Identifying the Biodiversity Research Needs Related to Forest Fragmentation

John A Kupfer  
*University of Arizona*

George P. Malanson  
*University of Iowa*

Scott B. Franklin  
*University of Memphis*
Identifying the Biodiversity Research NeedsRelated to Forest Fragmentation

John A. Kupfer

Dept. of Geography and Regional Development
University of Arizona
Tucson, AZ 85721
kupfer@email.arizona.edu

George P. Malanson

Dept. of Geography
University of Iowa
Iowa City, IA, 52242
george-malanson@uiowa.edu

Scott B. Franklin

Dept. of Biology
Univ. of Memphis
Memphis, TN 38152
sfrankli@memphis.edu

A report prepared for the National Commission on Science for Sustainable Forestry (NCSSF) and funded by the National Council for Science and the Environment (NCSE)

February 13, 2004
Chapter 1: Forest Fragmentation: The State of Knowledge

In recent decades, a tremendous amount of field research coupled with technological advances in remote sensing, ecological modeling, geographic information systems (GIS), and spatial analysis have clarified the effects of forest fragmentation on landscape pattern, biodiversity and ecological processes. Integrating results from such studies into land management plans and decision making, however, is not a trivial task because the effects of fragmentation: 1) are highly specific to the taxa, spatial scales, and ecological processes considered, 2) vary according to landscape type and landscape structure, and 3) may be obscured by local effects such as changes to microhabitat features or historical events (Villard 2002). Further, ecological responses to deforestation (the loss of forests) and forest fragmentation (the alteration of forest pattern across the landscape) may be interactive and highly nonlinear, i.e., where incremental change in the landscape will have disproportionately large effects on the biota and where the influence of one variable is largely dependent on the value of other factors (Franklin and Tolonen 2000; Malanson 2002a,b).

We believe that a synthesis of the patterns and effects of forest fragmentation is needed to bring together the diverse and rapidly growing literature on fragmentation effects and identify "research horizons" for fragmentation studies in the coming decade. In this paper, we use an explicitly landscape ecological approach because of its relevance to issues of changes in ecosystem pattern and function in fragmented landscapes (Kupfer 1995), recognizing the importance of addressing studies of ecological pattern and process at a range of spatial, temporal and ecological scales.
Figure 1.1. The mosaic of old-growth forest, second-growth forest, agricultural fields, pastures and villages in the landscape outside of Lamanai Archeological Reserve, Indian Church, Belize (photo: J. Kupfer).

Forest Fragmentation: From the Past to the Present

Many of the long-standing theories concerning forest fragmentation stem from island biogeographic representations of landscapes in which forested ecosystems are conceptualized as areas of suitable habitat embedded in an uninhabitable matrix of non-forested uses. Such a depiction of landscapes tends to overlook variability in habitat quality in both the forested and non-forested habitats. The non-forested habitat, for example, may be neither uniformly unsuitable nor serve as a fully-absorbing barrier to the dispersal of certain forest taxa (e.g., Kupfer 1995) while the remaining forest areas typically represent a gradient of conditions and habitat suitability. Studies of mosaic landscapes containing a range of old-growth forest, successional habitats, and agriculture (e.g., shifting cultivation systems: Fox et al. 2000; Kupfer et al., in press) exemplify how landscapes can represent a range of conditions from deforestation
to varying degrees of forest degradation in otherwise “intact” forest (Fig. 1.1). Further, it is important to recognize that the dynamics of a forest fragmented by agriculture or urban development may be vastly different from those associated with the mosaic of mature and regenerating stands resulting from timber harvesting. The first situation represents cases where the modified habitat may be indefinitely affected and have little or no habitat value for forest species whereas the latter situation may involve only a temporary reduction in habitat for species that rely on mature forests. This also helps to reinforce the dynamic nature of non-forested ecosystems, which may, through ecological succession, increasingly resemble forested areas (e.g., Moran and Brondizio 1998).

The “remnants as islands” analog is also limited in that it focuses attention almost solely on population (or metapopulation) dynamics within forested habitats while frequently ignoring dynamic linkages with the non-forested habitat (except for the outermost forest edge habitat). Often, the most important aspect of non-forested habitats, from the viewpoint of ecologists concerned with biodiversity in forest remnants, is whether species can move through the non-forested habitats to other forest habitats, and if not, how can such links be fostered. This concern is perhaps best represented by the rapid growth of interest in habitat corridors, which have a highly developed literature and are increasingly becoming cited as potential components of regional management plans (e.g., Davidson et al. 1996; Iverson et al. 2001; Hess and Fischer 2001). While most attention has been paid to movement through habitat in binary landscapes (e.g., Malanson and Cramer 1999a,b), some attempts have been made to use more classes (e.g., Wiegand et al. 1998) or to represent a continuous surface with discrete cells (With 1994; Malanson 2002). Such approaches are important because a spatially-explicit representation of habitat quality utilizing discrete cells may be more realistic for many species and because matrix
quality has been shown to have a significant effect on population processes such as dispersal in fragmented landscapes (Gustafson and Gardner 1996; Fahrig 2001).

If we recognize that the non-forested matrix represents a heterogeneous area that may be usable to some degree for habitat or movement, we must also recognize that not all areas within remnants of forested habitat provide the same degree of habitat quality. In addition to natural heterogeneity created by canopy gap openings and other disturbances (e.g., Farris et al., in press), silvicultural practices create patchiness (and variability in habitat suitability) within larger forested stands that can be quantitatively documented (e.g., Anderson et al. 2000; McGarigal et al. 2001). The extent to which such changes translate into changes in species habitat or alterations of ecosystem processes, however, remains more difficult to assess because of species-specific responses to such changes and potential feedback effects. For example, the role of thresholds is becoming increasingly recognized as a potential area for fragmentation research. Models utilizing percolation theory show that habitat destruction has little effect on movement until a threshold or critical point is reached when a gap wide enough to interrupt dispersal is created. In random landscapes, i.e., where the spatial patterns of the habitat cells/pathways are random, the threshold is found at c. 60% habitat. Aspects of the geometry of the habitat also change nonlinearly in the vicinity of this threshold; differences are seen in the number of clusters, the size and fractal dimension of the largest cluster, and the mean edge of all clusters (Gardner et al. 1987). Boutin and Hebert (2002: 396) recently made a call for a greater examination of threshold behavior with respect to fragmentation, noting:

“We think that the challenge to landscape ecologists studying fragmentation in managed forests is to determine possible thresholds of landscape change where landscape configuration becomes an important component over and above the absolute loss of habitat. If such thresholds can be identified, managers can then begin to plan their activities accordingly.”
Remote sensing and GIS have become indispensable tools for studying patterns of fragmentation, particularly at relatively large spatial scales. Lambin (1999) and Allen and Kupfer (2000) have addressed remote sensing methods for the detection of not only simple deforestation but also forest degradation. However, common sources of data such as satellite imagery are only a starting point; theory and case studies need to be developed and integrated into ecological modeling efforts to help identify the degree to which lowered habitat quality in remnants will further reduce their value (e.g., Riebsame et al. 1994). The effects of habitat destruction and extractive use of resources may create a “double bind” for species in which habitat is reduced and the quality of the remnant habitat is lessened (Malanson 2002a,b). Simulation results indicate that if such combinations lower the reproductive vigor in remnant habitat, the effect will be greatest on those species characterized as superior competitors. Binary landscapes potentially miss these cumulative effects. The conclusion that should be drawn from studies such as these, we believe, is that more emphasis on the effects of habitat heterogeneity and quality in fragmented landscapes is needed to help elucidate the ecological effects of fragmentation and assist in the development and implementation of methods, models and metrics related to habitat quality.

Forest Fragmentation: From the Present to the Future

Whether the explicit focus has been on specific species or more generally on various aspects of biodiversity, research on the effects of deforestation and forest fragmentation has typically concentrated on pattern and process within habitat remnants (e.g., Bierregaard et al. 1992; Laurance et al. 1998a,b). Understanding the effects of habitat destruction on remnants is critical to assessing impacts on the diversity of species and community composition, and
ambitious, ongoing, long-term experiments have even created habitat islands and are tracking their biology (e.g., Laurance et al. 1998a,b). A considerable amount of work on forest fragmentation has stressed how declining forest area and/or increasing isolation of forest remnants influences both richness and species survival. The underlying theory (stemming from applications of island biogeography and metapopulation theory) is that as forests are fragmented, populations decline in size and become increasingly isolated from one another, leading to higher extinction rates, lower immigration rates, and lower species richness in remaining forests, although such effects may not be immediately manifested (Tilman et al. 1994a).

The other widely studied impact of forest fragmentation is the increased susceptibility of forest remnants to edge effects – changes in microclimate, forest structure, biotic composition, and ecological function that occur along forest edges exposed to non-forested habitats such as agricultural fields, clear cuts, roads or pastures. Characteristics of edge effects such as depth of edge influence have been documented for a wide range of variables, locations and organisms (Forman 1995; Baker and Dillon 2000), and the stand-level importance of edge habitats has often been evaluated indirectly through the use of patch shape indices such as perimeter-area ratio and fractal dimension (e.g., Jorge and Garcia 1997). However, such analyses can be of varying usefulness and may be misinterpreted for a range of reasons (Kupfer and Runkle 2003). While edges are often characterized as sharp boundaries beyond forested and non-forested systems, the structure and composition of the adjacent habitats may very greatly, resulting in significant differences in edge characteristics and complexity (e.g., Matlack 1993, Kupfer 1996). Further, it is clear that studies of forest edges must not only document the characteristics of the edges themselves (the traditional edge effect) but also seek to uncover the dynamic manners by which edges alter key ecological processes in forest remnants and across the landscape as a whole.
(boundary dynamics: Wiens et al. 1985; edge-mediated effects: Fagan et al. 1999). For example, Ranney et al. (1981), Kupfer (Kupfer and Runkle 1996; Kupfer et al. 1997; Kupfer and Runkle 2003), Laurance (1997) and Goldblum and Beatty (1999) have all suggested that edges may influence canopy gap replacement processes within forest interiors by acting as seed sources for shade-intolerant plant species.

Issues of forest size, isolation and edge are frequently addressed in forest management planning, but their quantification still often involves relatively simplistic measures of forest fragmentation based on simplified, discrete depictions of the landscape that may or may not directly address the true underlying mechanisms for species loss (e.g., loss of habitat, altered trophic structures, lower population numbers). For example, the quantification of “forest area” or “suitable habitat” that typically accompanies GIS-based studies implies a readily identifiable and meaningful difference between forested and non-forested habitat and does not differentiate the quality of forested areas. One might, for instance, question the “true” or “effective” size of a 100 ha forest that contains 50 ha of native deciduous forest and 50 ha of non-native pine plantation, or question “equal” permeability [to animal movement] of a forest edge next to an interstate versus a forest edge adjacent to a regenerating cut forest. It is possible, however, to recast estimates of area, isolation and edge dynamics in light of a habitat heterogeneity and habitat quality perspective. Wiens (1997), for example, has suggested that the basic species-area relationship of island biogeography can be predictably modified if we take into account the degree to which the area around remnant habitat is habitable or useable, providing a starting point for linking the divergent conceptualizations of fragmented landscapes.

Perhaps more significantly, future research on forest fragmentation needs to better define and explore the dynamic relationships among the component parts of the landscape. Forest
fragmentation affects animal movement, propagule distribution, and local climate across the landscape (Forman 1995) and thereby influences local vegetation composition and dynamics. For example, Silva et al. (1996) and Kupfer et al. (in press) found that landscape structure strongly affected regeneration of adjacent agricultural lands and thus connected the importance of forest fragmentation with the conservation of forested landscapes. Habitat quality in non-forested habitats (or in successional habitats) may in turn feedback to alter ecological processes in remnant forests (Cantrell et al. 1998). Previous studies have proposed that forest fragments, often disturbed by winds and other factors from the surrounding modified landscape matrix, may be prone to invasions of successional species adapted to recurring disturbance (e.g., Janzen 1983; Laurance 1997). At this point, the literature on such linkages between fragmentation and community-level dynamics of regenerating lands is fairly dispersed and should be incorporated into a contemporary synthesis of fragmentation effects.

Purpose and Structure of This Paper

At a time when the needs of renewable resource utilization (e.g., timber harvesting) must be balanced against the various other functions that forested habitats provide, it is important to understand and incorporate concepts and measures associated with fragmentation into forest management plans, as both an aid to facilitating sustainable utilization of those resources and as a means for protecting susceptible species and ecosystems. Several recent national assessments, including *The USDA Forest Service 2000 RPA Assessment of Forest and Range Lands* (USDA Forest Service 2001), *The State of the Nation’s Ecosystems: Measuring the Lands, Waters and Living Resources of the United States* (Heinz Center 2002), and *The U.S. Roundtable on Sustainable Forests Draft Report* (http://www2.srs.fs.fed.us/2003/2003.htm), have cited the
importance of studying the relationships between biological diversity and landscape structure in fragmented landscapes and support the notion that the composition, extent, and spatial layout of land cover types have the potential to fundamentally affect the flow of ecosystem goods and services. These reports have in turn stimulated the development and implementation of indices for national assessment and monitoring of fragmentation (Riitters et al. 2002).

Despite the widespread recognition that forest fragmentation is a pressing environmental issue, there continues to be active debate concerning the most appropriate areas for future study of fragmentation effects and the manners by which theory can be applied to real-world situations. For example, at the same time that governments and land management agencies have been seeking measures of spatial configuration that can be used to monitor changes in fragmentation and assist forest managers in their decision-making processes, some scientists have argued that metrics of spatial configuration are of little value as a management tool because habitat loss is much more likely to result in declines of biodiversity at most levels of fragmentation (e.g., Fahrig 1997; Lindenmayer et al. 2002). Villard (2002: 320) thus recently noted in his introduction to a special issue of *Ecological Applications* focused on habitat fragmentation:

“One of these challenges (concerning fragmentation research) is to ensure that researchers do not focus on intellectually stimulating, yet spurious issues that play only a minor role in biodiversity conservation when considered in the broader context of landscape change. As the understanding of habitat loss and fragmentation effects improves, ecologists have to convey a loud and clear message to decision-makers, and this will only be achieved using well-focused, high quality research.”

To this end, the National Commission on Science for Sustainable Forestry (NCSSF) funded this project to provide a synthesis of the current state of knowledge on fragmentation effects and to help identify knowledge gaps that need to be addressed by additional research.
NCSSF is a non-profit organization convened and managed by the National Council for Science and the Environment with its mission being “to improve the scientific basis for the development, implementation, and evaluation of sustainable forestry in the United States”. Apart from its ecological significance, fragmentation was identified as a key research area by NCSSF because it is a key biodiversity indicator within the Montréal Process, which involves the Working Group on Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests. The Working Group was formed in Geneva, Switzerland, in June 1994 to develop and implement internationally agreed-upon criteria and indicators for the conservation and sustainable management of temperate and boreal forests. In February 1995 in Santiago, Chile, member countries of the Montréal Process endorsed a comprehensive set of criteria and indicators for forest conservation and sustainable management for use by their respective policy-makers (The Montréal Process: http://www.mpci.org/whatis_e.html, June 27, 2003). Indicators of fragmentation were included within Criteria 1: Conservation of Biological Diversity, and are considered separately from indicators of forest extent and protected status.

The primary charge of this project was to examine the relationships between forest fragmentation and biodiversity. However, forest fragmentation can be used to refer to either the broad process of forest loss and isolation (which includes the effects of species loss due to deforestation, i.e., area effects) or more specifically to changes in the spatial configuration of forest remnants that is a result of deforestation. Our general focus is on the latter, that is, the way in which patch isolation and connectivity are altered during deforestation plus the consequences of edge effects. However, such changes cannot be understood without considering the consequences of forest loss, and the combined effects are difficult or impossible to separate outside of simulations. As a result, our conceptual model of fragmentation as well as our
discussion of forest fragmentation effects include the broad range of effects that are associated with forest loss and disjunction.

The term biodiversity is also ambiguous in that it can be used to refer to everything from genetic diversity of populations to the diversity of cover types across a landscape, although it is often used interchangeably with species richness (the number of species in a defined area). Throughout this paper, we address the effects of fragmentation on a range of biodiversity aspects, but we focus primarily on aspects at the population and community levels (e.g., issues of species persistence and extinction, changes in species richness accompanying forest fragmentation). We do so primarily because these are the levels at which most forest managers have to make their decisions, for instance, in response to the Endangered Species Act. We also address the effects of fragmentation on a wide range of ecological processes such as dispersal and trophic fluxes because these are the fundamental processes that underpin patterns of species patterns.

Finally, the primary objective and mandate of NCSSF is to provide practical information and approaches that serve the needs of forest managers, practitioners and policymakers. Therefore, the information contained in this report comes not only from our review of the scientific literature but also from meetings organized by NCSSF with managers, practitioners and policymakers from a diverse range of fields, including government agencies, non-governmental organizations, small independent timber companies, and large commercial logging interests. It has also been shaped through discussion and interactions with Kurt Rüters (USDA Forest Service), graduate students in Dr. Kupfer’s forest fragmentation seminar in Fall 2002 (Kevin Anchukaitis, Jeff Balmat, Mike Crimmins, Francisco Delgado, Toby Finke, Erika Geiger, Kandres Halbrook, Christine Hansell, Dan Higgins, Choy Huang, Pepe Iniguez, Candice Koski,
Theresa Mau-Crimmins, Susan Taunton, and JD Trebec), NCSSF Commission members (especially Al Lucier, Hal Salwasser and Norm Christiansen), and scientists that were involved in special fragmentation symposia held at the 2003 U.S. Association for Landscape Ecology Meeting (organized and chaired by John Kupfer with participants Kurt Riitters, George Malanson, Andrew Fall, and Marc Bélisle) and 2003 Association of Southeastern Biologists Meeting (organized and chaired by Scott Franklin with participants John Pye, Brean Duncan, Glenn Matlack, Vic Rudis and Steve Seagle).
Chapter 2: Forest Fragmentation: Background and a 

Conceptual Model of Fragmentation Effects

The study of forest fragmentation is the study of habitat destruction and isolation of the resulting remnants. Bunnell (1999a), Fahrig (1997, 1999) and Haila (1999), while recognizing that both co-occur, argue that the ecological consequences of habitat loss and isolation should be distinguished. The key point, they contend, is to distinguish the effects of reducing habitat area (deforestation) from those of increasing isolation (“true” fragmentation effects). While we agree that this distinction is important and believe that it may be possible to separate the effects of deforestation and fragmentation in simulations, it is difficult or impossible to do so in real forests. Further, we argue that all effects must be considered in an attempt to understand forest fragmentation (in the broader sense of the term), and rather than trying to isolate each, more emphasis is needed on understanding their interaction across the range of effects.

While ecological research has focused attention on species in remnant fragments because the area of habitat destroyed may lose most or all of its plants and animals (e.g., Bierregaard et al. 1992, Laurance et al. 1998a,b), there is mounting evidence that management in fragmented landscapes needs to focus as much or more on processes in the intervening matrix (Crome 1997; Lindenmayer and Franklin 2002). For our purposes, the remnants will be forest areas not affected by a specific human-caused disturbance and the matrix will be the disturbed area, which may include recently logged areas, agricultural fields, and other areas of human disturbance. Although this usage of matrix does not necessarily agree with other formal definitions of this term (e.g., the matrix defined as the most extensive or dominant area sensu Forman 1995), it is rather intuitive and matches the usage of Lindenmayer and Franklin (2002), who have best
theorized it. This definition also recognizes that the matrix can take on a variety of forms and
contain a range of varying habitat quality.

In this chapter, we provide a brief review of some of the most important theoretical
advances in the study of deforestation and habitat fragmentation, including island biogeography
theory, metapopulation theory and source-sink dynamics. These concepts are discussed
throughout this paper so a concise summary of the key points is warranted at this point. After this
review, we present a working conceptual model, based on models developed by Zuidema et al.
(1996) and Lindenmayer and Franklin (2002), that addresses the major effects of fragmentation
on biodiversity.

Deforestation and Forest Fragmentation: Basic Concepts

Nineteenth century works by scholars such as George Perkins Marsh and Alexander
Woeikof were the first to systematically document the effects of habitat destruction on soil
erosion, stream hydrology, climate, and (to a lesser degree) plant and animal communities
(Kupfer and Malanson, in press). Insights provided by such works subsequently served as the
basis for later studies of habitat alteration in the early- and mid-twentieth century. For example,
the influential international symposium “Man’s Role in Changing the Face of the Earth”,
convened in 1956, included numerous contributions addressing deforestation and habitat
fragmentation, including Darby’s analysis of deforestation in Europe, Clark’s treatise on the
alteration of mid-latitude grasslands, and Strahler’s paper on the effects of habitat change on
fluvial geomorphic processes. Papers from this symposium also raised some of the earliest
concerns about how human actions were altering patterns of biodiversity and leading to species
extirpations and extinctions in both natural and semi-natural habitats. Curtis (1956), for instance,
drew attention to the spatial aspects of fragmentation by documenting changes in forest cover that had accompanied Euro-American settlement in Cadiz Township in southern Wisconsin, noting not only the decreasing amount of forested habitat (e.g. reduced patch size) but also the changing spatial relations among habitat patches (Fig. 2.1).

Ecological concerns about the effects of deforestation and other forms of habitat alteration grew during the mid- to late- twentieth century and, coupled with the quantitative revolutions in ecology and geography, led to efforts to develop prescriptive models for maximizing species diversity and protecting critical habitat for endangered species. The first quantitative links between habitat loss and species extinctions were developed out of concepts formalized within island biogeography theory, which stated that the number of species on oceanic islands is a function of island size (which was linked to extinction rates and habitat heterogeneity) and isolation (which was believed to influence the arrival of potential colonists).
MacArthur and Wilson 1967). Large islands located near the mainland were hypothesized to maintain the greatest number of species because of their size and proximity to colonization sources while small, isolated islands had the fewest species. Although the idea that species richness varied as a function of habitat area was well established at the time, the importance of habitat isolation and especially its quantification by distance to a potential colonizer source was a novel concept.

