This paper is a much abridged version of World Bank Environment Department Paper 75, "Biodiversity Conservation in the Context of Tropical Forest Management," by the same authors. It is the first paper in the bank's Impact Studies Series, which addresses the broader questions of the positive and negative effects of human activities on biodiversity. A more complete set of data supporting the arguments herein are in the appendices and text of the World Bank paper, which can be accessed from http://www.worldbank.org/biodiversity.

Tropical Forest Management and Conservation of Biodiversity: an Overview

Introduction

Parks and protected areas are essential for biodiversity conservation but inadequate to assure the continued existence of the majority of natural landscapes, ecosystems, communities, species, and genotypes in tropical forests. Even if a goal of 10–12% protection were attained and reserved areas were appropriately located and managed, up to 50% of tropical species would be expected to go extinct during the next few decades (Soulé & Sanjayan 1998). If biodiversity outside protected areas is neglected, thousands of species are likely to disappear. The first priority should be to increase the area of forests under strict protection while improving reserve management. Mechanisms should be developed to halt road building and commercial logging in forest wilderness areas as well as in centers of diversity and endemism. But promoting more biodiversity-sensitive management of forests outside protected areas is of almost equal priority, given the conservation potential of these still vast areas.

In the search for land-use practices compatible with biodiversity maintenance, many environmentalists have focused on logging (for comprehensive reviews of the environmental effects of logging in tropical forests, see Grieser Johns 1997; Haworth 1999). This emphasis is not surprising given that of all forest uses, logging is often the most financially lucrative and has the most severe environmental effects. The indirect effects of logging, particularly increased hunting (e.g., Robinson et al. 1999) and the greater likelihood of deforestation due to improved access (reviewed by Kaimowitz & Angelsen 1998), have also been highlighted recently.

What has emerged from the dust, mud, chainsaw noise, and diesel fumes is the idea that conservation of some components of biodiversity could be facilitated by collaboration between loggers and environmentalists. Some of the latter oppose the idea of promoting better forest management as a means for achieving overall conservation goals (or at least oppose financial investment in such efforts; Rice et al. 1997; Bawa & Seidler 1998; Bowles et al. 1998). This opposition notwithstanding, consideration of the inevitability of logging in much of the tropics, the many constraints on expansion of nature reserves in tropical countries, the challenges of protecting and managing the parks already demarcated on paper, sovereignty issues, development needs, and the implicit adoption of the "use it or lose it" assumption motivate other conservationists to continue holding sustainable forest management as a worthy conservation goal in forests outside of protected areas (e.g., Dickinson et al. 1996; Chazdon 1998; Poore et al. 1999; Whitmore 1999).

General conceptual approaches to zoning forests for different uses have been presented recently by various authors, including Noble and Dirzo (1997) and Frumhoff and Losos (1998). Methods for integrating conservation functions at different geographical scales were reviewed recently by Poiani et al. (2000). Our paper focuses on the forests zoned for timber production. Our goals are to (1) contribute to the development of a heuristic construct for considering the range of effects of forestry activities on tropical forest biodiversity at the levels of landscapes, ecosystems, communities, species, and genes; (2) indicate the topics on which further research will be particularly useful in evaluating the effects of different forestry activities on the various components and attributes of biodiversity; and (3) suggest ways to mitigate the deleterious effects of forestry activities on tropical forest biodiversity.

To help elucidate some of the factors on which the compatibility of tropical forest logging and biodiversity protection depend, we first attempt to disaggregate the terms *logging* and *biodiversity.* We discuss the wide range of logging intensities, logging methods, collateral damage, and silvicultural approaches appropriate for tropical forests. A framework for considering the effects of

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logging and other management activities on the various forest components (landscapes, ecosystems, communities, species/populations, and genes) and attributes (structure, composition, and function) of biodiversity is presented. We use the components and attributes of biodiversity to review the effects of logging and other silvicultural activities on tropical forests.

Disaggregating "Biodiversity"

Biodiversity refers to the natural variety and variability among living organisms, the ecological complexes in which they naturally occur, and the ways in which they interact with each other and with the physical environment. This definition and the elucidation below are based on work by the Office of Technology Assessment (1987), Noss (1990), and Redford and Richter (1999). Climate, geology, and physiography all exert considerable influence on broad spatial patterns of biotic variety; local ecosystems and their biological components are further modified by environmental variation (e.g., local climatic and stream flow fluctuations) and ecological interactions. This natural variety and variability is distinguished from biotic patterns or conditions formed under the influence of human-mediated species introductions and substantially human-altered environmental processes and selection regimes (Noss & Cooperrider 1994; Bailey 1996).

Biological diversity can be measured in terms of different components (landscape, ecosystem, community, population/species, and genetic), each of which has structural, compositional, and functional attributes (reviewed in Table 1). *Structure* refers to the physical organization or pattern of the elements. *Composition* refers to the identity and variety of elements in each of the biodiversity components. *Function* refers to ecological and evolutionary processes acting among the elements.

Disaggregating "Logging"

When properly planned and conducted, logging is an integral component of forest management systems designed to promote sustained timber yields (STY) or the more all-encompassing goal of sustainable forest management (SFM). Unfortunately, logging in tropical forests all too often represents a timber "mining" activity carried out without regard for renewability of this natural resource (Putz et al. 2000*a*). Due mostly to the desire to obtain voluntary third-party certification of good management from the Forest Stewardship

Table 1. Components and attributes of tropical forest biodiversity that might be influenced by logging and other silvicultural activities.*

