

Ecosystem Loss and Fragmentation: Synthesis

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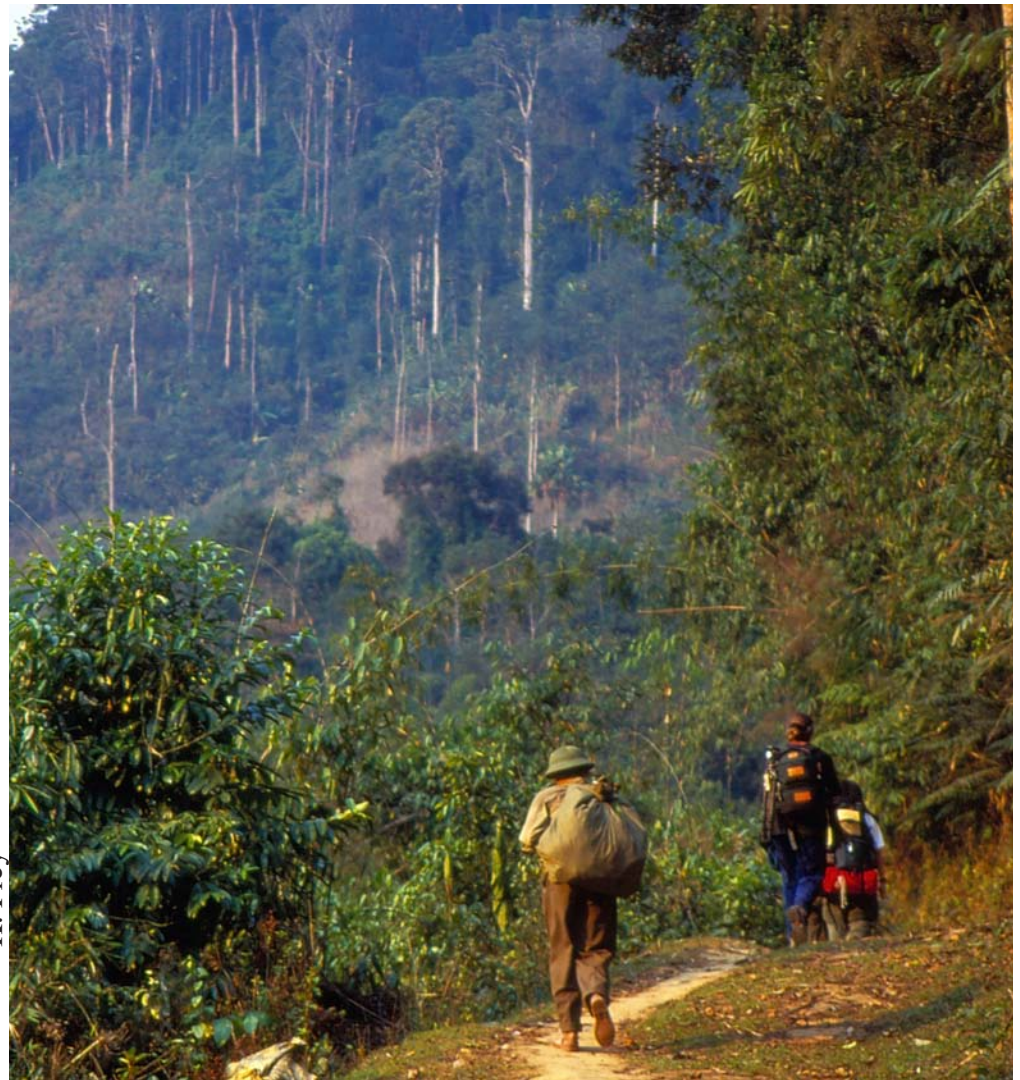
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Ecosystem Loss and Fragmentation

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Table of Contents

Introduction.....	74
Habitat Loss by Biome.....	74
Terrestrial.....	75
Forests -Tropical and Temperate.....	75
Grasslands -Tropical, Temperate, and Tundra.....	76
Aquatic.....	77
Wetlands.....	78
Riverine Systems.....	78
Causes of Fragmentation.....	79
Fragmentation Due to Natural Causes.....	79
Fragmentation Due to Human Activity.....	79
Natural Versus Human Fragmentation.....	80
Effects of Fragmentation.....	80
Decreasing Patch Size.....	80
Increased Edge Effects.....	81
Edge Effects.....	81
Edge Effects -Physical.....	81
Edge Effects -Biological.....	82
Invasion by Generalist Species.....	82
Alteration of Plant Communities.....	82
Alteration of Insect Communities and Nutrient Cycling.....	82
Isolation –Barriers to Dispersal.....	83
Species Response to Isolation.....	83
Effect of Time on Isolation.....	83
Effects of Different Types of Fragmentation.....	84
Effects on Species Abundance, Richness, and Density.....	84
Interactions Among Species and Ecological Processes.....	85
Box 1. Corridors and Connectivity.....	86
Box 2. The Futi Corridor – Linking Tembe Elephant Park, South Africa to Maputo Elephant Reserve, Mozambique.....	87
Box 3. Identifying Species Vulnerable to Fragmentation.....	88
Management of Fragmented Landscapes.....	88
Recommendations.....	89
Terms of Use.....	89
Literature Cited.....	90
Glossary.....	95

Ecosystem Loss and Fragmentation

Melina F. Laverty and James P. Gibbs

Introduction

Ecosystem loss and fragmentation has been termed the greatest worldwide threat to biodiversity and the primary cause of species extinction (Wilcox and Murphy, 1985; Rosenberg and Raphael, 1986; Simberloff, 1986). Today, as Laurence and Bierregaard (1997) have stated, “the fragmented landscape is becoming one of the most ubiquitous features of the tropical world – and indeed, of the entire planet.” Moreover, ecosystem fragmentation is as much an issue for biodiversity in aquatic, including marine, environments as it is for terrestrial ones (Bostrom et al., 2006).

Ecosystem loss and fragmentation are related processes and typically occur simultaneously. Indeed, some texts (e.g., Meffe and Carroll, 1997) define fragmentation as the loss and isolation of natural habitats. However, the two processes are distinct (Fahrig, 2003). Ecosystem loss refers to the disappearance of an *ecosystem*, or an assemblage of organisms and the physical environment in which they exchange energy and matter. Many studies, however, examine loss with respect to a specific organism’s *habitat*. *Habitat loss* is the modification of an organism’s environment to the extent that the qualities of the environment no longer support its survival. Habitat loss usually begins as *habitat degradation*, the process where the quality of a species’ habitat declines. Once the habitat’s quality has become so low that it no longer supports that species then it is termed habitat loss. *Fragmentation* is usually a product of ecosystem loss and is best thought of as the subdivision of a formerly contiguous landscape into smaller units. Ultimately, fragmentation reduces continuity and interferes with species dispersal and migration, thereby isolating populations and disrupting the flow of individual plants and animals (and their genetic material) across a landscape. Generally speaking, habitat loss is of far greater consequence to biological diversity than habitat fragmentation (Fahrig, 2003).

