Future Directions

In this brief review I have attempted to summarize how deforestation and fragmentation can influence biological systems. However the field of fragmentation biology remains a dynamic and exciting one, and there is still much to learn regarding the structure and functioning of fragmented forests. For instance the precise ecological mechanisms responsible for most local extinctions from fragments are still unknown, as are the details regarding the dispersal of plants and animals between the remaining patches of forest. Finally, while the populations of plants and animals surviving in fragments continue to be the subject of considerable research, one cannot understate the importance of the matrix habitat in which these fragments are embedded. Some types of matrix habitat are better at mediating the impact of abiotic changes, while others have a higher diversity of species regenerating in them. Perhaps most importantly, matrix habitat influences the movement of plants and animals in fragmented landscapes. These movements are critical, since they may be sufficient to ameliorate population declines or inbreeding depression in fragments. All of these differences are dependent on how the land was managed immediately following forest clearing, therefore understanding the biological dynamics of forest fragments will require not only a greater understanding of what happens inside them, but also of what goes on in the habitat that surrounds them.

See also: **Biodiversity**: Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Human Influences on Tropical Forest Wildlife; Plant-Animal Interactions in Forest Ecosystems; Reproductive Ecology of Forest Trees. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Forest Management for Conservation. **Landscape and Planning**: Landscape Ecology, the Concepts. **Soil Development and Properties**: The Forest Floor. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation.

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Human Influences on Tropical Forest Wildlife

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Introduction

Different patterns of anthropogenic forest disturbance can affect forest wildlife in both tropical and temperate regions in many ways. The overall impact of different sources of structural and nonstructural disturbance may depend on: (1) the groups of organisms considered; (2) the evolutionary history of analogous forms of natural disturbance; and (3) whether forest ecosystems are left to recover over sufficiently long intervals following a disturbance event. The wide range of human-induced disturbance events are widely variable in intensity, duration and periodicity and are often mediated by numerous economic activities including timber and nontimber resource extraction, other causes of forest degradation, forest fragmentation, and forest conversion to other forms of land use. Examples of human enterprises that can severely affect wildlife may include hunting, selective logging at varying degrees of intensity, slash-and-burn agriculture, plantation forestry, selective removal of the understory to produce shade-tolerant crops, and outright deforestation for large-scale livestock operations. The resulting faunal assemblages can be drastically disfigured in highly modified forest landscapes compared to those in truly undisturbed forest lands containing a full complement of plant and animal species, which are being rapidly confined to the best-guarded strictly protected areas or the remote, roadless wildlands in the last remaining pristine forests.

In this article, we focus on tropical forests rather than their temperate counterparts because tropical forests arguably present the greatest challenge to global biodiversity conservation. We also focus on forest vertebrates because the effects of human disturbance on tropical forest invertebrates remain poorly known. Within the terrestrial vertebrates, most of our examples come from bird and mammal studies because effects of disturbance on reptile and amphibian assemblages remain poorly understood. We illustrate this discussion and review the evidence from the literature and our own field studies on the basis of three increasingly ubiquitous types of human disturbance in forest lands with severe consequences to the vertebrate fauna – hunting, selective logging, and wildfires.

Hunting

Hunting is perhaps the most geographically widespread form of human disturbance in tropical forests, although the total extent of this form of nontimber resource extraction cannot be easily mapped using conventional remote sensing techniques. Many parts of west Africa, Southeast Asia, and the neotropics are becoming chronically overhunted, partly as a result of burgeoning human populations that often escape to and become marginalized in frontier regions. Exploitation of wild meat (the meat from wild animals often referred to as bushmeat) by tropical forest-dwellers has also increased due to changes in hunting technology, scarcity of alternative protein sources, and because it is often a preferred food. Large-bodied game birds and mammals providing highly desirable meat packages and hunted for either subsistence or commercial purposes are particularly affected, because they are the main target species and tend to be associated with low reproductive rates, thus recovering slowly from persistent hunting pressure (**Figure 1**).

Estimates of Wild Meat Harvest

Studies of wild meat harvest tend to be approached at the level of subsistence communities, where wild animals can be intercepted, or market and restaurant surveys. These studies tend to severely underestimate the true mortality because many of the animals intentionally or incidentally killed in the forest are not retrieved, thus not translating into meat consumed at the level of villages, markets, or informal sales. The species most threatened by hunting may also be rarely seen in markets, because they were already at very low population densities.

Figure 1 A young Kaxinawa Indian hunter showing a recently killed howler monkey (*Alouatta seniculus*) and a white-faced capuchin (*Cebus albifrons*), which are unsustainably harvested at his indigenous reserve in western Acre, Brazilian Amazonia.

