depend on weather and climate in addition to forest structure and composition. Fires are such an integral part of many seasonally dry tropical forest systems that some managers do not consider them a disturbance at all. Fire initiation and spread depend on the amount and frequency of precipitation, the presence of ignition agents, and conditions (e.g., lightning, fuel availability, forest distribution, topography, temperature, relative humidity, and wind velocity; Janssens 2000).

Fire effects on dry tropical forests include acceleration of nutrient cycling, mortality of individual trees, shifts in successional direction, induced seed germination, loss of soil seed bank, increased landscape heterogeneity, alteration of surface-soil organic layers, changes in underground plant-root and reproductive tissues, and volatilization of soil nutrients (Whelan 1995). Erosion can occur where soil disturbance accompanies fire (e.g., during fire fighting or timber salvage operations). Fire affects forest value for wildlife habitat, timber, and recreation; and through smoke, it affects human health (Moreno 2006).

The spatial and temporal heterogeneity created by fire is important to ungulates that occupy these forests (McShea and Baker, this volume). Although fires are not the prime cause of local extirpation of any plant species, the spatial heterogeneity created by fires in dry tropical forests over time is critical to providing habitat for the diverse animals that occur in these dry tropical forests (e.g., elephants and tigers; Fernando and Leimgruber, this volume; Smith et al., this volume).

Fire was found to have a strong effect on bamboo distribution in the tropical seasonal mixed deciduous forest of the Mae Klong Watershed Research Station in Kanchanaburi Province of western Thailand (Marod et al. 1999). Mortality was size dependent, with middle-sized trees (30–50 cm) having the lowest mortality and smallest trees (5–10 cm) having the highest mortality. Tree recruitment was mostly in the area where dieback of undergrowth bamboo occurred. Hence "both the fire disturbance regime and bamboo life-cycle greatly influence the structure and dynamics of this seasonal tropical forest" (Marod et al. 1999).

The rapid response of fire regimes to changes in climate (Flannigan et al. 1998, 2000; Stocks et al. 1998) can potentially overshadow the direct effects of climate change on species distribution and migration. Modeling results predict great variation in future fire-weather patterns. Some fire-history studies suggest that the frequency of fire might decrease despite warmer temperatures because of increased precipitation (see Bergeron and Archambault 1993). In a study of northeastern Cambodia, Maxwell (2004) determined that the greatest fire activity ended about 8,000 years ago, and the subsequent period experienced low levels of fire and a strong summer monsoon. There was then an increase in forest disturbance, and fire activity increased, commencing about 5,500 years ago. A small change in the record occurred about 3,500 years ago, and more marked change occurred about 2,500 years ago when fire frequency, and maybe human control over fire, became more important. It is difficult to extrapolate for all of Asia using this one study or to determine the long-term human impacts from burning. Nevertheless, Maxwell (2004) found that current charcoal input from fire activity is one of the lowest of the past 9,300 years. He suggests that "anthropogenic fire is an adaptation to the monsoonal environment."

Because fire is a frequent disturbance in the seasonally dry tropical forests of Central America, Otterstrom et al. (2006) conducted an experimental burn in a tropical dry forest of western Nicaragua to evaluate plant survivorship and recruitment. They found that the most common dry forest species are fire tolerant, for these species had high survivor rates or used seeding or sprouting as an alternative for persistence in the forest system. This phenomenon also occurs in Jamaica (McLaren et al. 2005). In addition, mechanisms for seed dispersal, particularly via wind, were important for recruitment success after the fire.

Aguilar-Fernandez et al. (2009) report that rates of land conversion from forest to cultivated land by slash-and-burn practices are higher in tropical dry forest than in any other neotropical forest type. The short-term consequences of the slash-and-burn process on arbuscular mycorrhizal fungi were that infective propagules were reduced in pasture plots during the first year after slash-and-burn, whereas spore abundance and intraradical colonization remained similar in forest and pasture plots over two years (Aguilar-Fernandez et al. 2009). These results suggest that forest conversion via slash-and-burn, followed by cultivation, resulted in few immediate changes in the arbuscular mycorrhizal fungi communities, likely because of the low heat conductivity of the soil and rapid combustion of plant residues (Aguilar-Fernandez et al. 2009).

Kennard and Putz (2005) monitored tree establishment and growth response to canopy opening, aboveground biomass removal, and experimental burns of low and high intensities in a lowland dry forest in Bolivia. Shade-intolerant species reestablished mostly from seed and had the highest survival and growth rates following high-intensity burns. Shade-tolerant species were abundant in gap control and plant removal treatments and showed little difference between the treatments in height growth. Trees with the ability to sprout roots were most abundant following plant removal and low-intensity burn treatments. This variety of regeneration strategies likely facilitates recovery from the diversity of disturbances to which these forests can be exposed.

Drought

Droughts occur in nearly all forest ecosystems. Extreme drought effects are influenced by soil texture and depth, exposure, species present, life stage, and the frequency, duration, and severity of the drought. Seasonally dry tropical forests are largely water limited; and in areas of forest disturbance, carbon fluxes respond more to seasonal water availability than to availability of sunlight (Huete et al. 2008). The primary immediate response of forests to drought is to reduce net primary production (NPP) and water use; both reductions are driven by reduced soil moisture and stomatal conductance. Under severe conditions, plants die. Small plants, such as seedlings and saplings, are usually the first to die and can succumb under moderate conditions. Deep rooting and stored carbohydrates and nutrients make large trees susceptible only to severe droughts. Secondary effects also occur. When reductions in NPP are extreme or sustained over multiple growing seasons, increased susceptibility to insects or disease is possible, especially in dense stands (see Negron 1998). Drought can also reduce decomposition processes and thus slow down the nutrient cycling process. However, reduced decomposition can also lead to a buildup of organic matter on the forest floor that may increase fire frequency or intensity, which thereby enhances nutrient cycling. Brandeis and Woodall (2008) found that forest litter decreased from wetter to drier forest life zones in tropical forests of Puerto Rico and the U.S. Virgin Islands. In addition, when compared to continental tropical forests, the island forests had fewer coarse woody fuels (2.91 Mg/ha) and relatively greater quantities of smaller-sized fine woody fuels (10.18 Mg/ha and 10.82 Mg/ha for duff and litter, respectively). These data suggest that continued decomposition of coarse woody debris from a previous hurricane is balanced by increasing inputs of fine woody debris from recovering and maturing secondary forest (Brandeis and Woodall 2008).

The consequences of drought depend on annual and seasonal climate changes and whether the current drought adaptations offer resistance and resilience to new conditions (Hanson and Weltzin 2000). Forests tend to grow to a level of maximum leaf area that almost fully uses soil water during the growing season (Neilson and Drapek 1998). A small increase in growing-season temperature could increase evaporative demand, triggering moisture stress.

Diversity in the lowland mixed dipterocarp forest at Lambir Hills National Park in Sarawak, East Malaysia, may have been enhanced by the 1998 drought (Potts 2003). The Lambir Hills forest is likely one of the richest forests in terms of tree species diversity left in the Old World. This is an area that experiences droughts almost every year, but the severity of the 1998 drought was on the order of once in every century (Nakagawa et al. 2000). Stem mortality was higher during this severe drought when compared to the pre-drought period, regardless of tree size or soil type. Smaller trees and large common trees experienced higher mortality, whereas the mortality of large rare trees did not differ significantly from other years (because of the small sample size; Potts 2003). Some species are more drought-mortality prone at maturity than others. In the middle of the Lambir forest, frequent slight droughts on deep sandy soils are associated with a diffuse but highly structured canopy supporting abundant but clumped emergent trees less than 70 m tall (Ashton and Hall 1992). Potts (2003) postulates that

extreme droughts enhance diversity via greater mortality of large trees and taxonomic differences in rates of mortality.