This process is well illustrated in southeastern Bolivia, where a landscape that was once continuously forested has been transformed into patches of forest surrounded by a matrix of agricultural land. A *patch* is usually defined by its area, perimeter, shape, and composition (e.g., a land cover type – such as water, forest, or grassland – a soil type, or other variable). The *matrix* is simply the most common cover type in any given landscape.

Loss and fragmentation are tightly coupled processes as the pattern of loss affects the degree of fragmentation. For example, in a 200-hectare forest, a single 100-hectare block could be cleared at one site for a farming operation. Alternatively, forest could be cleared into many small plots across the landscape, leaving 100 forest fragments of one hectare each. In both cases the landscape has lost 100 hectares of forest, but in the second scenario the landscape has a much higher level of fragmentation. The potential consequences for plants and animals are quite different in these two scenarios.

Habitat Loss by Biome

Loss and fragmentation impact most of the earth’s major *biomes* from tropical and temperate forests to grasslands and from wetlands to rivers. Quantifying the extent of this loss and fragmentation is difficult – one major problem is determining what vegetation existed historically to establish a benchmark for comparisons. Another issue is determining the extent that change is caused by humans versus natural forces (Clark and Matthews, 1990; Fukami and Wardle, 2005). Many textbooks show maps of the hypothetical distribution of the world’s biomes with today’s climate, if there were no humans. These maps refer to the “present potential” vegetation – that is the potential vegetation if there were no humans to remove it. Additional maps illustrate earlier times when climates were different and human impact was minimal: 5,000, 10,000 or

more years ago. What is the basis of these maps and how accurate are they?

Maps for 5,000 or more years ago are largely determined by past climate, as human influence was still limited. Evidence of past climate patterns are compiled from plant and zoological fossils, as well as soil and sedimentological analyses. Maps of present potential vegetation combine existing vegetation and climate patterns with remnant vegetation patches. With these maps there are obviously higher levels of uncertainty in areas that are heavily influenced by human activity versus those that have limited human impact. In other words, areas that have been heavily affected by human activity for thousands of years, such as Europe, are more difficult to recreate, while areas like the Arctic tundra or Canada's boreal forest are easier to establish. For a detailed discussion of the challenges in reconstructing and understanding global vegetation patterns, see Adams and Faure (1997).

Efforts have been made to quantify the extent and rate of loss of the world's major biomes at various scales and for different time periods (Turner and Clark, 1990; Skole and Tucker, 1993; Adams and Faure, 1997; Davidson et al., 1999; Steininger et al., 2001; Achard et al., 2002; Etter et al., 2006). This process is complex and estimates vary widely due to:

- differences in classification methods (for example, wetland inventories in the United States, Canada, and Mexico are all based on slightly different definitions for wetlands);
- limited data for some regions (for example, typically there is less data for Africa than North America);
- lack of comparable land cover data from different time periods (particularly historical data) that would allow

comparisons over time;

- limited groundtruthing of satellite data; and
- poor or erratic government reporting.

These factors must all be kept in mind when examining data on the extent and rate of ecosystem loss and fragmentation. Despite these challenges, these data are critical to conservation efforts and monitoring. Because of its importance, in recent years efforts have been made by several organizations, such as the World Resources Institute (WRI), Wetlands International, and Tropical Ecosystem Environment Observation by Satellite (TREES), to streamline habitat classification and



Deforestation in Madagascar (Source: L. Langham)

produce better comparisons on broad scales (Davidson et al., 1999; Matthews et al., 2000; White et al., 2000; Achard et al., 2003).

Terrestrial

Forests - Tropical and Temperate

Today forest cover has shrunk to approximately half of its *potential extent* (Adams and Faure, 1997; Roper and Roberts, 1999), replaced by agriculture, grazing, and settlement.

Table 1: Deforestation rates

Hotspot areas by continent	Annual deforestation rate for sample sites within hotspot area (range)
Latin America	0.38%
Central America	0.8-1.5%
Brazilian Amazon belt	
<i>Acre</i>	4.4%
<i>Rondonia</i>	3.2%
<i>Para</i>	1.4-2.7%
Columbia-Ecuador border	1.5%
Peruvian Andes	0.5-1.0%
Africa	0.43%
<i>Madagascar</i>	1.4-4.7%
Southeast Asia	0.91%
Southern Vietnam	1.2-3.2%
Source: Modified from Achard et al., 2002	

Primary forest blocks of a significant size exist in only a few countries, such as the boreal forests of Northern Canada and Russia, and the Amazon basin of Brazil (Bryant et al., 1997).

The world's forests began declining thousands of years ago, with the expansion of farming and herding in the Middle East and Europe. More recently, rapid population growth, industrialization, and globalization are contributing to rapid deforestation in many tropical regions, with forest loss in Brazil and Indonesia exceeding 3.5 million hectares in 1995 alone (Roper and Roberts, 1999, based on FAO figures). While there is no question that forest loss and fragmentation is substantial, determining the exact rate of these losses globally is complex (Roper and Roberts, 1999). While determining rates at smaller, local scales is often easier (Skole and Tucker, 1993; Steinger et al., 2001), they too can be controversial.

Furthermore, depending on how "forest" is defined, what forest cover data is presented, or how it is analyzed, the picture we obtain may end up being quite different; for example, by changing the time periods used in an analysis, deforestation

rates may differ dramatically. According to estimates from the Tropical Ecosystem Environment Observation by Satellite (TREES), a research program that uses satellite imagery to estimate the extent of the world's tropical humid forests, between 1990 and 1997, 5.8 (+/- 1.4) million hectares of humid forest were lost each year, which corresponds to a rate of 0.52% per year. A further 2.3 (+/-0.71) million hectares were obviously degraded, a rate of 0.20% a year (Achard et al., 2002; Eva et al., 2003). However, other scientists considered this result to be an underestimate of tropical forest loss, as it only included humid tropical forest, while dry tropical forests are disappearing more rapidly as those areas are often more conducive to agricultural activities (Fearnside and Laurance, 2003). For conservation planning, it is also critical to keep in mind the variation in deforestation rates at regional and local scales as different strategies might be needed. For example, the average deforestation rate across all of Latin America is 0.38%, yet there is a very different picture of deforestation if you look at the provincial level. Rates of deforestation in Brazil's Acre province are 4.4 percent, substantially higher (Table 1). Knowledge of this variation is essential for conservation planning.