Components	*Structure*	*Composition*	*Function*
Landscape	size and spatial distribution of habitat patches (e.g., seral stage diversity and area); physiognomy; perimeter-area relations; patch juxtaposition and connectivity; fragmentation	identity, distribution, and proportion of habitat types and multihabitat landscape types; collective patterns of species distributions	habitat patch persistence and turnover rates; energy flow rates; disturbance processes (e.g., extent, frequency, and intensity of fires); human land-use trends; erosion rates; geomorphic and hydrologic processes
Ecosystem	soil (substrate) characteristics; vegetation biomass, basal area, and vertical complexity; density and distribution of snags and fallen logs	biogeochemical stocks; life-form proportions	biogeochemical and hydrological cycling; energy flux; productivity; flows of species between patches; local climate effects
Community	foliage density and layering; canopy openness and gap proportions; trophic and food web structures	relative abundance of species and guilds; richness and diversity indices; proportions of endemic, exotic, threatened, and endangered species; proportions of specialists vs. generalists	patch dynamics and other successional processes; colonization and extinction rates; pollination, herbivory, parasitism, seed dispersal, and predation rates; phenology
Species/population	sex and age-size ratios; range and dispersion; intraspecific morphological variation	species abundance distributions, biomass, or density; frequency; importance or cover value	demographic processes (e.g., survivorship, fertility, recruitment, and dispersal); growth rates; phenology
Genetic	effective population size; heterozygosity; polymorphisms; generation overlap; heritability	allelic diversity; presence of rare alleles; frequency of deleterious alleles	gene flow; inbreeding depression; rates of outbreeding, genetic drift, and mutation; selection intensity; dysgenic selection

**Modified from Noss (1990) and Redford and Richter (1999).*

Council (FSC), the transition from forest mining to forest management has finally started to occur in some areas in the tropics (Nittler & Nash 1999). Even within certified forests there are questions about how to most effectively and efficiently minimize the deleterious environmental effects of logging and other silvicultural activities.

Forest interventions of all types, from harvesting of fruits for home consumption to clearcutting for timber, have effects on forests that need to be understood and often deserve mitigation (Peters 1996). Logging often is the most damaging and generally the most financially lucrative of such forest interventions (Pearce et al. 1999). The compatibility of logging with biodiversity conservation is complicated because logging is carried out over a huge range of intensities with a variety of techniques that may be applied carefully or in ways that result in a great deal of avoidable damage. The following sections focus on the issues of harvesting intensities, yarding methods (how timber is extracted from the stump to haul roads), and ways of reducing logging damage.

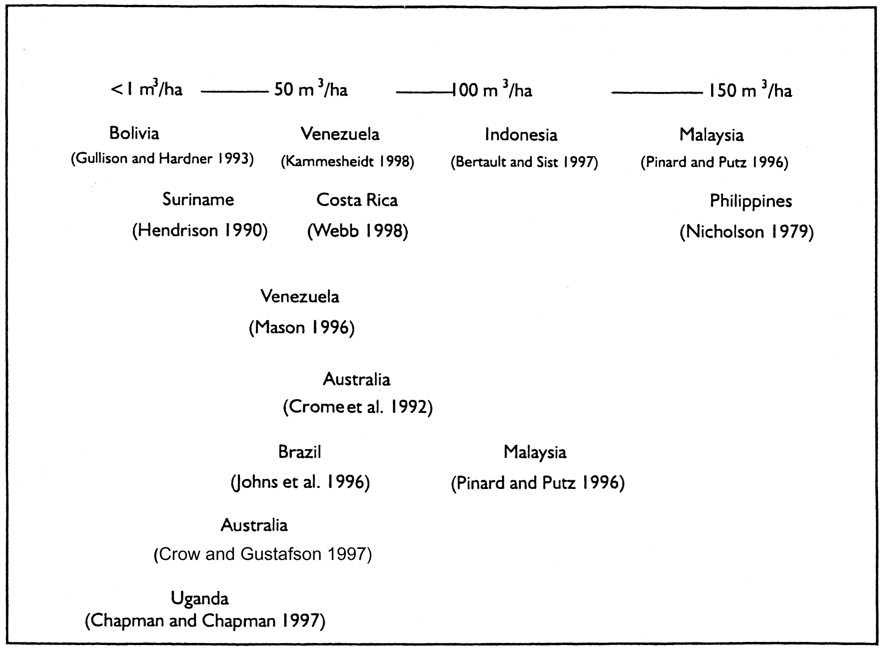

Figure 1. Logging intensities (m^3/ha) for tropical forests. In most of these studies, as in most logging areas in the tropics, felling was done with chainsaws and yarding with bulldozers or articulated skudders with rubber tires.

Logging Intensities

Logging intensities span more than two orders of magnitude (<1 m^3/ha to >100 m^3/ha; Fig. 1), complicating the challenge of generalizing the effects of such activities. At a small scale (1–10 ha), the typical aggregated distributions of tropical trees (Hubbell 1979) leads to locally severe logging effects unless harvesting controls are implemented. The localized but severe direct effects of roads, log landings, and skid trails hardly need to be emphasized (Guariguata & Dupuy 1997). At a slightly larger scale (10–100 ha), stands vary in stocking of commercial species and in their accessibility due to terrain or edaphic factors. Where logging is carried out in areas designated for each year of management (annual coupes), logging effects tend to be aggregated at larger scales. Logging intensities also vary over time, tending to increase with local timber shortages, improved access, and greater willingness of markets to accept lesser-known species (Plumptre 1996).

The substantial number of studies conducted on the effects of logging in tropical forests all conclude that soil effects and damage to the residual forest all increase with increasing logging intensity (Ewel & Conde 1980; Sist et al. 1998). Proportions of both soil and residual trees damaged by logging range from 5% to 50%, depending on harvesting intensity, yarding method, and the care with which the operations are carried out. Interpretation of data pertaining to the relationship between logging intensity and residual stand damage is complicated by concomitant change in residual stand density; at the extreme, there is no residual stand in clearcuts. Further complicating assumptions about logging damage is the fact that few tropical forests are logged only once.

Log Yarding Methods

Much of the direct damage to tropical forest caused by logging occurs while logs are being extracted from the stump to roads or riversides from which they are then hauled or towed out of the forest (yarding). Yarding methods utilized in tropical forests vary in technological sophistication, the collateral damages with which they are associated, and yarding costs (Conway 1982). The range of effects on biodiversity at the landscape, ecosystem, community, population/species, and genetic levels varies greatly along the continuum of technological sophistication of yarding methods that stretches from manual extraction to the use of helicopters (Fig. 2).