Windstorms

Scale and frequency of disturbance have profound impacts on the dynamics and composition of flora and fauna in wet tropical forests (Ashton and Hall 1992), but their role in seasonally dry forests is unknown outside of the Caribbean and Central America. In a study subsequent to Hurricane George's striking Puerto Rico, Van Bloem et al. (2005) found that hurricane-induced mortality of large trees was significant enough that the low, dense structure of Caribbean dry forest could be maintained by hurricane damage to larger stems. Furthermore, the dry forest trees of the Caribbean sprout near the base following hurricane disturbance even if the trees have not incurred structural damage (Van Bloem et al. 2006). Even though the density and proportion of surviving stems decreased over the ensuing seven-year period, the sprouting rate was still three times higher and the proportion of sprouting stems five times higher than before the hurricane (Van Bloem et al. 2007). Mortality of sprouting and non-sprouting stems was similar (13.9 percent and 15.4 percent) after seven years. These results demonstrate that, despite some thinning, hurricane-induced sprouts survive to influence the structural characteristics of Caribbean dry forests long after the hurricane disturbance (Van Bloem et al. 2007).

Forest structure itself is often a result of wind disturbance in these seasonally dry tropical systems. Lugo et al. (2006) report that the low floristic diversity and stature and high density of small- and medium-sized trees of Antillean dry forests are a result of periodic hurricanes, anthropogenic disturbance, and the fact that most of these forests occur on limestone substrate, which induces water stress and nutrient limitations. A great diversity of life forms, high resistance to wind, a high proportion of root biomass, high soil carbon and nutrient accumulation below ground, the ability of most tree species to resprout, and their high nutrient-use efficiency allow the plants to survive the stressful environment (Lugo et al. 2006). These attributes also make them resilient to disturbance (Lugo et al. 2006). On the other hand, the forests become less resilient and species invasion occurs subsequent to opening the canopy, eroding the soil, and removing root biomass (Lugo et al. 2006).

EFFECTS OF FOREST DISTURBANCES ON ANIMALS

Studies are limited (but see McShea and Baker, this volume; Bhumpakphan and McShea, this volume), but there is compelling evidence that animals respond strongly to disturbances in seasonally dry tropical forests. Sanchez et al. (2007) report a low abundance of bats in Patia, Columbia, compared to nearby dry tropical forest, which the authors relate to human disturbance. Also, two ground-dwelling sympatric couas species that occupy the dry forest of Madagascar are insectivores that feed at ground level but differ in size, and logging affects their foraging via changing their ability to climb in the vegetation (Chouteau 2009). Furthermore, the two species responded

differentially to burning, likely because of changes in microhabitat variables relating to the foraging sites of the two species as related to stem density, understory vegetation, cover, and prey detectability (Choutaeu 2007).

Andresen (2005) documented the effects of both rainfall seasonality and forest structure on the dung beetle community of a Mexican tropical dry forest. This study supports the concept idea that dung beetle communities are useful bioindicators of habitat disturbance for dry tropical forest, as already has been observed in tropical rain forests.

Zelikova and Breed (2008) measured how ant communities affect seed removals and seed dispersal distances for *Acacia collinsii* and papaya seeds in tropical dry forests of Guanacaste Province, Costa Rica, to determine if habitat disturbance affects ant community composition and associated interactions between ants and seeds. The forests differed with regard to land-use and disturbance history. Habitat disturbance affected the ant community and the relative abundance of key seed-dispersing ant species, with consequential effects on seed removals and seed dispersal distances.

Furthermore, Achury et al. (2008) found that disturbance increases the probability of dominance by the little fire ant, *Wasmannia auropunctata* (Formicidae: Myrmicinae), an indicator species of low-diversity ant communities in tropical dry forest fragments of the Cauca River Valley, Colombia. At each of four locations, three biotopes were distinguished: forest interior, forest margin, and the surrounding matrices (sugar cane or pasture). Competition ability indices were calculated for the 66 ant species in 30 genera that were attracted to bait traps. Ant species composition was found to be primarily influenced by disturbance conditions.

Suaz-Ortuno et al. (2008) documented impacts of forest conversion to agricultural mosaic on 18 anuran, 18 lizard, 23 snake, and 3 turtle species assemblages of neotropical dry forests. The assemblages each responded differently to disturbance. The species richness, diversity, and abundance of lizards were higher in disturbed forests. Anuran diversity and species richness were lower in disturbed forest, and abundance was similar in both disturbance types. The diversity, richness, and abundance of turtles were lower in disturbed forests, whereas the structure and composition of snake assemblages did not differ between forest conditions.

Finally, Suaz-Ortuno et al. (2007) examined the diet of the marbled toad (*Bufo marmoreus*) in conserved and disturbed tropical dry forest on the coast of Jalisco, Mexico. During 2000 and 2001, toads in the conserved area consumed greater proportions of ants (36.7 percent by volume), whereas toads in disturbed forest consumed greater proportions of beetles (53.1 percent by volume). Furthermore, the diversity of diet was significantly lower in the disturbed area. However, prey availability was not affected by disturbance because the abundance, size, and weight of the toads were similar in both areas.

EFFECTS OF DISTURBANCE ON ECOSYSTEMS

Disturbances, both human-induced and natural, shape forest systems by influencing their composition, structure, and functional processes. Indeed, forests throughout the world are molded by their land-use and disturbance history. Natural disturbances

having the greatest effects on forests include fire, drought, introduced species, insect and pathogen outbreaks, hurricanes and monsoons and other wind storms, landslides, and volcanoes (Dale et al. 1998). Each disturbance affects forests differently. Large disturbances such as hurricanes can result in massive tree mortality (see Van Bloem et al. 2005; Imbert and Portecop 2008), and most disturbances to dry tropical forests affect tree-size distribution (see Poorter et al. 2008; Chazdon et al. 2007).

Forest disturbance in seasonally dry tropical forests can lead to changes in ecosystem properties. In areas of forest disturbance of monsoon Asia, carbon fluxes closely track seasonal water availability (Huete et al. 2008). In addition, dipterocarp rain forest in southwest China, which has a species composition similar to that of forests in tropical Asia, has higher seed storage subsequent to intense disturbance and forest fragmentation (Tang et al. 2006). As another example, Sagar and Singh (2005) studied the impact of disturbance on the diversity patterns, forest structure, and regeneration of tree species in the Vindhyan dry tropical forests of India based on more than 1,500 quadrats spread over five sites that varied in disturbance level. Alpha diversity increased with decreasing disturbance intensity. Both the level of disturbance and the nature of the species strongly affect regeneration (as revealed in the regression analysis).

Forest disturbances influence how much carbon is stored in trees, dead wood, and soils. Abril et al. (2005) examined soil balance (CO_2 production as affected by soil and litter organic carbon) in areas under varying degrees of disturbance by overgrazing and fire in the Dry Chaco woodland, Argentina. Under undisturbed conditions, soil carbon was relatively constant throughout the year (range: 23–24 g/kg), whereas both burned and grazed sites experienced carbon values fluctuating markedly (range: 21–31 g/kg). In non-grazed, burned areas, soil carbon content increased 16 percent, whereas at burned and overgrazed sites, it decreased 38 percent. Hence overgrazing has a more-significant, adverse effect on soil carbon balance than does fire when both factors act separately. The apparent reason for this pattern is that burned but non-grazed areas appear to slowly recover their initial carbon balance, whereas in chronically overgrazed sites there is a tendency to permanent carbon loss.

