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

Further Reading

Brokaw N and Busing RT (2000) Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15: 183–188.
Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199: 1302–1310.
Everham EM III and Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. *Botanical Review* 62: 113–185.
Garwood NC, Janos DP, and Brokaw N (1979) Earthquake-caused landslides: a major disturbance to tropical forests. *Science* 205: 997–999.
Grime JP (1979) *Plant Strategies and Vegetation Processes*. Chichester, UK: John Wiley.
Hubbell SP (2001) *Unified Theory of Biodiversity and Biogeography*. Monographs in Population Biology no. 32. Princeton, NJ: Princeton University Press.
Hubbell SP, Foster RB, O'Brien ST, *et al.* (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554–557.
Johns RJ (1986) The instability of the tropical ecosystem in New Guinea. *Blumea* 31: 341–371.
Nelson BW (1994) Natural forest disturbance and change in the Brazilian Amazon. *Remote Sensing Reviews* 10: 105–125.
Sheil D and Burslem DFRP (2003) Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution* 18: 18–26.
Shugart HH (1984) *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. New York: Springer-Verlag.
Watt AS (1947) Pattern and process in the plant community. *Journal of Ecology* 35: 1–22.
White PS and Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62: 399–450.
Whitmore TC (1982) On pattern and process in forests. In: Newman EI (ed.) *The Plant Community as a Working Mechanism*, pp. 45–59. Oxford, UK: Blackwell Scientific Publications.
Whitmore TC and Burslem DFRP (1998) Major disturbances in tropical rain forests. In: Newbery DM, Prins HHT, and Brown N (eds) *Dynamics of Tropical Communities*, pp. 549–565. Oxford, UK: Blackwell Science.

Biological Impacts of Deforestation and Fragmentation

E M Bruna, University of Florida, Gainesville, FL, USA

Introduction

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

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

Physical Consequences of Deforestation

Habitat Loss and Insularization

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

Abiotic Changes in Forest Fragments

The abiotic conditions in forest fragments change dramatically once fragments are isolated, and these alterations are thought to drive many of the biological changes observed in fragmented landscapes. Sunlight penetrates forest fragments from above as well as laterally at the fragment's margins. Consequently, there is an increase in the amount of photosynthetically active radiation (PAR) at the forest understory. There is also an increase in understory air temperatures, frequently by as much as 8°C, and fragments become drier since the elevated temperatures and wind turbulence near fragment edges act synergistically to reduce relative humidity. Increased exposure of trees to wind results in wind throws and snapped crowns, leaving the canopy ragged and allowing additional sunlight to reach the understory. The temperature of the soil can increase markedly, and surface soil moisture can be diminished or even depleted.

These changes are not felt uniformly throughout the fragment. The intensity of these changes is spatially variable, and diminishes rapidly with increasing distance from the fragment's edge (**Figure 1**). As a result, these changes are frequently referred to as 'edge effects.' The extent to which fragments are influenced by edge effects will vary depending on fragment size, with small fragments more susceptible to environmental changes than large ones. It also depends on fragment shape, or more specifically the ratio of fragment perimeter to area. Fragments with high perimeter to area ratios, such as linear strips along roadsides, have much of their forest near edges and therefore have a greater amount exposed to harsh environmental conditions. In contrast fragments with lower ratios of perimeter to area have a greater amount of the fragment in the more buffered fragment interiors (**Figure 2**).

Abiotic changes in fragments can be ameliorated over time if vegetation outside the fragment regenerates and 'seals off' the fragment edge. Fragments surrounded by activities that maintain sharp fragment borders, such as cattle ranching or wheat farming, remain continually exposed to altered environmental conditions. Conditions in fragments can eventually return to levels similar to those found prior to fragment isolation, if cleared areas are allowed to regenerate or if agroforestry and other less intense forms of land use are adopted.