Yarding can be carried out in an environmentally and silviculturally sensitive manner, or it can be extremely destructive. The rankings of environmental effects in Fig. 2 are suggestions of the typical amounts of dam-

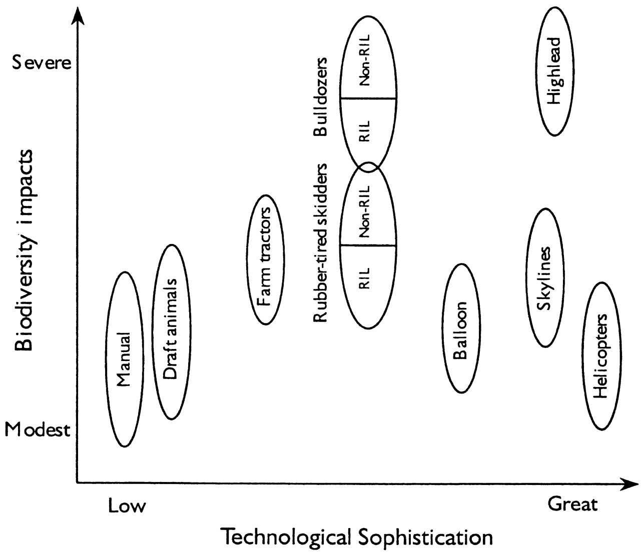

Figure 2. Generalized ranges of direct biodiversity effects of timber yarding methods used for tropical forest logging as a function of level of technological sophistication required (assumes equal volumes of timber yarded). For mechanized ground-based yarding operations, conventional (non-RIL), and reduced-impact logging (RIL) effects are contrasted.

age associated with different yarding techniques. Impact is affected by both choice of yarding equipment and the care with which yarding operations are carried out, as indicated by the contrasts between conventional and reduced-impact logging (RIL) in Fig. 2. Unfortunately, although the silvicultural, environmental, and economic benefits of the planning of log-extraction routes have been recognized for many decades (review by Putz et al. 2000*a*), well-planned logging operations are still the exception in tropical forests.

Most destructive yarding in tropical forests is carried out with bulldozers (crawler tractors). Bulldozers are excellent devices for constructing roads but are unfortunately versatile enough to yard timber as well. The excessive damage to soils and residual trees during conventional bulldozer yarding is well known, especially at high intensities on steep slopes logged during wet weather by untrained crews, but bulldozers still yard much of the timber in commercial logging areas in the tropics.

With the loss of forest in accessible areas in much of the tropics, logging is increasingly being relegated to flooded, steep, rocky, or otherwise adverse terrain. Because ground-based yarding from such sites can be prohibitively expensive, they often have been left as unlogged refugia within harvested areas. Their status as refuges is jeopardized by helicopter yarding, because helicopters can yard timber from even the most adverse sites. Obtaining timber from these sites is becoming more cost-effective under some conditions. Although areas from which timber is harvested by helicopters are not dissected by skid trails, haul roads are still needed, and with them come all the problems associated with increased access. An equally important concern about helicopter yarding is that areas traditionally avoided by loggers are rendered accessible and are likely to be harvested. Because helicopters leave no obvious trails, it will be challenging to monitor their harvesting effects.

Logging and Other Silvicultural Treatments

Logging can be either a cause of a great deal of avoidable damage or one of a series of silvicultural treatments designed to promote the regeneration and growth of commercial timber species while protecting ecosystem services and biodiversity. In logging areas where sustained yield of timber is a priority, various silvicultural treatments can be used in combination with the appropriate logging regime to promote the regeneration or growth of commercial species. Carrying out silvicultural treatments in conjunction with logging reduces their cost while reinforcing the idea that logging itself can be silviculturally useful.

The most common method for controlling timber harvesting in tropical forests is simply to set a minimum stem diameter for felling. Although theoretically easy to implement and monitor, minimum-diameter rules often are inimical to achieving silvicultural goals. The problem with this system is obvious where minimum-diameter limits are set below the sizes at which trees start to reproduce (Appanah & Manof 1991; Plumptre 1995). Minimum-diameter rules also do not prevent harvesting of clusters of trees and thereby create silviculturally unsatisfactory conditions, as when commercial species are favored by small canopy gaps or vines proliferate in large ones.

Logging is often the most severe of silvicultural interventions, but there are other prescriptions designed to increase the stocking of commercial tree species or to increase the growth of trees already present. Retaining seed trees in harvested stands is one possible way to increase stocking, but for species that require mineral soil seed beds or minimal competition for germination, establishment, and subsequent growth, seed-tree retention needs to be combined with various other treatments. Seed beds can be modified and competition can be reduced through controlled burning, mechanical scarification, or herbicide treatment of plants competing with seedlings of the crop species. Where natural regeneration fails, or where particularly high stocking levels are desired, many foresters have tried planting seedlings of commercial species in gaps or along lines cleared through the forest. For stands in which regeneration of the commercial species is already established, various thinning and weed-control treatments are often prescribed to accelerate tree growth and to promote "stand improvement." Thinning around potential crop trees, often referred to by tropical foresters as "liberation thinning," and vine cutting are two commonly prescribed but less commonly applied silvicultural treatments. In experimental areas where liberation treatments have been applied to enhance volume increments of commercial species, treatments are often prescribed at intervals of 10 years or more (de Graaf et al. 1999). As in the case of logging, all of these other silvicultural treatments have effects on biodiversity, but they have been much less well studied.

Reducing the Effects of Logging and Other Silvicultural Treatments

Substantial attention has been given recently to reduced-impact logging (RIL). Most of the practices in the various RIL guidelines that have been promulgated of late have long been recognized as being environmentally sound and silviculturally appropriate (Bryant 1914). Full application of RIL techniques represents a major step toward SFM, but RIL alone does not guarantee sustainability. Especially where tree species being harvested regenerate only in large clearings, the required silvicultural interventions to assure sustained yield of the same species often may be substantial (e.g., mimicking the effects of slash-and-burn agriculture or hurricanes followed by fires; e.g., Snook 1996; Fredericksen 1998; Dickinson & Whigham 1999; Pinard et al. 1999; Fredericksen & Mostacedo 2000). This silvicultural challenge notwithstanding, careful planning and implementation of harvesting guidelines would represent a big step toward sustainable forest management.