Subsistence Hunting

Subsistence game hunting can often have profound negative effects on the species diversity, standing biomass, and size structure of vertebrate assemblages in tropical forests that otherwise remain structurally undisturbed. This occurs mainly through local population declines, if not extirpation, of large-bodied vertebrate taxa which make a disproportionately large contribution to nonhunted forests in terms of their aggregate biomass and role in ecosystem functioning. Overharvested forest sites where large game species have been depleted thus tend to be dominated by small-bodied species that are either bypassed or ignored by hunters. Regardless of the nature of density compensation by small-bodied species following the local extinction of large vertebrates, important species interactions or ecosystem functions associated with large body size such as dispersal of large-seed plant species and herbivory of tree seedlings may no longer take place.

Overhunting

Overhunting of wildlife for meat consumption has reached an unprecedented scale across the humid tropics, causing local extinction of many vulnerable species. Yet productivity of tropical forests for wild meat is at least an order of magnitude lower than that of tropical savannas, and can only support fewer than 1 person per square kilometer if they depend entirely on wild meat for their protein. Reasons why the scale and spatial extent of hunting activities have increased so greatly in recent years include human population growth and migration; severe reduction in forest cover and nonhunted source areas; increased access via logging roads and paved highways into remote forest areas allowing hunters to harvest wild meat for subsistence or cash; the use of efficient modern hunting technologies especially firearms and wire snares; and, in some regions, greatly increased trade in wild meat. Forest defaunation driven by wild meat hunters has therefore become one of the most difficult challenges for tropical forest wildlife conservation.

In addition to drivers of the bushmeat harvest, wildlife depletion in tropical forests can be driven by extractive activities targeted to other desirable animal parts or products, including skins, feathers, ivory, horns, bones, fat deposits, eggs and nestlings, as well as live-captures of juveniles or adults for aviaries, aquaria, and the pet trade. These activities are often poorly regulated in the humid tropics, and have been responsible for wholesale extinctions of many target species.

Aggravating Effects

In frontier tropical forest regions, hunting and other forms of offtakes often co-occurs with different patterns of forest disturbance that can either aggravate or buffer the detrimental effects of faunal exploitation. For instance, effects of hunting are likely to be considerably aggravated by isolated forest fragmentation because fragments are more accessible to hunters, allow no (or very low rates of) recolonization from nonharvested source populations, and may provide a lower-quality resource base for the frugivore–granivore vertebrate fauna. On the other hand, selective logging may actually boost the local densities of large terrestrial browsers by puncturing and opening up the canopy, thus enhancing the understory productivity through a more favorable light environment. Likewise, slash-and-burn agriculture associated with long-term rotation of a successional mosaic can generate attractive foraging areas for populations of large herbivorous rodents and ungulates, as well as species preferring second-growth. We therefore turn to other important forms of anthropogenic disturbance involving structural changes to wildlife habitats in tropical forests.

Selective Logging

Selective logging is a major anthropogenic disturbance event in tropical forests, affecting around 15 000 km^2 a year of forest in the Brazilian Amazon alone. As only a small proportion of the remaining tropical forests is expected to be strictly protected within reserves, there is much debate over whether timber production can be reconciled with biodiversity conservation. For wildlife, the crucial issues are whether populations of species of conservation importance can be maintained within a matrix dominated by logged forests. However, despite the growing amount of literature documenting the effects of selective logging on the abundance and distribution of forest wildlife, the lack of agreement between studies means that few conclusions can be drawn. The disparity is highlighted by a recent review. In eight studies on the effects of logging on the forest avifauna, frugivorous birds were found to increase, decrease and to remain unaffected, whilst the same range of responses were demonstrated in different studies on forest chimpanzees (*Pan troglodytes*).

There are four major reasons why these studies have failed to find consistent results. Firstly, the effects of logging can be strongly influenced by the time elapsed since logging occurred, the number of recurrent logging events, the severity of the logging operation and extraction methods used, and the composition of the surrounding landscape. Secondly, sampling techniques are rarely standardized between studies. Effects may differ across different spatial and temporal scales, and by whether sampling focuses on understory species, canopy species, or species from all forest levels. Studies also differ depending on whether they examined tree fall gaps, or the entire logged forest matrix, in the latter case capturing many disturbance-intolerant species that are able to persist in unlogged refugia. Thirdly, some of the differences may be explained by geographic and historical factors. Production forests occur throughout the tropics, capturing many faunas that are unlikely to be equally adapted to disturbance. In the neotropics alone, logging appears to have greater impacts on the Amazonian avifauna than that in the Atlantic forest or in Belize, a difference that can be attributed to the more intensive history of natural disturbance events in those areas. Finally, few studies have incorporated the synergistic effects of other forms of disturbance that co-occurs with logging, including fires, edge effects, and area effects resulting from forest fragmentation (**Figure 2**).