Grasslands - Tropical, Temperate, and Tundra

Estimates of the extent of the world's grasslands range from 40 to 56 million km² or 30 to 40 percent of the earth's land area (Table 2) (Whittaker and Likens, 1975; Atjay et al., 1979; Olson et al., 1983; Davidson et al., 2002). These estimates incorporate temperate and tropical grasslands as well as shrubland and tundra (tundra occurs around the Arctic circle above the latitude where trees can survive, and is dominated by shrubs, sedges, grasses, lichens, and mosses). Temperate grasslands develop in climates that typically have cold winters and summer droughts, and are found in North America (prairies), Europe and Asia (steppe), South America (pampas), and South Africa (veldt) (Roxburgh and Noble, 2001). Tropical grasslands usually develop in areas with distinct seasons of drought and rain, and include savanna, as well as tropical woodland and savanna (this designation refers to grassland associated with shrubs and trees). Herbivory and fire are important elements of temperate and tropical grassland systems.

Grassland Type	<u>Whittaker and Likens</u> (1975) ^a		<u>Atlay et al.</u> (1979) ^a		<u>Olsen et al.</u> (1983)		<u>Davidson et al.</u> (2002) ^f	
	Million km ²	% of Total Land Area ^b	Million km ²	% of Total Land Area ^b	Million km ²	% of Total Land Area ^b	Million km ²	% of Total Land Area ^b
Savanna	15.0	11.6	12.0	9.3	-	-	17.9	13.8
Tropical Woodland and Savanna	-	-	-	-	7.3	5.6	-	-
Dry Savanna and woodland	8.5 ^c	6.6	3.5	2.7	13.2 ^d	10.2	-	-
Shrublands ^e	-	-	7.0	5.4	-	-	16.5	12.7
Non-woody grassland and shrubland	-	-	-	-	21.4	16.5	10.7 ^g	5.7
Temperate Grassland	9.0	7.0	12.5	9.7	-	-	-	-
Tundra	8.0	6.2	9.5	7.3	13.6	10.5	7.4	5.7
Total Grassland	40.5	31.3	44.5	34.4	55.5	42.8	52.5	40.5

^a Desert and semi-desert scrub not included
^b Total land area used for the world is 129,476,000 km² (excludes Greenland and Antarctica)
^c Includes woodland and shrubland
^d Includes dry forest and woodland
^e Includes hot, warm, or cool shrublands
^f Davidson et al. (WRI/PAGE) calculations based on GLCCD, 1998, Olsen, 1994 a and b, PAGE land area is based on land cover classifications for savanna, woody savanna, closed and open shrubland, and non-woody grassland, plus Olsen's category for tundra
^g Includes non-woody grassland only
Notes: - means data is not available or has been combined in another category

Some of the highest rates of habitat loss and fragmentation in the world have been in grassland areas, in large part because of their suitability for growing crops like wheat and corn, and for grazing (Parkinson, 1997). Conversion of grasslands to farmlands in Western Canada and the U.S. has left only remnants of the original prairie grassland. The U.S. Geological Survey (USGS) estimates that since 1830 over 1 million km² of the grasslands of the western US have disappeared.

- The tall-grass prairie grassland has decreased by 97 percent (from 677,300 km² to 21,548 km²)
- Mixed-grass prairie has declined 64 percent (from 628,000 km² to 225,803 km²)
- Short-grass prairie has declined 66 percent (from 181,790

km² to 62,115 km²)

Additional declines are occurring in grasslands in other parts of the world as well. The rate and extent of these declines is less well documented than in the U.S. and so is harder to quantify accurately.

Aquatic

Although we often think of loss and fragmentation only in a terrestrial context, as these areas are easier to observe, loss and fragmentation is also a concern for aquatic ecosystems. Wetlands, mangroves, seagrasses, rivers, coral reefs, kelp forests, and rocky shorelines are fragmented by natural forces such as

Table 3: Wetland extent (in hectares) in the United States and Canada based on the results of national wetland inventory information

Country	Wetland Extent (1780s)	Wetland Extent (1980s)	Wetland Extent (1985)	Wetland Extent (1988)	Wetland Extent (>1988)
United States (continental only)	89,488,127 ^a	42,238,851 ^a	41,356,092 ^b	-	40,9000,000 ^b
United States (includes Alaska and Territories)	158,389,525 ^a	111,056,479 ^a	-	-	-
Canada	-	-	-	127,199,000 ^c	150,000,000 ^d

^a published Dah, 1990;

^b USFWS, 1998;

^c published NWWG, 1988;

^d approximate number based on data indicating total wetland extent in Canada may be as much as 150,000,000 ha based on information indicating increase in peatland area (Polestar Geomatics, unpublished)

Source: Modified from Davidson et al., 1999

bottom topography, wave action, currents, tides, storm surge, as well as human activities such as draining, diversion, extraction of groundwater, dams, dredging, sedimentation, fishing (e.g., trawling, dynamite fishing), aquaculture, sea jetties, and boating. Here we highlight loss and fragmentation in two of the many aquatic systems: wetlands and rivers.

Wetlands

Wetlands have been drastically reduced in area and number in many regions of the world as they are drained and filled for human use. A recent global review of wetlands identified significant gaps in our knowledge of their extent and rate of loss (Davidson et al., 1999). Differences in classification schemes as well as gaps in data (data is especially limited for areas outside North America and Europe) mean that current estimates of global wetland coverage vary widely, from 560 to 1,279 million hectares. In the continental United States, where study of wetlands has been more extensive, wetlands have declined by more than half, from 89 to 42 million hectares between 1780 and 1980. The rate of loss is speeding up; by 1985 more than an additional one million hectares disappeared (see Table 3).

Riverine Systems

Many of the world's major riverine systems are highly frag-

mented or have had their flow modified by human intervention, primarily through the creation of dams (Dynesius and Nilsson, 1994; Pringle, 1997). According to the World Register of Dams, between 1950 and 1986, the number of large dams in the world increased seven-fold. Most dams are built for irrigation or for hydroelectric needs; they fragment rivers and surrounding environments and change natural water flow patterns, transforming *lotic* into *lentic* systems. Of the world's major rivers (those greater than 125 miles or 201 km long), only two percent are free flowing; the remaining 98 percent have been fragmented or diverted (Benke, 1990).

Fragmentation of rivers has impacted many species. In the Pacific Northwest of the United States, dams have seriously affected salmon populations by preventing salmon from returning to their native streams to reproduce. Dams have also contributed to declining freshwater mussel populations. Ninety percent of the world's freshwater mussels are found in North America, and 73 percent of these face extinction in the United States. Many North American freshwater mussels must spend a part of their lifecycle in fish gills to reproduce successfully. As an example, dams have blocked the movement of *anadromous fish*, which the dwarf wedge mussel (*Alasmidonta heterodon*) depends upon during its life cycle. This, coupled

with siltation and chemical runoff, has led to substantial declines in their population.