Ecologists subsequently drew parallels between oceanic islands and terrestrial habitats that had been fragmented by human land uses and began to study the relationships among biodiversity, remnant forest area and forest patch isolation (e.g., Lovejoy et al. 1986; Bierregaard et al. 1992). Island biogeography principles were applied to the design of nature reserves, for example, the idea that biodiversity in reserves would be highest in larger and less isolated reserves (Diamond 1975). The ensuing debate over the relevance of island biogeography theory to terrestrial habitats is lengthy and has been reviewed elsewhere (e.g., Gilbert 1980), but the final conclusion was that its direct applicability to nature reserve design is limited, although the basic tenets are highly relevant (Kupfer 1995). For example, spatial structure is now recognized as an essential element for contemporary theories addressing processes involving genes, individuals, populations and communities (Turner et al. 2001). Theories associated with metapopulation (Hanski and Gilpin 1991) and source-sink (Pulliam 1996) models of population dynamics as well as the roles of corridors and connectivity in fragmented landscapes (Forman 1995) have in fact grown directly out of the emphasis on isolation that was central to island biogeography theory (cf. Wiens 1995; Kupfer 1995) and perpetuated interest in landscape metrics that capture not only area but also isolation effects in fragmented landscapes.
While sharing a common theoretical basis with island biogeography theory, metapopulation theory (Levins 1969) focuses on interactions among populations rather than determinants of species richness. Metapopulations consist of a subset of habitat patches where populations may or may not exist and infrequent between-patch migrations. Each population has a finite probability of extinction, and each local extinction may be balanced by recolonization from neighboring populations. Extinction may occur due to loss of genetic variation, demographic fluctuation, or environmental fluctuation, all of which become more important as population size decreases. There is thus a direct relationship to fragmentation / habitat loss and the potential for a population to go extinct. Recolonization potential is based on size and suitability of patches as well as isolation from potential colonist patches, both of which are potentially affected by fragmentation. Metapopulation theory has been used to examine the extinction threshold for species as habitat is destroyed (Bascompte and Sole 1996) and subsequently minimum viable populations (Gilpin and Soulé 1987; Walters et al. 2002) using a range of simulation models. However, one of the main assumptions of basic metapopulation models, that suitable habitats are equally suitable and unsuitable habitats are equally hostile, is unrealistic for real landscapes.

The source-sink dynamic model is a slightly revised version of metapopulation dynamics that considers the implications of habitat-specific demography. That is, subpopulations occurring in different habitats are assumed to have different demographic rates. A source is a population in which births exceed deaths and emigration exceeds immigration; a source area is thus a net exporter of individuals. Conversely, sinks are habitats in which deaths exceed births and immigration exceeds emigration (Pulliam 1996). Source populations help to maintain sink populations (a rescue effect), and in the absence of immigration, sink populations disappear. An
important point is that defining an area as a source or sink is both temporally and spatially scale
dependent (Boeken and Shachak 1998). In addition, source-sink analyses (and metapopulation theory in general) still fail to explicitly consider the differential hostility of matrix habitat
between suitable patches that filter but do not stop plant and animal mobility.

**Forest Fragmentation: A Conceptual Model**

Based in part on principles from island biogeography theory, metapopulation models, and
source-sink dynamics, Zuidema et al. (1996) developed a conceptual model that identified four
interactive effects of forest fragmentation leading to the loss of biodiversity, all of which focused
most explicitly on patterns and processes associated with the remnants (Fig. 2.2). However,
recent analyses have begun to emphasize the importance of the characteristics of the area around
the remnants to their function and diversity. Lindenmayer and Franklin (2002), for example,
described in detail many of the ways in which the matrix can influence the effect of forest
fragmentation on species in remnants. Here, we will address the conceptual scheme of Zuidema
et al. (1996) by rethinking the effects of fragmentation and incorporating additional matrix
heterogeneity concepts, resulting in a modified model that is more inclusive of the full range of
fragmentation effects (Fig. 2.3).

**Forest Fragmentation: Primary Effects**

The four primary ways in which biodiversity may affect forest fragmentation are: 1) sample effects, 2) area effects, 3) isolation effects, and 4) edge effects. Each of these in turn
influences a range of population, community and ecosystem processes.
Figure 2.2. Scheme of forest fragmentation effects from Zuidema et al. (1996) as modified by Lindenmayer and Franklin (2002).

**Sample Effect.** When forest is cut, most individual plants in the cut area are lost and the extent of habitat for forest animals is changed. In some cases, species could become globally or locally extinct in this step alone (Connor and McCoy 1979). While the sample effect may lead directly to extinction or extirpation if all the individuals of a species are removed or if all of its habitat in an area is lost, sample effects are generally tied to reductions in population sizes and thereby loss of biodiversity through a range of processes that are most relevant for small populations (e.g., demographic stochasticity, genetic stochasticity, and susceptibility to environmental change and natural catastrophes; Ricklefs and Miller 2000). Additionally, the
Figure 2.3. Modified conceptual model of fragmentation effects.
populations in the remnants are merely a sample of the original population and may not be representative of the pre-cut populations, not only in terms of numbers but also in terms of a range of other characteristics (e.g., genetic diversity, demographic structure). Thus species interactions – predation, competition, and mutualism – are also potentially altered in the remnants.

Area Effect. Island biogeography (MacArthur and Wilson 1967) is a starting point and guide in the evaluation of area effects, as in so many considerations of spatial ecology. As MacArthur and Wilson (1967) noted, habitat loss has two consequences: 1) a reduction in resources for species even in a homogeneous habitat leads to smaller populations vulnerable to extinction; and 2) a reduction in the range of habitat types results in fewer species. The former must be considered in terms of niche packing and the inability of species to subdivide a habitat into extremely narrow niches if the total resources are limited. Smaller populations also may be less fecund than larger populations (the Allee effect) and more susceptible to local extinction. Thus, island biogeography theory postulates that species extinction rates are higher on small islands. While Fahrig (1997) and Haila (1999) argued that the area effect should not be considered as part of fragmentation in the strict usage of the phrase, it must be accounted for, in part because the nature of isolation effects may be based on the area effect (see below). We represent these two effects as change in the resource base in Fig. 2.3.

Reductions in forested area can also result in the subdivision of populations. Island biogeography theory and metapopulation models have demonstrated that patch area affects their role as target: larger patches are easier to locate. Patch size may also affect the presence of animal dispersal vectors as large mammals and some birds may require larger patches for
grazing, nesting, and mating and thus may not serve as vectors from smaller patches. Patch size and shape may also affect wind fields (Pielke et al. 1997); smaller patches with certain orientations will have less drag on wind and may have seeds more easily lofted above and away increasing dispersal.

The types, extents, frequencies and even intensities of disturbances can be constrained by the area of remnants, and disturbances that begin in the matrix can spread to influence processes in the remnant. Some types of disturbances may depend on area; for example, small areas may be more subject to wind destruction. Frequencies depend on area where the source and spread depend on contiguity (although this is difficult to separate from isolation in real landscapes). Specific disturbance characteristics such as fireline intensity may be influenced by the amount of area over which the disturbance develops, and the area of a disturbance per se can be part of a disturbance regime. Baker (1989), for example, illustrated how forest fragmentation could alter the potential fire disturbance regime for northern Minnesota. The combination of these aspects of disturbance regime will affect the dynamics of species and the resulting biodiversity (e.g., Malanson 1984).

Finally, reductions in forest area affect potential species interactions, with trophic effects being especially notable. Species that are at higher trophic levels, e.g., top carnivores, tend to require more area (Brown and Lomolino 1998). Because of the loss of energy at subsequent steps in the trophic pyramid, a large carnivore must cover an extensive territory to capture the small fraction of the primary productivity it accumulates. If the sample effect leaves top carnivores on small remnants, they are likely to become locally extinct should the remnants be too isolated for interpatch movement. Competition is also affected (Huxel and Hastings 1998); for example, some species may be released from competition by local extinctions subsequent to area and
sample effects (Hanson et al. 1990). Similarly, mutualisms can be lost if one interacting species becomes locally extinct and cannot be rescued (e.g., Anstett et al. 1997).

**Isolation Effects.** While sample and area effects are more directly related to deforestation, one of the primary results of fragmentation *per se* is the altered spatial configuration of habitats across the landscape, especially the increased isolation of forested patches. The immigration rate of an isolated remnant will almost surely be lower than an equal area surrounded by contiguous similar habitat, although this raises the important distinction between structural and functional connectivity. Structural connectivity refers to the degree of habitat connectedness. Fragmentation by its nature alters structural connectivity, with the degree of alteration itself being a function of the amount of remaining forest habitat (e.g., Andrén 1994). Functional connectivity, while related to structural connectivity, refers more directly to the ease with which organisms move across a landscape and is therefore of greater interest when assessing isolation effects.

The degree of isolation is dependent on factors that influence immigration such as distance of nearby patches and restrictiveness of the intervening matrix for habitat and movement. Some of the species in an area surrounded by contiguous homogenous habitat must be maintained by persistent immigration at some time scale. Because island biogeography assumes a completely uniform, inhospitable matrix (ocean), simple geometry and distance-decay in dispersal indicates that more isolated islands will have less immigration and a greater risk of extinction. Due to true isolation, ocean archipelagoes have stronger negative responses (loss of species) to isolation than mainland habitats (which have varying degrees of matrix uninhabitability), and steepness of response varies directly with degree of isolation. The role of isolation has also been debated around the question of habitat corridors. While corridors are
generally thought to be beneficial for reducing isolation and thereby maintaining biodiversity (Hanson et al. 1989; Taylor et al. 1993), there continues to be ongoing debate about the merits of corridors to facilitate connectivity for biodiversity (Simberloff et al. 1992; Beier and Noss 1998).

In addition to subdividing a population, isolation also affects disturbance regimes because disturbances spread through space. Isolation from fire or pests can protect a population and lower the disturbance frequency for areas by reducing the number of times a disturbance that begins in another area spreads to the area in question. Isolation can also affect post-disturbance recovery by limiting the possible recolonization of a remnant.

Finally, isolation effects may feedback to affect species interactions. Species that could interact because they were in a contiguous area may no longer be able to do so because of isolation. Among a group of interacting species, a particular spatial configuration will mean different degrees of isolation depending on the mobility of the species. Individuals may be in a remnant without a primary predator or competitor. The matrix affects the response primarily through modifying the degree of isolation. Species interactions can be altered to the extent that some local extinctions may occur if some species are missing and cannot be rescued by immigration.

*Edge Effects.* The other primary effect of changing the spatial configuration of forested landscapes through fragmentation is the creation of forest edge habitats. Remnants are subject to edge effects and the effects of edges on interiors (Murcia 1995). Edges are primarily distinguished by changes in microclimate (Chen et al. 1992). Depending on latitude, the age/closure of the edge, and the direction the edge faces, more light reaches the understory at an edge than under a canopy (Ranney et al. 1981). Greater incoming solar radiation creates higher
temperatures and provides a source of energy for plant species that can best photosynthesize in full sunlight. Trees also slow wind by friction, absorbing momentum so that wind speeds in the understory at an edge are higher than those for the interior understory. As a result of higher winds and temperatures, the potential evapotranspiration at an edge is much higher than in an interior so the conditions for plant growth are considerably drier. A wide range of studies have documented the depth to which various microclimatic edge effects may be observed (see Baker and Dillon 2000 and Laurance et al. 2002 for recent reviews), but it is important to recognize that edges represent gradients of multiple physical factors (e.g., Cadenasso et al. 1997) rather than discrete forest communities.

Edge species are those adapted to edge microclimates and are often species found in the early stages of forest succession in a given region (cf. Kupfer and Malanson 1993). Thus the diversity of a fragment may actually increase as these species are added. The responses of forest interior species to conditions that develop along the new edge vary, but some species are unable to survive in the newly created conditions. For these species, the amount of habitat lost to fragmentation is greater than that simply converted (Chen et al. 1992).

In addition to the changes in community structure and function induced by microclimatic effects, invasions by exotic species may also be enhanced by habitat destruction (Medley 1997). Many invasive plant species prolific seed producers that thrive in higher light conditions and have widely-dispersed seeds. All of these traits make them more likely to establish and thrive on edges than in interiors of forest. They may, however, be able to play an increasing role in remnants if they successfully establish along edges and subsequently influence gap succession in interiors (Burke and Nol 1998; Kupfer and Runkle 2003).
Zuidema et al. (1996) introduce “Increased Human Pressure” as a factor between forest fragmentation and reduction in population sizes without linking it to any of the main effects, but we consider it as an edge effect since the degree to which human pressures affect the remnant decline from the edge to the interior. These pressures can be from light, noise, pets, hunting or other activities (Theobald et al. 1997) and, as we discuss below, depend to a large extent on nature of the matrix.

Finally, edge effects alter species interactions by increasing the degree of interaction among edge and interior species, the most notable of which involve brood parasitism and nest predation of bird populations. Gustafson et al. (2002), in modeling the spatial aspects of cowbird nest parasites, summarized important knowns and unknowns on this phenomenon. Fagan et al. (1999) synthesized recent empirical results concerning the effects of habitat edges on population dynamics with contemporary theoretical developments to outline the ways in which species interactions, and the dynamics of the communities in which they are embedded, can be changed by habitat edges.

Interactions Among Primary Effects

Beginning with a species-area curve that would be expected based on area only, we can superimpose the hypothetical effects of forest fragmentation (Fig. 2.4). Moving to the left would reflect the effects of reduced area alone via reduced habitat and resources. Isolation decreases the number of species below what we would find on the same area surrounded by similar forest. The sample effect decreases the number of species in the landscape as a while and so would decrease immigration rates among remnants. Edge effects could have a positive or negative effect on raw diversity because the loss of area-sensitive forest species may be offset by increased numbers of
weedy or successional species. These results can be complicated by interactions among the different primary effects:

**Sample x Area Interaction.** If the area of remnants is large, the sample effect will be proportionally low. This interaction is scale dependent as we discuss below.

**Sample x Isolation Interaction.** This interaction depends on specific locations of populations in the area cut versus the remnants. The degree to which metapopulations are formed (rather than discrete, non-interacting populations) depends on which remnants have members of the species after cutting and the degree to which these individuals can interact with other remnants.

**Area x Isolation Interactions.** Island biogeography focuses on this interaction as the primary determinant of the number of species on a given remnant. If isolation is low, the remnants function as a larger whole, depending on the scale at which the species experience the landscape.

**Area x Edge Interactions.** The proportionate importance of edge effects in a patch is relative to the patch’s area and shape. Managers are often interested in maintaining the species that existed in an area prior to its becoming a remnant. Because of edge effects,
these species and their functions may be confined to a core. Edge-interior relationships for a forest fragment are thus often conceptualized using static metrics such as perimeter:area ratios or core-area models, the latter of which provides an approximation of total edge and core habitat based on a measure of edge penetration depths and forest geometry (e.g., Groom and Schumaker 1990; Laurance and Yensen 1991).

*Forest Fragmentation: Mechanisms of Biodiversity Change and the Importance of the Matrix*

Until very recently, comparatively little attention has been paid to how processes in the matrix affect the longer-term responses of forest remnants to fragmentation. This is rapidly changing. The effects of the matrix on the remnants and the whole landscape depend on how similar it is to the remnant and how well it supports fluxes among remnants (e.g., Ricketts 2001). The two are not necessarily directly related. We can consider how a matrix functions in these ways with a modified version of Forman’s (1995) typology for edge-related processes. One function of the matrix is habitat; the degree to which some forest species can live in or utilize the matrix as alternative habitat will affect landscape functioning. In terms of flux, we can think of the matrix as a conduit (allowing or facilitating the movement of species), a filter (a variably permeable membrane allowing selective movement of species), a source (serving as an origin of individuals that move into the remnants), a sink (accepting individuals from the remnants but not allowing them to leave; e.g., as a result of predation) or a nonpermeable barrier blocking all movement.

Having considered the four major categories of fragmentation effects, we now look at the second row of responses to fragmentation effects and examine how the effects on each are modified by characteristics of the matrix. Specifically, as we discuss the effects of altered species interactions, population subdivision, altered disturbance regimes, diminished resource base, altered microclimates, increased presence of invasives, and increasing human pressures on
remnants, we do so with the understanding that the extent to which each of these affects forest remnants is dependent on processes in the matrix itself.

*Resource Base.* The degree to which the matrix differs from the remnant may alter the resource base differently for different species. Species differ in the degree to which they are habitat specialists or generalists. Some may experience little difference between a remnant and a matrix even if the matrix differs somewhat in structure, while others respond to even minor differences. Thus the entire notion of remnant and matrix may not be so clearcut for some species. For example, Kupfer et al. (in press) found no differences in species diversity (richness, evenness) or vegetation structure (woody density, frequency, basal area) in regenerating slash-and-burn agricultural fields as a function of distance to forest due to seed inputs from surrounding early successional habitats which were acting as seed sources.

*Disturbance Regimes.* Altered disturbance regimes are likely to reduce diversity. As noted above, area and isolation affect the size, frequency, and intensity of disturbances. If isolation is low, the remnants function as a larger whole. The matrix alters disturbance regimes by modifying the degree of isolation. As with population subdivision, the degree to which a matrix operates as a barrier, filter, or conduit will vary with the type of disturbance. It is even possible that the matrix can act as a super-conduit, increasing the rates of flux over what would have occurred in a contiguous forest; this was probably true for the extensive fires in Wisconsin in 1871 following extensive logging that left a matrix of fine dead wood. Further, the matrix can have wholly new disturbances that were not a part of the pre-fragmentation landscape but yet significantly affect remnants in the fragmented landscape.
**Population Subdivision.** Isolation effects through population subdivision depend on the area and sample effects. The division of a population into smaller parts leads to more local extinctions that cannot be rescued if isolation is high. The matrix can reduce the effect of isolation on population subdivision if it is not impassible. For example, some plants may be able to persist in small areas within the matrix, in what McIntyre and Hobbs (1999) call the modified, variegated landscape. Even seeds that are carried by wind may be able to move in multiple steps (e.g., for seeds that can be carried by both wind and water). Species respond uniquely to the simple geometries of remnants in an impassible matrix, and species-specific scaling necessitates recognition of the varying passability of the matrix from the species-eye view.

**Microclimate.** The degree to which the matrix contrasts with the remnant in structure, roughness, albedo, and evapotranspiration will modify microclimatic (and therefore vegetational) edge effects (e.g., Cadenasso et al. 2003). For example, Didham and Lawton (1999) found that edge penetration distances for most microclimate and vegetation structure variables were as much as two to five times greater at open, fire-encroached forest edges than at closed, non-fire-encroached edges in central Amazonian forest remnants. The matrix can reduce the effect of small size and edge on microclimate, if the matrix’s albedo and roughness are similar to that of the remnant forest.

**Invasives.** As with native species, the matrix can serve as a habitat, conduit, barrier, or filter for invasive species. In fact, as a habitat or conduit, the matrix may function better, from the perspective of the invasive species, than would a contiguous forest; the edge itself may be the
best habitat and/or conduit. The matrix may have perhaps the greatest effect on the degree to which edges serve as suitable and accessible sites for invasives.

*Human Pressure.* The matrix is fundamentally associated with human pressure. Where forest clearing is for forestry or agriculture, increased human pressures may come from hunting; unless the remnants are small, the edges will have more activity than the interior. Where cutting is due to land use such as housing, human pressures in terms of light, noise, pets, and local recreation will also have a strong distance decay (Theobald et al. 1997). Thus the land use of the matrix for humans as a habitat where they live close to the remnants, as a conduit that they easily use to approach the remnants, as a filter that impedes movement, up to being a barrier, will alter these impacts.

*Additional Issues Regarding Perceptions of the Matrix*

*Extent versus quality.* In most studies of forest fragmentation, the remnant forest is treated as a unit of habitat. The type of habitat may vary, but emphasis is on extent, not changes of quality. When edge effects are considered, these are seen as reductions in the extent of the core rather than as part of a gradient of habitat quality. McIntyre and Hobbs (1999) represented the landscape as being intact, variegated, fragmented, and relictual as the amount of cutting increases; each portion could also be unmodified, modified, highly modified and destroyed. Not all combinations are possible, but one can have variegated or fragmented landscapes in which the degree of modification varies. Although they show modification only on edges, one can consider impacts across large remnants. It is also possible that one has highly modified but not destroyed forest. In fact, some impacts, such as acid rain or global climate change, may modify large intact
forest regardless of fragmentation. If we consider habitat destruction to reduce matrix quality to zero, then extent is the most important factor in determining forest function and diversity. However, if the matrix has a habitat value greater than zero and if the remnants have a habitat value less than 1, then a more realistic representation can be seen. Moreover, for a given purpose, some species may perceive the landscape as a continuous surface of quality and others as a few classes.

*Landscape Structure.* Even in a continuously forested landscape, spatial structure (e.g., pattern of heterogeneity or interspersion of forest types) is present. When the landscape is altered, sample effects will depend on where in the landscape clearing occurs. Area and edge effects will still depend on shape and core area, and isolation will depend on connectivity, which is more complicated than simple distance. Fahrig and Merriam (1994) argued that spatial structure is vital to understanding conservation dynamics, although Fahrig (1997) later noted that habitat destruction is the primary problem. The influence of landscape structure on each of the four primary effects includes:

i. Landscape structure-sample effects. Given a landscape with varying forest habitat quality, perhaps ranging from productive valley bottoms to rocky ridges to less productive wetlands, where cutting occurs will determine the initial sample effects of species loss. In timber harvesting, the most productive areas might be harvested, but these are not necessarily those most diverse or functionally important. In many harvest situations, however, only the very least productive areas plus some protected riparian zones are not cut. In other land use scenarios, such as agriculture, highly productive areas might also be cut within the constraints of topography. For exurban development, productivity is not such an important a factor so ridges and areas next to water may be cut; access is still important, however, so that valley bottoms are still focal areas.

ii. Landscape structure-area effects. We are often interested in maintaining the species that existed in an area prior to its becoming a remnant. Because of edge effects, these species and their functions will be confined to a core. The core
cannot be only the area of the remnant minus an edge of a certain width, however, because different edge effects penetrate different distances. To this, the structure effects are those linked to sample effects. The question becomes how much area and of what quality.

iii. Landscape structure-isolation effects. Remnants are usually not alone. The connectivity among remnants is an aspect of landscape structure that depends on their location from a species-level perspective. The connectivity of a given arrangement will vary in its connectivity among species. The nature of the matrix is crucial to this perspective. Pathways of higher habitat quality may be necessary for some species, but the quality for survival may not be a good indicator of usefulness or movement for all species.

iv. Landscape structure-edge effects. Edge effects depend on the contrast with the matrix and on the amount of edge versus core area. The effects of shape per se (i.e., separate from edge:interior ratio) have been variously argued, but there is not a consistent theory. The straight edges of human activities are often seen as potentially disruptive to interaction with the matrix. This may be good or bad, depending on the matrix. Often, the lower the quality of the matrix, the more abrupt and straighter is the edge. This may reduce the opportunities of invasives and negative edge effects. Where the matrix is not greatly lower in habitat quality, more irregular edges may facilitate boundary crossing.

Scale. Much of our understanding of forest fragmentation is scale dependent. Sample, area, isolation, and edge effects all have scale-related aspects. As a forest is fragmented, there is a range of habitat destruction where no effects are seen in the remnants apart from some local edge effects. As fragmentation continues, effects begin to increase. In theory, these effects at first seem linear with increasing fragmentation, but at some point nonlinear responses occur; large drops in diversity and/or function occur with small increases in fragmentation (e.g., Hanski et al. 1996). Most notably, as remnant area decreases linearly, connectivity, isolation, shape and edge change nonlinearly (Gardner et al. 1987 With et al. 1997; Malanson and Cramer 1999a,b).