For all yarding methods, logging damage can be substantially reduced, and logging costs reduced as well, by proper design, construction, and maintenance of road networks. Much of the cost of harvesting timber and a large proportion of the hydrological damage (e.g., stream sedimentation) due to logging is associated with roads (e.g., Bruijnzeel 1992). Guidelines for road construction are readily available and are well outlined in the FAO Model Code of Forest Harvesting Practices (Dykstra & Heinrich 1996). Unfortunately, forest engineering standards in most tropical logging areas are extremely low, and there are too few experienced forest engineers involved in most tropical logging operations. Because soil damage due to poor skid trail design or improper use, for example, reduces productivity, increases surface erosion, and has various other deleterious environmental effects, adhering to RIL guidelines has advantages regardless of whether the forest is allowed to regenerate or is replaced by an oil palm plantation or a maize field (e.g., Congdon & Herbohn 1993; Nussbaum et al. 1995; Pinard et al. 1996).

The effects of other silvicultural treatments on biodiversity (e.g., thinning and vinecutting) depend on the intensity with which they are applied and on the proper designation of areas deemed inappropriate for stand "improvement." For example, vine cutting can enhance tree growth but undoubtedly has negative effects on a wide variety of animals (Putz et al. 2000*b*). Both biodiversity effects and labor costs of vine cutting depend on whether only selected future crop trees are liberated or vine cutting is carried out as a blanket prescription.

Effects of Forest Management on Biodiversity

Human activities have an enormous effect on a global scale, as three examples illustrate: 40% of the Earth's terrestrial primary productivity is appropriated by humans (Vitousek et al. 1997); 25–35% of the primary productivity of continental-shelf marine ecosystems is consumed by humans (Roberts 1997); and 26% of total evapotranspiration and 54% of all runoff in rivers, lakes, and other accessible sources of water are appropriated by humans (Postel et al. 1996). Despite these statistics on current human effects, many people still maintain it is possible to both use and preserve biodiversity with no costs to either side (e.g., Huston 1993). This claim is made regardless of human overexploitation of resources that began in prehistory (Goudie 1990) and is manifested most recently in the negative effects of tropical logging (Frumhoff 1995; Bawa & Seidler 1998) and exploitation of nontimber forest products (Homma 1992; Coomes 1995). This thinking is dangerous because it allows its adherents to believe that there are easy, cost-free solutions to the problems intrinsic to exploitation of the planet.

Summarizing the effects of forestry activities on biodiversity in tropical forests is an effort fraught with problems, in large part because of the immense diversity found therein. Even at the species level, the diversity is difficult to imagine, and each of the literally millions of species in tropical forests responds to different logging effects in distinct ways. Although some general response patterns are obvious and others have emerged from field research, the idiosyncrasies and apparent inconsistencies of species responses need to be recognized. For example, chimpanzee (*Pan troglodytes*) populations have been reported to increase (Howard 1991; Hashimoto 1995), decrease (White 1992), and respond not at all to logging (Plumptre & Reynolds 1994). In contrast, studies of terrestrial and bark-gleaning insectivorous birds consistently report negative effects of logging (Putz et al. 2000*b*).

Landscape Effects

Logging affects the landscape component of biodiversity by changing land forms and ecosystem types across large geographic areas. Logging shifts the regional mosaic of land uses. Although the landscape component of biodiversity is the least sensitive to logging, changes in the size, spatial distribution, and connectivity of habitat patches across the landscape occur, especially as the intensity of management interventions increases. These changes in the habitat mosaic alter species distribution patterns, forest turnover rates, and hydrologic processes. The most severe effects described in this section, however, result from indirect consequences of logging, such as increased access to remote areas (leading to hunting and land conversion), fragmentation, and altered fire regimes (Holdsworth & Uhl 1997; Cochrane & Schulze 1999; Cochrane et al. 1999).

STRUCTURE

The size and spatial distribution of tropical forest patches and the juxtaposition and connectivity of different forest patches across the landscape are most affected by the indirect effects of logging. One of these effects—increased access for humans—often is deleterious, because logging is almost invariably accompanied by increased hunting pressure and is often followed by deforestation as lands are cleared for agriculture. Another indirect effect of logging—fragmentation of previously contiguous or otherwise connected forest patches—may have complex effects. For example, wide logging roads may represent uncrossable barriers for some forest-interior species, but roadsides with secondary vegetation attract many large ungulates, where they are more easily hunted (Robinson & Bennett 2000).

The degree of fragmentation depends on whether logging is dispersed over large areas or is concentrated in small areas (Fig. 3). Where preservation of forest-interior biodiversity is the priority, concentrating logging in small areas is generally the pattern recommended by conservation biologists (Noble & Dirzo 1997). Fortunately, due to associated cost savings, concentration of logging activities is one of the steps toward improved forest management that loggers may find acceptable.

Long-term species maintenance is also influenced by whether logged stands are interspersed within species-rich forest or in a low-diversity landscape dominated, for example, by pulpwood plantations. Even small, unlogged patches within harvest areas can serve as source populations for some species after logging.

COMPOSITION

Logging activities may directly and indirectly affect the identity, distribution, and proportion of habitat types in tropical forests. Forestry may directly affect the composition of the landscape component of biodiversity by intentional creation of new types of habitats (e.g., forests converted into plantations). Furthermore, if silvicultural objectives are uniform across the landscape, inter-stand diversity is sacrificed by widespread application of the same stand "improvement" treatments. Perhaps most important, improved access provided by logging roads indirectly fosters post-logging habitat changes by human forest colonizers, weeds, and wildfires.

Setting aside reserves within logging areas may mitigate some of the deleterious effects of logging and other silvicultural treatments. The specific location of reserves substantially influences their value in biodiversity conservation. Optimally, the full range of landscape features and habitats should be represented within protected areas.