Human disturbance of dry tropical forests can be intense. Between 1880 and 1980, the area of cultivated land increased by 106 M ha in South and Southeast Asia (Richards and Flint 1994). Human population density and livestock density in these forest systems have also tripled in the past century (Table 1). Yet because of the uncertainty of estimating carbon storage and forest density both in 1880 and for recent times, the exact magnitude of these changes is not entirely apparent (Table 2). Even so, there have been strong declines in carbon storage over thirteen countries in South and Southeast Asia (Flint and Richards 1994) during the past century. Combined with natural disturbances, these human-induced changes have greatly altered the ecosystem services provided by seasonally dry tropical forests in Asia. Furthermore, the changes in human population over recent decades have been even greater than in the past (Table 1), but their effects on livestock density, forest area, and carbon content are not recorded in a way that allows comparisons to estimates over the past century. Even so, the decline in forest carbon content and forest area is undoubtedly increasing—likely at a steep rate.

A critical effect of disturbances in dry tropical forest is change in water flow. Bruijnzeel (2004) found that in Southeast Asia the effects of forest disturbance and

Table 1. Estimated human and livestock densities and total populations for 13 South Asian nations (India, Bangladesh, Sri Lanka, Myanmar, Thailand, Cambodia, Laos, Vietnam, Malaysia, Brunei, Singapore, Indonesia, and the Philippines). Countries have a total area of 791.3 million ha.

Attribute	Year				
	1880	1920	1950	1980	2008
Human population density (millions/ha)	0.39	0.50	0.74	1.44	4.93
Livestock density in natural vegetation (millions/ha)	0.37	0.47	0.66	1.04	2.56
Total human population (millions)	310.4	397.3	589.3	1,140.5	3,908.2
Total livestock population (in natural vegetation, millions)	221.1	271.1	360.4	507.9	731.9

Source: Richards and Flint (1994) for 1880–1980; United Nations estimates for 2008.

Table 2. Carbon in the vegetation and soils of seasonally dry tropical forests.

Attribute	Value
Area of forest[a] (ha; in millions)	31
Carbon in vegetation[b] (tC/ha)	
High estimate	60
Low estimate	40
Carbon in soils[b] (tC/ha)	50
Estimated biomass density for undisturbed seasonally dry forests of tropical Asia[c] (Mg/ha)	
Ecologically based estimates from global land-use models:	
Potential biomass	120
Model projections for 1880	97
Model projection for 1980	84
Geographic information system—based estimates:	
Potential biomass	215
Model projections for 1880	150
Model projection for 1980	80

Note: Based on information in Houghton and Hackler (1994).
[a]Houghton et al. 1985, 1987; Palm et al. 1986.
[b]Food and Agriculture Organization / United Nations Environment Programme 1981.
[c]Dale et al. 1994.

conversion from undisturbed to disturbed forest on rainfall infiltration and subsequent water flow are less than those for conversion from forest to grassland because, after disturbance, the radiative properties of the secondary forest are similar to those of the original forest. Actual amounts of annual water yield differ between sites and years because of differences in rainfall and degree of surface disturbance, with the greatest yield associated with complete forest clearing. However, with limited surface disturbance, most increases in water yield occurs at times of low flows, and if groundwater reserves are not replenished during the wet season, declines in dry-season flows may be extreme. Bruijnzeel's survey (2004) of more than sixty catchment sediment yield studies from Southeast Asia demonstrates the significant effects of common forest disturbances, such as selective logging and clearing for agriculture, plantation creation, urbanization, mining, and road construction. He finds that the "low-flow problem"

is a critical watershed issue that requires further research to address the time delay between upland soil conservation measures and potential changes in downstream sediment yield, particularly at increasing distances from the disturbance. The net effect on forests of changes in water storage include the potential for vegetation dieback and species shifts, although the high diversity in these tropical dry forests means that disturbances are not a key factor in maintaining alpha diversity (Leigh et al. 2004).

In contrast, however, sal (*Shorea robusta* Gaertn. f.) forest occurs in Nepal as part of dry deciduous systems typical at elevations of less than 1,000 m. Webb and Sah (2003) found that the disturbance associated with forest management and regeneration of the sal forest in Nepal resulted in a severe decline in botanical diversity and robust regeneration of *Shorea*. Even though total tree density was high, all species except *S. robusta* declined in abundance in managed forest after twenty years of protected regeneration. Although successional sal forest recovered most of its species richness in twenty years, most tree species were in lower abundances. Thus Webb and Sah (2003) call for a full analysis of forest "value" to establish optimal land-use practices. It should be noted that rainfall and past disturbances (fire and anthropogenic use) are mainly responsible for different community types of sal forest in lowland Nepal.

Virtually all dry tropical forests, whether at stand or regional scale, are in some state of seral succession because of more or less occasional landscape-scale catastrophes (Ashton 1993). Sagar et al. (2003) found that the disturbance gradient explained both tree diversity and density in a dry tropical forest in India. They compared community composition and species diversity of the understory vegetation among five dry tropical forest sites in northern India using data from 1,500 quadrats distributed over 15 one-ha permanent plots differing in degree of disturbance. Both human disturbance intensity as well overall disturbance regimes combined with the soil's water-holding capacity to explain understory composition and organization. Understory species diversity decreased with increasing human disturbance intensity, reflecting utilization pressure and decreased soil fertility. The high correlation between overstory and understory tree diversity suggests that understory trees may soon replace the overstory.

Most landscapes are a mosaic of historical catastrophic events, which create a diversity of tree ages and species and follow the intermediate disturbance hypothesis that local species diversity is at a maximum at an intermediate level of disturbance (Connell 1979). Bongers et al. (2009) tested this hypothesis in tropical forests using data from 2,504 one-ha plots and found that it explains more variation in the diversity of seasonally dry rather than wet tropical forests because early-successional species diversity increases with disturbance, shade-tolerant species decrease in number, and intermediate species diversity does not change. In summary, Connell (1979) is right: intermediate disturbance (toward but not at the low end) favors tree species diversity and, therefore, insect, microorganism, and overall biodiversity.

CLIMATE INFLUENCES ON FOREST DISTURBANCES

Forest disturbances are influenced by climate and in some cases might be exacerbated by climate change. The effects on each type of disturbance are partly tempered by prior

adaptations. The species present in a dry tropical forest often reflect past disturbances. Drought-prone sites typically support species that survive well under dry conditions with variable rates of annual rainfall. Thus, if climate change alters the distribution, extent, frequency, or intensity of any of these disturbances, large impacts (such as loss of species regeneration) could be expected. The effects on species or communities already at the margin of their range may be particularly severe. For example, a synergistic convergence of climatic, technological, and socioeconomic factors explains the loss of the dry tropical Chaco forests of central Argentina (Zak et al. 2008). During the past three decades of the twentieth century, about 80 percent of an area that was originally undisturbed forest became occupied by crops, pastures, and secondary scrub.

As another example, Poorter et al. (2008) compared size distribution of tree species in forty-four Ghanaian tropical forest communities based on data from 880 one-ha plots and more than 118,000 trees of 210 species. The variation in the size distribution of these forest species is continuous and log-normal and related to both rainfall and disturbance. Size distributions in dry forests were more skewed than those in wet forests, with more tall species and a wider height range.