Patterns of Adaptation

Despite these problems, some general patterns have become apparent. By opening up the canopy, and shifting much of the primary production to the understory, logging tends to simplify the vertical stratification of forest species. Both bird and butterflies typical of the canopy layer may begin to forage at lower levels, replacing many of the highly specialized shaded understory species that are adapted to foraging within the dark forest interior of undisturbed primary forest. This shift in productivity may also favor many large terrestrial browsers, and may boost the abundance of elephants, okapis, and duikers in African forests, or pacas, brocket-deer and tapirs in neotropical forests. The same may be true for highly folivorous arboreal mammals such as colobine primates and howler monkeys in African and neotropical forests, respectively. Across all taxa, specialists with narrow niches tend to decline whilst generalists that are able to switch between resources tend to increase. This is illustrated in primate populations; unripe seed and ripe fruit specialists such as bearded sakis (*Chiropotes* spp.) and spider monkeys (*Ateles* spp.), respectively, tend to decline in highly selectively logged forests, whilst generalists such as brown capuchins (*Cebus apella*) may increase.

Effect of Logging Method

One crucial factor in the overall impact of a logging operation is the method used for timber harvest and extraction, which will determine the proportion of the forest area affected by canopy gaps where the understory light environment is significantly different.

Figure 2 A roundlog loading bay and logging road in the Brazilian Amazon.

Selective logging operations targeting commercially valuable species accounting for considerably less than 1% of the forest basal area can result in as little as 5% and as much as 40% of collateral damage to nontarget species in the remaining stand. The level of collateral damage is context-dependent in terms of the size of trees, abundance of woody lianas spreading over adjacent tree crowns, terrain topography, and hydrology, but tends to increase with heavy mechanized machinery such as operations in which roundlogs are dragged out over long distance by bulldozers. Collateral damage is lowest where the extracted roundlogs can be floated out in the case of seasonally inundated forests, or removed by a system of steel cables or even cargo helicopters, or where the timber can be sawed *in situ* and removed by less destructive methods. Another important factor is whether the timber species targeted by loggers are important food sources for forest wildlife, and how crucial these are for a particular vertebrate assemblage when these food resources become available. For instance, the systematic offtake of important fruiting species may have a far greater impact on highly frugivorous species, particularly if these fruit crops would otherwise become available during annual periods of food scarcity.

Although changes in species abundance and distributions are common, the complete extirpation of species from logged forest has been rarely recorded. Most primary forest specialists merely exist at low population densities, utilizing small unlogged patches until the forest becomes suitable for recolonization. As a result, timber production has been promoted as a means of biodiversity conservation, as it is seen to provide an economic justification for large tracts of tropical forest outside protected areas. Management of the logging methods can substantially reduce their impact on forest structure (actually increasing long-term yields), whilst careful planning of unlogged refugia and corridors may ensure the survival and recolonization of disturbance-sensitive species. Despite these mitigation measures, timber production cannot be seen as a panacea to the problems of forest wildlife conservation in the tropics. Reduced impact methods are rarely used, and still account for a very small proportion of the logging concessions in the tropics. Furthermore, very little data exist on the effects of repeated timber harvests at variable intervals, a necessary component if production forests are to remain economically viable. Indeed, this may lead to structurally homogeneous forests unlikely to maintain the full array of biodiversity found in primary forest. Logging may also disrupt many of the complex interactions between species, the effects of which may not be noticeable in the short term.

Finally, logging cannot be examined in isolation from other forms of forest disturbance. The creation of logging camps, logging roads, and skidding trails generates greater demand for bushmeat and access to previously undisturbed forest, which greatly increases local hunting pressure. The logging access matrix also accelerates the rate of forest clearance for agriculture, and the associated effects of forest edges and fragmentation, which combined with the higher density of tree-fall gaps can greatly enhance both the risk and potential severity of wildfires in seasonally dry forest. These secondary effects are not restricted to conventional selective logging, but can also result from reduced-impact logging operations associated with lower levels of canopy damage. Without appropriate and enforceable postlogging restrictions, the role of timber production in conserving forest wildlife will be diminished well beyond the immediate impact of logging itself.

Forest Wildfires

Historically, fire events in tropical forests have been rare and largely associated with the mega El-Niño Southern Oscillation (ENSO) events of the past 7000 years. However, within recent years understory wildfires have become increasingly common events in tropical forests: in the 1997–1998 ENSO year fires burned around 17 million ha of lands in Indonesia and Latin America alone, much of which was tropical forest. Three factors explain this unprecedented increase of tropical forest fires, all of which can be related to anthropogenic activity:

1. Human-induced climate change exacerbates wildfire hazards by increasing the frequency and intensity of ENSO events, which cause abnormally long droughts in the dry season and allow normally fire-resistant forests to become flammable.
2. Selective logging lowers the flammability threshold of forests by reducing canopy cover and understory humidity, whilst increasing the amount and continuity of fine and coarse fuel loads on the forest floor.
3. Tropical agricultural practices are often heavily reliant on fire, ensuring that seasonally flammable forests are never far from ignition sources.