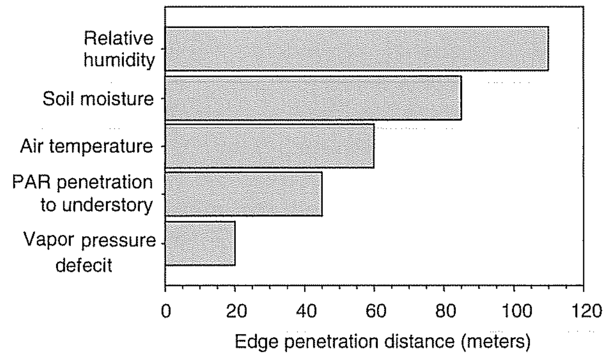

Figure 1 Edge penetration distances of abiotic changes in forest fragments. The *x*-axis indicates the distance (in meters) into forest fragments at which changes in abiotic parameters could be detected. PAR, photosynthetically active radiation. Adapted from Figure 32.1 in Laurance WF, Bierregaard RO (1997) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. Chicago, IL: University of Chicago Press with permission from the University of Chicago Press.

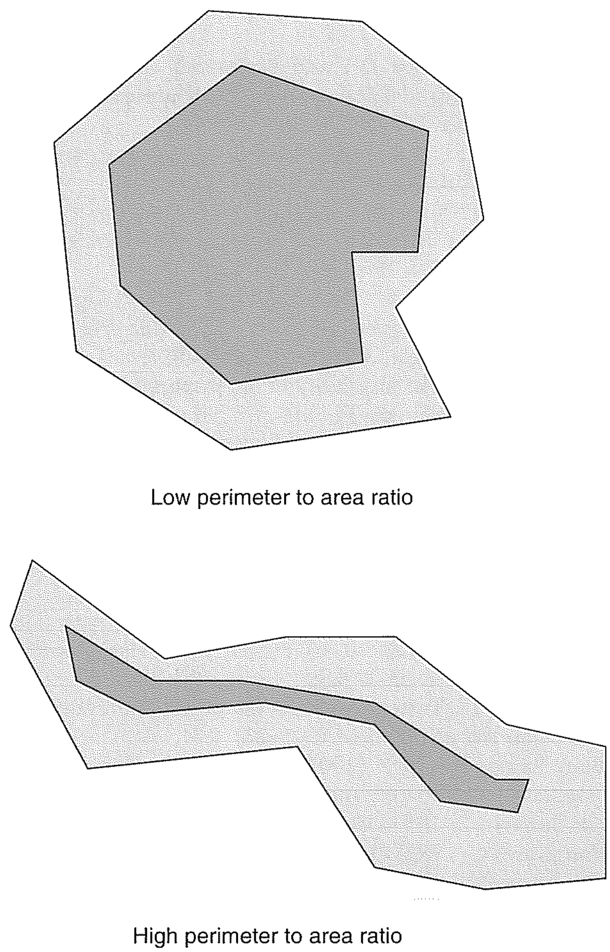

Figure 2 Influence of fragment shape on edge to perimeter ratio. The two fragments shown have approximately the same area, however the top one has a lower perimeter to area ratio. As a result, a greater proportion of the fragment is in the central core area that is buffered from edge effects (dark gray region).

Biological Consequences of Fragmentation

Changes in Individual Physiology and Behavior

As might be expected, the dramatic environmental changes in fragments can have serious consequences for the physiological condition of individuals that live there. For instance lizards in Australian rainforest fragments (*Gnypetoscincus queenslandiae*) have been found to be smaller than those in continuous forest, which could result from increased thermal variance during gestation or perhaps the reduced abundance of temperature-sensitive prey items. Similarly, temperature-related reductions in the abundance of insects could be responsible for the lower feather growth rates of the insectivorous birds *Glyphorynchus spirurus* and *Pipra pipra* in Amazonian forest fragments, though they could also have resulted from higher rates of evaporative water loss.