Finally, analysis of palaeoecological records for the Amazon by Mayle and Power (2008) suggests the forests in most of Amazonia appear to have been resilient to climatic conditions that were significantly drier than they are today, even though there is widespread evidence of forest burning. The authors surmise that the great spatial and temporal variation in patterns of vegetation disturbance and fire in the Amazon Basin likely reflect complex heterogeneity in precipitation and seasonality patterns across the basin, as well as interactions among climate change, drought and fire susceptibility of the forests, and Palaeo-Indian land use.

INTERACTIONS AMONG DISTURBANCES

Many disturbances are cascading. Drought often weakens tree vigor, leading to insect infestations, disease, or fire. Insect infestations and disease promote future fires by increasing fuel loads, and fires promote future infestations by compromising tree defenses. Increased fire intensity or extent can enhance the potential for landslides. Also, changes in land use, forest management, and atmospheric chemistry can interact with these natural disturbances. Agriculture and road establishment in landslide-prone areas, coupled with increased wetness, can result in more landslides. In some cases, however, a combination of disturbances may ameliorate impacts. Under drought-prone conditions, stomata tend to close, reducing the effects of high ozone exposure.

Zimmer and P. Baker (2009) found statistical evidence of synchronous recruitment at stand and site scale, but not at a regional scale, for seasonal tropical pine forests of northern Thailand. Recruitment success was often related to favorable climatic conditions, such as multiyear periods of cool and wet dry seasons. Nevertheless, there are clearly complex interactions among local disturbance history, regional climate variability, and pine recruitment (Zimmer and P. Baker 2009).

When ecosystems experience more than one disturbance, the compounded effects can lead to new ecological states (Paine et al. 1998). A new ecological state is entered

when the system has not recovered from the first disturbance before a second perturbation occurs, leading the system to a new long-term condition. For instance, a combination of climatically driven wildfires, fragmentation caused by agricultural settlement, and logging often results in significant and unprecedented changes in forest composition (see Weir 1996). Invasive nonnative species are sometimes able to modify existing disturbance regimes or introduce entirely new disturbances (Mack and D'Antonio 1998). Under climate change, these compounded interactions may be unprecedented and unpredictable. They are likely to appear slowly and be difficult to detect because trees live for so long.

Some disturbances can be a function of both natural and human conditions. On the slopes of the Javan volcanoes of Indonesia, where disturbances are endemic, people opportunistically grow crops in response to volcanic activity and El Niño–related forest fires or longer climatic anomalies, while land degradation from state-organized deforestation is often buried by new volcanic activity (Lavigne and Gunnell 2006). Such responses are also seen in Latin American dry forests that lie in the shadow of volcanoes.

At the current time, a human disturbance to dry tropical forests that appears to be on the rise is the establishment of bioenergy crops in areas that were previously forests (Lim 2001). It is not clear from remote-sensing studies how much forest degradation or clearing occurred prior to the establishment of the bioenergy crops. In some cases it may be that establishment of commercial perennial bioenergy crops on land that had previously been used for slash-and-burn agriculture may actually provide a sustainable lifestyle that effectively reduces pressure for deforestation (Kline and Dale 2008). Developing policies that reduce pressure for forest degradation or clearing requires a broad-scale perspective and consideration of the role of the diversity of human activities and forest-ecosystem benefits. As an example, Urquiza-Haas et al. (2007) assessed the effects of combined disturbances on forest basal area, stand-level wood specific gravity, and aboveground biomass of forests of the Yucatan, where the predominant land use is still slash-and-burn agriculture. Intensive logging and fire reduced aboveground biomass in late-successional plots (30–50 years) by 36 percent and 37 percent, respectively.

In addition, Imbert and Portecop (2008) studied forest recovery in old-growth dry forest subsequent to Hurricane Hugo on the calcareous island of Grande-Terre, Guadeloupe, which has experienced several centuries of anthropogenic disturbances, as well as natural, catastrophic disturbances such as hurricanes. The authors measured floristic composition, litterfall, stem density, basal area, and tree growth for trees ≥ 10 cm dbh in a set of 2,400 m^2 permanent inventory plots from 1987 to 1998. The hurricane disturbance in these dry forests affected the forest structure on a longer time-scale than the functioning of the forest ecosystem.

The effects of livestock grazing, fuelwood extraction, and burning on vegetation in Bandipur National Park in southern India were analyzed using data from two hundred sites in four watersheds spanning a degradation gradient (Mehta et al. 2008). Vegetation plot height, canopy cover, and tree diameter were negatively correlated with field disturbance, resulting in stunted forest stature in degraded sites. Vegetation composition in degraded watersheds was dominated by small-stature woody tree species and a greater diversity of shrub species.

Laurance et al. (2006) report that even moderate hunting pressure can markedly alter the structure of mammal communities in central Africa, based on the authors' studies in southern Gabon. Roads also reduced the abundance of some species, with avoidance of roads being stronger where hunting was permitted outside wildlife reserves.

MANAGEMENT NEEDS RELATED TO DISTURBANCES

Management plans need to include the potential for disturbances. Infrequent disturbances may not be included in planning because people's perceptions are most influenced by what has occurred during their lifetimes (Christensen et al. 1989). Management goals typically do not consider what aims are appropriate in the face of disturbance, but they should identify the components, time frame, and spatial resolution needed to achieve specific goals (Rogers 1997).

The realization of the integral nature of disturbance alters the way we consider management of disturbance-prone systems in that both disturbances and their management are often part of the overall management system rather than a result and response subsequent to a particular disturbance. Sagar and Singh (2006) documented the relationships between forest basal area and diversity components (number of species and evenness) for a disturbed dry tropical forest of northern India. Recurring disturbances concentrated biomass or stems in only a few strong competitors. The conservation activities the authors deemed to be important were management of fuelwood plantations near human settlements, deferred grazing, and canopy enrichment through multispecies plantations of desirable species within the forest patches of low basal area. As might be expected, small, frequent disturbances are easier to study, understand, and incorporate into planning and management than are large or infrequent disturbances. Aspects of silviculture are designed to replicate small disturbances in forests, yet large disturbances are seldom a part of forest management plans (W. Baker 1992).

When disturbances do occur, they may trigger large departures from average events, and these changes can result in an outcry from the media and the public for immediate and costly action to quickly return the situation to seemingly normal conditions (Schullery 1989). Yet the costs and benefits of management actions are assessed at relatively small temporal and spatial scales. Planning for response to disturbances typically does not consider the length of time or full cost required for repair to occur naturally (Dale et al. 1998).

For management purposes, the conditions that lead to or result from disturbances need to be understood so that alternatives for manipulation can be developed when possible. Our poor understanding of some disturbances emphasizes the need for simultaneous programs of system management and research. Ideally, active adaptive-management efforts (Walters and Hilborn 1978) could be focused on systems where a large disturbance is either imminent or recent. Such a focus would allow evaluation of the implications of management actions. Management plans may focus on the potential for managing the system prior to the disturbance, the disturbance itself, the system immediately after the disturbance, or the recovery process. Sabogol (1992) found that management strategies for natural forests in the tropical dry zones of Nicaragua could

focus on encouragement of advanced growth of desirable tree species, inducement of natural regeneration, coppice management, and compensatory planting as a way to avoid the disturbance created by traditional utilization.