Freshwater systems are also fragmented by groundwater removal, which often modifies the temperature structure of streams. For example, in the Southeastern United States extraction of groundwater has reduced the amount of cold water that feeds many streams. Important game species, like striped bass, use spring-fed areas of rivers as refuges during hot summer months, as they have high oxygen needs and higher oxygen levels are found in colder water (Pringle, 1997). As these colder areas disappear, it affects species that depend upon these conditions.

Causes of Fragmentation

Fragmentation is caused by both natural forces and human activities, each acting over various time frames and spatial scales.

Fragmentation Due to Natural Causes

1. Over long time frames (thousands or millions of years), landscapes are fragmented by geological forces (e.g., continental drift) and climate change (e.g., glaciations, changes in rainfall, sea level rise).
2. Over short periods (decades or months), natural disturbances, such as forest fires, volcanoes, floods, land slides, windstorms, tornadoes, hurricanes, and earthquakes, modify and fragment landscapes.

In addition, landscapes are naturally fragmented by mountain ridges, canyons, rivers, and lakes. Some ecosystems also commonly occur in discrete patches and are thus naturally fragmented. Natural processes create the habitat heterogeneity and landscape diversity upon which many species depend.

Fragmentation Due to Human Activity

Humans have modified landscapes for thousands of years. Early hunters influenced the landscape by burning areas to

favor certain game species, and today ranchers keep grasslands open in the same way (Schüle, 1990). Many human activities—agriculture, settlement (e.g., construction of buildings, fences etc.), resource extraction (e.g., mining, timber), industrial development (e.g. the construction of hydroelectric dams)—alter and fragment landscapes. Of these activities, agriculture is the leading cause of ecosystem loss and fragmentation throughout much of the world today (Vitousek et al., 1997; Tilman et al., 2001).

The process of human-caused fragmentation often proceeds in a fairly predictable manner. First, an opening is formed in a matrix of natural habitats: perhaps a road is built that crosses the landscape. This opening becomes larger as settlement and deforestation occur along the road. Still, the landscape remains largely forested and although there is habitat loss, fragmentation is minimal. Second, smaller roads are constructed off the main road, increasing access to the forest. The newly accessed areas are subsequently cleared for crops. The landscape begins to appear fragmented, even though the remaining patches of original forest are still large. This process of subdivision repeats itself at a finer and finer scale until the landscape shifts to one predominated by cleared or degraded land, with patches of isolated forest. Eventually, all of the landscape may be converted for human use, except those spots that are too wet, too dry, or too steep to be useable.

Humans also create distinctive patterns as they fragment landscapes, typically leaving patches that are non-random in size and distribution. An analysis of deforestation in the Tierras Bajas region of Southwest Bolivia revealed different land cover patterns created by four principal groups of people (Steininger et al., 2001). Colonization by peasant farmers, in some cases planned and in others not, left a complex mosaic of cropland, secondary forest, and forest remnants. The planned settlements formed pinwheel patterns of linear farms, radiating from a central town, while the unplanned settlements appeared as small, square or rectangular fields along roads. Mennonite colonies, on the other hand, had settlements along the road with large, rectangular farms extending behind them, leaving larger forest remnants than the peasant settlement pat-

terns. Industrial soybean farms were distinguished from the others by their lack of settlements; these farms formed linear strips with marked boundaries and windbreaks of trees 20 to 40 meters wide between the strips. Like the Mennonite farms, the industrial farms left larger forest remnants.

There are several technical terms commonly used in the field of landscape ecology to define different stages of the fragmentation process or different forms of fragmentation of a landscape. These include perforation (holes punched in a landscape), dissection (initial subdivision of a continuous landscape), fragmentation (breaking into smaller parts), shrinkage (reduction in size of patches), and attrition (loss of patches).

Natural Versus Human Fragmentation

Several differences exist between human-caused and naturally fragmented landscapes:

1. A naturally patchy landscape often has a complex structure with many different types of patches. A human-fragmented landscape tends to have a simplified patch structure with more distinct edges, often with a few small patches of natural habitats in a large area of developed land.
2. Patch types in human-modified landscapes are often unsuitable to many species, while in a heterogeneous natural landscape most patch types are suitable to a more diverse group of species.
3. The borders (or edges) of patches in naturally patchy landscapes tend to be less abrupt than in those created by humans. (Edge effects are discussed in detail later in this document.)

Certain features of human-fragmented landscapes, such as roads, are novel in the evolutionary history of most wild species and pose additional threats. Not only do they restrict movement between populations, but heavily traveled roads are a direct danger to wildlife (Forman and Alexander, 1998; Gibbs and Shriver, 2002). Furthermore, some animals avoid habitats near roads due to noise pollution. Roads also have secondary impacts on ecosystems and species. They are an ac-

cess point, increasing a region's vulnerability to invasion by exotic species, and perhaps most importantly, making wildlife habitats accessible to people for hunting or resource extraction (Findlay and Bourdages, 2000). In West Africa, for example, new roads for logging act as conduits for the bushmeat trade, which has contributed to the extirpation of many duiker species (*Cephalopus spp.*) and the extinction of at least one primate species, Miss Waldron's red colobus monkey (*Procolobus badius waldroni*) (Newing, 2001; Whitfield, 2003).

Effects of Fragmentation

Fragmentation and loss of ecosystems are coupled processes: fragmentation is a consequence of loss (Haila, 1999). It is often difficult to distinguish between the effects of these two processes, since they often happen simultaneously. Loss of habitat impacts species principally by reducing available resources and microenvironments. Fragmentation has additional consequences for species on top of those caused by loss—most importantly, affecting movement and dispersal and modifying behavior.

As fragmentation progresses in a landscape, three major consequences are apparent:

1. decreasing patch size;
2. increased edge effects; and
3. increased patch isolation

Decreasing Patch Size

Once a landscape has been fragmented, the size of the remaining patches is a critical factor in determining the number and type of species that can survive within them. For all species—large or small—that cannot or will not cross a forest edge or leave a patch, all requirements to complete their life cycle must be met within the patch, from finding food to mates. This is especially important for species with complex life cycles, each with distinct habitat requirements. For example, many amphibian species have an aquatic larval stage and an upland adult phase. Also, some species require large

areas of continuous habitat and cannot survive in small patches—they are referred to as *area-sensitive species*. Furthermore, large patches typically support larger populations of a given species and thereby buffer them against extinction, *inbreeding depression*, and *genetic drift*.