Additional sample-scale effects exist. The number and functional roles of species lost by initial habitat destruction vary directly with area cut, but the broader context is important. Local species diversity and losses due to fragmentation depend on the regional species pool (Ricklefs
1987; cf. MacArthur and Wilson 1967, Hanski 1991). The amount and pattern of cutting in a landscape that extends across a region will have less effect than the same amount and configuration in a landscape type that is confined to a small locale. Any population-level threshold effects will depend on the spatial configuration, including both extent and isolation, of the remnant forest (Moilanen and Hanski 1998). In real landscapes, because of the complexity of shapes and the varying degrees in which species experience a landscape, the nonlinearities should not be as abrupt as the threshold responses seen in some theoretical models (Malanson and Cramer 1999a,b).

**Summary**

As scientists, we know the general forces and impacts of forest fragmentation. Most of our knowledge, however, comes from theory and models; experimental work has been valuable, but the multiplicity of factors make illuminating experiments difficult (Debinski and Holt 2000). As a result, the application of our knowledge to particular cases is limited. For conservation purposes, we can be fairly certain that more forest left in natural conditions will promote better forest diversity and function and that as forest declines in extent and quality impacts accumulate nonlinearly. Nonlinear responses are often seen as thresholds, and their location in term of management decisions is unknown. It is also clear that conservation efforts will need to take into account matrix characteristics; for example, factors such as the degree to which the matrix can serve as habitat or partial habitat or as a conduit between remnants is variable and as yet unpredictable. Future research will best focus on considering the ways in which remnants are embedded in their matrix as whole functioning landscapes. Applications to management might
take into account the nature of the matrix based on theory, but variations based on local conditions and history may prove dominant.
Chapter 3: Populations, Communities and Ecosystems in Fragmented Landscapes

Research over the last three decades has documented a broad range of ecological responses to fragmentation, with effects manifested at scales ranging from genes to entire ecosystems. Turner et al. (2001) deduced four general insights from this sizable body of previous research: 1) larger, more heterogenous patches support more species; 2) the shape of forest boundaries can influence relative population abundance; 3) landscape connectivity effects are based on a critical threshold, and 4) characteristics of the surrounding landscape can strongly influence local populations in remnant patches. The lack of additional general insights illustrates the complexity of fragmentation effects, although we believe there are other generalities that can be added to this list. In the previous chapter, we presented a generic conceptual model of the various manners by which forest fragmentation affects biodiversity; here, we look in greater depth at how forest fragmentation alters ecological pattern and process, citing a more extensive range of case studies to illustrate fragmentation effects. While we occasionally discuss the effects of fragmentation on genetic diversity, our primary focus is on the scales most commonly employed by scientists and managers: (1) the population/community level, through the restriction of organismal movement, alteration of landscape-level population dynamics, and introduction of edges, and (2) the ecosystem level, through the effects on energy and matter fluxes and through interactions and feedbacks with natural disturbance processes.

Populations and Communities in Fragmented Landscapes

Effects of landscape fragmentation on biotic components of the landscape have been examined via three major themes: (1) effects on movement and pattern of habitat use (both
within individual remnants and among groups of remnant patches), (2) effects on population and community dynamics in heterogenous landscapes, and (3) changes in ecological processes at forest edges (Berrett and Peles 1999). We structure this section around these three themes.

**Movement and Patterns of Habitat Use**

There is little doubt from recent research that understanding the effects of landscape change on biota requires knowledge of population-level processes. Landscape structure has been shown to affect plant and animal dispersal for colonization, movement patterns, and gene flow, but in a species-specific manner. Changes in population dispersal and dynamics ultimately affect community assembly and interactions. Processes occurring at the population and community level drive landscape-level processes (e.g., metapopulation dynamics) while landscape pattern (e.g., distance to seed pool) constrains population (e.g., extinction) and community (e.g., succession) processes. There exist, however, feedback mechanisms among all these processes.

There are two primary research foci regarding the effects of fragmentation on movement and pattern of habitat use: (1) how fragmentation affects populations within resulting patches and (2) how fragmentation affects movement among patches.

**Within-patch processes.** Research on the effects of deforestation and forest fragmentation has typically concentrated on pattern and process within habitat remnants (e.g., Bierregaard et al. 1992; Laurance et al. 1998a,b). Understanding the effects of habitat destruction on remnants is critical to assessing impacts on the diversity of species and community composition, and ongoing, long-term experiments such as the Biological Dynamics of Forest Fragments Project have monitored changes in a range of ecological variables in fragmented landscapes for more
than two decades (e.g., Laurance et al. 1998a,b). A considerable amount of work on forest fragmentation has stressed how declining forest area and/or increasing isolation of forest remnants influences both richness and species survival (e.g., Kattan et al. 1994, Matlack 1994a, Yahner 1997). Davies and Margules (1998) list three intuitive generalizations from previous fragmentation research: 1) the theory of metapopulation dynamics suggests that subpopulations in forest remnants have a higher probability of extinction due to environmental and population stochasticity; 2) the theory of island biogeography predicts smaller, more isolated fragments retain fewer species than larger, less isolated fragments, and 3) fragmentation modifies physical conditions creating habitat edges different from habitat interiors.

The underlying theory and interpretations of remnant patch research suggest that as forests are fragmented, populations decline in size and become increasingly isolated from one another, leading to higher extinction rates and lower immigration rates, although such effects may not be immediately manifested (Tilman et al. 1994). Abundances of many species have been linked to forest habitat loss and fragmentation, although local extinction following fragmentation is species-specific, as some taxa are more vulnerable than others (Thiollay 1997, Marsden 1998). Species with abnormally small populations, species at their distributional limits (Kattan et al. 1994), large frugivores (Willis 1979), sallier canopy foragers (Medin 1985), rare species (Newmark 1991), poor dispersers (Tilman et al. 1997) and habitat specialists (e.g., forest interior species, Newmark 1991) are generally at greater risk of local population extinctions.

Laurance (2002) suggests that fragmentation also leads to hyperdynamism of population dynamics. The frequency and/or amplitude of dynamics increase following landscape fragmentation, resulting in elevated dynamics that remain indefinitely or only gradually return to a level typical of intact landscapes. Periodic low population numbers make a population
susceptible to extinction from random events and loss of genetic variability. Indeed, it is the low population numbers that drive conservation biology and endangered species management.

Population theory suggests that small populations may suffer from genetic drift, changes in gene frequency due to random variation in fecundity, and mortality due to small populations being less resilient to random events. The loss of genetic variability can lead to inbreeding depression, reducing the ability of populations to increase, expand, or recover from disturbance (Ricklefs and Miller 2000). Knutsen et al. (2000), for example, examined genetic differentiation among beetle (*Bolitophagus reticulatus*) populations and found that differentiation was three times greater in fragmented forest patch populations compared to populations in contiguous forest fragments. It was unclear, however, if the cause was due to a founder effect (where one or a few individuals colonize a new suitable site, resulting in low genetic diversity) or random genetic drift.

Behavior may be another factor driving changes in population dynamics and genetic diversity in fragmented landscapes (Wolff 1999). Hooded warblers (*Wilsonia citrina*), for example, did not travel more than 500 m across open fields for extra-pair copulations, although they made forays within 500 m quite often (Norris and Stutchbury 2001). Compared to males, however, females spent significantly less time off territory and traveled shorter distances across nonforested gaps, highlighting the importance of examining the potential effects of fragmentation on different sexes (Norris and Stutchbury 2002). In this case, isolation affected their behavior, which could in turn affect metapopulation genetics.

Because isolation is hypothesized to be such an important effect of fragmentation, use of suitable habitat should be affected by the characteristics of the adjacent habitat (Lord and Norton 1990, Barrett et al. 1994, Wiens 1994). Indeed, several studies have found that populations are strongly influenced by surrounding habitat (Hinsley et al. 1995, Stouffer and Bierregaard 1995,
Bellamy et al. 1996). Estades and Temple (1999) examined the distributions of birds in remnant hualo (*Nothofagus glauca*) and adjacent planted pine forest patches of Chile and found that the abundance of cavity-nesting species in the latter was positively correlated with proximity to the former. Watts et al. (1996) studied species richness and total abundance of wintering sparrows in habitat patches as a function of the type of adjacent edge vegetation and noted that sparrow diversity was greater in all habitats adjacent to weedy vegetation compared to habitats adjacent to open areas. These results support the use of a mosaic approach for the study of fragmentation and an understanding that a gradient of effects may be created by variations in the intensity of fragmentation.

These various population-level responses to forest fragmentation in turn may be manifested as declines in species richness and diversity in fragmented landscapes. Loss of diversity has been an important component of fragmentation research, stemming mostly from analyses of remnant patches following fragmentation (Laurance 1998a,b). Loss of species may be due to isolation as described above or due to insufficient size of patches (Verboom et al. 1991, Thompson et al. 1995). The latter is an area effect although also logically tied to the interior-to-edge ratio (and thus edge effects) because the 'area' must be of a suitable quality.

Suitable habitat (patch) size relates to organism size (suggesting an allometric relationship, Foster and Gaines 1991), resource needs, and mobility of species (Carey et al. 1992). Larger plants and animals tend to need more space for growth and movement. Klein (1989), for example, found smaller beetles in fragments compared to intact forest. General results from the literature suggest that small, isolated patches hold fewer species, contain higher densities of populations, and higher numbers of transient species compared to larger, less isolated patches (Foster and Gaines 1991, Forman 1995). The mechanism behind these results
may be explained by the natural distribution of species in a landscape due to species life history characteristics. The core-satellite hypothesis (CSS, Hanski 1991) suggests that species in the landscape are either locally abundant and regionally common (core species) or sparse and occurring at only a few sites (satellite species). This dichotomy is synonymous with Grime's (1998) dominant and transient classification, although Grime also had a subordinate group that the core-satellite hypothesis ignores (Gibson et al. 1999).

The CSS model has been supported in a variety of areas, suggesting a universal relationship between regional distribution and local abundance. The bimodality occurs due to increased migration rates and decreased local extinction as the fraction of occupied patches increases. Satellite (transient) species are a source of colonizers following disturbance while core species might be particularly susceptible to the effects of fragmentation (Collins and Glenn 1997). These predictions are contrary to those of Howe (1984) and Vallan (2000), who found species common in forest patches were also common in large nearby forest. The contradiction lies perhaps in the life history characteristics, specifically: is the core species common because it was a strong dominant prior to fragmentation, but is a poor disperser and thus sensitive to fragmentation? Or, is the core species dominant due to its generalist strategies and, thus, likely less affected by fragmentation? A functional group approach allows some prediction of fragmentation effects on population fluctuations and diversity, but the CSS model will need to incorporate life history strategies to be useful in predicting population changes (Gibson et al. 1999).

While biodiversity has been a major focus of fragmentation research, we support the suggestion of Margules (1994) that emphasizing population responses to fragmentation will more likely provide an understanding of processes that lead to extinction and persistence in
fragmented landscapes. There are two reasons. First, richness may not necessarily be a reliable indicator of community dynamics and function. Rather, as has been suggested by Huston (1997), Tilman et al. (1997b) and Grime (1998), compositional changes may be better indicators of functional changes. For example, Davies and Margules (1998) found no effect of fragmentation on carabid beetle richness but noted significant species-specific responses, which would be expected if species had evolved to heterogeneous landscapes (a point we discuss later in this chapter).

Secondly, the loss of diversity may sometimes be explained by confounding factors simultaneously occurring with fragmentation. For example, fragmentation is always coupled with a decrease in habitat, leading to a greater impact on species survival than can ever be attributed to fragmentation alone (Lord and Norton 1990, Boutin and Hebert 2002, Fahrig 2002, McGarigal and Cushman 2002). For wide-ranging species, it is perhaps not the isolation or size of ‘patches’ that affects their population sustainability, but the overall area of suitable habitat, which may include matrix and patch habitat. In addition, several cases of historic fragmentation were accompanied by hunting of large predators (e.g., wolves, mountain lions) or other species (e.g., beaver, bison). Their decreasing numbers may have little to do with fragmentation but instead result from severe hunting pressure (although hunting pressure itself can be related to the presence of fragmenting agents such as roads). Recent increases in wolf (Canis lupus) populations in the Great Lakes region, for example, suggest that fragmentation was not the sole (or perhaps even the major) cause of this animal’s extirpation.

Due to these confounding factors, the remainder of our discussion will concentrate on population processes and interactions among populations to highlight pertinent areas of needed experimental research. In light of the fact that immigration is so important for sustainable
populations, the question becomes: can species move across the landscape to colonize other locations?

Among-patch processes. Plant and animal movement across heterogeneous landscapes depends on the species’ dispersal ability, the isolation and characteristics of suitable patches, and barriers to movement, all of which have species-specific components. Based on results of a model of animal responses to forest fragmentation in the Brazilian Amazon, Dale et al. (1994) showed that the amount of available habitat decreased only as a function of total remaining forest for animals with gap-crossing ability proportional to area requirements. Species with large area requirements but short dispersal capabilities were more adversely affected by fragmentation, with available habitat for such species decreasing at a rate disproportionately greater than the rate of forest clearing. These results match other modeled expectations based on life-history trade-offs between competitive ability and dispersal ability (Tilman et al. 1997a). The spatial adjacency of existing patches, especially source patches, is an important factor affecting animal movement so if landscape fragmentation is severe, the adjacency of existing habitat patches is crucial for maintaining populations.

Isolation through fragmentation is also important because it increases (forces more) cross-landscape movement (Forman 1995). The increased movement may be energetically costly or increase risks of predation (one factor that makes matrix habitat a barrier to dispersal). Both effects suggest that the matrix habitat, while not a complete barrier, certainly affects populations. Dispersal ability defines the isolation of suitable habitat based on the species' tolerance to matrix habitat and edges as landscape barriers.
The incorporation of corridors and stepping stones in landscape conservation projects is an effort to increase dispersal ability across a heterogeneous landscape (Turner et al. 2001). Mech and Hallett (2001) showed the effectiveness of corridors for red-backed vole populations in the forests of Washington. Red-backed voles are forest specialists that do not cross large areas of non-forest habitat; consequently, their genetic diversity was greatest in an intact landscape, least in a landscape of isolated forest fragments, and in-between for the fragmented landscape with corridors, implying that corridors moderated the effects of fragmentation. Contrarily, the genetic variation of deer mice, a habitat generalist, was unaffected by fragmentation in the same study. The discrepancy was attributed to different responses of generalist (deer mouse) and specialist (red-backed vole) species to fragmentation.

In her study of the movement of Fenders’ blue butterfly in the Willamette Valley of Oregon, Schultz (1998) underscored the importance of recognizing the relationship between landscape structure and species dispersal in fragmented landscapes. Records of the naturally heterogeneous landscape suggested that lupine patches of suitable (source) habitat were historically less than 0.5 km apart, easily within the 2 km dispersal potential of the butterfly across non-lupine (sink, but not truly hostile) habitat. Fragmentation, however, has resulted in lupine patches that are isolated by 3-30 km, dividing the metapopulation into discrete, non-interacting populations. Schultz suggested stepping stones (of lupine patches) to reconnect the populations rather than corridors, as stepping stones would mimic historical landscape structure.

Finally, while most attention has been paid to movement through habitat in binary landscapes (e.g., Malanson and Cramer 1999), some attempts have been made to use more classes (e.g., Wiegand et al. 1998) or to represent a continuous surface with discrete cells (With 1994; Malanson 2002). Azevedo et al. (2000) developed eight habitat suitability classes to
determine a functional heterogeneity index for red-cockaded woodpeckers (*Picoides borealis*) of eastern Texas. The functional heterogeneity index incorporated the woodpecker’s response to the heterogeneous landscape. In this case the species 'perception range' included the spatial structure, avoiding sections of the landscape with more isolated patches. Such approaches are important because a spatially-explicit representation of habitat quality utilizing discrete cells may be more realistic for many species and processes.

*Population and Community Dynamics in Heterogeneous Landscapes*

The ways in which forest fragmentation affects animal movement, propagule distribution, habitat suitability and local climate across the landscape (Forman 1995) in turn influence local population and community dynamics. For example, red squirrels (*Tamiasciurus hudsonicus*) have expanded their range into the central hardwoods region while gray squirrel (*Scurius carolinensis*) populations have declined, perhaps because the latter (e.g., Goheen et al. 2003). Such interspecific differences in mobility and sensitivity to habitat loss coupled with complex interactions among populations drive community dynamics and provide one example of the manners by which fragmentation-driven changes in species movement and habitat use may influence population and community dynamics. Two specific examples are the effects of fragmentation on trophic structures and plant successional pathways and trajectories.

*Trophic aspects: predator-prey, herbivory, parasitism.* By altering population numbers and persistence, fragmentation has the ability to alter a range of interspecies relationships (e.g., predator-prey, herbivore, and host-parasite systems). Much of our knowledge of these interactions stem from simplistic models of a few species that fail to incorporate temporal or
spatial dynamics (Morin 1999). However, there is little doubt that spatial structure affects population interactions. As an example, Louda (1982) studied the frequency of *Haplopappus squarrosus* across four climatic zones in California. The numbers of flowers were counted and compared to the numbers of plants observed. Contrary to what was expected, *H. squarrosus* was least abundant in climatic zones where it flowered best. The incongruity was explained by the distribution of herbivorous insects that attacked the flowers and seeds, which maintained fairly high populations where the shrub flowered well. Indeed, predators (carnivores, herbivores and parasites) have long been thought to strongly control prey populations under top-down control theories (Morin 1999). As another example, the invasion potential of exotic species is often linked to the lack of predators and parasites when introduced to a new area (Elton 1958). Kudzu (*Pueraria montana*), which has taken over large areas in the Southeast, may have over 300 species of animals feeding on its roots in native climes, but none thus far in the United States. Reintroduction of predators (biological control) can again lead to population control (e.g., Fenner 1983), but the important point for this discussion is that these key ecological interactions depend on the spatial arrangement of the participants.

By changing patterns of habitat use and species movement, fragmentation may affect trophic structure by altering biotic interactions (e.g., decreased pollination in fragments, Powell and Powell 1987, Aizen and Feinsinger 1994). Loss of species within fragments may affect trophic interactions through bottom-up controls. Komonen et al. (2000) examined the food chain beginning with a forest specialist bracket fungus, *Fomitopsis rosea*. The food chain included a moth larva that eats the fungus and a parasitic fly specializing on the moth larva. They found that the frequency of *F. rosea* was reduced in fragmented forests of eastern Finland, and its reduction accounted for half the population extinctions at higher trophic levels in forest fragments. Limited
dispersal for recolonization was likely also a factor. The resulting median number of trophic levels was reduced from three in control areas to one in fragments; in other words, the food chain was truncated. They further noted that ecological specialization at all trophic levels makes species vulnerable to extinction.

If fragmentation reduces population sizes, it will be most keenly felt at higher trophic levels where sizes are inherently smaller (i.e., predators are more likely to go locally extinct). Zanette et al. (2000) studied the sensitivity of eastern yellow robin (*Eopsaltria australis*) in small and large forest fragments of New South Wales, Australia. They found that small fragments contained only half of the invertebrate biomass compared to large fragments, and incubating females received 40% less food from males. Additional evidence suggesting nutrient limitation in fragments was the poorer physiological condition of birds found in forest fragments versus continuous forest of Central Amazonia (Stratford and Stouffer 2000), smaller weights of chipmunks in forest fragments of Pennsylvania (Mahan and Yahner 1998), and smaller body dimensions of skinks in forest fragments of Australian wet tropics (Sumner 1999).

Colonization of new species following fragmentation may conversely cause top-down controls. Local extinction of passerine birds from forest fragments is generally a result of trophic dynamics, and these dynamics are extremely variable in space and time (Fauth 2001). Avian sensitivity has been linked to nest predators and brood parasitism (Paton 1994) and food abundance (Burke and Nol 1998), although results of such studies show a great deal of variability (e.g., Chalfoun et al. 2002). Patten and Bolger (2003) examined nest predation of four bird species in relation to a fragmentation gradient, from large interior habitat blocks > 2300 ha to small habitat fragments 5-17 ha in size. Avian nest predator abundance increased across the gradient while snake abundance decreased. The result was a higher nest success for the spotted
towhee and rufous-crowned sparrow, whose principal nest predators were snakes, in habitat fragments. Fragmentation has resulted in creating suitable habitat in forest edges for black rat snakes (*Elaphe obsoleta obsoleta*) in eastern deciduous forests, increasing contact between snakes and nesting birds (Blouin-Demers and Weatherhead 2001).

Finally, it is important to note that habitat fragmentation (and more broadly, spatial heterogeneity) can have complex effects on trophic relationships. Homogeneous spatial arrangements such as monocultures can facilitate the dispersal of predators and parasites and lead to quickly declining prey communities. Diseases can sweep rapidly through monocultures, a lesson learned with the Irish potato blight. Contrarily, the persistence of predator-prey relationships may be attributed to the existence of spatial refuges that give prey a temporary respite from predators (Gause 1934, Morin 1999). Huffaker (1958) and later Holyoak and Lawler (1996) provided examples of how metapopulation dynamics can stabilize a predator-prey relationship. They developed ‘temporary refuges’ for prey by setting up elaborate schemes of isolation and barriers to movement. The system rendered a continual game of hide-and-seek, where prey immigrated to new areas, built their populations, and predators later colonized. What these studies suggest is that a certain amount of isolation may act to stabilize trophic interactions, which may partially explain why fragmentation does not always negatively affect populations until a certain threshold is reached (Turner et al. 2001).

**Plant Succession.** Succession is driven by processes of mortality, colonization, and the abiotic characteristics of the area, all of which are significantly altered by forest fragmentation. We concentrate in this section on vegetative dispersal and subsequent vegetation dynamics in areas regenerating from disturbance, but deforestation and fragmentation also change abiotic
conditions in forest remnants and across the landscape as a whole, influencing vegetation
dynamics in both the fragments and the matrix.

One of the main factors controlling succession in a mosaic of disturbed areas is distance
from the seed pool, in large part because it is a key determinant of patch colonization (Hewitt
and Kellman 2002). Seed dispersal involves primary dispersal (the initial movement of the seed
away from its parent tree and subsequent deposition) and secondary dispersal (the post-
deposition movement of seeds by water, wind and animals), both of which are significantly
altered by fragmentation and edges. The distance that a seed is dispersed is a function of a
number of factors, many of which are tied to the dispersal vector(s) (wind, water, animals,
gravity). Hewitt and Kellman (2002), for example, ranked the dispersal abilities of seeds by
dispersal mechanisms and seed size from (highest to lowest): bird > light-seeded rodent = wind >
large-seeded rodent = unspecialized.