Plants surviving in fragments also appear susceptible to physiological changes. Some understory herbs, such as *Heliconia acuminata* (Heliconiaceae), shrink in response to the droughtlike conditions in fragments, and their leaves show signs of solar damage to the photosynthetic system. Their seeds also germinate less frequently in fragments than in continuous forest, which could be because they become buried under the leaf litter created by water-stressed trees or the light and temperature levels they use as cues to induce germination have changed. Plant mortality can also be sharply elevated in fragments, especially for the seedlings of shade-tolerant tropical trees such as *Pouteria caimito*, *Chrysophyllum pomiferum*, and *Micropholis venulosa*. Large adults of these species are also susceptible to increased mortality, since the inflexible trunks can be snapped by the gusts of wind that buffet fragment edges. Although the consequences of these changes for the long-term persistence of plant populations are unclear, they could be substantial – body size and physical condition are frequently correlated with reproductive success. It is worth noting, however, that the effects of fragmentation are not detrimental for individual physiology in all cases. For instance, individuals of *Pachira quinata*, an important timber species found in the dry forests of Central and South America, were found to develop crowns with more reproductive branches when isolated by fragmentation than when in continuous forest. This increased reproductive effort can probably be attributed to a lack of competitors in disturbed areas.

Perhaps less intuitive is the fact that forest fragmentation can also influence the behavior of individuals. An increasing number of studies have found that animals, even highly mobile ones such as migratory birds, are frequently averse to traversing roads, pastures, and the other types of clearings made by humans in forest landscapes. For example, mixed flocks of birds led by *Thamnomanes* antshrikes avoid crossing dirt roads through tropical rainforests if the vegetation along roadsides is regularly cleared. This aversion to clearing in the forest may lead to altered territory shapes and sizes, which can in turn increase the frequency of aggressive encounters between conspecifics. As might be expected, the birds will readily cross the roads again if the vegetation is allowed to regenerate.

Changes in Population Size and Genetic Structure

Ecological theory predicts that small or isolated populations are most likely to decline and become extinct, due in part to the effects of environmental and demographic stochasticity. It has therefore been hypothesized that populations in fragments will decline as well, particularly those that are in smaller or more isolated remnants. Empirical results partially support these conclusions, and the abundance of some organisms does decrease dramatically in forest fragments.

Species highly susceptible to population declines include large-bodied animals, which frequently require large areas in which to establish feeding or mating territories. Many of these species, such as the Florida panther (*Puma concolor coryi*) and black bear (*Ursus americanus floridanus*), can actually survive in a landscape that is only partially forested. However, the reduced amount of forest cover puts them in frequent contact with human populations, particularly when the cause of fragmentation is increased urbanization. As a result, they often have elevated rates of mortality due to poaching, collisions with automobiles, or exposure to pollutants and agricultural runoff.

Populations of species specializing on particular host-plants for oviposition or with highly specialized diets may also decline precipitously in fragmented landscapes. This is particularly true in tropical forests, where host plants and preferred food items are often patchily distributed and at extremely low densities. For example, the tropical butterfly *Hamadryas februa* utilizes the vine *Dalechampia scandens* for oviposition and larval development. Recent studies have found that butterfly populations in small fragments were not limited by their colonization ability or environmental conditions. Instead, it was the lack of host plants and high rates of emigration from fragments that constrained butterfly populations. While the 'fragments' in which these studies were conducted were a set of forested islands recently created by a hydroelectric project, they nonetheless demonstrate the importance of considering resource utilization in addition to habitat heterogeneity when evaluating the consequences of forest fragmentation.

Finally, populations of species with limited tolerance to abiotic changes may also be susceptible to declines in forest fragments. The increase in temperature and decrease in relative humidity that often accompany fragmentation are thought to be particularly detrimental to animals such as amphibians and invertebrates, which do not have the capacity to thermoregulate. One such example is of the Amazonian leaf-litter frog *Colostethus stepheni*, which has been found to have lower abundance in forest fragments than in continuous forest up to 19 years after fragment isolation. While a number of mechanisms could explain these reductions, one intriguing possibility is that altered abiotic conditions in fragments have delayed the sexual maturation of females. This delayed breeding would result in reduced per capita reproductive rates, ultimately driving the declines in growth rates of isolated populations.