Increased Edge Effects

One of the most obvious changes to a fragmented landscape is the increase in edge environment. *Edge environments* or *ecotones* mark the transition between two different habitats. In a naturally forested landscape, edge is usually limited to a small area, such as along streams or landslides (Laurance and Bierregaard, 1997). Natural edges are usually less abrupt than human-formed edges and show a gradual transition from one habitat type to another. In Rondonia, Brazil, deforestation patterns show a herringbone pattern that closely follows the road that was cut through the original forest. Along agricultural frontiers, the original landscape may be fragmented into long narrow strips or shreds, interspersed with areas of agriculture (Feinsinger, 1997). These strips may separate different crops, thus serving as windbreaks, or the boundary between two landowners. As a result this remaining fragment is entirely made up of edge environment. Residual trees along rivers provide another example of narrow, edge-dominated environments.

The extent of edge environment in a fragment patch is determined in part by its shape. The ratio of the perimeter to area (or the amount of edge environment to the amount of interior) is one measure of patch shape. A circular patch has the maximum area per unit edge and will have less edge environment and fewer edge effects than a rectangular patch of the same size. Because edge effects may extend 200 meters (and sometimes more), small patches may be entirely composed of edge environment. For example, a new reserve is being created with an area of one square km. The reserve can either be rectangular: Reserve A (2 km by 0.5 m), or square: Reserve B (1 km by 1 km). As illustrated, both have the same total area but Reserve A will be composed entirely of edge environment and its core size will be 0 square km, whereas Reserve

B will have a core area of 0.25 square km.

Edge Effects

Many studies have examined the effects of edges on the physical environment and biological communities that remain after fragmentation (Lovejoy et al., 1986; Bierregaard et al., 1992; Malcolm, 1994; Camargo and Kapos, 1995; Murcia, 1995; Didham, 1997; Laurance et al., 1998; Carvalho and Vasconcelos, 1999). The longest running and perhaps the most detailed study of fragmentation effects ever conducted is the Biological Dynamics of Forest Fragments project, which began in 1979. This pioneering project, located in the Amazon region north of Manaus, Brazil, has generated some of the findings described here and informed much of our general understanding of the effects of forest fragmentation. Edge effects is a general term used to describe a number of different impacts, and can be categorized into several types: physical (e.g., microclimatic changes), direct biological (changes in species composition, abundance, and distribution), and indirect biological (changes in species interactions such as predation, competition, pollination, and seed dispersal) (Matlack and Litvaitis, 1999). Moreover, many of the effects of fragmentation are synergistic; for example, fragmentation can lead to increased fire risk, increased vulnerability to invasive species, or increased hunting pressure (Hobbs, 2001; Laurance and Williamson, 2001; Peres, 2001).

Edge Effects - Physical

Some of the most significant edge effects are the microclimatic changes that take place along a fragment's edge (Harper et al., 2005). Edge areas in forests are typically warmer, more exposed to light and wind, and drier than interior areas. Gradients of these microclimatic conditions extend into the interior approximately 15 to 75 meters (Kapos, 1989; Laurance and Bierregaard, 1997). Microclimatic changes along edges often have secondary effects, such as altering vegetation structure and, eventually, plant and animal communities (Matlack, 1993).

Increased wind along the edge of fragments physically dam-

ages trees, causing stunted growth or tree falls (Essen, 1994; Laurance, 1994). This is especially obvious when a fragment first forms, since interior plant species are often not structurally adapted to handle high wind stress. Furthermore, wind tends to dry out the soil, decrease air humidity, and increase water loss (evapotranspiration rates) from leaf surfaces, creating a drier microclimate. This drier environment has a higher fire risk. Several studies have examined the increased risk of fires in fragmented environments, particularly those that border grazing lands (Uhl and Bushbacher, 1985; Cochrane and Schulze, 1999; Nepstad et al., 1999; Cochrane, 2001; Hobbs, 2001).

Edge Effects - Biological

The creation of “edge” following fragmentation causes a number of biological changes (Harper et al., 2005). These changes are often similar or coupled to the biological changes that result from the creation of the fragment itself.

These include changes in species composition, abundance, and distribution, as well as changes in species interactions such as predation, competition, pollination, and seed dispersal. Along the edge of a fragment, biological changes may extend farther than the physical ones. In one study, invasion by a disturbance-adapted butterfly species extended nearly 250 meters into the forest (Laurance et al., 2000). Here we examine three biological changes particularly associated with the formation of edge: invasion by generalist species, alteration of plant communities, and alteration of insect communities and nutrient cycling. Additional biological changes as a consequence of fragmentation are detailed in subsequent sections: “Effects on Species Abundance, Richness, and Density” and “Interactions Among Species and Ecological Processes.”



Bolivian road (Source: E. Sterling and K. Frey)

Invasion by Generalist Species

Edges are more susceptible to invasion by generalist or “weedy” species that are better adapted to handle disturbance and the new microclimate. These species might be plants (such as lianas, vines, creepers, and exotic weeds), animals, or diseases. Simultaneously, long-lived interior canopy species, epiphytes, and other mature forest taxa decline in abundance (King and Chapman, 1983). Wind along edges also increases the transfer of seeds from outlying areas, thereby aiding invasion of foreign, generalist, or weedy species. Introduction of animals,

adapted to disturbed environments and human presence, such as domestic cats, rats, and mice, is often a problem along edges, as is disease transmission between wildlife and domestic animals.

Alteration of Plant Communities

The increased light along edges affects both the rate and type of plant growth, favoring fast-growing light-

loving species at the expense of slower-growing shade-loving ones (Harper et al., 2005). Studies of forest fragments in the Amazon noted a dramatic loss of plant biomass overall; although secondary vegetation (especially vines and lianas) proliferated, this new biomass did not compensate for the loss of “interior” tree species (Laurance et al., 1997). Since many tree species have long life spans, it is important to examine the changes in plant communities over extended periods. It may take hundreds of years for the full consequences of fragmentation to be revealed.

Alteration of Insect Communities and Nutrient Cycling

Only a few studies have been conducted to date on the effect of fragmentation on insect communities (Aizen and Feins-

inger, 1994; Gibbs and Stanton, 2001). Fragmentation, however, appears to alter both the abundance and composition of insect communities, thus affecting leaf litter decomposition and hence nutrient cycling (Didham, 1998).

Beetles (of the families, Carabidae, Staphylinidae, Scarabaeidae) that are common to continuous interior forest disappear from forest fragments, a surprising result given their small size and generalist habitat requirements (Klein, 1989). Their disappearance may be the result of the drier microclimate or loss of species they depend on (i.e., less mammal dung and fallen fruit on which to reproduce). Another possible reason for their disappearance is that these insects actually travel tremendous distances in search of decaying material for their reproduction and may not be able to cross the matrix between patches. Whatever the cause, there are a number of implications for ecosystem function, including a decreased rate of nutrient cycling. Also, the incidence of disease may be elevated, as dung is left on the ground longer, allowing flies to breed there.