For both wind- and animal dispersed species, fragmentation affects seed dispersal at the
landscape-level, which in turn can influence species patterns across a landscape (e.g., Hanson et
al. 1990). The dissemination of animal-dispersed species across a landscape can be constrained
by how the dispersal agent (e.g., a blue jay or squirrel) responds to landscape structure. For
example, it has been shown that blue jays are more likely to cache acorns in certain types of
habitats while avoiding others (Darley-Hill and Johnson 1981). _Lonicera_ and _Rubus_ produce
berries that are consumed by birds and then dispersed in close proximity to forest edges and
perching sites (Hughes and Fahey 1988, McClanahan and Wolfe 1987). With respect to wind-
dispersed species, the typical dispersal distance of individual wind-dispersed seeds may actually
increase following forest clearance because of greater exposure to higher wind speeds resulting
from the disturbance. However, the potential benefits of increased dispersal distance must be
evaluated within the context of the decreased number and altered locations of potential seed sources. Woody perennial seeds are usually larger than annual and herbaceous perennial species, less abundant, are not viable for long periods of time and are limited by dispersal distance and/or dispersing organisms from seed source (McClanahan 1986 a, b). These characteristics may contribute to low woody perennial abundance during early succession.

At the patch level, patterns of seedling establishment, growth and survivorship following a disturbance will vary spatially because seeds will not be uniformly dispersed into the adjacent matrix. Seed density generally decreases with distance from a seed source, and patterns of arrival will vary by species because of differences in seed morphometry. As a result, plant recruitment and colonization vary spatially within the disturbed matrix. Silva et al. (1996), for example, found that landscape structure strongly affected regeneration of adjacent agricultural lands and thus connected the importance of forest fragmentation with the conservation of tropical landscapes while Kupfer et al. (in press) have documented that successional pathways on fallow Belizean fields are influenced by the proximity of forest remnants. In addition, predation of seeds and seedlings will also vary spatially (Ostfeld et al. 1999), further affecting recruitment.

Similarly, dispersal into the remaining fragments and subsequent recruitment are affected as well. Cadenasso and Pickett (2001) quantified the flux of seeds moving from the matrix into the forest interior using seed traps and found that the structure of vegetation along forest edges influenced seed flux. Ranney et al. (1981), Kupfer (Kupfer and Runkle 1996; Kupfer et al. 1997; Kupfer and Runkle 2003), Laurance (1997) and Goldblum and Beatty (1999) have all suggested that edges may influence canopy gap replacement processes within forest interiors, at least temporarily, by acting as seed sources for shade-intolerant plant species. Cordeiro and Howe (2001) examined differential recruitment into small and large African forest fragments and noted
that the recruitment of animal-dispersed taxa was three times greater in continuous forest and large forest fragments than in small forest fragments. For wind and gravity-dispersed taxa, however, no differences existed based on landscape structure. They suggested that the disappearance of large frugivores explained the dynamics.

*Ecological Processes at Habitat Edges*

The effects of fragmentation on species movement, habitat use and population and community dynamics mentioned thus far have largely been discussed within the context of area and isolation effects. However, as we briefly discussed in Chapter 2, forest fragmentation results in the increased susceptibility of forest remnants to edge effects: changes in microclimate, forest structure, biotic composition, and ecological function that occur along forest edges exposed to non-forested habitats. Characteristics of forest edges have been documented for a wide range of variables, locations and organisms (Forman 1995), with some studies finding edge effects that penetrate hundreds of meters into fragments (Wilcove et al. 1986; Janzen 1986). Forman (1995) suggests that sunlight and wind are the overriding controls of edge microclimate, directly affecting photosynthetically active radiation and evapotranspiration and indirectly affecting nutrient cycling and animal use (e.g., Malanson and Kupfer 1993). Edges will generally have greater variability and unpredictability in climate and other characteristics (e.g., litter decomposition rates, Didham 1998) than interiors, but often not as variable as open habitats. Edge gradients of microclimate (Foggo et al. 2001), vegetation (Gelhausen et al. 2000), invasive species abundance (Brothers and Springarn 1992) and seed and seedling predation by small mammals (Ostfeld et al. 1999) in turn have been shown to have feedbacks on edge characteristics.
Holland et al. (1991) recognized that edges are important for satisfying life-cycle needs for many organisms, which suggests an evolutionary adaptation to landscape structure rather than a simple mixing of two adjacent communities. Most of the species found on edges are common in the landscape, have generalist habitat preferences, and tolerate frequent disturbances. In addition, boundaries are often characterized by high biological diversity (Brothers 1993, Kupfer and Malanson 1993a; Forman 1995). Indeed, wildlife management, including the increased development of edges, dates back to Aldo Leopold’s book *Game Management* (1933). Many of the game herbivores are found at higher densities in edges than patch interiors. Due to the alterations of herbivory and microclimate, regeneration and success of plant species differ in edges compared to interior forest, often favoring disturbance-adapted flora that are less palatable and less sensitive to trampling (Belsky 1986). Brothers (1993) found edges of an old-growth forest in Indiana acted as refuges of shade-intolerant species such as oak while the shade-tolerant competitor *Fagus grandifolia* was less abundant and had lower regeneration.

While edges are often characterized as sharp boundaries between forested and non-forested systems, the structure and composition of the adjacent habitats may very greatly, resulting in significant differences in edge characteristics (e.g., hard or soft) and complexity (e.g., Matlack 1993, 1994b, Kupfer 1996). Because the type of edge affects permeability and adjacent vegetation defines the edge type, a neighborhood approach to edge function must be used. The edge itself may change over time in structure and composition, affecting its habitat suitability and permeability (Matlack 1994b).

In an effort to understand edge complexity between farmland and natural areas, Duelli et al. (1990) proposed six categories of edge influence based on a study of arthropods. The classification suggests a gradient of species-specific edge permeability and would lead to
complex models of plant and animal mobility in heterogeneous landscapes (perhaps similar to forest gap succession models). Lidicker and Peterson (1999) suggested a more parsimonious separation of edge effects into matrix and ecotonal. Matrix effects can be explained by either the patch or adjacent habitat while ecotonal effects are new (they use the term emergent) to either of the adjacent habitats. Matrix effects tend to occur where the two habitats are quite different, such as farmland/forest ecotones (Heske 1995), and represent “hard” borders. The hardness of an edge is directly related to the similarity of two adjacent habitats; soft borders have more similar juxtaposed habitats and hard borders extremely different juxtaposed habitats. Ambrose (1987) evaluated the penetration of species from a farmland-forest matrix into the Great Smoky Mountains National Park (i.e., permeability) and found that greater numbers of vertebrates and exotic plant species had crossed and penetrated further into the Park along soft borders.

Studies of forest edges must not only document the characteristics of the edges themselves (the traditional edge effect) but also seek to uncover the dynamic manners by which edges alter key ecological processes in forest remnants and across the landscape as a whole (boundary dynamics: Wiens et al. 1985; edge-mediated effects: Fagan et al. 1999). Edges affect a range of biotic and abiotic processes (Yahner 1988; Cadenasso and Pickett 2000), but they do so in complex ways because edges vary in their structure compared to the patch in question and adjacent habitat (Mesquita et al. 1999). Forman (1995) offers five functions of edges with respect to their active roles in fragmented landscapes, as: 1) habitat, 2) filters, 3) conduits, 4) sources, and 5) sinks. Lidicker and Peterson (1999) posed several pertinent questions for current and future research: 1) How far from an edge are the effects of edges felt? 2) Are edges barriers to movement? 3) Do corridors enhance population movement or simply exacerbate edge effects (which are often negative for species within the forest remnant)? 4) Do edges increase the
likelihood of invasions? All of these are questions that need to be addressed at the population level. The answers will differ depending on the species of interest, but since it is the mobility of species that drive landscape dynamics, the capacity of edges to filter use of edge and adjacent habitat is extremely important. The dynamic role of edges in fragmented landscapes has been demonstrated in a number of studies. They may provide a screen or filter for seed rain from adjacent patches and a source of seed rain to patch interiors (Kupfer et al. 1997). Wind that moves seeds across an open area, or seeds that are blown across a snow covered field, will be slowed and retained by forest edges. In other cases animals preferentially cache transported seeds in edges, as blue jays have been observed to do with acorns (Johnson and Webb 1989). Because of the non-random distribution of seeds produced by these processes, mortality due to high densities of established plants (Ranney et al. 1981, Kupfer and Malanson 1993a) can be expected to be quite high unless a seed is secondarily moved (i.e., deposited and then moved again). As sources, edges may be preferentially used by some animals, and updrafts generated at edges may allow longer distance dispersal by wind. Still, edge effects are notoriously species-specific (e.g., Schlaepfer and Gavin 2001, Woodward et al. 2001).

Thresholds, Populations and Communities in Fragmented Landscapes.

Finally, it should be noted that population and community dynamics may be subject to threshold effects and nonlinear responses associated with ongoing fragmentation. Zanette (2000), for example, suggested that a threshold of fragment sizes occurred, below which eastern yellow robin populations were not viable (recruitment of individuals < loss). Thresholds are depicted by comparing some spatial response variable (y-axis) to the percentage of initial land type (horizontal axis gradient, Forman 1995). The threshold is an area along the gradient where the
spatial attribute changes rapidly. Thresholds have been linked with minimum viable population levels and several examples have been illustrated (Franklin and Forman 1987, Turner et al. 2001). Forman (1995) suggests most thresholds occur within the first 40% of land transformation, which matches with major truncation of landscapes in simple models of percolation theory (Stauffer and Aharony 1992). The value of being able to predict thresholds in an expectedly unpredictable fragmented system is high, but the effects of isolation and size of suitable habitat area in a remnant will be species-specific so that much work needs to be completed before thresholds become useable.

One approach to operationalizing thresholds is the proposed ecological neighborhoods of Addicott et al. (1987). Their work recognizes that various behaviors (especially in animals) and life stages require different resources and habitats, so, for example, thresholds in a single population may differ based on foraging compared to mating. Thresholds may also help separate the confounding factors associated with fragmentation. Andrén (1994), for example, found that once landscapes had been reduced to < 30% of the original cover, populations declined more rapidly than could be explained by habitat alone. Such threshold levels will undoubtedly vary among landscape types and species (Andrén 1999), from 60% for more sensitive taxa to perhaps as little as 10% for others (Bennett and Ford 1997). They will also vary according to the number and arrangement of patches, the spatial scale at which the organisms perceive and use the landscape, and the movement capabilities of the species (Lamberson et al. 1994; Cale and Hobbs 1994; Andrén 1999).
Dealing With the Species-Specific Nature of Fragmentation

An important point that has been elucidated by previous research is that few species view the landscape at the same scale and in the same form that humans do; we should thus not be surprised if maps of land use and land cover are imperfect tools for understanding animal and plant movement across landscapes. Instead, a species-specific ‘perception range’ exists (McIntyre and Hobbs 1999, Peles et al. 1999). The specificity of a population in their perception and use of landscape elements is likely one reason experimental and observational studies fail to corroborate predictions of general models (Lamberson et al. 1994, Schumaker 1996, Morrison and Bolger 2002). However, obtaining species-specific knowledge for a wide range of members in an entire community is difficult, so attempts to understand movement and use have recently focused on life history strategies (e.g., behavior, dispersal ability, trophic level) to characterize responses of species in fragmented landscapes (e.g., Davies et al. 2000). For example, studies suggest that habitat generalists may disperse through fragmented habitat more easily and thus be less dependent on corridors. Rare and isolated species populations are more likely to decline than abundant, common species, unless the abundant species are the poorest dispersers and best competitors (Turner et al. 1997), and predators are more likely to decline than non-predator taxa (potentially due to their generally smaller populations sizes: Komonen et al. 2000).

Wolff (1999) proposed a behavioral model system (BMS) that lists characteristics of species that make them good or poor colonizers in fragmented landscapes. The crux of his model is that different life history strategies render different dispersal capabilities and thus different colonizing potential. Similarly, researchers studying invasions of non-native taxa have developed ‘characteristics’ of successful invaders, also stressing dispersal ability and generalist strategies (Mack et al. 2002). Tilman et al. (1997) suggest that a trade-off between competitive ability and
dispersal ability explains species response to habitat destruction: poor dispersers are more likely to go extinct in highly fragmented landscapes even if they are superior competitors because of their inability to recolonize patches from which they have gone extinct. As we will discuss in a subsequent chapter, however, species-specific responses to the range of conditions in a heterogeneous landscape (and their associated interactions) make even such simple and straightforward generalizations more complicated.

**Ecosystems: Energy and Matter**

Thus far, we have focused on the ways in which fragmentation affects population and community dynamics, including the movement of organisms through landscapes, the importance of edge effects, and the ways in which movement, edges and the altered landscape structure in fragmented areas affect overall population dynamics. In the second major section of this chapter, we address the consequences of spatial heterogeneity on ecosystem processes. We consider the movement of plants and animals as the main vector for horizontal movement of energy and matter. Further, we recognize that changes in community composition and diversity may alter the functioning of ecosystems (Chapin et al. 1997, Grime 1998). Thus, understanding the effects of fragmentation on population and communities as discussed above, along with metrics of energy use, will allow some prediction of landscape-level effects on ecosystem function. We do not consider the well-studied gravitational transfers in watershed/ecosystem analyses (e.g., Likens and Bormann 1995) nor the importance of buffer zones, as these research endeavors are not studying fragmentation *per se* and because there is a sizable body of work already addressing these topics. Since we have already discussed the mobility of plants and animals and their effects on community processes, in this section we concentrate on studies of nutrient and energy
exchanges linked to such movement. In addition, we briefly examine abiotic alterations to fragment patches that affect nutrient cycling. One thing is clear, however: compared to our knowledge at the population and community-levels, the study of fragmentation effects on ecosystem processes is in its infancy (Turner et al. 2001).

A number of studies have elucidated the potential for organisms to move energy and matter horizontally. Indeed, the various adaptations of seeds to use animals for mobility substantiate animal vector potential. Willson et al. (1998) examined the transfer of phosphorus from streams to uplands in the Pacific coastal region of North America. They suggested salmon carcasses moved by bears (*Ursus arctos* and *U. americanus*) and bald eagles (*Haliaeetus leucophalus*) potentially added 6.7 kg P/ha to uplands, an application rate similar to commercial fertilizers for trees. A recent study by Seagle (in press) suggests that the current juxtaposition of high nutrient agriculture areas and forest patches of the Maryland landscape results in a spatial subsidy of nitrogen into forest patches. Based on an allometric model of deer consumption and deposition within a simple landscape of soybean fields and forest, selectively foraging white-tailed deer (*Odocoileus virginianus*) numbering 100 individuals per hectare transferred > 20 kg N/ha/yr from field to forest with 20% of the landscape forested. The calculated rate of deposition was actually above annual atmospheric deposition. These substantial horizontal transfers highlight their importance toward our understanding of exchanges among patches in a heterogeneous landscape.

Landscape structure also affects the heterogeneity of resources and microclimate. Forest fragments tend to have altered hydrologic regimes, altered radiation balance, and altered wind patterns (Hobbs 1993). Generally, these changes occur when a continuous landscape is fragmented into small blocks, and the populations are exposed to very different climatic regimes.
The increased variability of temperature and generally drier conditions in these patches have been shown to affect plant productivity and nutrient cycling because they affect the suitability of the habitat and trophic dynamics of local communities. Direct effects (e.g., lower evapotranspiration causing lower nutrient immobilization) and indirect effects (e.g., loss of species lowering productivity) may account for the differences. Because small fragments are more susceptible to wind disturbance, are more likely to completely burn if fire occurs, and may lack predators to control herbivore outbreaks, they tend to be less productive (Forman 1995). Further, litter turnover times and dung decomposition have been shown to be slower in forest fragments than continuous forest, altering the nutrient cycling process (Klein 1989; Didham 1998).

_Ecosystems: Feedback mechanisms with disturbance_

Most studies involve communities that are in some dynamic response to past disturbance events (_this is discussed further in Chapter 5_). Early research in the field recognized the importance of disturbance (Cooper 1926, Watt 1947), but only recently has disturbance been treated as a fundamental ecosystem process (Heinselman 1973, Pickett and White 1985, Pickett et al. 1989). Disturbance may occur at various spatial and temporal scales (e.g., Pickett et al. 1989, Collins 1992). For example, studies of fire include measures of the fire cycle (spatial) and the average fire interval (temporal) (Johnson 1992). Most forms of biota have adapted to disturbance. Some, such as longleaf pine (_Pinus palustris_) and ponderosa pine (_P. ponderosa_) have adaptations that give them an advantage under frequent, low to moderate intensity fires. Thus, the frequency and intensity of the disturbance affects the community of individuals found in a given area (White and Pickett 1985, Chaneton and Facelli 1991). This is also easily observed.
in floodplains where small differences in elevation (i.e., frequency and intensity of inundation) lead to different forest communities (Robertson et al. 1979; Wharton et al. 1982).

In many natural systems, disturbance occurs with such frequency that it maintains a certain structure and composition (van der Maarel and Sykes 1993). Sheep grazing in England’s grasslands (Gibson 1988b) and fire in the North American boreal forest (Johnson 1992) are examples of disturbances that maintain a system. Vegetation dynamics still occur in these systems, but they are constrained by disturbance intensity and frequency (Franklin and Tolonen 2000). Without continual disturbance, systems may succeed to a different composition and structure. For example, removing fire from a boreal forest ecosystem results in succession to shade tolerant species (Franklin and Tolonen 2000). In fact, evidence suggests that fire, wind and insect outbreaks, which create a high light and low litter microsite, are necessary for the long-term maintenance of many eastern United States pine populations, which otherwise would succeed to oak communities (Gibson and Good 1987, Burns and Honkala 1990, Franklin et al. 1993). Because fragmentation can alter the dynamics of disturbance (i.e., disturbance regime, Lord and Norton 1990), community composition and dynamics are also affected.

We suggest that disturbance catalyzes landscape structure, including fragmentation, affecting both patch size and adjacency. There are two important points here: 1) patchiness and fragmentation have been a factor for centuries in forested landscapes due to natural disturbance regimes, and 2) changes in the disturbance regime as witnessed in many anthropogenically-modified landscapes affects ‘natural’ landscape patterns. This results in a more difficult issue concerning fragmentation and edge effects. Specifically, the important question perhaps should not be how fragmented is the landscape at the current time, but rather how different is the landscape structure from some temporal frame of reference (e.g., pre-European settlement
conditions). For example, it is difficult to determine exactly what constituted an edge in pre-
European settlement upland forests of the southeast that were described as open, savanna, park-
like, or barrens by early land surveyors (Franklin 1994). Although roads were nonexistent, trails
extensively dissected the landscape, especially those developed by bison. Thus, because the
natural landscape exhibited a certain degree of “fragmentation”, anthropogenic effects need to be
examined within the context of natural heterogeneity.

A similar idea involves the natural range of variability in aspects of the disturbance
regime such as magnitude, timing, frequency, duration, and rate of change (e.g., Swetnam et al.
1999). Flooding and fire remain a part of many terrestrial systems but function differently due to
their altered periodicity (Poff and Allen 1995, Nesler et al. 1998, Franklin and Tolonen 2000,
Franklin et al. in press). Because the temporal dynamics of disturbance (the creation of edges and
development of mosaic landscapes) are quite important for the life cycles of species that have
evolved particular responses, it is important to have an understanding of the natural disturbance
regime (and its variability, rather than just mean values) and the ways in which local biota are
adapted to (or a product of) fragmented systems due to past disturbance history.

As an example of the ways in which fragmentation alters natural disturbance regimes and
effects, Duncan and Schmalzer (in press) simulated historical and recent fire spread patterns on
Merritt Island, FL using the FARSITE model. They described European anthropogenic changes
to fuel type (new exotic species) and fuel amount (removal of fuels via towns), both resulting in
a fragmentation of fuels that were once much more continuous and estimated that fuel
fragmentation has decreased the area burned during simulated fires from 68% to 14% of the
burnable area (percentages are an average of four sites they examined).
Vegetation dynamics in non-forested habitats (or in successional habitats) may in turn feedback to alter ecological processes in remnant forests. Previous studies have proposed that forest fragments, often disturbed by winds and other factors from the surrounding modified landscape matrix may be prone to invasions of successional species adapted to recurring disturbance (e.g., Janzen 1983; Laurance 1997). Indeed, studies of exotic species mobility in the landscape corroborate this relationship (Ambrose 1987; National Research Council 2002). Many of the most invasive exotics have similar life histories that we have described for fragmentation-positive taxa, including generalist habitat preferences and adaptations for disturbances (Bazzaz 1986, Ehrlich 1986, Usher 1988, Rejmanek and Richardson 1996). Thus, fragmentation, and disturbance in general, tend to result in increased numbers of exotics (Pyle 1995). Exotic species often out-compete native species because they are aggressive in their growth habits, have no natural controls on population growth such as disease or predators, and put out large numbers of seed with long viability (many are annuals). The invasion of other exotic species, whose primary use is aesthetic, may be ignited by their intensive use in urban centers. For example, Rudis and Jacobs (in review) found that privet (Ligustrum sinense and L. vulgare) dominated near-urban centers of the upper coastal plain section of the southeast US while several of the exotic invasive bamboos (Bambusa spp. and Pseudosasa japonica) may also follow an urban ignition trend (SBF, personal observation), although this has not yet been studied.

In some cases, subdivision of populations (natural or anthropogenic) may act to decrease threats from environmental fluctuations and catastrophes (Akcakaya and Baur 1996). Perkins and Matlack (2002) describe an historical landscape of loblolly and slash pine forests restricted to stream bottomlands prior to European settlement in southern Mississippi. These species now cover a greater area of the landscape extending into the uplands. Distances between stands have
shrunk from > 610 m prior to settlement to < 50 m in modern forests, greatly increasing the spread of southern pine beetle and fusiform rust across the landscape and the subsequent loss of pine forest. Research in western forests and northern forests has linked the amount of cutover area and forest susceptibility to bark beetle and fungal attacks (Franklin and Forman 1987, Forman 1995).

A final issue is the heterogeneity of past disturbances. Most disturbances tend to increase landscape heterogeneity and variability (Forman 1995). Historical accounts suggest burns were quite heterogeneous due to variability of fuel types, fuel moisture, and topography (Arno 1980). Occasional, severe disturbances tend to homogenize the landscape (Heinselman 1973, Turner et al. 1989, Forman 1995). Increased fuel loads in combination with a decreased heterogeneity of fuels in the West have obviously resulted in very different fire intensity and frequency. Unfortunately, the process has been made cyclic. The large landscape level effort to suppress fire has resulted in large, landscape level disturbance patterns that have decreased the overall heterogeneity of the system. We should now expect periodic, large-scale disturbances to persist unless small-scale disturbances are implemented to create more heterogeneity.