The consequences of these fires to forest structure and composition will depend on their severity, as well as the history of fires in a given forest ecosystem. Initially, low-intensity surface fires move slowly through the leaf litter, burning the fine and coarse fuel layer. Under normal fuel loads and humidity conditions, flame heights rarely exceed 10–30 cm. However, these fires serve to increase greatly the fuel load and open up the canopy, so that recurrent burns will become much more intense, scorching the canopy layer, and killing many of the surviving trees that remain after the first burn. Because of their recent historical rarity, very few studies have documented the effects of accidental fires on forest wildlife; the following is based on information from a small number of studies conducted in Amazonia and Southeast Asia, and outlines the effects of fires in their immediate aftermath, up to 1 month, and 1 to 3 years thereafter. However, considering that this is a recent phenomenon and the possible range of postburn responses, these conclusions cannot be generalized to all contexts.

Fire-Induced Mortality

Reports of the initial fire-induced mortality appear to be inconclusive. In Sumatra, the lack of animal carcasses following the fire was taken as evidence that most birds and mammals were able to escape the fire. However, in the Brazilian Amazon there is evidence of substantial mortality in several groups of terrestrial vertebrates including tortoises, tinamous, armadillos, and caviomorph rodents, whilst even more mobile arboreal species such as toucans, parrots, and some primate species can succumb to the fires, presumably through smoke asphyxiation. In high-intensity fires in forests burning for the second time, even large, highly mobile mammals, such as the collared peccary (*Tayassu tacaju*) and brocket deer (*Mazama* spp.), can be killed by the fires.

Many understory birds and forest lizards appear to be absent 1 month after the fires, perhaps reflecting the conspicuous lack of foraging opportunities in the scorched understory. Some canopy frugivores are also less abundant. In Sumatra, two hornbill and two primate species had either declined or become absent from burned forest, whilst in Amazonian forests many surviving canopy trees shed or aborted their fruit crops, leading to declines in the abundance of frugivorous primate species. These declines may have been exacerbated by hunting, as the open understory rendered many game species as easy targets for subsistence hunters.

Post-Burn Survival

Up to 1 to 3 years after the fires, many primary forest specialists appear able to persist in lightly burned forest, though most are found at much lower densities than in adjacent unburned forest. Considering the understory avifauna, highly specialized insectivores such as the dead-leaf gleaning and ant-following species, which often contain many regionally endemic species, appear to be the most vulnerable, and often disappear from burned forest. However, species richness at small spatial scales may actually increase in burned forest, as many gap specialists and edge species invade from more disturbed areas. As with logging, fires open up the canopy and shift primary productivity to the understory. This dense postburn regeneration, often spearheaded by bamboo and some pioneer tree and liana species, appears to cause an increase in the abundance of many terrestrial browsers in an Amazonian forest, most notably collared peccaries and both species of brocket deer. It also provides these species with a temporary refuge from hunting. Frugivorous primates appear to be far more susceptible than their folivorous counterparts, although most primates species manage to persist in forests succumbing to a single fire event, and may also benefit from reduced hunting pressure.

Where fire severity increases, either because of a recurrent fire, or a high level of preburn logging activity, the effects on wildlife is considerably greater. Most primary forest species, and even many gap and specialist species, are extirpated from the dense early-successional regeneration that follows these fires, and are replaced by species typical of young second-growth. The understory avifauna in twice-burned forest is almost entirely dissimilar with that found in the unburned forest, and becomes dominated by the second-growth specialists such as the wren *Thryothorus genibarbus*. Most primate species are also absent in this highly modified habitat, and only small-bodied species typical of young second-growth such as marmosets (*Callithrix* spp.) and titi monkeys (*Callicebus* spp.) are particularly abundant.

Overall, initial low-intensity fires appear to act in a similar manner to logging, puncturing the canopy, severely altering the understory light environment, and changing the abundance of many species. This, however, only rarely results in the local extinction of disturbance-intolerant species. In contrast, recurrent fire events from as early as a second burn appear to have a much greater effect in substantially disfiguring forest structure, and represent a serious threat to forest wildlife. While no information is available on the recovery of these forests it appears that the potential for the establishment of a recurrent burn regime in many tropical forests represents one of the largest contemporary threats to wildlife, as it can lead to the conversion of extensive closed-canopy forest lands into scrub savannas. This occurs concomitantly with the local extinction of almost all the forest wildlife typical of undisturbed forest. To a large degree wildfires in the humid tropics can represent an irreversible transition into replacement fire-climax ecosystems that provide considerably lower value both in terms of wildlife habitat and key ecosystem services.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Landscape and Planning**: Landscape Ecology, the Concepts.

Further Reading

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