In managing the system prior to disturbance, actions should be designed so that the system responds to disturbances in ways that do not compromise management goals. Therefore, it is useful to think of potential management options in view of a conceptual framework for management of potential disturbance to a system (Figure 1). The seasonally dry tropical forest system can be manipulated to alter its vulnerability, its resistance, or its response to a disturbance. An example of changing a system's vulnerability is the alteration of fuel loads in a forest so that fire is more or less intense when it occurs. Resistance can be increased at the location in the system where the agent first exerts the disturbing force (e.g., through fire breaks, spraying for insects, or planting windbreaks). Then the disturbing force can still occur, but the system will not be altered to the extent it would have been without management intervention. Maxwell (2004) argues for consideration of the importance of indigenous land-use customs as a part of forest management and biological conservation.

The disturbance itself can be managed in one of two ways: no action, or prevention and thus some control of the disturbance. Action should not be taken when nothing can be done about preventing the disturbance (as in the case of many volcanoes and hurricanes), or when one can accept the consequences of the event. Prevention is usually motivated by the desire to satisfy or protect a human concern. Managers attempt to prevent disturbance when the costs of such efforts are perceived to be balanced or exceeded by the anticipated benefits. As examples, dams, levees, reservoirs, and coastal barriers are implemented to prevent disturbances caused by water action.

Managing the system after the disturbance requires recognition of the potential for natural processes of recovery. Sometimes management actions have been both costly
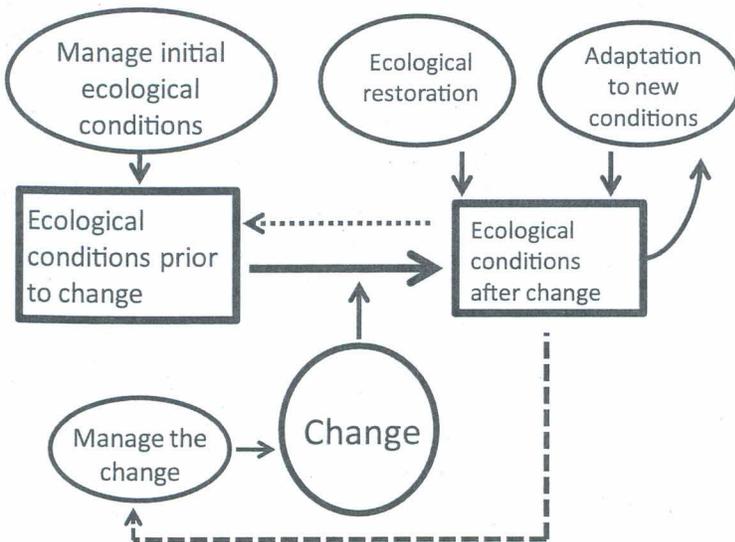

Figure 1. Diagram of how managers can deal with disturbances to seasonally dry tropical forests. As indicated by the dashed line, over time future changes as well as changing ecological conditions may alter these managed systems.

and detrimental to the natural recovery process. An example of such management is that, after Hurricane Hugo hit Puerto Rico in 1989, stream channels in the Luquillo Experimental Forest were filled with trees knocked down by the high winds. Some of the logjams were removed, but those left in place provided the environmental benefit of greater cover and food for stream organisms and retained valuable nutrients, sediments, and organic matter (Covich et al. 1991; Covich and McDowell 1996; Covich and Crowl 1990).

Because managing recovery can be thought of as managing succession, knowledge of natural succession processes increases the likelihood that the management plan will be achievable (see Luken 1990). The first step in managing recovery is evaluating the site potential, which includes the spatial pattern of the disturbance effects, the biological and physical residuals of the disturbance, the site's environmental conditions, the potential for propagule rain to aid in the recovery, and the influence of structural heterogeneity on the reestablishment of plants and animals. A common goal of recovery management is to shorten the process of succession or to maintain the process of succession at one particular state that is considered desirable for human purposes.

In developing recovery plans for seasonally dry tropical forests, managers should focus on critical stages of the successional process (MacMahon 1987; Luken 1990): migration, establishment, biotic interactions (such as competition, predation, and mutualism), and the reaction of the systems to the changes that occur over successional time. For each successional stage, a management prescription can be developed that offers three alterative interventions: add something to the system, kill or remove a biological component, or alter the structure of the system. Alternatively, one could physically remove existing propagules from the system, exclude animals that might eat the propagules, or remove the dispersal agent of undesirable seeds.

Successional trajectories after a disturbance event can follow a variety of directions (McCune and Allen 1985), but in many cases they appear to culminate in functional communities similar in structure and composition to the original ones. Alternatively, the successional trajectory can involve novel or unfamiliar seral communities when a disturbance sets succession back to early or uncommon stages. For example, after Hurricane Hugo in Puerto Rico, stands in the Luquillo Experimental Forest were invaded by vines and herbaceous species not previously observed at that site in more than fifty years of research (Scatena et al. 1996). Yet this early stage in the recovery of the forest quickly gave way to more-familiar successional trees, such as *Cecropia peltata*. Seven years after the hurricane, vines and herbaceous vegetation had assumed their previous low abundance, yet their dominance after the hurricane was critical in the immobilization of nutrients released by the disturbance and in the reestablishment of forest conditions (Scatena et al. 1996). Thus, while not always predictable, succession events after a disturbance often shape the reestablishment process.

CONCLUSIONS

The research on disturbances to seasonally dry tropical forests has been limited because of the difficulty of studying these long-lived systems and the prevailing cumulative

human influences on these forests. A key research need identified by Bruijnzeel (2004) is including the role of underlying geological controls of catchment hydrological behavior when analyzing the effect of land-use change on (low) flows or sediment production. Baker et al. (2005) emphasize the importance of understanding the role of legacies from prior disturbances in changes to these dry tropical forests. Clearly, the interactions of human activities with forest disturbances and changes thereafter will continue to be a critical part of understanding and managing seasonally dry tropical forests. There is also a need to characterize disturbance rates, intensities, and extents. Much of the current theory on how forest systems respond to disturbances was developed in temperate systems; there needs to be more testing and data collection to examine how these theories play out in seasonally dry tropical forests.

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REFERENCES

Abril, A. P., and E. H. Bucher. 2005. The Effect of Fire and Overgrazing Disturbes on Soil Carbon Balance in the Dry Chaco Forest. *Forest Ecology and Management* 206:339–405.

Achury, R., P. Chacon de Ulloa, and Á. M. Arcila. 2008. Ant Composition and Competitive Interactions with *Wasmannia auropunctata* in Tropical Dry Forest Fragments. *Revista Colombiana De Entomologia* 34:209–16.

Aguilar-Fernandez, M., V. J. Jaramillo, L. Varela-Fregoso, and M. E. Gavito. 2009. Short-Term Consequences of Slash-and-Burn Practices on the Arbuscular Mycorrhizal Fungi of a Tropical Dry Forest. *Mycorrhiza* 19:179–86.

Alvarez-Yepiz, J. C., A. Martinez-Yrizar, A. Burquez, and C. Lindquist. 2008. Variation in Vegetation Structure and Soil Properties Related to Land Use History of Old-Growth and Secondary Tropical Dry Forests in Northwestern Mexico. *Forest Ecology and Management* 256:355–66.

Andresen, E. 2005. Effects of Season and Vegetation Type on Community Organization of Dung Beetles in a Tropical Dry Forest. *Biotropica* 37:291–300.