Conclusion: Biodiversity of a Fragment

Island biogeography, metapopulation dynamics, and source-sink dynamics theories are the theoretical basis to our understanding of fragmentation effects on biodiversity of patches. These population-based concepts provide a simple basis to explain the effects of fragmentation on biodiversity, but they continue to be too simplistic to predict population dynamics. Their main fault is the failure to incorporate the variability of patch and matrix habitat suitability and the variability of barriers to plant and animal dispersal. Studies strongly suggest the effects of
deforestation, fragmentation and edge creation are increasingly ameliorated as adjacent habitat becomes more similar to patch habitat, a process that naturally occurs through succession. Testing species-specific responses to heterogeneous landscapes and edges of varying permeability, specifically looking for thresholds of species response, will lead to much greater predictability of fragmentation on populations and communities. This daunting task should also involve the development of life history groupings (functional groups) to make predictions easier and establish mechanisms behind fragmentation effects.
Chapter 4: Fragmentation: Landscape Pattern and Quantification

While forest fragmentation involves changes in the area and isolation of forest ecosystems across a landscape, it is more than a state of landscape pattern – it is a dynamic process driven by a range of interacting natural and anthropogenic factors. The dynamics of forest removal, the nature of secondary succession, and the introduction of new types of land uses are part of human history, and any attempts to understand the effects of fragmentation must be set within the context of ongoing change. In the past, large-scale forces such as European migration to North America, westward expansion, and demands for timber drove forest cutting (Williams 1989, Franklin 1998). Today, the latter plus exurban expansion coupled with the continued expansion of road networks are important. Local decisions resulting in deforestation respond to local economic, demographic, and cultural factors, but these are also set in a larger context. For instance, local economies are part of the national and international economies so demands for wood products reflect global processes and pressures. Changes in international trade agreements and tariffs, national and regional shifts in population distribution, and cultural changes such as the propensity to own second homes or recent interest in protecting large area of wilderness all affect the extent and patterns of local deforestation.

The objectives of this chapter are twofold. First, we examine common patterns and processes associated with forest loss and recovery. Neither the process of cutting nor the process of recovery can be easily generalized (*a detailed discuss of the latter, for example, would involve a lengthy review of succession theory that is well outside the scope of this paper and has already been done by numerous authors, e.g., Glenn-Lewin et al. 1992*), although we attempt to provide a general framework for describing both. The steps of forest cutting and isolation that collectively
are called fragmentation often overlap and interact in space and time. Their initial impact
depends on the inertia and resilience of the forest cut as well as the ongoing processes of cutting
itself. Second, we describe the development and implementation of spatial pattern metrics that
have been used to quantify patterns of deforestation and fragmentation. In particular, we examine
the aspects of spatial pattern that are addressed by such metrics and evaluate their ability to
capture the effects of fragmentation on biodiversity.

Forest Fragmentation: Landscape Patterns

The natural background of a landscape is that of a shifting mosaic shaped by abiotic
conditions, biotic processes and interactions, and disturbance (Spies and Turner 1999; Urban et
al. 2000). The degree of stability of this mosaic in time and space varies among landscape
elements, but change is a constant feature. Differences in resource distribution set the
background, with climate, geology and topography serving as the large-scale constraints that
determine the distribution of resources, especially in terms of soils, water and solar radiation.
Against this background, natural disturbances continually alter the mosaic by creating new initial
patches in sizes, shapes and places that do not necessarily reproduce the previous mosaic pattern.
The most dynamic elements are those that undergo frequent disturbance and succession,
including large tracts of forest subject to fire or windthrow. Although the resulting patterns can
appear random, even natural disturbances can have larger-scale constraints such as topography
(Lindemann and Baker 2002).

The effects of human activities are further superimposed upon and interact with natural
patterns and processes, resulting in a complex and dynamic landscape mosaic whose structure
reflects to varying degrees the influences of natural and anthropogenic agents. With respect to
deforestation and forest fragmentation, Forman (1995) described a series of loosely-ordered stages: perforation, dissection, fragmentation, shrinkage, and attrition (Fig 4.1a). We describe these below and link each to types of land use that change forest to other land cover types (e.g., agriculture, timber harvest, settlement, road building). It is also worth reinforcing that this sequence need not be followed through to the end in all landscapes.

Perforation

Perforation involves cutting holes in a largely forested landscape, as would occur with isolated land use change in advance of a contiguous frontier. Consequently, the number of forest patches remains essentially unchanged and average patch size decreases only as a function of forest removal (Fig. 4.1b). Riitters et al. (2002) identified perforation as a primary factor in forest change and, where road density is relatively low, it is the process that initially decreases the amount of interior forest habitat while introducing a large number of forest edges, thereby increasing the interactions between forest edge and interior areas. Connectivity of forested habitats, however, remains generally high during this process. Because perforation is typically one of the first stages of clearing in a forested landscape, it occurs with initial forestry operations in an unlogged area or in low density, dispersed logging regimes. Low-density settlement and more isolated instances of exurban development also represent examples of forest perforation. In the past, initial clearing for agriculture and settlement would have been cases of perforation, but such cases are less common now, at least in the United States.
Figure 4.1 (a). The relative importance spatial processes at varying stages of deforestation and fragmentation. (b) Major spatial process in land transformation and their effects on spatial attributes. + = increase, - = decrease, 0 = no change. Effects are measured for the black cover type. White represents the surrounding landscape type. Both figures from Forman (1995).
Dissection

By definition, subdivision – and thus fragmentation – occurs where a block of forest is dissected. What Forman implies as dissection largely includes the isolating effects of roads, although other linear features such as transmission lines can have some of the same effects. As such, dissection has small sample and area effects but potentially significant isolation and edge effects, depending on the characteristics of the feature (e.g., road width) and the species or process under consideration. Roads are known to have a wide range of associated effects on biodiversity and ecological processes (e.g., Vermeulen 1994; Knops et al. 1995; Baker and Knight 2000; Delgado et al. 2001), including roadside vegetation and animals as well as water, sediment and chemical fluxes (Forman and Alexander 1998; Forman 2003). Trombulak and Frissel (2000) identified seven general ways that roads affect terrestrial and aquatic ecosystems: (1) mortality from road construction, (2) mortality from collision with vehicles, (3) modification of animal behavior, (4) disruption of the physical environment, (5) alteration of the chemical environment, (6) facilitation of the spread of exotic species, and (7) changes in human use of land and water.

Forman’s classification of stages does not allow for the development of a road network connecting perforations that does not dissect a forest, but such a network would exacerbate perforations by dissecting the remaining forested areas. The spatial pattern of a developing network is different from the general ideas of patterns of fragmentation, but it is probably the most common spatial development. Networks take many shapes, however. Dendritic road networks may develop in topographically rugged areas in order to efficiently link perforations to external places (e.g., for either timber harvest or isolated settlement). In other areas grids may develop, which while not necessarily efficient, are common (e.g., for both agriculture and
forestry in flatter regions such as the Southeast or Midwest). The road networks and the type of
dissection thus do not necessarily depend on the type of land use. Dissection occurs with
forestry, early stages of extensive agriculture, and low to moderate density settlement.

*Fragmentation*

Forman’s third category is fragmentation, in which pieces of forest become isolated from
one another. Perforations and dissections grow wider, and fragmentation occurs when the
expansion links cleared areas. Patch size decreases and the amount of interior forest drops as
edge density often reaches its peak in fragmented landscapes. Fragmentation will occur with
extensive forestry and with medium- to high- density settlement. As a road network develops and
associated forest cutting occurs, multiple intersections and adjacent cut parcels can occur that
leave isolated remnants. Fragmentation can be thought to occur when the dissection or secondary
linkage of cut areas is complete, but is better thought of as the process of expanded cutting after
the initial road building and perforation stage. At this stage all cutting effects can be strong.
Fragmentation was also a key stage during settlement and agricultural transformation of the
United States.

*Shrinkage and Attrition*

Shrinkage is the inverse of the expansion of existing cutting and picks up where
fragmentation leaves off. The isolates created by fragmentation can be seen to shrink, edges may
actually decrease in length throughout the landscape and never stabilize, and as implied, area
declines while isolation increases. Some forestry operations, extensive agriculture, and high-
density settlement all lead to shrinkage. Attrition is then the endpoint of the process, when
individual remnants disappear. This stage is most likely with very extensive agriculture and urban-suburban (rather than exurban) development. Thus, there are in fact three key processes: cutting patches, cutting lines, and cutting the edges of patches and/or lines. Curtis’ classic study of forest transformation in Cadiz Township, WI exemplifies the area in a pre-agricultural state and three conditions illustrative of fragmentation, shrinkage and attrition (Fig 2.1). Such changes are imposed over the shifting mosaic, which can include areas of disturbance and non-forest.

In addition to the basic patterns and processes associated with these different stages of deforestation and forest fragmentation, there are two other points to recognize. First, it is important to acknowledge that the patterns created by different fragmentation agents and processes may have different scaling properties. For example, the scale of resource-oriented deforestation will depend on the interaction of the purpose and the technology available. Current forest cutting for timber in the Northwest has a different scale of spatial pattern (and thus differences in perforation, edge, and interior) than agricultural clearing in New England 300 years ago. Similarly, exurban fragmentation in many eastern areas, which often occurs where development results from clearing forests on land abandoned from agriculture, has a different scale of spatial pattern than the primary fragmentation that occurred during initial settlement and cultivation.

Second, within the processes of forest loss and fragmentation, we can expect nonlinear responses in the resulting patterns. Percolation theory shows that with a random process of habitat destruction many characteristics of the landscape begin to change rapidly when approximately 40% of the forest cover is removed. Reducing forest cover from 100% to 90% or from 15 to 5% results in relatively little change in mean forest patch area or connectivity whereas a much larger change in both characteristics would be expected when forested area decreases.
from 65% to 55% (on a random landscape). With nonrandom patterns (as would be expected in real-world landscapes), the changes are not as abrupt and occur at lower proportions of remaining forest, but the responses are still nonlinear.

Forest Fragmentation and Recovery of Disturbed Areas

Although the primary focus in fragmentation research tends to be on the pattern of fragmentation and the resulting effects on remnant forest ecosystems, non-forested ecosystems in fragmented landscapes are not static and may, through plant succession, increasingly come to resemble the forested remnants (e.g., Moran and Brondizio 1998). This is especially likely if the disturbance is temporary and does not substantially alter site characteristics or resource availability. This could be the case with agricultural clearing or logging, although the post-disturbance response depends on characteristics of the plant community and disturbance itself. While persistent or irreversible changes in plant community structure or composition following disturbances may once have been regarded as rare incidents that only occurred following exceptional events or particularly extreme disturbances, research has shown that past human land uses and disturbances can be important determinants of species composition, biodiversity, community pattern, and ecosystem function even in landscapes that outwardly appear “natural” (e.g., Duffy and Meier 1992; Goodale and Aber 2001; Foster et al. 2003).

As an example of these lasting legacies of human disturbance, natural reforestation of agricultural lands in New England over the past 150 years has created a predominantly forested landscape. Bellemare et al. (2002), however, documented persistent compositional differences between the vegetation of primary and post-agricultural secondary forests, indicating that the distribution patterns for many plant species still reflect the open, agricultural environment of the
nineteenth century despite the current predominance of forest cover in the study area. Hall et al. (2002) emphasized the importance of recognizing scale when studying land use history effects. They found that broad patterns of variation in vegetation composition at the regional scale were largely controlled by environmental conditions, but at finer spatial scales, historical land-use practices, which were relatively homogenous across the study area and averaged out at broad spatial scales, had strong and persistent impacts on vegetation composition and structure.

It is therefore important to understand not only the processes or steps associated with fragmentation but also how these relate to the recovery of cut areas. The recovery of cleared areas will depend to some degree on the same processes and effects as the remnants, with the primary mechanism being plant succession. The rate and trajectory of succession are generally controlled by the responses of individuals to changing abiotic conditions, but succession is also constrained by spatial relationships and processes (e.g., the location of seed sources). Thus, as we discussed in the previous chapter, forest fragmentation can greatly influence plant succession in both the remnant forests and in the disturbed matrix. However, rather than focusing specifically on the various factors influencing succession, which will be specific to a given location and situation, we wish to place the processes of change in a more general framework analogous to that of the previous section.

The linked processes of forest loss and recovery, we argue, can be categorized by the degree of habitat destruction and the amount and rate of recovery. McIntyre and Hobbs (1999) described potential landscapes as Intact, Variegated, Fragmented, and Relictual. These are meant to indicate a gradient of proportion of habitat destroyed. They then overlaid the remnant habitat with degrees of change such as Unmodified, Modified, and Highly Modified. Their areas of Destroyed Habitat remained the same in both. This description needs to be taken further to
explicitly recognize that there are degrees of destruction as well as degrees of modification within the non-remnant habitat. Then, another range of categories is needed to account for the stability of the altered land, especially relative to its recovery to some type of forest cover. The processes of destruction can vary from complete to variegated; the processes of recovery can be zero, arrested, or complete and vary by rate. Examining ecosystems in terms of their inertia and resilience (\textit{sensu} Westman 1978) provides a useful approach that has been used to examine ecosystem responses to broad range of disturbances and stressors (e.g., Cooper-Ellis et al. 1999; Hirst et al. 2003).

\textit{Inertia / Resistance}

In terms of ecosystem response to a disturbance, inertia (or resistance) describes how much a landscape changes given a specific force (e.g., a disturbance) (Milchunas and Lauenroth 1995; Zobel and Antos 1997). The concept was developed for ecosystems subject to stress or the application of a given amount of energy as an impact (and thus the physics/mechanics analogy). For a landscape, the concept can be extended so that the amount of area cut and the degree to which it is modified are the energy applied. Inertia represents how the landscape elements, especially the remnants, respond to a given amount of impact. We could look to the tenets of island biogeography as an approach to quantifying inertia, or, as discussed below, use more axes for a state space (Malanson and Trabaud 1987). Because the impact itself has multiple axes (area and intensity being perhaps the two most important for deforestation), a simple energy-inertia measure will not be possible, but a degree of change in multiple dimensions should be.

With respect to natural disturbances, we might expect to see differences in inertia dependent on the disturbance regime, on natural productivity, and on history. Inertia in forests
varies, for example, as a function of forest structure and age, which will depend on these same factors. Thus, forests subject to a fire regime with occasional stand-destroying crown fires (e.g., lodgepole pine communities) will have different inertia than stands characterized by a regime of frequent but low intensity surface fires (e.g., ponderosa pine communities). The inertia of forests to human fragmentation agents such as logging will be a function of characteristics of both the disturbance itself (e.g., logging type or intensity) and the response of the remnant vegetation to changes effected by the disturbance (e.g., altered microclimatic conditions).

Resilience

Resilience or recovery of the landscape is due primarily to the characteristics of the matrix (e.g., Dale et al. 1998), but remnants can recover simultaneously. Resilience has four components:

- **Elasticity** is the rate of recovery. It can be measured as the similarity to the pre-impact landscape over time. Elasticity is related to the rate of succession in the pre-deforestation ecosystem and will depend on factors such as the biotic and abiotic conditions for establishment.

- **Malleability** is the degree to which the recovered landscape differs from the pre-impact state. Some species may become globally or at least regionally extinct during fragmentation. Some landscapes never approach a pre-deforestation condition, and changes in the abiotic environment may make exact recovery impossible (e.g., when a severe wildfire sterilizes the soil). It must also be kept in mind that the pre-fragmentation forests may not have been in equilibrium with the environment due to climate change, and the recovered forest may represent effects of a changing climate as well as fragmentation effects.

- **Amplitude** is the amount of change that can occur before the landscape cannot recover toward its pre-impact condition. It thus depends on inertia and the level of fragmentation. In theory, at some level of fragmentation, a forest should be able to recover toward the pre-fragmentation state, even though it may never approach it completely, but with any more fragmentation the forest would not recover toward the pre-fragmentation state. This theory implies a threshold in the system.
**Hysteresis** is the degree to which the path of recovery varies from the path of impact-change. It is best seen in chronic disturbances where retrogression and succession have different pathways. For fragmentation, the concept can best be applied to examining differences among pathways of recovery. Small differences in initial conditions or subsequent history combined with nonlinear dynamics will cause pathways to differ even from nearly identical conditions of fragmentation.

These dynamics can be seen in the trajectories in a state space of characteristics of cut areas through time (e.g., Malanson and Trabaud 1987). For example, trajectories in terms of diversity, species composition, structural characteristics, and/or ecosystem functions could be used, and the changes in state space could indicate much about inertia and resistance.

The characteristics of inertia and resilience as proposed by Westman did not take into account the system behaviors caused by nonlinearities. For that reason, some of the characteristics interact more than originally implied. For example, hysteresis and malleability will interact because different pathways will lead to forests that differ from the pre-fragmentation forest in different degrees; the threshold in amplitude is a nonlinearity. Because of nonlinearities in response to spatial habitat destruction, we should expect that recovery would vary with the amount of destruction as well as the inherent characteristics of the landscape. To the degree that landscapes are variegated rather than relictual and the level of modification is low, the recovery will be more elastic, less malleable, less likely to exceed its amplitude, and have less hysteresis. The opposite will be true for relictual, highly modified landscapes. The important point about nonlinearity is that any of these characteristics can change greatly with a small amount of additional forest cutting.
Quantification of Fragmentation: Landscape Metrics

Because forest fragmentation involves the subdivision of forests into smaller, disjunct units by road construction, clearing for agriculture, timber harvesting, urbanization, and other human developments, the spatial extent and distribution of ecosystem types and seral stages across a landscape is reshaped, interactions among the component landscape elements are modified, structural and functional connectivity of the landscape are often altered, and abundance and ecological importance of edge habitats change. Fragmentation is thus an inherently spatial process requiring appropriate approaches, tools and methodologies.

The maturation of remote sensing techniques and GIS over the past twenty years has greatly increased the availability of spatially-explicit, landscape-level data on land use and land cover (discussed in depth in Chapter 6) and given scientists the means to document patterns of forest fragmentation at scales ranging from watersheds to regions, nations and the globe (e.g., Ripple et al. 1991; Riitters 1997; Tinker et al. 1998; Riitters et al. 2000; McGarigal et al. 2001). Numerous metrics have been developed and made available through specialized landscape analysis packages, facilitating the quantification of landscape pattern and composition resulting from fragmentation. We thus believe that the major obstacles now facing scientists and land managers with respect to quantifying patterns and effects of fragmentation are no longer limitations associated with technology or data availability, although better assessments of error in existing datasets and the concomitant effects on landscape metrics are needed (e.g., Wickham et al. 1997). Rather, we contend that the major issues that need to be addressed in the upcoming decade are:

1) the continued documentation of fragmentation effects above and beyond those attributable to deforestation. This includes clarifying the complex manners that fragmentation effects interact with habitat loss effects to affect biodiversity and ecological processes (Andrén 1994; With et al. 2002), and
2) the linkage of fragmentation effects to quantitative measures of landscape pattern. This includes coming to a better understanding of the inherently nonlinear relationships between landscape structure, fragmentation effects and landscape metrics, developing ways of dealing with the species-specific nature of fragmentation effects, and facilitating the use of fragmentation measures in the development and implementation of forest management and monitoring plans. This will also entail evaluating the utility of existing landscape metrics and likely developing additional metrics that characterize fragmentation in new ways, recognizing that most fragmented landscapes are dynamic mosaics composed of habitats that vary in quality rather than discrete patches of “habitat” and “non-habitat”.

The assertion that we as scientists still don’t fully understand fragmentation effects may be somewhat surprising given that the linked processes of deforestation and forest fragmentation are among the most important conservation issues of our time. The reality, however, is that our understanding of fragmentation effects is still largely based on intuition, partially-tested theory, results from simulation models and correlative studies (D’Eon 2003). As Haila (2002) emphasized, much of what has been ascribed to “fragmentation effects” in the literature has included the effects of both deforestation and fragmentation, and several authors have called for additional well-focused, high quality research that addresses the ways in which fragmentation directly affects biodiversity and ecosystem function (McGarigal and Cushman 2002; Villard 2002). This crucial idea is discussed at greater length in other chapters of this paper and in the overall summary chapter but is important to bear in mind as we begin to explore the proliferation of landscape metrics.

The second challenge, the linkage of deforestation and fragmentation effects with quantitative measures of landscape pattern, is the subject of this section. Many forest managers consider fragmentation to be one of the major issues they face in their regular decision-making processes (Hagan and Whitman 2003). Governments and management agencies have therefore
sought generic measures of forest fragmentation to monitor changes in forest cover measures that may also be informative in the decision-making process (Lindenmayer et al. 2002; Heinz Center 2002). Even with the tenuousness of the evidence concerning the unique contribution of fragmentation effects to biodiversity maintenance, there is an existing body of circumstantial evidence relating landscape metrics to various effects on biodiversity and ecological processes in fragmented landscapes, and there are an increasing number of studies that have addressed the importance of spatial configuration over and above habitat loss, especially in heavily deforested landscapes (e.g., Villard et al. 1999; K.B. Jones et al. 2000; Collingham and Huntley 2000; Cooper and Walters 2002; Mac Nally and Horrocks 2002). As with other vital environmental issues, many managers feel a need to address the potential consequences of fragmentation whether or not specific effects have been fully validated through the scientific process, and landscape metrics are one potential tool by which the importance of spatial configuration in fragmented landscape can be interpreted and incorporated into forest management and monitoring plans (e.g., Baskent and Jordan 1995; Borgesa and Hoganson 2000; Herzog et al. 2001).

It has been argued, however, that overemphasizing the importance of measures of spatial configuration may be misguided because habitat loss is the primary cause of biodiversity losses at most levels of deforestation and forest fragmentation (Fahrig 1997; Trzcinski et al. 1999; McGarigal and Cushman 2002; Schmiegelow and Mönkkönen 2002). Further, while landscape metrics may be useful when the aim is to quantify current landscape patterns from a human perspective or to monitor the rate and extent of change in pattern over time, it is not clear that most metrics have consistent ecological or statistical significance (Tischendorf 2001; Lindenmayer et al. 2002). Thus, one of the most difficult issues facing landscape ecologists,
conservation biologists, foresters, land managers and others dealing with forest fragmentation is how (and if) landscape metrics can be tied to specific fragmentation effects.

*Landscape Metrics and Forest Fragmentation: A Background*

In the same way that biologists and ecologists use indicators to quantify the status of an ecosystem, landscape ecologists use indices or “metrics” of landscape structure to quantify patterns of landscape structure and change (e.g., Franklin et al. 2000). The assumption in the first case is that the complexity of ecosystem characteristics and processes can be captured using indices that are easier to interpret and less expensive to gather. For example, the amount of downed woody debris or standing decadent logs on a site can be an indicator of a wide range of ecosystem attributes and functions that may be too complex, difficult, or expensive to quantify, including habitat availability, nutrient cycling, or disturbance history (Harmon et al. 1986). By monitoring and comparing indicator values through time or across space or by projecting the effects of different actions on index behavior, forest managers can assess the impact of different management strategies or competing management scenarios on ecosystem attributes of interest (e.g., Steyer et al. 2003).