FUNCTION

Logging may markedly alter several landscape-level ecological processes subsumed under the functional attribute of the landscape component of biodiversity. For example, logging roads and activities associated with their construction can greatly influence the permanence of the forest fragments they create by altering landscape-level disturbance regimes. In large part, disturbance is altered because roads and skid trails provide ready access to the forest for both colonists and fire. High-intensity and widespread logging, especially if not carefully controlled, also influences hydrological processes at all levels, perhaps including the regional climate. Where logging roads are wide and logging intensities are high,

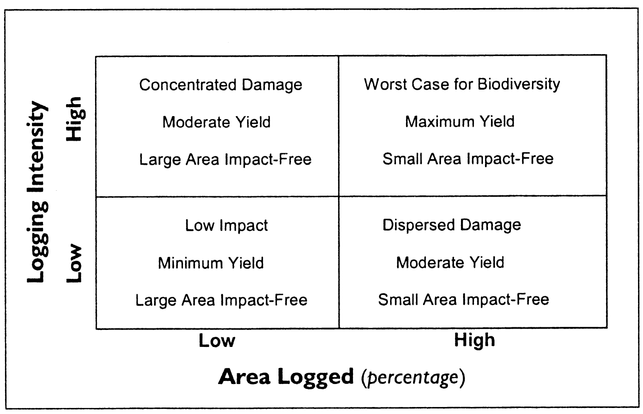

Figure 3. Some effects of logging on biodiversity as a function of distribution of logging activities (percentage of area logged) and logging intensity (m^3/ha of timber harvested).

landscape-level movements of animals can be disrupted (Goosem 1997), as can gene flow in plants when pollinators are restricted to isolated fragments by inhospitable surroundings. It should be noted, however, that the effects of roads depend on where and how they are constructed and change with time as the road and its margins mature (Lugo & Gucinski 2000).

Ecosystem Effects

The deleterious ecosystem-level effects of logging on tropical forests are widespread, substantial, enduring, and well studied, especially compared with landscape and genetic components. The ecosystem component of biodiversity is somewhat more sensitive to logging than the landscape component in part because management activities are usually implemented at this scale. In contrast to the landscape component, most ecosystem-level effects are a direct consequence of logging activities. Logging purposely removes biomass from ecosystems, but it also alters their vertical complexity and soil characteristics. Depending on the silvicultural objectives, changes in structural heterogeneity may be intended. Whether intended or not, the structural effects of logging alter the relative proportions of life forms, biogeochemical stocks, nutrient and hydrologic cycling, productivity, and energy flows.

STRUCTURE

Logging may affect the structural attribute of the ecosystem component of biodiversity by changing the biophysical properties of soils, spatial heterogeneity of forest stands, and biomass. The extent and types of ecosystem damage to these structural attributes depend on logging intensity, the yarding system, and the care with which the operations are conducted. Soil compaction, for example, is a major problem during ground-based yarding operations, especially where skid trails are unplanned and yarding continues during wet weather. Compaction negatively affects hydrology, which in turn alters the characteristics of watercourses. Where compaction is severe, soil permeability and bulk density often require many decades to recover. Exposure of mineral soil after litter layers and root mats are bladed off by bulldozers is also a concern. Disruption of mineral soil occurs during bridge building, road construction and maintenance, and skidding operations—forest-management activities that affect ecosystem structure and thereby biodiversity.

Another effect of logging on ecosystem-level structure is reduction in biomass and alteration of necromass. Losses of biomass due to forest-management activities include the amounts in the removed timber, damage to trees in the residual stand that result in mortality, and silvicultural treatments that result in tree death. Biomass losses range from 5–10 Mg/ha at the lowest logging intensities to substantially greater amounts where heavy logging is followed by poison girdling of noncommercial trees in the residual stand. Necromass, including coarse woody debris, increases immediately after logging but may then decrease to levels below prelogging conditions because of increased temperatures near the ground and associated increases in decomposition rates. Wildfires promoted by construction of logging roads and canopy opening and controlled burns carried out for silvicultural purposes can have obvious effects on biomass and necromass stocks in tropical forests.

Maintenance of healthy communities, species populations, and gene pools is predicated upon protection of hydrological functions, nutrient cycles, and other ecosystem properties. Fortunately, methods for mitigating the ecosystem-level effects of logging on tropical forests are well known. Switching from ground-based to skyline yarding techniques, for example, greatly reduces damage to residual stands, soils, and streams but allows harvest on steep slopes. The opposite trend in technological change also can have environmental benefits: log yarding with draft animals or by manual means generally results in substantially less logging damage than yarding with bulldozers (Cordero 1995). To reap these potential benefits, the expertise of experienced forest engineers should be called upon more often where logging does have to occur.

COMPOSITION

Logging affects ecosystem-level compositional attributes of biodiversity by changing biogeochemical stocks. For example, soil compaction reduces water-holding capacity, which in turn leads to increased surface runoff. Limited storage capacity in natural streams is further reduced by sedimentation, which means flow regimes can be greatly modified by logging, especially during the first years after logging is completed. Various RIL techniques, such as installation of cross drains on skid trails, can greatly diminish these effects.

FUNCTION

Logging affects the functional attributes of ecosystem-level biodiversity by adversely affecting hydrological and biogeochemical fluxes as well as productivity. Reduced plant productivity results in part from impeded root growth, a further consequence of logging-induced soil compaction. Because most of the available nutrients are usually found near the top of the soil profile, blading of the soil surface also diminishes nutrient availability in local areas and otherwise interferes with nutrient cycling. In more extensive portions of logging areas where RIL guidelines are not followed, nutrient cycling and hydrological functions are greatly modified by reduced canopy interception of rain and mist, decreased uptake of water and nutrients by the diminished biomass, and increased occurrence of surface erosion and landslides associated with improperly located and poorly constructed roads and skid trails.

Changes in carbon storage and flux associated directly and indirectly with logging and other silvicultural activities influence whether forests are net sources or sinks of "greenhouse" gases. For example, substantial logging-induced transfers of living trees to coarse woody debris can have substantial effects on understory structure and dynamics, leading to more carbon release. The deleterious effects of logging on forest carbon balance can be greatly diminished by application of RIL techniques (Pinard & Putz 1996). Substantial biodiversity benefits are also likely to result from RIL, but they have not been well studied. Other silvicultural treatments, such as fire management, weed control, thinning, and enrichment planting, have various effects on both greenhouse-gas emissions and biodiversity which should be investigated.

Community Effects

Logging, especially if followed by silvicultural treatments such as liberation of future crop trees from competition, can substantially change the physiognomy, composition, and trophic structure of forest stands. To a large extent, these modifications represent the goal of forest "refinement" treatments applied to increase volume increments and relative densities of commercial timber species. This "stand domestication" by nature reduces species richness; rare, threatened, and endangered species may become locally extinct, especially if they have no perceived commercial value. These changes in composition and structure affect numerous community-level ecological processes, including colonization, predation and mortality rates, pollination, seed dispersal, and timing and abundance of flower and fruit production.