Anitha, K., S. Joseph, E. V. Ramasamy, and S. N. Prasad. 2009. Changes in Structural Attributes of Plant Communities along Disturbance Gradients in a Dry Deciduous Forest of Western Ghats, India. *Environmental Monitoring and Assessment* 155:393–405.

Arredondo-León, C., J. Muñoz-Jiménez, and A. García-Romero. 2008. Recent Changes in Landscape-Dynamics Trends in Tropical Highlands, Central Mexico. *Interciencia* 33:569–77.

Ashton, P. S. 1993. The Community Ecology of Asian Rain Forests, in Relation to Catastrophic Events. *Journal of Biosciences* 18:501–14.

Ashton, P. S., and P. Hall. 1992. Comparisons of Structure among Mixed Dipterocarp Forests of North-Western Borneo. *Journal of Ecology* 80:459–81.

Baker, P. J., S. Bunyavejchewin, C. D. Oliver, and P. S. Ashton. 2005. Disturbance History and Historical Stand Dynamics of a Seasonal Tropical Forest in Western Thailand. *Ecological Monographs* 75:317–43.

Baker, W. L. 1992. The Landscape Ecology of Large Disturbances in the Design and Management of Nature Reserves. *Landscape Ecology* 7:181–94.

Bergeron, Y., and S. Archambault. 1993. Decreasing Frequency of Forest Fires in the Southern Boreal Zone of Québec and its Relation to Global Warming since the End of the "Little Ice Age." *Holocene* 3:255–59.

Bongers, F., L. Poorter, W. D. Hawthorne, and D. Sheil. 2009. The Intermediate Disturbance Hypothesis Applies to Tropical Forests, but Disturbance Contributes Little to Tree Diversity. *Ecology Letters* 12:798–805.

Bormann, E. H., and G. E. Likens. 1979. *Pattern and Process in a Forested Ecosystem*. New York: Springer-Verlag.

Brandeis, T. J., and C. W. Woodall. 2008. Assessment of Forest Fuel Loadings in Puerto Rico and the U.S. Virgin Islands. *Ambio* 37:557–62.

Bruijnzeel, L. A. 2004. Hydrological Functions of Tropical Forests: Not Seeing the Soil for the Trees? *Agriculture Ecosystems & Environment* 104:185–228.

Chazdon, R. L., S. G. Letcher, M. van Breugel, M. Martínez-Ramos, F. Bongers, and B. Finegan. 2006. Rates of Change in Tree Communities of Secondary Neotropical Forests following Major Disturbances. *Philosophical Transactions of the Royal Society B—Biological Sciences* 362:273–89.

Chouteau, P. 2007. The Impact of Burning on the Microhabitat Used by Two Species of Couas in the Western Dry Forest of Madagascar. *Ostrich* 78:43–49.

———. 2009. Impact of Logging on the Foraging Behaviour of Two Sympatric Species of Couas (*Coua coquereli* and *Coua gigas*) in the Western Dry Forest of Madagascar. *Comptes Rendus Biologies* 322:567–78.

Christensen, N. L., J. K. Agee, P. F. Brussard, J. Hughes, D. H. Knight, G. W. Minshall, J. M. Peek, S. J. Pyne, F. J. Swanson, B. F. Thomas, S. Wells, S. E. Williams, and H. A. Wright. 1989. Interpreting the Yellowstone Fires of 1988. *BioScience* 39:678–85.

Connell, J. H. 1979. Intermediate-Disturbance Hypothesis. *Science* 204:1345.

Covich, A. P., and T. A. Crowl. 1990. Effects of Hurricane Storm Flow on Transport of Woody Debris in a Rain Forest Stream (Luquillo Experimental Forest, Puerto Rico). In *Tropical Hydrology and Caribbean Water Resources*, ed. J. H. Krishna, V. Quiñones-Aponte, and F. Gomez-Gomez, 197–205. San Juan, Puerto Rico: American Water Resources Association.

Covich, A. P., T. A. Crowl, S. L. Johnson, D. Varza, and D. L. Certain. 1991. Post-Hurricane Hugo Increases in Atyid Shrimp Abundance in a Puerto Rican Montane Stream. *Biotropica* 23:448–54.

Covich, A. P., and W. H. McDowell. 1996. The Stream Community. In *The Food Web of a Tropical Rain Forest*, ed. D. P. Reagan and R. B. Waide, 434–59. Chicago: University of Chicago Press.

Dale, V. H., S. Brown, E. P. Flint, C. A. S. Hall, L. R. Iverson, and J. Uhlig. 1994. Estimating CO_2 Flux from Tropical Forests. In *Effects of Land Use Change on Atmospheric CO_2 Concentrations: Southeast Asia as a Case Study*, ed. V. H. Dale, 365–74. New York: Springer-Verlag.

Dale, V. H., A. Lugo, J. MacMahon, and S. Pickett. 1998. Ecosystem Management in the Context of Large, Infrequent Disturbances. *Ecosystems* 1:546–57.

Denslow, J. S. 1980. Patterns of Plant Species Diversity during Succession under Different Disturbance Regimes. *Oecologia* 46:18–21.

Farwig, N., C. Braun, and K. Boehning-Gaese. 2008. Human Disturbance Reduces Genetic Diversity of an Endangered Tropical Tree, *Prunus africana* (Rosaceae). *Conservation Genetics* 9:317–26.

Flannigan, M. D., Y. Bergeron, O. Engelmark, and B. M. Wotton. 1998. Future Wildfire in Circumboreal Forests in Relation to Global Warming. *Journal of Vegetation Science* 4:469–76.

Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate Change and Forest Fires. *Science of the Total Environment* 262:221–29.

Flint, E. P., and J. F. Richards. 1994. Trends in Carbon Content of Vegetation in South and Southeast Asia Associated with Changes in Land Use. In *Effects of Land Use Change on Atmospheric CO_2 Concentrations: Southeast Asia as a Case Study*, ed. V. H. Dale, 201–300. New York: Springer-Verlag.

Food and Agriculture Organization / United Nations Environment Programme. 1981. *Tropical Forest Resource Assessment Project: Forest Resources of Tropical Asia*. Rome: Food and Agriculture Organization.

Hanson, P. J., and J. F. Weltzin. 2000. Drought Disturbance from Climate Change: Response of United States Forests. *Science of the Total Environment* 262:205–20.

Houghton, R. A., R. D. Boone, J. R. Fruci, J. Hobbie, J. M. Melillo, C. A. Palm, B. J. Peterson, G. R. Shaver, G. M. Woodwell, and B. Moore. 1987. The Flux of Carbon from Terrestrial Ecosystems to the Atmosphere in 1980 Due to Changes in Land Use: Geographic Distribution of the Global Flux. *Tellus* 39B:122–39.

Houghton, R. A., R. D. Boone, J. M. Melillo, C. A. Palm, G. M. Woodwell, N. Myers, B. Moore, and D. Skole. 1985. Net Flux of CO_2 from Tropical Forests in 1980. *Nature* 316:617–20.

Houghton, R. A., and J. L. Hackler. 1994. The Net Flux of Carbon from Deforestation and Degradation in South and Southeast Asia. In *Effects of Land Use Change on Atmospheric CO_2 Concentrations: Southeast Asia as a Case Study*, ed. V. H. Dale, 301–28. New York: Springer-Verlag.