Landscape metrics are quantitative indices meant to capture various aspects of landscape structure under the premise that there are strong links between ecological pattern and ecological function and process (Gustafson 1998). With respect to fragmentation, the expectation is that changes in metric values can in some way be linked to changes in fundamental ecological processes. For example, the percentage of a forested landscape that remains in forest following some human activity (e.g., logging, land use conversion) can be interpreted as the degree to which forests have been fragmented. The underlying assumption is that reducing forest cover
leads to (among other things) a loss of species habitat, a loss of resources, smaller populations of forest species, and a decrease in species diversity of forest-dependent species. Thus, from a scientific standpoint, the crucial connection to make is how changing spatial patterns in fragmented landscapes affect ecological pattern and process. This understanding in turn may have practical and applied value if managers can begin to alter or manipulate landscape pattern to reach some desired goal (e.g., for use as the basis for evaluating conservation value of different scenarios) (Baskent and Jordan 1995).

Since the 1980’s, dozens of landscape metrics have been proposed to quantify landscape pattern and structure (see http://www.umass.edu/landeco/research/fragstats/fragstats.html for a list and descriptions). Popular commercial GIS (e.g., ArcInfo) and remote sensing (e.g., Idrisi) packages generate basic landscape measures such as patch area and perimeter while more specialized landscape analysis packages (most of which now have GIS or remote sensing interface capabilities) such as Fragstats (McGarigal and Marks 1995; McGarigal et al. 2002), r.le (Baker and Cai 1992), and APACK (http://flel.forest.wisc.edu/projects/apack) provide a broad spectrum of metrics that have been used for landscape quantification more generally and fragmentation studies more specifically (e.g., Reed et al. 1996; Knutson et al. 1999; Cushman and Wallin 2000; Griffith et al. 2000; Graham and Blake 2001; Herzog et al. 2001; McGarigal et al. 2001; Leimgruber et al. 2002). The study of land use and land cover patterns and changes has now become a prominent topic for research by landscape ecologists, foresters, geographers, and remote sensors (among others), and various measures of landscape pattern are often an integral part of such studies (e.g., Brown et al. 2000; Evans et al. 2001; Leitao and Ahern 2002).

Haines-Young and Chopping (1996), Turner et al. (2001) and McGarigal et al. (2002) all provide excellent reviews of common landscape metrics that are included in widely used analysis
packages like Fragstats. Despite the large number of metrics that have been developed, most can generally be grouped according to what aspects of landscape structure and pattern are measured, with the most basic classes separating indices that measure: (1) the composition of the landscape, referring to the amount of different cover types found in the landscape, (2) the configuration of the landscape, that is how patches of the same or different cover types are arranged in the landscape in relationship to each other, and (3) the shapes of patches and characteristics of edges in the landscape (Lindenmayer et al. 2002). Baskent and Jordan (1995) differentiate areal indices (measures of landscape or patch size, shape and core area), linear indices (measures of boundary length, width, and shape as well as landscape-level connectivity), and topological indices (measures of the spatial relationships between landscape components, including interspersion, spatial association and isolation). Haines-Young and Chopping (1996) and McGarigal et al. (2002) provide slightly more detailed classifications in which they distinguish metrics that measure area, edge characteristics, shape, core area, isolation and proximity of cover types, diversity and evenness, contagion and interspersion, connectivity and circuitry, and contrast.

Within each of these groups, metrics can be grouped according to the spatial scale of analysis, including patch-level metrics (calculated for each individual patch in the landscape), class-level metrics (average values calculated for each cover type in the landscape), and landscape-level metrics (calculated for the landscape as a whole irrespective of specific cover types). Rather than using these generic indices, some studies employ metrics that more directly focus on specific variables of interest. For example, measures such as road density and distance of forested areas from the nearest roads have been utilized as indicators of fragmentation and road effects (e.g., McGurk and Fong 1995; Reed et al. 1996; Tinker et al. 1998; McGarigal et al. 2001; Saunders et al. 2002).
For a landscape metric to be an effective indicator of fragmentation, it should be easy to calculate, work over the full range of all possible situations (e.g., from 0-100% forest cover), be readily and consistently interpretable, and be able to adequately characterize the fragmented landscape structure (Forman 1995). No single metric has all of these properties so multiple indices are needed to capture various aspects of landscape pattern. However, landscape metrics tend to exhibit a great deal of redundancy (Fig 4.2), and a few indices can often capture most of the variation in landscape characteristics. Riitters et al. (1995) addressed the issue of landscape metric redundancy by performing factor analysis on a suite of 26 metrics for 85 maps of land use/land cover to identify common axes of pattern and structure. They identified six independent factors that explained about 87% of the variation in the metrics and represented composite measures of average patch compaction, overall image texture (from coarse to fine), average patch shape, patch perimeter-area scaling, and number of cover types. Studies by Hargis et al. (1998) and Trani and Giles (1999) support their conclusion that many landscape metrics are highly correlated and thus do not measure unique qualities of spatial pattern. Consequently, analyses of fragmentation pattern should involve complementary metrics that are independent of one another but yet can collectively quantify differences in landscape pattern.

In addition to problems of redundancy, some metrics suffer from: 1) ambiguity, which involves cases where different landscape structures result in the same metric values or cases where correlations between a landscape index and response variable range from highly positive to highly negative when derived from different spatial patterns (Fig. 4.2) (Tischendorf 2001), and 2) scale sensitivity, where metric values change significantly with the grain size of the data (i.e., resolution) (Moody and Woodcock 1995; Wickham and Riitters 1995; Benson and MacKenzie 1995) and the spatial extent of the study area (Turner et al. 1989; Saura and
Fig. 4.2. Changes in landscape metric values at various levels of forest cover loss. The metrics, the percentage of interior forest, the mean forest patch size, the Shannon diversity index, and the Shannon evenness index, provide examples of redundancy, when two metrics exhibit a high degree of correlation, and ambiguity, where metrics can take on the same values at very different values. Adapted from Trani and Giles (1999).
Martinez-Millan 2001). Metrics are sensitive not only to spatial scale but also to the detail of the land cover classification (Huang et al., in review), including the amount of error in the classification (Wickham et al. 1997; Turner et al. 2001). Finally, although a meaningful interpretation of metrics is possible only when the limitations of each measure are fully understood and the user is aware of potential shifts in the range of values due to characteristics of the landscape patches themselves (Hargis et al. 1998), the statistical properties and sensitivity of most metrics to changing landscape patterns continues to be poorly understood (Turner et al. 2001; Lindenmayer et al. 2002). In particular, we have very little understanding of the degree to which landscape pattern must change to be able to detect an ecologically- or statistically-significant change in the value of the metric (Wickham et al. 1997).

The majority of the metrics commonly calculated by landscape analysis packages are more appropriate for assessing the effects of deforestation (e.g., patch size, core area) than the changes in spatial configuration resulting from fragmentation. There are, however, a number of metrics that are more clearly related to habitat isolation and connectivity, especially measures of inter-patch or mean nearest neighbor distance and patch cohesion (because fragmentation is generally thought to decrease landscape connectivity) and measures of edge characteristics, especially edge length and density (because fragmentation alters the abundance and importance of edges). Metrics addressing these attributes have been shown to be responsive to changes in forest structure associated with forest fragmentation (e.g., Hlavka and Strong 1992; Schumaker 1996; Ranta et al. 1998; Villard 1999; Griffith et al. 2000; Ripple et al. 2000; Swenson and Franklin 2000; Hansen et al. 2001; Lofman and Kouki 2001; Ochoa-Gaona 2001; Graham and Blake 2001; Ferreras 2001), and both inter-patch distance and edge density have been proposed as national fragmentation indices by a Technical Work Group facilitated by the Roundtable on
Sustainable Forests to address Indicator 5 (Fragmentation of Forest Types) of Criterion 1 (Conservation of Biological Diversity) of the Santiago Declaration of the Montréal Process (see Riitters 2003). Patch density, shape, and fractal dimension also address characteristics of fragmented landscapes (e.g., Rex and Malanson 1990) but could be considered to fall somewhere between deforestation and true fragmentation indices. Bender et al. (2003) provide a more general overview of recent patch isolation studies, applied patch isolation measures, and results.

While the ability of landscape metrics to capture landscape structure and pattern is important for documenting and monitoring changes related to forest fragmentation (Noss 1999), a more fundamental issue is whether changes in metric values can actually be linked to changes in biodiversity or key ecological processes. Of particular relevance to fragmentation effects are whether:

(1) metrics such as interpatch distance and patch cohesion that largely address structural connectivity (the degree of habitat connectedness) can be used to understand changes in functional connectivity (which addresses how easy it is for organisms to move across a landscape), and

(2) metrics of edge abundance can be related to significant changes in forest structure, composition and function due to microclimatic edge effects and subsequent edge-mediated effects.

Isolation and Connectivity Metrics

Both field and simulation studies have documented that inter-patch distance and landscape connectivity influence the dispersal of species, with the specific effects being highly variable among species. Studies relating landscape metrics of patch isolation and connectivity to population properties (e.g., size, persistence) and ecological processes (e.g., dispersal), however, have yielded mixed results, with many researchers finding weak or non-existent relationships. Schumaker (1996), for example, tested for correlations between nine common metrics of habitat
pattern and the results of simulated spotted owl dispersal through fragmented old-growth forest landscapes in the Pacific Northwest. His results indicated that dispersal was only weakly correlated to the indices examined. Bender et al. (2003) and Tischendorf et al. (2003) similarly examined the ability of isolation metrics to predict animal dispersal in fragmented landscapes, with the latter also including variation in matrix habitability. Their results suggested that area-informed isolation measures, such as the amount of available habitat within a given radius around a patch, were generally more reliable than distance-based metrics, but that the habitability of the matrix also had a strong influence on patch immigration.

The sometimes-inconsistent relationships between metrics of isolation/connectivity and ecological pattern and process response variables should not be surprising given the complicated nature of species dynamics in fragmented landscapes. These metrics by their nature tend to assess the degree of structural connectivity across a landscape in an effort to capture the effects of reductions in patch immigration rates. The movement of organisms across a landscape, however, is determined by the landscape’s functional connectivity for each species, which is related to a range of factors that are not easily captured by existing landscape metrics (e.g., stepping stones, matrix characteristics, width and quality of corridors, gap crossing willingness of the species: Aberg et al. 1995; Tischendorf and Wissel 1997; Haddad 2000; Ricketts 2001; Sondgerath and Schroder 2001; Bowman and Fahrig 2002; Bélisle and Desrochers 2002). Measures of structural connectivity are thus probably important only to the extent that they capture the underlying functional connectivity.

A second complicating factor is that both the value of fragmentation metrics and their ecological significance may be dependent on other attributes of the landscape such as patch size or shape (Hargis 1999), making direct interpretations of fragmentation indices problematic. In
the early stages of habitat destruction, the remaining habitat is perforated but generally remains well connected (Metzger and Décamps 1997). Populations are affected mainly by habitat loss, with population sizes reduced by some proportion of deforestation. With increasing forest destruction, the degree of connectivity is rapidly reduced, and habitat fragmentation begins to amplify the impact of habitat loss (Hanski 1999). As we described earlier, percolation theory-based landscape models indicate that connectivity in random maps decreases rapidly after about 40% of the habitat is removed, with thresholds being different for non-random, spatially-structured landscapes. Andrén (1994) suggested that landscapes remain relatively well connected until 60-80% of the habitat is removed (although the specific values will vary depending on the species examined), after which distinct fragmentation effects become more notable.

Subsequent studies have documented a range of nonlinear responses in fragmented landscapes, including both thresholds where small changes in habitat loss lead to rapid changes in biodiversity or ecological processes as well as thresholds related to the interactions between habitat loss and fragmentation effects (e.g., With and Crist 1995; With et al. 1997; Wiens et al. 1997; Villard et al. 1999; Collingham and Huntley 2000; Flather and Bevers 2002). Bender et al. (2003) found that simulated animal immigration rates were adequately predicted by nearest neighbor distance when patch size and shape were variable. The complexity and species-specific nature of these types of threshold effects place severe limitations on the development of “cookbook prescriptions” in management plans based on landscape metrics of isolation and connectivity (With and King 2001).
Edge Metrics

With respect to edges, there are two primary concerns in fragmented landscapes: (1) the development of edge effects where forests abuts non-forested land uses, and (2) the effects that the edge and adjacent land use have on the movement, behavior and survival of forest organisms. As with the effects of isolation and connectivity, the ecological effects associated with forest edges related to road construction, logging, agricultural activities and other human activities are well documented. In small fragments, edge effects may even be more important in modifying forest dynamics (e.g., tree mortality and recruitment, biomass loss, and community composition) than deforestation effects related to patch size (Gascon and Lovejoy 1998).

The potential effects of edge creation and subsequent influences on forest structure, function and composition are often quantified using perimeter to area ratios or core area-indices (Laurance and Yensen 1991). The latter subtract the area ascribed to edge effects using a user-specified buffer to derive the amount of “interior” area not affected by edge. Such indices, however, have a number of limitations in that they are highly correlated with patch area, are sensitive to the specified depth of edge influence (which itself is specific to the individual property or species being examined), ignore the heterogeneity inherent in the edge to interior transition, and do not account for the dynamic aspects of some edge effects (e.g., Kupfer and Runkle 2003). These limitations make edge density and other edge metrics more attractive as relatively generic indicators of the range of changes associated with edge creation, but as with patch isolation metrics, the linkage between edge density and ecological response variables is imperfect due to several complicating factors.

Regardless of the index used, specific edge effects are highly dependent on factors that are not typically captured by the edge metrics used, such as contrast with the adjacent habitat
type. Thus, a landscape composed of a mosaic of old-growth and second-growth forests will have very different ecological characteristics than a mosaic of old-growth forests and open fields or logging cuts (Matlack 1993; Kupfer 1996; Bayne and Hobson 1997), even though the landscapes may have a similar edge density. Further, edge effects are highly dynamic through time as an edge ages (Esseen and Renhorn 1998), meaning that generic measures of edge density may miss important ecological differences among different edges within a heterogeneous landscape. All of these complications mean that metrics such as edge density will likely serve as reasonable indicators of fragmentation effects, but that specific impacts will be difficult to relate to metric values in a prescriptive sense.

**Summary**

Effective forest management requires reliable information on the status and condition of forests and of changes in conditions over time (Noss 1999). In the case of forest fragmentation, this has led to: (1) the documentation of spatial patterns of fragmentation using GIS, remote sensing and a number of landscape metrics designed to quantify landscape pattern and composition, and (2) attempts at linking landscape metrics with measures of biodiversity and ecological processes at a range of scales, both as a means of validating landscape-level fragmentation effects (i.e. by linking changes in pattern to ecological responses) and as an effort to develop tools and indices that can be used as aids in the forest management decision-making process. The results of previous studies suggest that landscape metrics addressing isolation, connectivity and edge density can capture changes in landscape structure that result from fragmentation, although some variation occurs as a function of other factors more directly related to deforestation (e.g., two landscapes with the same amount of remaining habitat may have
different edge densities as a function of differences in patch size, shape or arrangement).

Previous studies have also shown that the effects of fragmentation on biodiversity and ecological processes can be linked in a general way to fragmentation metrics. There are, however, many uncertainties involved that should be kept in mind when incorporating fragmentation metrics into the decision-making process. For example, distance-based metrics can only be interpreted within the context of the organisms being studied because different organisms perceive and utilize the landscape at different scales, making generalizations difficult (Kotliar and Wiens 1990; Villard et al. 1999).
Chapter 5. History and Pattern of Forest Fragmentation in the United States

History shapes every forest community to some extent, through selection of those species that survive a disturbance, by influencing which species can colonize developing communities, or by setting the sequence of species arrival to developing communities. Reconstructions based on a range of proxies as well as long-term successional studies using permanent plots and chronosequences have helped to elucidate the effects of past climate, land use and disturbance regimes on current landscape structure and community composition. Such studies demonstrate the dynamic nature of communities in response to factors operating at a range of spatial and temporal scales, underscoring the ephemeral nature of plant assemblages and highlighting the necessity of understanding the limits of our abilities for management (e.g., the limitations of our abilities to repeat history and the legal and societal constraints on our actions).

Understanding the interactions among climatological, physiographical and historical factors controlling forest structure and composition is a major challenge to ecologists, conservationists and land managers, and the implications of such knowledge for sustainable forest management are poorly understood but potentially significant. As Foster (2002a) notes in his summary of work carried out in New England:

“(T)he region’s dynamic history raises challenges for conservationists and land managers that are shared by decision makers for any region that bears the legacies of environmental change, natural disturbance and human activity. These challenges include several basic questions:

- What do we conserve in dynamic landscapes and how do we accomplish this?
- To what extent should we value and conserve cultural landscapes and habitats that have been shaped by land-use activities that are no longer current practice?
• How do we protect different biotic communities and conservation values in a varied landscape while still accommodating human development and natural resource extraction?

• What are the regional and global consequences of local land management and conservation policy?”

For many regions of the U.S., the history of land use changes and fragmentation is a key to understanding current landscape patterns and predicting future changes. Agriculture has been responsible for some of the most extensive forest conversions. This type of change, in combination with settlement, occurred over most of the eastern U.S., and much of what we see now is regrowth of forest after agriculture was abandoned. Timber harvesting also occurred, and still occurs, in the eastern U.S., especially in the Southeast, and it is an extensive land use in the Northwest. Decoupled from agriculture and timber harvesting, especially during the last century, the conversion of forest to housing has increasingly become a prominent issue in many areas, especially in the more populated East and around growing metropolitan areas of the West. This is a more complicated land use, however, because densities vary greatly, the existence of trees not cut or planted varies, and actual use varies. In recent years, this process has also been complicated by increasing parcelization, the subdivision of privately owned lands into smaller parcels.

The purpose of this chapter is to document the history and pattern of forest transformation in the U.S., beginning with the arrival of European settlers in the early seventeenth century. We also discuss the effects of these changes on American forests, with specific discussions of forests in New England, the Great Lakes states, the Southeast, and the West, including the Pacific Northwest and the Rocky Mountains.
Historical Context of Deforestation and Forest Fragmentation in the United States

Within the current boundary of the United States, it is estimated that forests covered ca. 425 million ha (46% of the total land area) at the beginning of European settlement in the early 1600’s (Figure 5.1); as a result of forest clearing for agriculture, timber production, industrial uses and other human activities, this area had declined to an estimated 300 million ha by 1907 (Smith et al. 2001). By the 1930’s, the decline in U.S. forest area due to agricultural conversion had largely stopped as draft animals were replaced by combustion engine-driven machinery and farm productivity increased with the development of hybrid crops, fertilization, and other practices resulting from agricultural research (Frederick and Sedjo 1991). Smith et al. (2001) place the current amount of “forest land” (defined as “land … at least 10 percent stocked by forest trees of any size, including land that formerly had tree cover and that will be naturally or artificially regenerated”) around 300 million hectares (Table 5.1), although studies using more stringent definitions of forest area place the forested area within the U.S. closer to 210 million ha (e.g., Roberts 1998). Most estimates of the amount of virgin, uncut forest in the U.S. vary from around 2-20%, but less than 1% and perhaps as little as 0.05% remains of the original eastern forests, with the vast majority in stands < 100 ha (Alverson et al. 1994).

Spatio-temporal patterns of deforestation and forest conversion largely followed but sometimes preceded the pattern of settlement in the U.S., although the causes of forest loss and transformation varied geographically. Logging efforts began in New England in the seventeenth century. Following extraction of the most commercially valuable species (e.g., white pine), primary forests were often cut to provide firewood or cleared for agriculture and settlement. As many of the original forests were logged, wood resources became more scarce and had to be brought in from greater distances (Alverson et al. 1994). Thus, prior to 1850, lumber production
Figure 5.1. Map showing the amount of primary (uncut) forest in the continental United States in 1620. Figure from Greeley (1925).


<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Northeast</td>
<td>34594</td>
<td>34513</td>
<td>34119</td>
<td>33019</td>
<td>30984</td>
<td>29225</td>
<td>24119</td>
<td>47729</td>
</tr>
<tr>
<td>North Central</td>
<td>34334</td>
<td>32464</td>
<td>32325</td>
<td>34057</td>
<td>34094</td>
<td>35076</td>
<td>32011</td>
<td>72704</td>
</tr>
<tr>
<td>Southeast</td>
<td>35880</td>
<td>35837</td>
<td>36610</td>
<td>38340</td>
<td>37620</td>
<td>35252</td>
<td>37242</td>
<td>55531</td>
</tr>
<tr>
<td>South Central</td>
<td>50763</td>
<td>49610</td>
<td>51224</td>
<td>54099</td>
<td>53849</td>
<td>54315</td>
<td>58153</td>
<td>87736</td>
</tr>
<tr>
<td>Great Plains</td>
<td>1942</td>
<td>1712</td>
<td>1820</td>
<td>1938</td>
<td>2110</td>
<td>2497</td>
<td>2713</td>
<td>2416</td>
</tr>
<tr>
<td>Intermountain West</td>
<td>56028</td>
<td>54796</td>
<td>54098</td>
<td>54862</td>
<td>55179</td>
<td>56294</td>
<td>57428</td>
<td>60104</td>
</tr>
<tr>
<td>Alaska</td>
<td>51549</td>
<td>52223</td>
<td>52245</td>
<td>52245</td>
<td>52245</td>
<td>52245</td>
<td>52245</td>
<td>52245</td>
</tr>
<tr>
<td>Pacific Northwest</td>
<td>20887</td>
<td>20758</td>
<td>21445</td>
<td>21768</td>
<td>21905</td>
<td>22284</td>
<td>22662</td>
<td>22768</td>
</tr>
<tr>
<td>Pacific Southwest</td>
<td>16307</td>
<td>16644</td>
<td>17053</td>
<td>18018</td>
<td>18025</td>
<td>20299</td>
<td>20639</td>
<td>21841</td>
</tr>
</tbody>
</table>

1 Subregions:
Northeast: CT, DE, ME, MD, MA, NH, NJ, NY, PA, RI, VT, WV
North Central: IL, IN, IA, MI, MN, MO, OH, WI
Southeast: FL, GA, NC, SC, VA
South Central: AL, AR, KY, LA, MS, OK, TN, TX
Great Plains: KS, NE, ND, SD
Intermountain West: AZ, CO, ID, MT, NV, NM, UT, WY
Pacific Northwest: OR, WA
Pacific Southwest: CA, HI
(Fig. 5.2) and forest conversion for agriculture (Fig. 5.3) were most prominent in the Northeast and the eastern Lake States (Pennsylvania, Indiana, Ohio) (Williams 1989).