As with individual physiology, however, the effects of fragmentation on population size are not uniformly negative. Populations of generalist invertebrates can increase dramatically in forest fragments, as can those of lianas, vines, rattans, and other pioneer plant species commonly found in natural forest gaps. The increased amount of edge habitat may also favor nest parasites such as cowbirds (*Molothrus ater*) or nest predators such as ravens (*Corvus corax*) and skunks (*Mephitis mephitis*), though the effects can vary considerably between species and locations. Still other populations show no change in density at all, although it is unclear if this is because the species under consideration are tolerant to fragmentation's consequences or because the studies have not continued long enough for changes in density to be detected.

The extent to which population size declines or increases in fragments may depend in part on how well individuals of each plant or animal species disperse across the intervening matrix habitat. This may be especially important for species that act as metapopulations, in which several subpopulations are linked to each other by dispersal. Unfortunately, detailed information regarding the movements of plants and animals between populations found in different forest fragments is rare, and the efficacy of habitat corridors connecting remnants of habitat to promote dispersal between isolated reserves remains the subject of ongoing debate. There is some indication that corridors may be useful in promoting the dispersal of at least some species, such as frogs, moths, small mammals, bush-crickets, and some birds. However there is little empirical evidence that dispersal alone will reduce the risk of population declines resulting from local changes in environmental conditions.

Isolated populations have been shown to suffer from increased rates of inbreeding depression, genetic drift, and reduced genetic diversity. These changes, which could result from reductions in population size following fragment isolation or because the movement of individuals between different forest fragments is limited, can have both short- and long-term consequences. In the short-term, populations of plants and animals may show an increase in fluctuating asymmetry (departures from bilateral symmetry) and other developmental problems due to reduced genetic diversity, as well have reduced fecundity. In the long term, genetic erosion could restrict evolutionary responses to changing environmental conditions and the potential for speciation, since genetic diversity provides the raw material upon which natural selection operates.

Changes in Community Composition and their Consequences

Using as a model MacArthur and Wilson's theory of island biogeography, researchers studying islands of forest have predicted that smaller fragments would support lower numbers of species than large fragments. This prediction has held true in a broad variety of temperate and tropical sites, with fragments often containing only a limited subset of a region's biota. These reductions in diversity have shown to affect disparate groups of plants and animals, including birds (e.g., insectivores, frugivores, cavity nesters), insects (e.g., beetles, fruit flies, ants), and plants (e.g., herbs, forbs, shade-tolerant trees).

Two different mechanisms have been invoked to explain this general pattern. First, populations in fragments could have become locally extinct following fragment isolation. Alternatively, lower diversity in fragments could also result from differences in the initial species composition of the patches that were isolated. This may be especially common in tropical forests, where regional species diversity is very high but many species are locally rare or patchily distributed. In this case a species may be missing from a fragment not because it went locally extinct, but because it was absent when the fragment was originally isolated.

Species diversity is not always lower in fragments, however, and there are numerous cases in which it has actually been found to increase following fragmentation. Many amphibians, insects, small mammals, and plants are habitat generalists tolerant of a broad range of habitat types. In some cases species diversity even increases despite the loss of forest-interior species, because their absence is compensated by an influx of generalists from the surrounding matrix. Perhaps one of the best examples of this phenomenon is tropical pool-breeding frogs, of which disturbed-habitat specialists (e.g., *Scinax rubra, Adenomera hylaedactyla*) can be found in recently isolated forest fragments and on the edges of continuous forest. Similar results have also been documented for small terrestrial mammals (e.g., *Oecomys* spp.), perhaps due to their preference for foraging in sites with abundant leaf litter and fallen branches.

Shifts in community structure may also depend on what trophic level a species occupies. Top predators such jaguars (*Panthera onca*) and gray wolves (*Canis lupus*) are hypothesized to be particularly vulnerable to extinction because they are found at lower population densities, forage in large territories, or are dependent on prey that can also be detrimentally affected by fragmentation. When these species become locally extinct, medium-sized predators (also known as mesopredators) such as coyotes (*Canis latrans*) and opossum (*Didelphis virginiana*) may increase in abundance. As a result, the abundance of the species preyed upon by the mesopredators will in turn decrease.