Huete, A. R., N. Restrepo-Coupe, P. Ratana, K. Didan, S. R. Saleska, K. Ichii, S. Panuthai, and M. Gamo. 2008. Multiple Site Tower Flux and Remote Sensing Comparisons of Tropical Forest Dynamics in Monsoon Asia. *Agricultural and Forest Meteorology* 148:748–60.

Imbert, D., and J. Portecop. 2008. Hurricane Disturbance and Forest Resilience: Assessing Structural vs. Functional Changes in a Caribbean Dry Forest. *Forest Ecology and Management* 255:3494–3501.

Janssens, M. L. 2000. *Introduction to Mathematical Fire Modeling*, 2nd ed. Boca Raton, FL: CRC Press.

Kennard, D. K., and F. E. Putz. 2005. Differential Responses of Bolivian Timber Species to Prescribed Fire and Other Gap Treatments. *New Forests* 30:1–20.

Kline, K. L., and V. H. Dale. 2008. Biofuels: Effects on Land and Fire. *Science* 321:199–200.

Kozlowski, T. T., and S. G. Pallardy. 2002. Acclimation and Adaptive Responses of Woody Plants to Environmental Stresses. *Botanical Review* 68:270–334.

Laurance, W. F., B. M. Croes, L. Tchignoumba, S. A. Lahm, A. Alonso, M. E. Lee, P. Campbell, and C. Ondzeano. 2006. Impacts of Roads and Hunting on Central African Rainforest Mammals. *Conservation Biology* 20:1251–61.

Lavigne, F., and Y. Gunnell. 2006. Land Cover Change and Abrupt Environmental Impacts on Javan Volcanoes, Indonesia: A Long-Term Perspective on Recent Events. *Regional Environmental Change* 6:86–100.

Leach, M. K., and T. J. Givnish. 1996. Ecological Determinants of Species Loss in Remnant Prairies. *Science* 273:1555–58.

Leigh, E. G., Jr., P. Davidar, C. W. Dick, J.-P. Puyravaud, J. Terborgh, H. ter Steege, and S. J. Wright. 2004. Why Do Some Tropical Forests Have So Many Species of Trees? *Biotropica* 36:447–73.

Lim, K. O. 2001. Biomass—A Fuel with a Bright Future, ed. K. Sopian, M. Y. H. Othman, S. A. Rahman, and S. Shaari. *Advances in Malaysian Energy Research* 2000:255–62.

Lugo, A. E., E. Medina, J. C. Trejo-Torres, and E. Helmer. 2006. Botanica and Ecologica Basis for the Resilience of Antillean Dry Forests. In *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation*, ed. R. T. Pennington, G. P. Lewis, and J. A. Ratter, 359–81. Systematics Association Special Volume Series. Boca Raton FL: CRC Press.

Lugo, A. E., and F. N. Scatena. 1996. Background and Catastrophic Tree Mortality in Tropical Moist, Wet, and Rain Forests. *Biotropica* 28:585–99.

Luken, J. O. 1990. *Directing Ecological Succession*. London: Chapman and Hall.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of Biological Invasions on Disturbance Regimes. *Trends in Ecology and Evolution* 13:195–98.

MacMahon, J. A. 1987. Disturbed Lands and Ecological Theory: An Essay about a Mutualistic Association. In *Restoration Ecology*, ed. W. R. Jordan, M. E. Gilpin, and J. D. Aber, 221–37. Cambridge: Cambridge University Press.

Marod, D., U. Kutintara, C. Yarwudhi, H. Tanaka, and T. Nakashizuka. 1999. Structural Dynamics of a Natural Mixed Deciduous Forest in Western Thailand. *Journal of Vegetation Science* 10:777–86.

Martini, A. M. Z., R. A. F. Lima, G. A. D. C. Franco, and R. R. Rodrigues. 2008. The Need for Full Inventories of Tree Modes of Disturbance to Improve Forest Dynamics Comprehension: An Example from a Semideciduous Forest in Brazil. *Forest Ecology and Management* 255:1479–88.

Maxwell, A. L. 2004. Fire Regimes in North-Eastern Cambodian Monsoonal Forests, with a 9300-year Sediment Charcoal Record. *Journal of Biogeography* 31:225–39.

Mayle, F. E., and M. J. Power. 2008. Impact of a Drier Early-Mid-Holocene Climate upon Amazonian Forests. *Philosophical Transactions of the Royal Society B—Biological Sciences* 363:1829–38.

McCune, B., and T. F. H. Allen. 1985. Will Similar Forests Develop on Similar Sites? *Canadian Journal of Botany* 63:367–76.

McLaren, K. P., M. A. McDonald, J. B. Hall, and J. R. Healey. 2005. Predicting Species Response to Disturbance from Size Class Distributions of Adults and Saplings in a Jamaican Tropical Dry Forest. *Plant Ecology* 181:69–84.

Mehta, V. K., P. J. Sullivan, M. T. Walter, J. Krishnaswamy, and S. D. DeGloria. 2008. Impacts of Disturbance on Soil Properties in a Dry Tropical Forest in Southern India. *Ecohydrology* 1:161–75.

Miles, L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos, and J. E. Gordon. 2006. A Global Overview of the Conservation Status of Tropical Dry Forests. *Journal of Biogeography* 33:491–505.

Moreno, A. R. 2006. Climate Change and Human Health in Latin America: Drivers, Effects, and Policies. *Regional Environmental Change* 6:157–64.

Nakagawa, M., K. Tanaka, T. Nakashizuka, T. Ohkubo, T. Kato, T. Maeda, K. Sato, H. Miguchi, H. Nagamasu, K. Ogino, S. Teo, A. A. Hamid, and L. H. Seng. 2000. Impact of Severe Drought Associated with the 1997–1998 El Niño in a Tropical Forest in Sarawak. *Journal of Tropical Ecology* 16 (3): 355–67.

Negron, J. F. 1998. Probability of Infestation and Extent of Mortality Associated with the Douglas-Fir Beetle in the Colorado Front Range. *Forest Ecology and Management* 107:71–85.

Neilson, R. P., and R. J. Drapek. 1998. Potentially Complex Biosphere Responses to Transient Global Warming. *Global Change Biology* 4:505–21.

Otterstrom, S. M., M. W. Schwartz, and I. Velazquez-Rocha. 2006. Responses to Fire in Selected Tropical Dry Forest Trees. *Biotropica* 38:592–98.

Paine, R. T., M. J. Tegner, and A. E. Johnson. 1998. Compounded Perturbations Yield Ecological Surprises: Everything Else Is Business as Usual. *Ecosystems* 1:535–45.

Palm, C. A., R. A. Houghton, J. M. Melillo, and D. L. Skole. 1986. Atmospheric Carbon Dioxide from Deforestation in Southeast Asia. *Biotropica* 18:177–88.

Poorter, L., W. Hawthorne, F. Bongers, and D. Sheil. 2008. Maximum Size Distributions in Tropical Forest Communities: Relationships with Rainfall and Disturbance. *Journal of Ecology* 96 (3): 495–504.

Potts, M. D. 2003. Drought in a Bornean Everwet Rain Forest. *Journal of Ecology* 91:467–74.

Richards, J. F., and E. P. Flint. 1994. A Century of Land-Use Change in South and Southeast Asia. In *Effects of Land Use Change on Atmospheric CO$_2$ Concentrations: Southeast Asia as a Case Study*, ed. V. H. Dale, 15–66. New York: Springer-Verlag.

Rogers, K. H. 1997. Operationalizing Ecology under a New Paradigm: An African Perspective. In *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity*, ed. S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, 60–77. New York: Chapman and Hall.