With increasing settlement in the Midwest and the overexploitation of northeastern forests, the pace of forest clearing for agriculture and timber production accelerated in the mid-1800’s and shifted the logging frontier into the North Woods of the Lake States (Michigan, Wisconsin, Minnesota) (Fig. 5.4). Fueled by the vast areas of virgin forest and ease of transport provided by the Great Lakes, logging in the Midwest began in earnest in the 1840’s and 1850’s and intensified from the 1870’s through the 1890’s, resulting in sweeping changes in forest communities (described below). By the end of the nineteenth century, logging had depleted many Midwestern forests, and settlement pressure had moved toward the Plains states. The greatest amount of clearing in forested states therefore shifted to the Southeast (Williams 1989) (Fig. 5.4). Many of these southern pinelands had already been cut once for agriculture, but logging accelerated in the 1880’s and 1890’s with the redirection of capital and technology from Northern forests. As a result, more than 36 million hectares of longleaf, shortleaf, loblolly and slash pine were cut over by 1920; only one-third, however, was restocked with saw timber, leaving extensive scrub woods and barrens and leading to a drop in lumber production (Alverson et al. 1994).

The decline in logging in the Lake States also shifted some attention to forests in the Pacific Northwest and Rocky Mountains. Forest conversion for agriculture in these areas has never been high because most lands were unsuitable for cultivation, and difficulties in transportation and access limited extraction of timber resources to lowland areas near good harbors (Alverson et al. 1994). Nonetheless, logging along the Pacific coast increased in the early 1900’s, and production rivaled that in the South beginning in the 1920’s and has remained
Figure 5.2. Lumber production in the United States, 1839-1849, 1859; value shown as percentage of total U.S. production. Figure adapted by Williams (1989).

Figure 5.3. Amount of land cleared by state (millions of acres) before 1850. Data from U.S. Census, adapted by Williams (1989).
Fig. 5.4 Lumber production in the U.S. by region and decade from the 1860’s through 1930’s. Data from USDA Agricultural Yearbook; figure adapted by Williams (1989).
high since. Timber harvesting and land conversion in the Rocky Mountains has remained comparatively lower, although logging also increased beginning in the early- to mid-1990’s with the implementation of new technologies.

Forests in New England: Past and Present

History

Before European settlement, New England was almost completely forested. Significant changes to the vegetation patterns were initiated by large and small-scale natural disturbances such as hurricanes, ice storms and climate change (Hill 1985). Native American populations also influenced the forested landscape by clearing small areas for agriculture and using fire to clear the understory to facilitate hunting. During the late 17\textsuperscript{th} century, European colonists began clearing forests for agricultural fields and cutting timber for building, fuel and other commercial needs. This process began what would become a 300-year process of ecosystem disturbance and environmental change that is unparalleled in scope and impact to that of other disturbances, such as wind, fire, and Native Americans (Fuller at al. 1997).

During the 18\textsuperscript{th} and 19\textsuperscript{th} centuries New England forests experienced increasing rates of deforestation. Forests were selectively logged for high demand and high valued tree species such as oak and white pine. The late 18\textsuperscript{th} century to mid 19\textsuperscript{th} century was a period of broad-scale agricultural development, when forests were clear-cut or burned to provide land for livestock and crops. It was during this period of agricultural intensification when forest cover was at its minimum (Foster 1992). At the beginning of the industrial revolution in the late 19\textsuperscript{th} century, New England moved away from an agricultural economy to an industrial and commercial economy, and agriculture became more economical and ecologically feasible in the midwestern
states. There was a corresponding abandonment of agricultural fields, which allowed for reforestation of much of New England. Throughout the 20\textsuperscript{th} century, the transition from firewood to heating oil and New England’s increased reliance on imports for lumber allowed for the reforestation of much of New England (Foster et al. 1997).

New England forests are still subject to less intensive (comparatively) deforestation and fragmentation due to logging, agriculture, and recreation, but the primary agents of change are now suburban and exurban development and road construction. Much of the New England landscape is now reforested, but due to the relatively short period for forest recovery (100-150 years), much of this forest is young second-growth forests and differs greatly from pre-European settlement forests (Foster et al 1997).

*Forest Structure and Composition*

Before widespread disturbances by European settlers, New England forests were characterized by older growth, large-stature forests. Old-growth northern hardwoods, hemlock, white pine, beech and sugar maple were prevalent. These forests exhibited regional vegetation patterns related to climate, physiography, natural disturbances and Native American populations. Forest vegetation patterns were strongly dictated by a broad climate gradient, and tree distribution was related to growing degree days (Bürgi et al. 2000).

European disturbances to New England forests included forest cutting, altering the fire regimes (burning to clear land, suppression of natural fire), agricultural activity, introduction of alien species, alterations in herbivore populations, urban development, atmospheric pollution, soil erosion, higher rates of vegetation change, and salvage logging. Impacts from these disturbances varied from region to region based on local land use regimes. It is important to note
how this broad-scale human disturbance differs from natural disturbances. Human disturbance has the ability to reach magnitudes and intensities larger than the most severe natural disturbances, and unlike the relative randomness of natural disturbances, human disturbance targets certain areas and may be relatively homogeneous across space (Cronon 1983).

Logging was not only nonrandom in terms of spatial pattern; certain tree species such as oak, hemlock and white pine were favored and selectively cut. Beech and sugar maple were clear-cut for agricultural land, as the presence of these species on land indicated good agricultural soils. The abandonment of agricultural lands by settlers was also selective, with the first fields to be abandoned generally being those on the steepest slopes. The composition of the reforestation of these lands was also selective, favoring pioneer species that could colonize and grow in open, grassy landscapes (Bürgi et al. 2000). Disturbance by European settlers thus disrupted existing relationships between biota and environment, initiating significant, long-term shifts in community composition and dynamics that selectively promoted species uncommon in the Colonial forest (e.g., Foster et al. 1997).

It is important to note that human disturbance to New England forests is not bound to physical disturbance of the forest. Disturbance in internal processes of the forest is and was common. Most modern New England forests have arisen from previously ploughed land or clear-cut land, thus forest soils lack the structure and properties of pre-agricultural forests. The broad impact of global warming and nitrogen deposition on New England forests due to industrialization has altered nutrient cycling and gas fluxes within these forests. It is also the case that these alterations in forest structure change the ways in which natural disturbances, hydrology, microclimates, biotic and abiotic environment affect them (Matlack 1997).
The forests of New England today are much different from the ones encountered by the Europeans centuries ago. The structure, composition and pattern of forest vegetation have been dynamic over the past three centuries in response to human and environmental disturbance. Most taxa that were abundant in pre-settlement times have changed in abundance and distribution, but species have responded in a highly individualistic fashion to disturbances (Foster et al. 1992). The forests are dominated by young second growth forests, due to the relatively short period (100-150 years) of reforestation after agricultural abandonment. Current low intensive selective cutting maintains a forest that is tall and contains trees of many ages. Tall and old forests (with species such as hemlocks) have only increased in the past 50 years as growth has exceeded forest cutting. Forests do not appear to be returning to conditions of the pre-settlement period despite the lower levels of disturbance. The youthfulness of these forests suggests impoverished understory species and most modern forests exist in fragments, allowing for little interior forest which decreases ecosystem diversity and stability (Matlack 1997). In general, the composition, structure and patterns of New England forests have shifted toward regional homogeneity.

The vegetation patterns of New England prior to European settlement had a close relationship with climatic variables; this relationship has decreased while the vegetation pattern’s relationship to regional and species-specific land use/human disturbance history has increased (Foster et al. 1997). Physiognomic classes of vegetation have not changed very much in the face of massive human disturbance, but species abundances have changed dramatically (Russell et al. 2001). The consequences of human disturbance, however, are scale dependent. Regionally, the distribution of pre-settlement and post-settlement forest types is similar, with a few structural changes and the loss of some tree species. At a landscape scale, modern forest characteristics are dictated by land use. This land use history has lead to a decrease in white pine, beech, sugar
maple, hemlock and northern hardwoods due to the 1938 Hurricane, selective logging, disease, and these species low tolerance to fire. Fire tolerant and successional, sprouting species such as oak, chestnut, birch and red maple have increased in abundance in New England forests (Foster et al. 1997). The continually dynamic nature of vegetation patterns in New England forests is a very important element to the post-European settlement landscape, as Foster (1992) noted:

“The effects (of land use) are long-lasting as they continue to control the way in which humans use sites and the ways in which natural processes affect them. The ramifications of this history in terms of contemporary ecological processes are too great to be dismissed by modern-day ecologists.” (p. 770)

Forests in the Great Lakes States: Past and Present

History

At the time of Euro-American settlement, forests throughout the Great Lakes states were fairly young, dating to the retreat of glaciers following the Wisconsin Glacial Epoch 10,000-14,000 years ago. As the ice retreated, existing southern forest populations moved northward as individual, separate populations. At this time, forest communities were short-lived and changed as the climate shifted and other species migrated into their particular area. Glacial landforms are recognized as a dominant factor in determining soils, topography, and subsequently, the potential natural vegetation in this region. Natural disturbances and stresses that have influenced the structure and composition of these forests historically and presently include wind (particularly catastrophic wind), fire, disease, insect infestation, and climatic fluctuations (Stearns 1997). Humans have subsequently been the cause of much disturbance in the Great Lakes forest. From the earliest American Indians, who intentionally burned forests for hunting and agricultural purposes, to the increasingly commercial utilization of forest resources and fire prevention in the last century and a half, humans have reshaped the forest landscape of the Great Lakes region.
Great Lakes forests currently cover about 20 million ha, compared to the 32.7 million ha present in pre-settlement times, and many continue to be support early successional forest types, dramatically altering patterns of vegetation diversity in many areas. Old growth forests make up about 5-8% of the forests today as compared to the 68% that they made up in pre-settlement times. Primary forests only make up about 1% as much as they did in pre-settlement times. The most extensive forest types in the Great Lakes States are secondary growth forests primarily consisting of oak-hickory and northern hardwood forests, but even these stands are highly fragmented due to the increase in urban and regional development (Frelich 1995). In general, Great Lakes forests have seen an increase in aspen/birch and non-forest upland land covers and a decrease in coniferous lowland, spruce-fir/other upland conifer, white/red pine, and northern hardwoods, jack pine and oak/other hardwoods.

Humans have altered the forest composition in the Great Lakes region and continue to do so today. The extent of this impact is realized through a significant decline in amount of forest cover, the transition in forest composition from northern hardwood and conifer types to early successional species (such as aspen), a shift toward younger stand age, and increased fragmentation due to urban and regional development. Future concerns for the Great Lakes forests include the ongoing effects of timber harvesting and forest fragmentation and of global climate change on the composition of forest species.

Forest structure and composition

Pre-settlement forests were diverse in species, from pines on sandy soils to hardwood and mixed hardwood conifers on the more fertile soils (till plains and moraines), to the swamp forests of cedar, spruce, and larch. Forests varied in age from young stands of aspen/birch, pine or maple
to older stands of pine, hemlock, or northern hardwoods ranging in age from 250-400 years. Pre-settlement forests were dominated in different periods and locations by jack, red/white pine, spruce-fir and aspen birch forests, barrens, and savannas. Long-lived species (hemlock-hardwood forests) were found on moraines and till plains. Forest composition on moraines and till plains was quite stable through time, aside from catastrophic blow downs.

The “Little Ice Age” was characterized by a cooler climate, which favored the development of massive stands of white pine and hemlock within the Great Lakes forests. Pre-settlement cycles of forest growth and disturbance were influenced by natural succession, wind, and fire. The dry, sandy soils on which pines are rooted promoted a forest type, which was extremely flammable and susceptible to intense fires at intervals of 20-150 years. Fire eliminated many of the competing hardwood forests when pine forest began to burn. This burning created the mineral seedbed required by the pine and allowed the few remaining trees which escaped the fire to restock the land. Fire frequency was very critical in determining the kinds and numbers of conifer species occurring in pine barrens (Cleland et.al 1995).

During the early 1800’s the United States was rapidly industrializing and much of the eastern forests had been logged to keep up with the growing population and increasing rates of consumption. White pine was considered the only tree species worth logging in quantity because it was light, strong and easily transported. By the 1840’s lumbermen in Pennsylvania, New York, and Maine found their supplies of white pine to be scarce so they looked westward to supply their ever-growing demand. It was also during this same period that major federal land purchases and various treaties involved the Great Lakes forests with the purpose of encouraging settlement and utilization of the Great Lakes forest resources. Many eastern lumber companies relocated to the Great Lakes where there was an ample supply of white pine. Logging in these forest has been
continual and can be characterized by four eras: the White Pine Era (1836-1890’s), the Hemlock-Hardwood era (1890’s-1920’), the Reforestation Era (1920’s-1950’s), and the Pulpwood Era (1950’s-present) (Whitney 1987).

White pine logging in the Midwest began around 1836 with selective logging to support explosive population growth in the Midwest. This era has been characterized as a “rapid and often wasteful exploitation of the forest resource” (Stearns 1997:8). Harvesting accelerated and continued for 50 years, progressing from small mills that produced a few hundred board feet per day to large mills that produced hundreds of thousands of board feet per day. This selective logging reached a peak around 1890, when all merchantable pine had been cut or destroyed by fire. Often cut-over land was converted to cropland or pastures, although agriculture was not sustainable on the sandy, unproductive soils that the pines left behind. (Whitney 1986).

By the 1890’s, the white pine supply in the Great Lakes region had been exhausted, and white pine blister rust had infected many of the remaining white pines in the region, killing many individuals and discouraging the replanting of this particular tree species. Logging in the 1890’s thus saw a transition from pine to hemlock and hardwood species. Specific species that were targeted for logging were maple, birch, ash, basswood, elm, conifers, hemlock, cedar and fir. Hemlock bark was a major source of tannin for leather industry, making it an economically profitable substitution for the white pine. During the Hemlock-Hardwood Era, clear cutting was the most common harvesting method, utilizing most small trees and some of the slash, leaving few standing trees. Fires were ignited in the dry slash, consuming surface debris and resulting in “stump pastures” that were often used for farming (Whitney 1987).

By 1920, logging had removed most of the merchantable pine, hemlock and smaller hardwoods in the Great Lakes forests. This logging history permanently changed the species
composition of the pine, hemlock and hardwood forests. For example, the drying of exposed soil eliminated the seedlings and saplings of more sensitive species such as hemlock. The widespread logging disturbance favored the more aggressive, sprouting and wind-dispersed sugar maple as opposed to the less mobile, animal dispersed beech. Old growth forests of hemlock, beech and sugar maple were converted to second growth forests of sugar maple. Fires also frequently followed logging in quick succession, thus supplying favorable conditions for the easily sprouting trees such as the oak and maple and not so favorable conditions for the seed producers such as the white pine. Fires also prompted the spread of pioneer species such as aspen, white birch, and cherry and helped maintain the more fire dependent jack pine. Land economic survey reports of the 1920’s likewise emphasized the conversion of pinelands to large expanses of sweet fern and open stands of aspen suckers, scruffy oak and red maple (Whitney 1986).

The Great Depression was the major catalyst for reforestation through federally funded programs, including the Works Progress Administration and Civilian Conservation Corps, which developed a large number of forest nurseries. The Weeks Act of 1911 authorized the purchase of private lands east of the Great Plains to be turned into national forests, and the Clark/McNary Act of 1924 increased the purchases of forests and increased federal-state cooperation on issues such as reforestation and fire control. These acts were a move toward the protection rather than exploitation of forest resources. Throughout this era, the incidence of fires and total acres of forests burned decreased and reforestation expanded dramatically.

The decrease in fire frequency during the Reforestation Era provided time for the re-growth of many forests, increasing the density and sizes of forests over the last 50 years. Many stands of forests are 40-60 years old due to effective implementation of fire control programs. Since 1950’s the formerly worthless stands of aspen and jack pine have become economically
valuable resources as inputs for pulpwood (paper, fiberboard and wafer board.). These forests are managed or clear-cut on a 30-60 year rotation cycle. In recent years, the low fire frequency in the jack pine and aspen forest has prompted concern about the difficulty of maintaining these short-lived shade-intolerant species (Whitney 1986). Fire suppression has had a large impact on the patterns of fires in the Great Lakes forests. Some researchers warn that without the reintroduction of fire, “…major unnatural, perhaps unprecedented changes in the ecosystem could occur…continuing fire control may allow spruce and fir to replace broadleaf species in the area” (Cleland et al. 1995:3).

Southeastern Forests: Past and Present

History

Reconstructions from pollen data have provided a general picture of vegetation changes in the southeastern United States over the last 40,000 years. Delcourt and Delcourt (1981) identified a mixed hardwoods deciduous forest type along major southern rivers, a mixture of jack pine and spruce in the northern Coastal Plain, and a broad band of communities typical of contemporary Coastal Plain forest types extending across the eastern sections into Texas about 40,000 years ago. During the last major glacial extension, c. 18,000 years ago, a zonation of boreal, northern deciduous/pine and southern deciduous/pine forest types similar to that in North America today was compacted below the Laurentide Ice Sheet. Boreal or northern hardwood species dominated in the north (spruce taxa dominated the floodplains and northern hardwood taxa, e.g., _Acer saccharum_ and _Fagus grandifolia_, dominated the uplands) while most of the vascular plant constituents of the mixed mesophytic forest association (_sensu_ Braun 1950) could be found in river bluff habitats throughout the southeast (Christensen 1988, Greller 1988).
Climate became warmer and drier beginning around 12,500 BP, resulting in widespread extinction of boreal elements in the South and the onset of human occupation (Christensen 1988). During the height of this period, the Hypsithermal (8,700 – 5,000 BP), mesophytic species retreated to bottomlands and protected coves while oak, hickory, and herbaceous species dominated uplands. Following the Hypsithermal, the climate became cooler and more moist, initiating a period of paludification and bog formation along the Atlantic Coastal Plain. Southern pine and oak species migrated north and invaded prairie and open forest, although plant migration and establishment were sometimes delayed by Native American disturbances such as annual burning and swidden agriculture (Pyne 1982). Natural disturbance regimes consisted of essentially the same factors active at the time of Euro-American settlement, including wind (tornados and hurricanes), insect outbreaks (e.g., southern pine beetle) and fire. Around 500 BP, a decentralization of the Mississippian culture into small agricultural villages took place. Native American Indian settlements cleared small patches of forest, 8-80 ha in size, and there are numerous records of anthropogenic fires (Greller 1988). In fact, it is difficult to separate the natural and anthropogenic fire regimes prior to European settlement. While many fires may have been localized, several were described as widespread. Thus, fire was likely a prominent landscape-level factor shaping pine forests in the South, especially in areas with longleaf (Pinus palustris) and slash (P. elliotii) pine. In the oak forests, however, fires were perhaps more local and their incidence driven by Native American uses.

Prior to Euro-American settlement, the vast swamplands and floodplains of the South covered approximately 15% of the total area, and vegetation dynamics were largely controlled by flooding regimes. Geomorphic processes (e.g., development of sandbars) and a dynamic hydrology produced a diverse array of environments within a small range of elevation (< 1 m,
Robertson et al. 1978). The inundation regime includes the amount of time soils are saturated, water quality, and water velocity, all of which affect the vegetation composition. While fires were infrequent in floodplain settings, catastrophic fires did occur periodically during major droughts, exerting some control on floodplain vegetation patterns.

The most significant disturbances following European settlement included deforestation for agriculture, timber operations, suppression of fire, and alterations to the hydrologic regime of floodplains. Significant settlement of the Southeast began in the 1700s along the Atlantic coastline, with settlement of inland areas not occurring until the latter part of that century. Early timbering was restricted to areas along the coastlines and along larger rivers where navigation was possible and transfer of logs easier. These early forestry operations were mainly on pinelands dominated by longleaf, shortleaf (*P. echinata*), loblolly (*P. taeda*) and slash pine. Forestry was the fastest growing trade in the South following the Civil War, and several other industries developed in response to the resources provided by forests, including terpentine, tanning, ship building, shingles, iron industry (wood used to make charcoal) and whiskey. At the start of widespread logging operations in the 1870’s, Sargeant (1886) reported a total of 237 billion board feet of pine timber in the Southern states, three times that of the Lake States. Predictions of the vast resource ranged from pine supplies lasting 300 years in Arkansas to 30 years in Florida.

As has been previously discussed, increased exploitation of southern forests occurred as the productivity of northern forests declined. Tens of millions of acres of “swampland” around the Gulf were sold for twenty-five cents per acre, with nearly 69% of the 3.7 million acres of land sold in lots > 5000 acres purchased by northern timber companies. Between 1880 and 1920, production of lumber increased nearly tenfold, with an estimated 90 million acres cut during this
period. Increased rail lines, nearly 39,000 miles of track in the 13 southernmost states by 1910, rendered another means to move wood and another avenue of accessibility to southern lands; areas within five to eight miles of the railroad were cleared. After the boom of the timber industry in 1914, predicted timber supplies dropped below 30 years.

Because forests were a valuable commodity, fire was seen as a negative factor consuming or damaging valuable board feet, especially in deciduous forest. Suppression policies were implemented in the early 1920s to keep fire out of forests prior to harvesting. Two-large-scale successional patterns have emerged from fire suppression. First, because pines are shade intolerant and can not regenerate under their own canopy, most pine forests succeed to oak without the periodic disturbance. Second, while more tolerant of shade than pine, most oaks also have difficulty regenerating under a closed canopy, which is likely quite different from the more open canopy forests described in the historical literature. Thus, many oak forests of the Central Hardwoods are succeeding to various mesophytic species, including sugar maple (Acer saccharum), beech (Fagus grandifolia), and red maple (Acer rubrum). Prescribed fires are currently being used by the timber industry to maintain pinelands and by natural area managers to maintain oak forest and savanna-like pine forest (e.g., longleaf pine).

Agricultural and logging practices, especially prior to the dust bowl (1930s), also often led to extensive erosion with concomitant problems of deposition in streams. For example, it has been estimated that every section of the Piedmont, has lost 25% or more of its topsoil in the last century (Walker 1999). The problems were exacerbated by the compaction of soil with large machinery, which decreased the infiltration and percolation of water into and through the soil. Thus, water was forced to flow over the soil surface (overland flow), causing greater erosion. The legacies of severe soil erosion, which sometimes exceeded 50 tons ha$^{-1}$ yr$^{-1}$, dating to this
period are still reflected in vegetation patterns in some areas of the South (e.g., Kupfer and Franklin 2000).