STRUCTURE

The most obvious logging-induced effect on the structural attributes of community-level biodiversity is the change in proportions of successional stages in forest stands. Depending on harvesting intensities, planning of roads and skid trails, and training and supervision of workers, logging can result in large changes in the proportion of forest in mature, recovering, and early successional stages. In some severely disturbed areas, succession might be "arrested" by post-logging proliferation of vines, bamboo, and other nonarboreal growth forms. Silvicultural treatments such as thinning and vine cutting can increase the rate of succession and increase the proportion of stand growth concentrated in commercial species, but not without affecting biodiversity in more than the intended ways.

COMPOSITION

In the community component of biodiversity, logging affects composition by changing (often purposefully) the relative abundance of species and guilds inhabiting forest stands. The relative abundance of tree species with light-demanding versus shade-tolerant regeneration, wind- versus animal-dispersed seeds, vertebrate- versus invertebrate-pollinated flowers, and thick versus thin bark, for example, are all subject to change in logged and otherwise silviculturally treated forests. Likewise, representation of different guilds of animals (e.g., understory insectivores and arboreal folivores) is influenced by forestry activities. Depending on a great number of factors related to the intensities, spatial scales, and modes of forest intervention, as well as characteristics of the focal taxa, effects of forestry activities can be negative, positive, or neutral. For example, in eight studies that considered the effects of logging on frugivorous birds, two reported positive effects at the guild level, three reported negative effects, and three reported no change at all (Putz et al. 2000*b*).

FUNCTION

The functional aspects of community-level biodiversity include numerous key ecological processes, such as pollination, herbivory, seed dispersal, and predation, all of which are affected by logging, especially under the most intensive management interventions. Many of the effects on these processes are a direct consequence of altered resource abundance (e.g., fruit for frugivores or young leaves for folivores), which in turn result from the logging-induced changes in community structure and composition. In addition to being influenced by resource-base changes, these ecological processes are also affected by changes in forest microclimates that are a result of exploitation, silvicultural treatment, and hunting.

Species Effects

The species component of biodiversity has received the most attention from researchers concerned about the effects of logging and other silvicultural treatments in tropical forests. The most obvious species-level effect of logging is on the abundance and the age and size distribution of harvested and damaged trees. Depending on the intensity of logging and the care with which it is carried out, the reproduction, growth, and survival of many species can be adversely affected. In reviewing this literature, it is important to note that the taxa studied were not selected at random. Instead, in many cases the species chosen were expected to be sensitive to and thus good indicators of the effects of logging.

STRUCTURE

The most immediate and direct effects of logging on the structural attribute of the species component of biodiversity are suffered by the harvested tree species. Their populations are often left greatly depleted, especially in the larger size classes of reproductive individuals, when management is based solely on minimum-diameter felling rules. Because of the spatial clustering characteristic of many commercial timber trees, the richest patches of forest are generally the most severely disturbed unless logging guidelines specify minimum spacing between harvested trees.

Changes in forest structure are suffered most by specialist species of the forest interior. After logging, many formerly shaded microenvironments in the forest interior become drier, brighter, warmer, and more easily exploited by some predators. For example, severe canopy opening adversely affects litter invertebrates and their predators. For species that are generalists in their diets and wide-ranging in their habitat use, such as many frugivorous canopy birds, the direct effects of logging vary from somewhat negative, to neutral, to positive. For the understory species that are adversely affected by logging, the effects may persist for decades (Wong 1985; but see Lee et al. 1998).

The effects of logging and stand-refinement treatments on species are of particular concern in small forest management units. Private landowners with <100 ha to manage, for example, may be unwilling to set aside 10% of their forest for species preservation. If their forests are surrounded by similarly managed or deforested areas, then blanket application of stand-refinement treatments or heavy logging can take a substantial toll on commercial and noncommercial species alike.

COMPOSITION

Logging affects the composition of species-level biodiversity by changing the abundance and distribution of species. Unless logging is accompanied by other silvicultural treatments designed to foster their reproduction and growth, the abundance and population structure of the harvested tree species are greatly modified by logging. Logging effects on tree populations continue for many years after logging is completed because damaged trees suffer high mortality rates, proliferation of weeds (e.g., vines) interferes with tree reproduction and survival, and population size reduction and fragmentation can decrease pollination levels and change the pattern and intensity of seed dispersal and predation. The species composition of animals also changes in response to the direct effects of logging such as canopy opening and associated indirect effects such as increased fire frequency and intensity, hunting, and forest conversion. Changes in species composition in response to forestry operations are by no means consistent across or even within taxa. Our review of the literature on primates, for example, revealed few cases of consistent responses of species to logging. This variation can be attributed to differences in logging intensity and to differences in the duration of post-logging population monitoring. Silvicultural treatments other than logging, especially vine cutting and crown liberation of future crop trees, might have more consistent deleterious effects on canopy animals, but such effects have been little studied.

Small fragments of untouched forest that remain within even heavily logged forests serve as important refugia for plants and animals. Wildlife densities in these unlogged fragments can be very high during and shortly after harvesting, but then diminish as animals recolonize the surrounding matrix. Many "unplanned" reserves are on steep or otherwise adverse sites, which certainly influences their function as refugia.

FUNCTION

Demographic processes (e.g., survivorship, fertility, and recruitment) and growth rates are two key functional attributes of the species component of biodiversity that are affected by logging. Populations of many organisms are susceptible to large fluctuations after logging due both to the direct effects on forest conditions such as microclimate and fragmentation and to the indirect effects of increased hunting, fire, and forest conversion. The proliferation of disturbance-adapted taxa in logged forests, some species of which are not native or were not previously common in the area, can have large but as yet little-studied effects on the resident flora and fauna.