Isolation-Barriers to Dispersal

The degree of isolation of a patch helps determine what biological communities it can sustain. While patches may appear isolated, their actual biological *connectivity* depends on the habitat that separates them. In fragmented landscapes, patches of high-quality habitat are typically interspersed with areas of poor habitat. In a very isolated patch, species that cannot disperse may be unable to find adequate resources or mates. They may become separated from other populations and thus prone to genetic inbreeding and possibly local extinction.

Species Response to Isolation

A species' response to fragmentation depends on its dispersal ability as well as its perception of the environment. For example, species that fly (e.g., birds, bats, flying insects) are typically less affected by patch isolation than less mobile species (e.g. frogs and beetles). For some species, crossing an open field for two kilometers is not a problem. However, species that spend most of their time in treetops (e.g., some species of primates and marsupials) or in dark, interior forest may

never cross such a large opening. A species that disperses over long distances, such as an African elephant (*Loxodonta sp.*), will perceive a particular landscape as more connected than a species with short-range dispersal, such as a shrew (species of the family Soricidae).

Species without the benefit of an aerial view of a landscape make decisions primarily based on the habitat directly in front of them (Gibbs et al., 1998). A study in the Amazon conducted by Malcolm (1998) revealed distinct responses of similar animals to fragmentation. Two species of opossum—the woolly (*Didelphys lanigera*) and the mouse (*Didelphys murina*)—were tracked using radio transmitters to determine if they would travel a gap of 135 to 275 meters to reach the fragment on the other side. Mouse opossums were able and willing to cross the gap, while the more strictly arboreal species, the woolly opossum, was not.

In the marine environment, responses to fragmentation are more complex because the environment is three-dimensional, and many marine species are mobile or have a mobile larval stage, and breed far from where they complete their adult life cycle. These traits mean that marine species are less likely to experience the kind of isolation that occurs in a fragmented terrestrial system. The circumstances depend largely on the particular marine system or species (e.g., fragmentation of mangroves mimics terrestrial fragmentation more closely than that of other marine systems) and the degree of fragmentation (small or large scale). Studies of larval dispersal that examine the link between physical oceanography (e.g., currents) and reproductive life cycles of marine species are shedding new light on the level of connectivity of marine systems (Roberts, 1997; Cowen et al., 2000; Taylor and Hellberg, 2003).

Effect of Time on Isolation

Fragmentation is a dynamic process, often with delayed effects; knowing the amount of time a patch has been isolated is critical to understanding the consequences of fragmentation. In long-lived species, such as trees, it may take a hundred years to observe the impact of fragmentation. Individual trees continue to survive immediately following fragmentation; how-

Table 4: A comparison of matrix habitats from a wildlife conservation perspective

Matrix Habitat	Benefits						Total Score
	Allows Gene Flow	Provides Ecosystem Services	Provides Wildlife Habitat	Provides Climatic Extremes	Provides Protection From Exotic Species	Provides Fire	
Fully protected forest	4	4	4	4	4	4	24
Low intensity selective logging	4	4	3	4	3	3	21
Traditional forest management	3	4	3	4	3	3	20
Medium-high intensity logging	3	3	3	3	3	1	16
Low-diversity agroforestry	2	2	2	2	2	2	12
Plantation Forests	1.5	3	1.5	3	2	3	14
Row crops	1	0	1	0	0	1	3
Cattle pastures	1	1	1	0	0	0	3

Note: Each habitat was scored by a panel of 15 researchers. The most favorable habitats received the highest number and the least favorable received the lowest.

Source: Modified from Laurance et al., 1997

ever, they may no longer reproduce – perhaps they are too spread apart to exchange pollen by wind, or their pollinators or seed dispersers have disappeared. In this case, it is only a matter of time before the population becomes locally extinct. Janzen (1986) coined the term “living dead” to describe the fates of species in such situations.

Effects of Different Types of Fragmentation

The effects of fragmentation also vary depending on the cause of fragmentation (for example, fragmentation for agriculture versus for logging). It is difficult to make generalizations about the effects of a specific type of fragmentation on a particular landscape, since the consequences may be very different in a temperate versus a tropical region or in a grassland versus a forest, largely because the plants and animals present have different sensitivities to fragmentation.

Keeping these issues in mind, we can estimate the potential effects of a particular type of fragmentation based on how the new environment is perceived by the original species present

and whether the change to the landscape is permanent or temporary. For example, selective logging is typically less disruptive than clear-cutting forested areas. This is because after selective logging the forest is still relatively intact. While differing from the original forest, selectively-logged forest does not form a large, unusable gap in habitat, as often occurs when a forested area is replaced with agricultural land (Table 4.).

The matrix that surrounds fragments has a large effect on what species remain within the fragments and their dispersal ability between fragments. Table 4 illustrates some of the benefits provided by different matrix types as subjectively ranked by a panel of 15 researchers from the Biological Dynamics of Forest Fragments project. The table displays a hierarchy of matrix habitats from most favorable to least favorable for many species.

Effects on Species Abundance, Richness, and Density

Fragmentation’s impact on species abundance, richness, and density is complex, and there is no clear rule what these ef-

fects may be. Studies of the effects of fragmentation on species abundance, richness, or density relative to fragment size have had inconsistent results (Debinski and Holt, 2000), some indicating an increase in species, in others, a decline. However, it is important to keep in mind that simply counting the number of species does not measure impacts of fragmentation on behavior, dispersal ability, or genetic diversity.

Some species respond positively to fragmentation (Brown and Hutchings, 1997; Laurance and Bierregaard, 1997; Lynam, 1997; Malcolm, 1997). Fragmentation may increase species richness by allowing generalist species to invade. In a study of the impact of fragmentation on frogs in a lowland Amazonian forest, species richness was strongly and positively related to fragment area (Tocher et al., 1997). After fragmentation, species richness increased largely as a result of invasion by frog species from the surrounding matrix into the remaining forest fragments. It is unclear if this increase will be sustained over time. For example, if this same spot were re-surveyed in 50 years, total species richness might decline as interior forest species disappear.

Immediately following fragmentation, the density of individ-

uals may increase as animals “crowd” into the remaining forest (Schmiegelow et al., 1997; Collinge and Forman, 1998). This inflation of density will ultimately prove short-lived because patches are rarely adequate to support the same population density as more extensive habitats. This phenomenon underscores the need to monitor fragmentation effects over long time scales.