Sabogol, C. 1992. Regeneration of Tropical Dry Forests in Central-America, Examples from Nicaragua. *Journal of Vegetation Science* 3:407–16.

Sagar, R., A. S. Raghubanshi, and J. S. Singh. 2003. Tree Species Composition, Dispersion and Diversity along a Disturbance Gradient in a Dry Tropical Forest Region of India. *Forest Ecology and Management* 186:61–71.

Sagar, R., and J. S. Singh. 2006. Tree Density, Basal Area and Species Diversity in a Disturbed Dry Tropical Forest of Northern India: Implications for Conservation. *Environmental Conservation* 33 (3): 256–62.

Sagar, R., and R. S. Singh. 2005. Structure, Diversity, and Regeneration of Tropical Dry Deciduous Forest of Northern India. *Biodiversity and Conservation* 14:935–59.

Sahu, P. K., R. Sagar, and J. S. Singh. 2008. Tropical Forest Structure and Diversity in Relation to Altitude and Disturbance in a Biosphere Reserve in Central India. *Applied Vegetation Science* 11:461–70.

Sánchez, F., J. Alvarez, C. Ariza, and A. Cadena. 2007. Bat Assemblage Structure in Two Dry Forests of Colombia: Composition, Species Richness, and Relative Abundance. *Mammalian Biology* 72:82–92.

Sapkota, I. P., M. Tigabu, and P. C. Oden. 2009. Spatial Distribution, Advanced Regeneration and Stand Structure of Nepalese Sal (*Shorea robusta*) Forests Subject to Disturbances of Different Intensities. *Forest Ecology and Management* 257:1966–75.

Scatena, F. N., S. Moya, C. Estrada, and J. D. Chinea. 1996. The First Five Years in the Reorganization of Aboveground Biomass and Nutrient Use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28:424–40.

Schullery, P. 1989. The Fires and Fire Policy. *BioScience* 39:686–94.

Stocks, B. J., M. A. Fosberg, T. J. Lynham, L. Mearns, B. M. Wotton, Q. Yang, J. Z. Jin, K. Lawrence, G. R. Hartley, J. A. Mason, and D. W. McKenney. 1998. Climate Change and Forest Fire Potential in Russian and Canadian Boreal Forests. *Climatic Change* 38:1–13.

Suaz-Ortuno, I., J. Alvarado-Diaz, and M. Martinez-Ramos. 2008. Effects of Conversion of Dry Tropical Forest to Agricultural Mosaic on Herpetofaunal Assemblages. *Conservation Biology* 22:362–74.

Suaz-Ortuno, I., J. Alvarado-Diaz, E. Raya-Lemus, and M. Martinez-Ramos. 2007. Diet of the Mexican Marbled Toad (*Bufo marmoreus*) in Conserved and Disturbed Tropical Dry Forest. *Southwestern Naturalist* 52:305–9.

Tang, Y., M. Cao, and X. F. Fu. 2006. Soil Seedbank in a Dipterocarp Rain Forest in Xishuangbanna, Southwest China. *Biotropica* 38:328–33.

Tilman, D. 1989. Ecological Experimentation: Strengths and Conceptual Problems. In *Long-Term Studies in Ecology: Approaches and Alternatives*, ed. G. E. Likens, 136–57. New York: Springer-Verlag.

Timilsina, N., M. S. Ross, and J. T. Heinen. 2007. A Community Analysis of Sal (*Shorea robusta*) Forests in the Western Terai of Nepal. *Forest Ecology and Management* 241:223–34.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems* 1:511–23.

Turner, M. G., V. H. Dale, and E. H. Everham. 1997. Fires, Hurricanes, and Volcanoes: Comparing Large Disturbances. *BioScience* 47:758–68.

Urquiza-Haas, T., P. M. Dolman, and C. A. Peres. 2007. Regional Scale Variation in Forest Structure and Biomass in the Yucatan Peninsula, Mexico: Effects of Forest Disturbance. *Forest Ecology and Management* 247:80–90.

Van Bloem, S. J., A. E. Lugo, and P. G. Murphy. 2006. Structural Response of Caribbean Dry Forests to Hurricane Winds: A Case Study from Guanica Forest, Puerto Rico. *Journal of Biogeography* 33:517–23.

Van Bloem, S. J., P. G. Murphy, and A. E. Lugo. 2007. A Link between Hurricane-Induced Tree Sprouting, High Stem Density and Short Canopy in Tropical Dry Forest. *Tree Physiology* 27:475–80.

Van Bloem, S. J., P. G. Murphy, A. E. Lugo, R. Ostertag, M. R. Costa, I. R. Bernard, S. M. Colon, and M. C. Mora. 2005. The Influence of Hurricane Winds on Caribbean Dry Forest Structure and Nutrient Pools. *Biotropica* 37:571–83.

Velázquez, E., and A. Gómez-Sal. 2008. Landslide Early Succession in a Neotropical Dry Forest. *Plant Ecology* 199:295–308.

Vieira, F. D., and D. de Carvalho. 2008. Genetic Structure of an Insect-Pollinated and Bird-Dispersed Tropical Tree in Vegetation Fragments and Corridors: Implications for Conservation. *Biodiversity and Conservation* 17:2305–21.

Walters, C. J., and R. Hilborn. 1978. Ecological Optimization and Adaptive Management. *Annual Review of Ecology and Systematics* 9:157–88.

Weatherhead, P. J. 1986. How Unusual Are Unusual Events? *American Naturalist* 128:150–54.

Webb, E. L., and R. N. Sah. 2003. Structure and Diversity of Natural and Managed Sal (*Shorea robusta* Gaertn.f.) Forest in the Terai of Nepal. *Forest Ecology and Management* 176:337–53.

Weir, J. M. H. 1996. The Fire Frequency and Age Mosaic of a Mixed Wood Boreal Forest. Master's thesis, University of Calgary.

Werneck, M. D., and E. V. Franceschinelli. 2004. Dynamics of a Dry Forest Fragment after the Exclusion of Human Disturbance in Southeastern Brazil. *Plant Ecology* 174:337–46.

Werner, F. A., and S. R. Gradstein. 2009. Diversity of Dry Forest Epiphytes along a Gradient of Human Disturbance in the Tropical Andes. *Journal of Vegetation Science* 20:59–68.

Whelan, R. J. 1995. *The Ecology of Fire*. Cambridge: Cambridge University Press.

White, P. S., and S. T. A. Pickett. 1985. Natural Disturbance and Patch Dynamics: An Introduction. In *The Ecology of Natural Disturbance and Patch Dynamics*, ed. S. T. A. Pickett and P. W. White, 3–13. New York: Academic Press.

Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of Disturbance on River Food Webs. *Science* 273:1558–61.

Zak, M. R., M. Cabido, D. Cáceres, and S. Díaz. 2008. What Drives Accelerated Land Cover Change in Central Argentina? Synergistic Consequences of Climatic, Socioeconomic, and Technological Factors. *Environmental Management* 42:181–89.

Zelikova, T. J., and M. D. Breed. 2008. Effects of Habitat Disturbance on Ant Community Composition and Seed Dispersal by Ants in a Tropical Dry Forest in Costa Rica. *Journal of Tropical Ecology* 24:309–16.

Zimmer, H., and P. Baker. 2009. Climate and Historical Stand Dynamics in the Tropical Pine Forests of Northern Thailand. *Forest Ecology and Management* 257:190–98.