Genetic Effects

The genetic component of biodiversity is likely to be the most sensitive of all components to logging because of reductions in effective population size and interruptions in gene flow. At present, however, little is known about the genetic structure of any tropical organisms, even commercially valuable timber trees (Ledig 1992). Furthermore, the techniques required for assessing the genetic structure of populations are sophisticated and expensive. Except in a few cases, concerns about dysgenic selection, genetic drift, and other genetic problems are based on controversial theory that is developing rapidly as evidence accumulates.

STRUCTURE

Logging affects the structural attribute of the genetic component of biodiversity by reducing effective population sizes and heterozygosity. Effective population sizes of both commercial and noncommercial species are reduced by harvesting, other silvicultural treatments, forest fragmentation, weed proliferation, and wildfires. There are also good reasons to be concerned about the effects of logging and stand-improvement treatments on dioecious species and in small forest-management units in which population sizes of all species are correspondingly small. Allelic frequencies of commercial species change after removal of a large proportion of healthy reproductive adults. For species with high densities of advanced regeneration, the genetic structures of their populations are unlikely to change dramatically after selective harvesting unless collateral damage is severe. Timber stand-improvement treatments also may affect the genetic structure of species targeted for removal (e.g., woody vines) and their associates, but these effects apparently have not been studied. Given the high proportion of vines and other plants that resprout after cutting (coppice), large effects on genetic structure are unlikely.

COMPOSITION

The fact that most species are rare in tropical forests implies that allelic diversity will decrease with increasingly intensive management interventions. Unregulated harvesting of all merchantable individuals of a commercial species, for example, has immediate effects on allelic frequencies that continue to change due to decreased effective population sizes. Deleterious recessive genes may become more apparent as a result of dysgenic selection, and heterozygosity may decline due to the bottleneck effect in the small, isolated populations that result from harvesting, forest fragmentation, and other direct and indirect effects of forestry activities (Styles & Khosla 1976; Murawski et al. 1994*a*, 1994*b*; but see Newton et al. 1996).

FUNCTION

Logging may affect the functional attribute of the genetic component of biodiversity by interrupting gene flow, which in turn influences outbreeding rates. Decreased effective population sizes, coupled with losses of pollinators and seed-dispersal agents, can result in reduced gene flow and inbreeding depression in populations of both commercial and noncommercial species. Especially vulnerable are populations represented by scattered mature individuals and few juveniles (e.g., many "long-lived pioneers" such as the mahoganies). Given the high proportion of tropical tree species that are dioecious or obligate outcrossers, only severe reductions in effective population size are likely to have much effect on gene flow (Ghazoul et al. 1998).

Overview of Biodiversity Conservation in Relation to Logging and Other Silvicultural Treatments

Figure 4 graphically displays the effects of logging on tropical forests based on the various components and attributes of biodiversity. Along the vertical axis of our framework, the five components of biodiversity are arrayed in the order of increasing susceptibility to logging effects: landscape, ecosystem, community, population/species, and genetic. The horizontal axis arrays a variety of approaches to silviculture in order of increasing intensity.

We assessed the effect of these silvicultural approaches on each biodiversity component based on three categories. First, each biodiversity component was scored as "mostly conserved" for cases in which their attributes were expected to usually stay within their natural range of variation. Second, biodiversity components were scored as "affected" for cases in which their attributes were expected to frequently fall outside their natural range of variation. Finally, biodiversity components were scored as "mostly lost" for cases in which their attributes were expected to almost always fall outside their natural range of variation.

The scoring process used for Fig. 4 was admittedly subjective; the scores were based on a reading of the literature and the authors' experience. We fully recognize that particular situations might warrant dif-

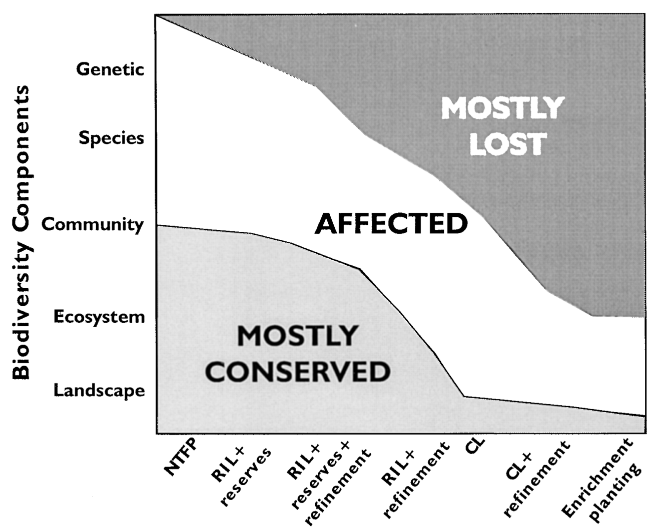

Figure 4. Expected effects of a range of forest uses on the components of biodiversity. Abbreviations: NTFP, nontimber forest products; RIL, reduced-impact logging; reserves, protected areas with forests managed mainly for timber; refinement, silvicultural treatments such as liberation of future crop trees from competition, which can substantially change the physiognomy, composition, and trophic structure of forest stands that are applied to increase volume increments and relative densities of commercial timber species; CL, conventional logging; enrichment planting, increasing the stocking of commercial species by planting seedlings (or seeds) in logging gaps or along cleared lines.

ferent scores, and we emphasize that our purpose is to illustrate what is believed to be a useful analytical process rather than to obtain perfectly accurate scores. This framework also serves to suggest important research topics for conservation biologists from a number of disciplines.

The responses summarized in Fig. 4 actually represent a multitude of effects from a diversity of silvicultural approaches applied with varying degrees of concern for biodiversity over a large range of scales. Figure 4 addresses neither the issue of profitability of different forest uses nor issues related to land-use capability, biodiversity value, or the capabilities and desires of local stakeholders. At least two other dimensions of this multidimensional topic are captured in Fig. 5, which indicates that every forest activity can be carried out over a range of intensities. Correspondingly, each forest-use activity generates timber volumes and financial profits that also vary widely (Fig. 6). Recognizing that forest-use practices vary over time with, for example, market fluctuations and political change, and that biodiversity effects are a function of a multitude of interacting factors operating at different temporal and spatial scales, we hope that Figs. 4–6 present an accurate "snapshot" of the relationship between biodiversity conservation and forest management.