Interactions Among Species and Ecological Processes

Fragmentation causes the loss of animal populations by a process termed *faunal relaxation*, the selective disappearance of species and replacement by more common species (Diamond, 2001). Large-bodied vertebrates, especially those at high *trophic levels*, are particularly susceptible to habitat loss and fragmentation, and are among the first species to disappear. Thus, predators are often lost before their prey, and those species that do survive on small fragments (usually herbivores) tend to become far more abundant than populations of the same species on larger species-rich fragments. There are two principal explanations for this increased abundance. The first is *ecological release from competition*: when competing species are removed, the resources they utilized become available

to the persisting species. The second is that prey escape predators that normally limit their abundance on larger fragments. Lack of predators in small fragments can also lead to an overabundance of herbivores that tend to weed out palatable plant species and convert the landscape into a forest of “herbivore-proof” plants. Furthermore, as large predators disappear, smaller predators often increase; this is known as *mesopredator release* (Soulé et al., 1988; Terborgh et al., 1997). For example, in California, as coyotes disappear from fragments, there is an overabundance of smaller predators, such as skunks, raccoons, grey fox, and cats (Saether, 1999).



Cassava field burning in Vietnam (Source: K. Frey)

These smaller predators then prey on scrub-breeding birds. Fragmentation thus triggers distortions in ecological interactions that drive a process of species loss, the end point of which is a greatly simplified ecological system lacking much of the initial diversity (Terborgh et al., 1997; Terborgh et al., 2001).

While predator-prey relationships are often altered in fragmented landscapes, it is not always possible to predict what the change will be. A number of review papers have examined nest predation in fragmented landscapes; however, the results have been inconsistent (Andren, 1994; Paton, 1994; Major and Kendal, 1996; Hartley and Hunter, 1998; Chalfoun et al., 2002). Studies in Central Canada, for example, found that nests in forest patches adjacent to agricultural land had increased predation, while those next to logged areas did not (Bayne and Hobson, 1997, 1998). It appeared that the predator community did not change in the logged areas, while forest patches next to agricultural land had increased densities of red squirrels that preyed on the nests. Other studies have shown that songbirds are subject to increased predation along edges, particularly in deforested areas. In other words, the type of fragmentation and the habitat adjoining the fragment in-

fluences predator-prey relations: nest predation is less affected by a single road bisecting an area, but is greatly affected along edges of areas that have been deforested (Hartley and Hunter, 1998).

Overall a combination of landscape type and structure, predator community, and level of parasitism are important in anticipating the outcomes of fragmentation. For example, unlike studies in the Midwest and Northeast of the United States, a study in the American West, where the landscape has historically been patchy, found that predation rates actually decreased as human-caused fragmentation increased (Tewksbury et al., 1998). This study indicated that the type of predators in an area, as well as the habitat structure, were key inputs to anticipate the impact of fragmentation on bird nest predation rates.

In addition, not all groups of species experience an increase in predation due to fragmentation. A recent analysis of the literature found that avian predators were more likely to benefit from fragmentation than mammalian predators (Chalfoun et al., 2002). Another study surprisingly found that turtle nests located along roads had lower predation rates than those lo-

Box 1. Corridors and Connectivity

When existing protected areas are small, connecting them to other protected areas may increase their ability to sustain their fauna and flora. Connectivity between protected areas is critical as few of them are large enough to sustain species on their own (Hunter and Gibbs, 2006). Four basic species movements are important to consider to ensure landscape connectivity: daily, small-scale home range movements; annual seasonal migrations; dispersal of young from their parents; and geographic range shifts (Hunter, 1997). These different species movements as well as the types of species found in a particular landscape are all important factors when increasing connectivity or designing protected area networks. One way to increase connectivity is by creating wildlife corridors. *Corridors* are linear strips of land that allow species to move among different habitat types for breeding, birthing, feeding, roosting, annual migrations, dispersal of young animals away from their parents, and as an escape path from predators or disturbance. Riparian zones are good examples of corridors that link forest patches. The value of corridors has been the center of considerable debate (Noss, 1987; Simberloff and Cox, 1987; Soulé and Gilpin, 1991; Simberloff et al., 1992; Tewksbury et al., 2002). Part of this debate is due to the theoretical nature of the corridor concept. There are few studies that show that animals actually use corridors, or that can separate between the effect of the corridor itself from that of the additional habitat provided by its creation.

cated in edges or in forests (Hamilton et al., 2002).

An increase in invasive plants following fragmentation may indirectly enhance predator success on bird nests. Schmidt and Whelan (1999) found that invasive plants of the genera

Lonicera and *Rhamnus* were not only preferred nesting sites for American robins (*Turdus migratorius*) and Wood thrushes (*Hylocichla mustelina*), but also facilitated predator access to nests. The invasive plants leaf out earlier, and so are frequently chosen as nesting sites; the lack of thorns and lower nest height

Box 2. The Futi Corridor – Linking Tembe Elephant Park, South Africa to Maputo Elephant Reserve, Mozambique

Landscapes have naturally occurring borders that are not determined by political boundaries. Many political borders are freely crossed by animals to access the resources they need for survival, while others, such as many international borders, not only appear on maps, but are bounded by fences or other obstacles that fragment landscapes and ecosystems. These boundary markers may present an impenetrable barrier to species that can limit a population's access to needed resources or prevent migration and movement through a landscape. In these situations removal of border obstacles and creation of designated corridors to facilitate animal movement has sometimes proven to be a worthwhile solution.

The border between Mozambique and South Africa is an example of such a solution. A fence constructed along the border divided a population of elephants, the only indigenous population remaining on the coastal plain of Southern Mozambique and Kwa-Zulu Natal province in South Africa. These elephants traveled along the “Futi Corridor” (a seasonal river and marshland) that links Tembe Elephant Park in South Africa to Maputo Elephant Reserve in Mozambique.

With the end of political unrest an opportunity arose to assess the need for the fence and the potential for reunifying the elephant population. On June 22, 2000, the governments of Mozambique, Swaziland, and South Africa signed the Lubombo Transfrontier Trilateral Protocol, an agreement whose goal is to remove borders to support conservation. Scientists at the Conservation Ecology Research Unit (CERU) at the University of Pretoria spent three years tracking the movements of elephants along a section of the Mozambique/South Africa border (Van Aarde and Fairall, 2002). Using satellite radio tracking, they found that the populations still traveled the traditional routes they had used prior to installation of the fence. Examining the elephant population's movement patterns, and their impact on the landscape and interaction with humans, a series of recommendations to facilitate movement across the boundary while minimizing disruptions to the landscape and the human population were proposed. The recommendations included removing the border fences entirely, formal designation of the “corridor” as a protected area in Mozambique, and specific boundary parameters for the corridor. Plans are currently underway to implement the recommendations and establish a conservation area that will cross the political boundaries (Peace Parks, 2003).

Cross border conservation solutions have been used more and more frequently to facilitate conservation cooperation between countries around the world. Typically solutions like this are called Transfrontier Conservation Areas (TFCA's) or Transboundary Natural Resource Management solutions. These cross border efforts are instrumental in reunifying artificially-divided landscapes and can facilitate development of coordinated conservation practices. Other benefits include improved political relationships between countries, increased tourism opportunities, and the involvement of local communities in crafting conservation solutions that will provide direct local benefits. [For more details see the module on Transboundary Protected Areas].