One of the defining features of forest habitats is the myriad interactions in which resident species are involved. Predation, herbivory, competition, and mutualisms all play an important role in structuring forest communities and promoting evolutionary change. As a result, it is widely believed that the disruption of these interactions in fragmented landscapes, particularly mutualistic ones related to plant reproductions and establishment, could have major repercussions for ecosystem functioning. In fact some authors have gone so far as to suggest that fragmentation-related reductions of these interactions will lead to 'ecological meltdown' or 'cascades' of further extinctions in forest fragments.

Some interactions relating to plant recruitment can be substantially modified in fragmented areas. For instance, the pollination of plants can decrease in fragments, either because pollinators are less abundant, they visit plants less frequently, or because they transfer less pollen per visit. Interestingly, a number of studies have also documented the opposite effect – dramatic increases in pollination in both fragments and the intervening matrix. The increase in these cases is usually due to a superabundance in the disturbed areas of exotic pollinators, such as the African honeybee (*Apis mellifera scutellata*). Seed dispersal and predation can be modified as well, although results to date have been somewhat contradictory. The quantity and composition of the seed rain has been shown to vary in disturbed habitats, due to changes in the abundance, diversity, or diet of dispersing animals such as monkeys, bats, birds, and dung beetles. Once these seeds are successfully dispersed, an influx of predators from the habitat surrounding fragments, particularly rodents and insects, can rapidly depress the seed numbers. This may be why the abundance of seedlings of understory plants is frequently much lower in fragments than in continuous forest. However, seedling numbers can also be lower if herbivory is higher in fragments and near edges, as might be expected given the larger populations of generalist browsers such as white-tailed deer (*Odocoileus virginianus*) or meadow voles (*Microtus pennsylvanicus*) in these areas.

Changes in Ecosystem Dynamics

Deforestation and fragmentation can also influence ecosystem processes at fragment, landscape, or continental scales. Within fragments, nutrient cycling can be substantially altered, since there is an increase in the amount of leaf litter on the forest floor and this litter often takes longer to decompose. At the regional scale, fragmentation can influence temperature and rainfall patterns. It is estimated that as much as 50% of rainfall in the parts of the Amazon is produced by the respiration of trees, and that by removing half the forest and replacing it with pastures total rainfall could be reduced by as much as 25%. Since forests are major reservoirs of the earth's terrestrial carbon, deforestation can also contribute significantly to global warming. As downed wood decomposes, it releases greenhouse gases such as carbon dioxide and methane. In fact it is hypothesized that as a result of this decomposition, deforestation alone contributes approximately one-fourth of all greenhouse gas emissions. Since tree mortality is elevated in fragments, this carbon is released by decomposing trees long after the original process of deforestation has been completed. These dead and downed trees, coupled with an increased accumulation of litter in fragments, also make fragments more susceptible to fires, which further alters the cycling of carbon and other nutrients. All of these changes in ecosystem processes can have major direct and indirect consequences for biodiversity. Increased fire frequency, for example, may directly cause the mortality of plants and animals in fragments. It may also indirectly drive reduced rates of individual growth and survivorship by altering the distribution of resources on which these individuals depend.

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.

Further Reading

Aizen MA and Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine 'Chaco Serrano'. *Ecological Applications* 4: 378–392.

Anciaes M and Marini MA (2000) The effects of fragmentation on fluctuating asymmetry in passerine birds of Brazilian tropical forests. *Journal of Applied Ecology* 37: 1013–1028.

Andresen E (2003) Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography* 26: 87–97.

Bierregaard RO, Gascon C, Lovejoy TE, and Mesquita R (eds) (2002) *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. New Haven, CT: Yale University Press.

Cunningham SA (2000) Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society Biological Sciences Series B* 267: 1149–1152.

Debinski DM and Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342–355.

Develey PF and Stouffer PC (2001) Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology* 15: 1416–1422.

Harrison S and Bruna E (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225–232.

Laurance WF and Bierregaard RO (1997) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. Chicago, IL: University of Chicago Press.

Laurance WF, Lovejoy TE, Vasconcelos HL, *et al.* (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16: 605–618.

Terborgh J, Lopez L, Nunez VP, *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science* 294: 1923–1926.

Human Influences on Tropical Forest Wildlife

C A Peres and J Barlow, University of East Anglia, Norwich, UK

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