The effects summarized in Fig. 4 and the ranks and ranges of effects and profits in Fig. 5 are based on a combination of literature reviews and the authors' subjective estimations. For example, under the range of stocking levels, terrain, and accessibility in which logging is carried out, reduced-impact and conventional logging overlap in both effects and profitability. Nevertheless, particularly where logging is conducted on steep slopes or under otherwise adverse conditions, application of most RIL guidelines results in immediate profits lower than those of unconstrained conventional logging. This observation helps explain why areas where regulations are nonexistent or unenforced are likely to be logged by conventional methods. Correspondingly, some of the effects of high-intensity RIL overlap those of low-intensity conventional logging, but the former generally has fewer adverse environmental effects than the latter.

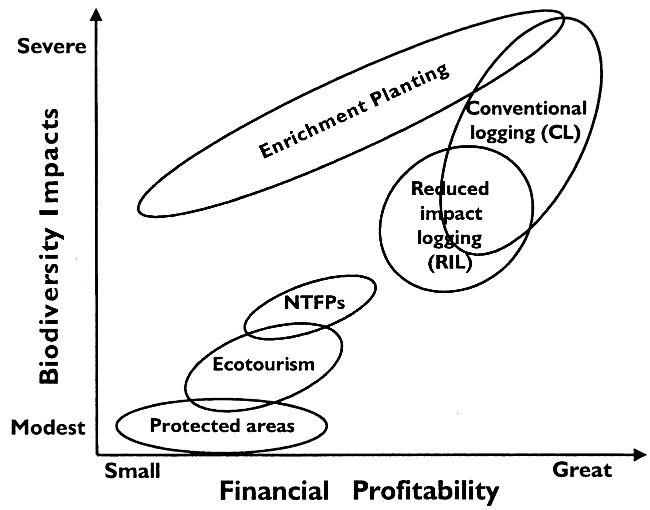

Figure 5. Generalized biodiversity effects plotted against expected short-term financial returns to forest owners or concessionaires (NTFPs, nontimber forest products).

Conclusions

Recognizing that all significant interventions in natural forests have effects on biodiversity, all silvicultural decisions necessarily represent compromises. Management for some goods or services necessarily involves management against some others. What are "weeds" to timber-stand managers are food sources, rare species, carbon stores, or intercrown pathways for other human and nonhuman stakeholders. The biodiversity compromises involved in deciding whether to cut vines, retain seed trees, or enhance seedling establishment by carrying out controlled burns should be informed by research. Unfortunately, little is known about how tropical forests can be best managed to enhance biodiversity. Researchers have instead focused on enumerating the deleterious environmental effects of uncontrolled logging by untrained and unsupervised crews. To inform decisions about tropical forest management and to assure that biodiversity is protected to the maximum extent, more research is needed on how to maintain diversity in forests selected for logging. The large and rapidly growing body of literature on ecosystem management in both northern and southern temperate forests (Kohm & Franklin 1997; Lindenmayer 1999) should provide inspiration and starting points for tropical researchers intent on solving forest-management problems associated with biodiversity.

The primary conclusions to derive from these analyses are that (1) different intensities and spatial patterns of timber harvesting, along with other silvicultural treatments, result in different effects on the different components of biodiversity; (2) some components and attributes of biodiversity are more sensitive than others to forest-management activities; and (3) only extremely limited use will protect all components (i.e., large protected areas are essential for biodiversity conservation).

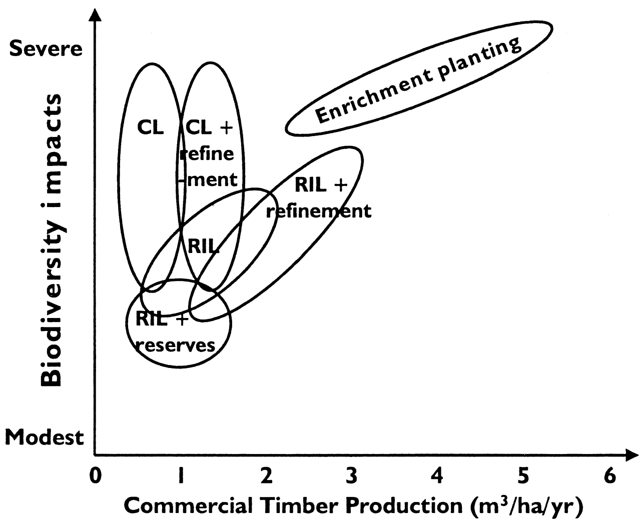

Figure 6. Generalized biodiversity effects resulting from different approaches to forest management for timber (CL, conventional logging; RIL, reduced-impact logging; refinement, any of a variety of silvicultural treatments applied to increase rates of timber volume increment; reserves, set-asides within harvested areas).

The capacity to mitigate the deleterious environmental effects of logging and other silvicultural treatments should not be construed as constituting support for sustainable forest management as a conservation strategy. Such an endorsement is unwarranted given widespread illegal logging in the tropics, widespread frontier logging and logging of areas of high priority for biodiversity protection, the persistence of poor logging practices despite substantial efforts in research and training, and the general slow rate at which most loggers are transforming themselves from timber exploiters into forest managers. Nevertheless, even the most harshly treated forests maintain more biodiversity than tree farms for pulpwood, oil palm plantations, maize fields, or cattle pastures. Furthermore, logging is often the least environmentally damaging of land uses that are also financially viable (Pearce et al. 1999). Given these conclusions, effective mechanisms for financing forest protection and environmentally sound forest management are needed.

By focusing on the deleterious environmental effects of tropical forest management activities, we often lose sight of the fact that, from the perspective of biodiversity maintenance, natural forest management (i.e., maintaining forests as forests) is preferable to virtually all land-use practices other than complete protection. As forest-management practices improve under market pressure or pressure from landowners, the deleterious environmental effects of logging and other silvicultural activities are likely to be substantially reduced. Forests that are carefully managed for timber will not replace protected areas as storehouses of biodiversity, but they can be an integral component of a conservation strategy that encompasses a larger portion of the landscape than is likely to be set aside for strict protection. In other words, forests managed primarily for timber will supplement and effectively extend the conservation estate if they are managed properly. Finally, it should be recognized that landscape management is consistent with the ecosystem approach emphasized by the Convention on Biological Diversity.

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