Box 3. Identifying Species Vulnerable to Fragmentation

Knowing which species are most vulnerable is critical to understanding the impact of fragmentation. Behavioral patterns, resource needs, reproductive biology, and natural history can be used to identify species that are most vulnerable to fragmentation. Below is a list of characteristics that are typical of species more vulnerable to fragmentation (modified from Laurance and Bierregaard, 1997):

- Rare species with restricted distributions (Andersen et al., 1997)
- Rare species with small populations (Andersen et al., 1997)
- Species with large home ranges (Soulé et al., 1979; Newmark, 1987)
- Species that require heterogeneous landscapes
- Species that avoid matrix habitats (Warburton, 1997)
- Species with very specialized habitat requirements
- Species with limited dispersal abilities (Laurance, 1990, 1991)
- Species with low fecundity (Sieving and Karr, 1997)
- Species with variable population sizes using patchy resources
- Ground nesters vulnerable to medium-sized predators at edges (Bayne and Hobson 1997, 1998)
- Species vulnerable to hunting (Redford and Robinson, 1987)
- Species that are arboreal (canopy dwellers)
- Co-evolved species (e.g., plants with specific pollinators) (Gilbert, 1980)

of these shrubs in turn seems to aid predators in reaching the nests.

Fragmentation can also take an indirect toll on plants whose pollinators or seed dispersers are forced to navigate an increasingly fragmented landscape in search of their host plants (Aizen and Feinsinger, 1994). In western Australia, only small, isolated populations of the cone-bearing shrub, Good's banksia (*Banksia goodii*), remain, and many of these no longer reproduce because their pollinators have disappeared (Buchmann and Nabhan, 1997).

Fragmentation often alters animal behavior, due to changes in the environment or predator activity. For example, Hobson and Villard (1998) found that one bird, the American Redstart (*Setophaga ruticilla*) acted more aggressively when confronted with a model of a nest parasite—the Brown-headed Cowbird

(*Molothrus ater*)—in fragmented landscapes than in unfragmented ones. This appears to be because Cowbirds are more common in fragmented areas, and are thus a greater threat to the Redstarts' breeding success.

Management of Fragmented Landscapes

Increasingly, conservation professionals are faced with managing fragmented landscapes. This challenge is complicated by the diverse responses of species to fragmentation and the complex decisions surrounding conservation of land. As with any conservation management plan, when examining a fragmented landscape, it is essential to identify clear goals. For example, for a wide-ranging species, such as the black bear (*Ursus americanus*), habitat connectivity is critical, so it is important to maintain a large unfragmented area; however, to conserve a rare species with specific habitat needs, it may be

more important to preserve a specific place than a large area, so that smaller fragments are more valuable than larger fragments (Dale et al., 1994; Laurance and Bierregaard, 1997). While there are many different conservation strategies and options (Laurance and Gascon, 1997), here we will explore some of the strategies specially aimed at fragmented landscapes [For a detailed discussion of conservation management strategies see modules on Conservation Planning in and outside Protected Areas].

Recommendations

The following are important considerations to manage fragmented landscapes (Laurance and Gascon, 1997; Meffe and Carroll, 1997):

- *Conduct a landscape analysis* to determine where the big blocks of land suitable for protection exist and where potential connections among them lie.
- *Evaluate the landscape and each patch in a regional context.* If all surrounding landscapes are heavily fragmented and your focal landscape is not, its role in biodiversity conservation is important at a regional level. Protection and conservation action should be elevated accordingly. In contrast, if surrounding areas are largely unfragmented, fragmentation issues in your focal region may be less important.
- *Increase connectivity.* Examine different planning options to avoid or reduce fragmentation. Can roads be re-routed, alternative land uses be found, or protected areas be placed strategically? [See Box 1. Corridors and Connectivity]
- *Minimize edge effects.* Land managers often have some control over which land uses will be adjacent to one another. Land management policies can be established to ensure that a fragment's size and shape maximizes the effective area of protected land and reduces edge effects. Adequate buffer zones (where land use is compatible with species' needs) around protected land also minimize edge effects.
- *Remember small fragments.* They may not sustain jaguars or tapirs, but they still retain huge diversities of invertebrates, small vertebrates, plants, and perhaps rare or unique eco-

systems and species.

- *Identify species most vulnerable to fragmentation.* It is important to identify those species most likely to be impacted by fragmentation and to consider them when designing management and monitoring plans. [See Box 3. Identifying Species Vulnerable to Fragmentation]

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- Corridors: linear strips of protected land.
- Ecological release from competition: when competing species are removed, the resources they utilized become available to the persisting species.
- Ecosystem: an assemblage of organisms and the physical environment in which it exchanges energy and matter.
- Ecosystem loss: the disappearance of an assemblage of organisms and its physical environment such that it no longer functions.
- Edge environments or ecotones: the transition between two different habitats.
- Faunal relaxation: the selective disappearance of some species and replacement by more common species.
- Fragmentation: the subdivision of a formerly contiguous landscape into smaller units.
- Genetic drift: a random change in allele frequency in a small breeding population leading to a loss of genetic variation.
- Habitat: there are two common usages of the term habitat. The first defines habitat as a species' use of the environment, while the second defines it as an attribute of the land and refers more broadly to habitat for an assemblage of species. For a discussion of different usages of habitat see Corsi et al., (2000). In this module we use habitat and "habitat type" to differentiate between the two common usages of the term.
- Habitat degradation: the process where the quality of a species' habitat declines.
- Habitat loss: the modification of an organism's environment to the extent that the qualities of the environment no longer support its survival.
- Inbreeding depression: reduction in reproductive ability and survival rates as a result of breeding among related

Glossary

Anadromous fish: fish that return from the sea to the rivers where they were born to breed (e.g. salmon).

Area-sensitive species: species that require large areas of continuous habitat and cannot survive in small patches.

Biome: a major biotic classification characterized by similar vegetation structure and climate, but not necessarily the same species.

Connectivity: the degree to which patches in a landscape are linked.

individuals.

Lentic: relating to or living in still or slow-moving water.

Lotic: relating to or living in swift-flowing water.

Matrix: the most common cover type in any given landscape. As it occupies the most area, it is the dominant feature of the landscape and usually the most connected cover type.

Meso predator release: as large predators disappear, the population of smaller predators often increases.

Patch: usually defined by its area, perimeter, shape, and composition, such as a land cover type (such as water, forest, or grassland), a soil type, or other variable.

Potential extent: the extent of coverage of a particular biome type, assuming there were no humans and based on current climatic conditions.

Trophic level: stage in a food chain or web leading from primary producers (lowest trophic level) through herbivores to primary and secondary carnivores (highest trophic level).