Forest clearing for logging and agriculture were not limited to upland areas, however. While the vast floodplains and swamplands of the South at first proved difficult for timber extraction, these difficulties were soon overcome. Virgin timber throughout large areas of the Coastal Plains was cut between the 1920s and 1950s (Walker 1999), and second bottoms were put into production of soybeans and cotton. Such agricultural development required the construction of artificial levees to control flooding, as well as channelization of waterways to speed the flow of stormwater off the land. Indeed, fear of swamps (due to diseases such as yellow fever) and want of wood products and more agricultural land led many government agencies to straighten, deepen, widen and levee all or portions of many waterways in the southeast (Simon and Hupp 1992, Shankman 1996). Among other things, these channel modifications were made to accelerate storm water drainage, to increase overbank flood stage, to protect agricultural land from flooding and to lower the water table in bottomland areas, thereby increasing the amount of acreage suitable for cultivation. Timber harvesting also benefited from these hydrological modifications. Bald cypress (*Taxodium distichum*) was cut out of deep swamps that were drained or floated out via canals. Removal of cypress peaked at 1 billions board feet per annum from 1905 to 1913, and then declined as supplies were exhausted. By the 1950s, the bald cypress swamps of the south were nearly gone.

The effects of these human activities on fragmenting Southeastern forests are notable. A recent study integrating remote sensing and U.S. Forest Service data collected periodically at over 26,000 forest locations across the Southeastern U.S. showed that the median (ha) size of forest stands in the mid-1980's was < 20 ha in Virginia, North Carolina, South Carolina and
Georgia, and only slightly higher in Florida (32) (Pye and Sheffield 1992). Remeasurements in
the early 1990’s showed significantly reduced median stand sizes for SC (14) and FL (26) and
for the three principal hardwood types region-wide. Rudis (1995) focused more explicitly on
fragmentation of southern bottomland hardwood habitat and developed two regional-scale
hypotheses: (1) forest fragmentation occurs more frequently in drier habitats and dry zone
(inundated ≤ 2 months annually), younger seral stage bottomland community types; and (2)
forest fragmentation induces establishment of drier habitats or dry zone, younger seral stage
community types. His results led him to suggest that regional forest fragmentation impacts
survival of distinct community types, anthropogenic uses, and multiple resource values.

Forest Structure and Composition

The southeastern forests consist of the Central Hardwoods, Appalachian Mountains, and
Coastal Plain Provinces. In general, distributions of tree species in the east are unchanged from
pre-colonial times (Greller 1988), although the size of trees was much larger in the past (e.g.,
various sources suggest deciduous trees often reaching 2 m in diameter). The Central Hardwood
Forest has a gradient from north to south in growing season length (3-5 months in the north to 6
months in the south) and snow cover. The forests consist of broadleaf deciduous trees, needleleaf
evergreen trees, and various mixtures of the two. Deciduous forests dominate this region, but
extensive clearing for agriculture, grazing, and logging have reduced, modified and fragmented
the original vegetation.

With nearly 2000m of relief in some areas, the Appalachian Mountains provide
significant gradients in precipitation and temperature that act to structure vegetation communities
(e.g., Whittaker 1956). The vegetation of the mountains includes mixed hardwood and Tsuga
canadensis stands in cool coves, Acer saccharum and Quercus rubra on cooler northern-facing slopes, Quercus alba and Q. velutina on somewhat drier sites, Q. prinus and Q. coccinea on even drier sites, and Pinus echinata and Pinus virginiana on the driest sites. At the highest elevations, Abies fraserii and Picea rubens dominate, although the former has been decimated by an introduced insect pest, the balsam woolly adelgid. Several of the Quercus spp. have developed stands following the demise of the American chestnut (Castanea dentata). Many forests, even in the area currently occupied by Great Smoky Mountains National Park, were severely cut, and some severely burned during the 1800s and early 1900’s (e.g., Pyle 1985).

High humidity and the absence of exceedingly cold winters characterize the southern pine–hardwood forest throughout the southern Atlantic and Gulf Coastal states. Soils are older and strongly leached Ultisols. These soils are quite poor of most essential nutrients. There are seven major Pinus spp. (P. echinata, P. taeda, P. virginiana, P. rigida, P. palustris, P. clausa). While inland areas have deciduous forest species (especially Quercus spp.), Pinus palustris, Pinus taeda, and Pinus elliotii typically dominate coastal areas. Prescribed fires are necessary to suppress the succession from pine to oak, as Quercus species are generally more shade tolerant than the Pinus spp.

While bottomland hardwoods are not a particular physiographic section, the bottomland forests of the eastern United States, generally restricted to the Coastal Plain province, are both economically and ecologically important. The bottomland hardwood forests consist primarily of flood plains adjacent to rivers and streams, but also include poorly drained areas. There are a large number of species found in this system. Within the bottoms, due to the past meandering of the main channel and its tributaries, occur secondary site types due to micro and meso-topography: ridges, flats, sloughs, and swamps. The wetlands have long acted like a buffer,
mitigating the effects of upland activities (e.g., fire and cutting) on adjacent river and stream systems by catching nutrients and eroding sediments (Sharitz and Mitsch 1993). However, many of these forests have been converted to farmland.

The amount of forested land is actually greater now in the east than during the timber boom of the early 20th century. However, the pattern of forest on the landscape has been drastically altered. Windthrow, fire, and flooding controlled the local distribution of historical landscapes and processes. Several authors described historical forests as being more open with widely spaced trees and greater density of understory flora. Perhaps the combination of periodic fire and large herbivores, since extirpated, maintained such a landscape. Whatever the controlling forces, several questions need to be answered. How fragmented was the historical landscape? How do you delineate an edge in a more open forest structure? Have changes in landscape structure altered landscape ecosystem functions, such as propagule dispersal?

It is now thought that fire-sustained forests of the southeastern U.S. were more fragmented historically, with closed forests dominating along streams and more open forest grasslands dominating uplands. Following a decrease in fire occurrence, uplands succeed to more closed forest, then cutover, and are now reforested again. The landscape is more homogeneous in physiognomy and composition, and this increased proximity of contemporary forests may be implicated for more widespread pathogen outbreaks. Franklin (1994) suggested that the suppression of fire and transformation of floodplains to agriculture has resulted in a switch in the topographic location of forest. Alternatively, Duncan and Schmalzer (2003) provide a good case study on how fragmentation alters the fire disturbance regime in the scrublands of eastern Florida. Anthropogenic activities that essentially developed fire breaks have reduced the spread of fire by 40%, thus reducing suitable habitat for fire-maintained taxa. The take-home message
from these studies is that landscape heterogeneity is an important structural feature affecting other ecosystem properties. Indeed, at a recent symposium on fragmentation held at the 2003 Meeting of the Association of Southeastern Biologists, Glenn Matlack, summarized from his work that the most severe impacts of fragmentation in coastal plain forest seem to involve alteration in the flow of landscape-integrating, spatially extensive processes such as the spread of a pathogens or fire. Thus, ‘flow’ (dispersal, movement) is perhaps the most important component for studying fragmentation effects, and perhaps where studies need to be concentrated to understand historical changes.

Forests in the Pacific Northwest and Rocky Mountains: Past and Present

*History*

In the last two decades, a substantial amount of work throughout the western United States has focused on reconstructing Holocene vegetation patterns and natural disturbance regimes, both of which reflect the influence of variations in the large-scale controls of climate (*see Whitlock et al. 2003 for an excellent overview of this literature*). Among these controls are millennial-scale variations in the seasonal cycle of incoming solar radiation and the size and position of the Laurentide and Cordilleran ice sheets, which affected regional climates directly, through changes in temperature and net radiation (Whitlock and Bartlein 1997), and indirectly, by altering atmospheric circulation (e.g., the strength and position of the jet stream and thus winter storm tracks; Thompson et al. 1993; Bartlein et al. 1998). Generally speaking, the lateglacial period was a time of biotic reorganization in the northwestern U.S., as the influence of large ice sheets on climate was waning and summer solar radiation was increasing (Whitlock 1992). In areas of the Cascades and the Rockies that had been glaciated, plant taxa colonized
regions vacated by the glaciers, creating new pioneer communities. Regions outside the glacial limits were also undergoing rapid change, and in some cases, the vegetation combined present-day subalpine and lowland taxa in assemblages that have no modern counterpart (e.g., Whitlock 1992, 1993). As climate continued to warm, species distributions became arranged along gradients of latitude and elevation.

While the importance of fire in most contemporary western ecosystems is widely recognized, its role in maintaining and altering forest vegetation is also evident in the paleoecological record. When synthesized across the entire northwestern U.S., past fire regimes were strongly controlled by climate and vegetation changes occurring on multiple time scales. For example, long-term reconstructions of Holocene fire regimes based on analyses of charcoal, pollen, and other fire proxies in a network of lake records indicate that the Pacific Northwest and summer-dry regions of the northern Rocky Mountains experienced their highest fire activity in the early Holocene (11,000–7000 years ago) and during the Medieval Warm Period (ca. 1000 years ago) when drought conditions were more severe than today. In contrast, in summer-wet areas of the northern Rocky Mountains, the period of highest fire activity was registered in the last 7000 years when dry woodland vegetation developed (Whitlock et al. 2003).

At the time of Euro-American settlement, fire was the primary disturbance affecting forests in the Pacific Northwest west of the Cascade crest (e.g., Agee 1993), although windstorms (in the form of both catastrophic events and smaller chronic disturbances) and, to a lesser degree, pathogens also initiated and shaped forest development (Halpern and Spies 1995). Research using a range of techniques (e.g., dendrochronology, charcoal analysis) has focused on documenting fire regimes of forests in the Pacific Northwest and indicates that fire intervals ranged from <50 years along the crest of the Coast Range in southern Oregon and in coast
redwood stands in northern California to as much as 750 years in moist, coastal forests in the northern Oregon Coast Range, the Olympics, and the Washington Cascades (Morrison and Swanson 1990; Swetnam 1993; Agee 1993; Halpern and Spies 1995; Long et al. 1998; see Appendix 4.1 in Alaback et al. 2003 for a summary of dendrochronological fire history studies in the western U.S. and Canada). Forests generally included diverse mixtures of conifers of different age and size classes, with each class occurring in large patches (Ripple et al. 1991; Ripple 1994; Spies et al. 1994).

The eastern slopes of the Cascades lie in the mountains’ rain shadow and are much drier. Wildfire, periodic droughts, and insects and pathogens (e.g., western spruce budworm, mountain pine beetle, spruce beetle) interacted to influence forest structure, composition and spatial pattern (Mutch et al. 1993; Agee 1994; Lehmkuhl et al. 1994). Frequent (< 20 years) low-intensity fires helped to maintain xerophytic, parklike stands of ponderosa pine, western larch and lodgepole pine with grassy understories. The typical landscape pattern in these areas was thus a fine-scale mosaic of stands of varying ages and stages of development, with young stands resulting from infrequent, stand-replacing fires occurring at intervals of 100-300 years (Smith et al. 2001).

Disturbance regimes in the Rockies generally show patterns similar to those in the Pacific Northwest, with fire (often in conjunction with insect infestations) as the dominant natural disturbance influencing forest structure and composition (Peet 1988). Dominant fire type and return interval differ between subalpine and montane forest zones in the Rockies (Romme and Knight 1981). In the subalpine zone, the continuous fuels characteristic of dense Engelmann spruce, subalpine fir and lodepole pine forests generally favored large stand-replacing fires sometimes exceeding 10,000 ha, with intervals often greater than 100 years (Arno 1980; Kipfmueller and Baker 2000; Kipfmueller and Kupfer, in press). In contrast, most fires in the
lower elevation montane zone dominated by ponderosa pine were surface fires carried mainly through grass fuels (Veblen 2000), although stand-replacing fires have been documented for the prehistoric landscape in some areas (e.g., Shinneman and Baker 1997). Recurrence intervals for these fires is generally shorter than for those in the subalpine zone (e.g., Romme and Knight 1981; Peet 1988). Superimposed upon and often interacting with the natural fire regime were insect outbreaks recurring at intervals from 50-300 years (Veblen 2000).

While western forests have been affected to varying degrees by many of the same human disturbances as forests in other regions (e.g., urbanization, introduction of exotic species), the two most significant effects of Euro-American settlement have been alterations in the fire regime and forest habitat loss and fragmentation by timber harvesting. After depletion of forests in the upper Midwest in the late 1800’s, logging efforts shifted not only to the Southeast but also to forests in the Pacific Northwest and Rocky Mountains. At roughly the same time, public sentiment had grown to protect some remaining forested areas as national parks or forests, particularly in areas of the western U.S. As policies to retain western forests on public lands became clearer, large timber companies moved to purchase remaining private lands (Alverson et al. 1994). The history and consequences of timber harvesting and reforestation on such private industrial forests (and indeed on many National Forests in the western United States) span a gradient related to technology available at the time of logging and specific strategies and practices implemented for timber cutting and removal (Rajala 1998). However, within less than a century, the natural disturbance regime characterized by wildfire, windstorms and insect outbreaks with varying size, frequency and intensity was largely replaced by short-rotation, even-aged management of forest stands using clear cuts and prescribed burning, disturbances that are more frequent and less variable in size and intensity (Halpern and Spies 1995).
Much of the pattern in today’s coastal and western Cascades forested landscape reflects 40-50 years of harvest with the “staggered setting” approach, in which units of 15 ha or more were dispersed in space and time to produce a mosaic of even-aged, structurally-uniform stands (Franklin and Forman 1987). Logging slash was typically broadcast burned to reduce fuel loadings and control competition from surviving understory plants, with subsequent management activities (e.g., the application of herbicides or fertilizers) further altering natural rates and patterns of stand development (Halpern and Speis 1995). Reforestation was initially left to reseeding from adjacent stands or, more recently, by replanting, often with only one or a few species (e.g., Douglas-fir). The effects of decades of such timber management on patterns of forests in the Pacific Northwest are now clear and have been discussed in greater detail elsewhere (e.g., Spies and Franklin 1988, 1991; Morrison and Swanson 1990; Noss 1994; Ripple 1994; Spies et al. 1994). However, in general, the distribution and viability of some wildlife and plant species may be adversely affected by forest habitat loss and fragmentation (Harris 1984; Lehmkuhl and Ruggiero 1991), and for species that depend on habitat characteristics that are unique to old-growth forests, a patchwork of small, disjunct stands of old-growth may not be equivalent to one solid patch of equal area (Smith et al. 2001).

On the east side of the Cascade crest and in the Rockies, a long history of selective harvesting of mature pines and larches, intensive grazing, fire suppression, and later clear cutting has also greatly altered this forest landscape. On the east side of the Cascades, 74% of the commercial forest was classified as ponderosa pine timber sixty years ago, much of which was old growth (Cowlin et al. 1942). This value has decreased greatly. For example, recent estimates suggest that 92%-98% of the old-growth ponderosa pine that once existed in the Deschutes, Fremont, and Winema National Forests has been logged or lost (Henjum et al. 1994). Similarly,
due to a mix of natural and anthropogenic disturbances, more than 60% of forests in National Forest lands in Colorado and Wyoming have stand origination dates since the 1860’s, with an even higher percentage for low- to mid-elevation forests dominated by ponderosa pine, lodgepole pine and aspen (Smith 2000).

The suppression of low-intensity fires and selective harvesting of large, old trees have generally homogenized forested landscapes east of the Cascade crest, especially in mid-elevation mixed-conifer forests that are now frequently overstocked with second-growth pines and shade tolerant firs (Lehmkuhl et al. 1994; Mason and Wickman 1994). Unnaturally large, adjoining areas of densely stocked and stressed trees provide an increased food base for defoliating insects (Mason and Wickman 1988; Gast et al. 1991; Hessburg et al. 1994) and are more favorable to the growth of parasitic plants (Zimmerman and Laven 1984; Gast et al. 1991) and fungal pathogens (Filip and Schmitt 1990).

Perhaps just as significant as the actual changes in forest cover due to logging that perforate or fragment forested landscapes in the Northwest are the effects of the dense network of roads that accompany logging activities, including their role in dissecting forest patches and the creation of associated edge effects. Baker and Knight (2000) and Reed et al. (1996) provide examples of the commonness of roads (Table 5.2) and edge effects (Fig. 5.5) even in National Forests for southern Rocky Mountain landscapes, but the problem is pervasive throughout the western U.S.

Forest Structure and Composition

Cool, wet winters and warm, dry summers in the Pacific Northwest result in a landscape dominated by large conifers, with forest structure and composition varying along gradients of
Table 5.2. Roads in forested parts of Region 2 of the U.S. Forest Service (Colorado, Wyoming, South Dakota as of 1997. Data are from the U.S. Forest Service R2TF database, and densities are for the entire forest, including roadless areas. Table from Baker and Knight (2000).

<table>
<thead>
<tr>
<th>Forest</th>
<th>Length</th>
<th>Road density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>km</td>
<td>km/km²</td>
</tr>
<tr>
<td>Shoshone</td>
<td>2,581</td>
<td>0.26</td>
</tr>
<tr>
<td>Pike–San Isabel</td>
<td>3,956</td>
<td>0.44</td>
</tr>
<tr>
<td>White River</td>
<td>3,541</td>
<td>0.45</td>
</tr>
<tr>
<td>Grand Mesa, Uncompahgre,</td>
<td>5,607</td>
<td>0.47</td>
</tr>
<tr>
<td>Gunnison</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arapaho-Roosevelt</td>
<td>3,681</td>
<td>0.50</td>
</tr>
<tr>
<td>Rio Grande–San Juan</td>
<td>8,288</td>
<td>0.55</td>
</tr>
<tr>
<td>Bighorn</td>
<td>2,606</td>
<td>0.58</td>
</tr>
<tr>
<td>Routt–Medicine Bow</td>
<td>7,190</td>
<td>0.80</td>
</tr>
<tr>
<td>Black Hills</td>
<td>7,435</td>
<td>1.47</td>
</tr>
<tr>
<td>Total</td>
<td>44,885</td>
<td>90.84</td>
</tr>
</tbody>
</table>

Fig. 5.5. The percentage of the landscape in the Tie Camp area on the Medicine Bow National Forest occupied by clearcuts, roads and edge habitat (with varying depths of edge influence). The percentage of loggable area is defined as the percentage of area suitable for logging that is occupied by clearcuts, roads and edge habitat. From Baker and Knight (2000).
climate, soils, topography and disturbance regime. West of the Cascades, temperatures remain consistently mild throughout the year in most of this region (as a function of maritime proximity), and precipitation and humidity are high. Where the summer drought becomes more severe in northern California, fog helps to reduce moisture stress. At higher latitudes, the summer dry season is shorter, and the proportion of precipitation falling as snow increases (U.S. Forest Service Ecoregion Provinces: www.fs.fed.us/colormap/ecoreg1_provinces.conf?80,81).

Dense, mesic forests in the Coast Range and on the west slope of the Cascades are composed of various combinations of Douglas-fir, western hemlock, western red cedar, grand fir, silver fir, Sitka spruce and Alaska-cedar, although the Klamath Mountains ecoregion supports a mixture of drought-resistant conifers and hardwoods due to its lower precipitation and a complex geological and ecological history (Smith et al 2001). The Douglas-fir dominated forests that comprise much of the low- to middle-elevation area west of the Cascades appear to be the result of long fire intervals punctuated by catastrophic fires (Franklin and Dyrness 1973; Spies and Franklin 1988; Long et al. 1998), although periodic, low-intensity surface fires were also common in places (Teensma 1987; Morrison and Swanson 1990). Higher elevations in the Cascades have a well-marked subalpine forest belt with mountain hemlock, subalpine fir, whitebark pine, and Alaska-Cedar that reaches into British Columbia (U.S. Forest Service Ecoregion Provinces; www.fs.fed.us/colormap/ecoreg1_provinces.conf?80,81). Oak woodlands, grasslands, herb-dominated wetlands and riparian forests with species such as black cottonwood and red alder replace the conifers that dominate the region in lowland river valleys of western Oregon and Washington. Increasing aridity and temperature variability east of the Cascade Range result in frequent fires that promote open, parklike stands of ponderosa pine, lodgepole
pine, and western larch in montane areas and juniper woodlands, sagebrush-steppe, and grasslands at lower elevations.

Vegetation patterns in the Rocky Mountains can similarly be explained as a function of complex interactions among gradients in temperature, precipitation, solar radiation, wind, soils, and hydrology. Forest community types vary with latitude, elevation, aspect and exposure and have been described by a number of authors (e.g., Alexander 1985; Peet 1988; Stohlgren 2001). The most common forest types include: 1) low-elevation pinyon-juniper communities, 2) ponderosa pine woodland and forest (occasionally with a significant oak component), which occupies much of the montane zone, especially in the southern and central Rockies, 3) mixed conifer forest dominated by Douglas-fir, often in mixed stands with ponderosa pine, blue spruce, or lodgepole pine, which generally occurs from near lower treeline upward in elevation to spruce-fir forests, 4) higher elevation subalpine spruce-fir forests, characterized by Engelmann spruce and subalpine fir, 5) seral lodgepole pine forests that dominate in even-aged stands following stand-replacing forests, especially in the central and north-central Rockies, 6) subalpine white pine forests on dry slopes at high elevations that include whitebark pine (northern Rockies), limber pine (central and north-central Rockies) and bristlecone pine (southern Rockies), and 7) Cascadian forest that grows on the mesic west slopes of the northern Rockies and is floristically and structurally similar to forests in the Cascades.

Due to conflicts among groups representing a range of different interests, preservation of old-growth forests has been a major issue in western forests over the last two decades. For example, forests in the Pacific Northwest contain some of the largest and oldest trees in the U.S. and harbor many endemic species. There is substantial evidence that habitat degradation and loss of structural diversity in forest plantations results in a lower diversity of certain taxa (e.g., Norse
1990; Ruggiero et al. 1991; Noss 1994), although there is a range of factors that affect the degree
to which such changes are evident and how long such differences may persist (Halpern and Spies
1995). In addition to forest losses on private lands beginning in the mid- to late-1800’s, the area
of old-growth forests on all forms of land ownership in Washington, Oregon, and California has
declined by > 50% since the 1930’s and 1940’s (Bolsinger and Waddel 1993). Scientists estimate
that only about 17% of the old-growth Douglas-fir forests that existed in the early 1800's
remained in 1988 (Spies and Franklin 1988; Marcot et al. 1991) and that 96% of the original
coastal rain forests in Oregon and 75% in Washington had been logged by 1988 (Kellogg 1992).

Because of their status, federal lands are often viewed as key areas for the protection of
old-growth forests in the Pacific Northwest. About 51% (2.38 million ha) of the federal lands in
western Oregon and Washington currently support older forests (average tree diameter > 51 cm;
Forest Ecosystem Management Assessment Team 1993), and about 56% (1.3 million ha) of
these older stands (28% of total forest cover on federal lands) is classified as old-growth
(Bolsinger and Waddell 1993). However, the lands protected as Wilderness or National Parks
occur mostly at higher altitudes, in contrast to the patterns of plant and animal diversity, which
decline with elevation (Harris 1984; Alverson et al. 1994). Further, declines in old growth on
National Forests, which began with timber harvesting in earnest after World War II (Williams
1989; Alverson et al. 1994), accelerated beginning in the 1970’s. For example, Spies et al. (1994)
noted that 13% of coniferous stands on the Willamette National Forest, most of which were
natural stands with dominant trees > 150 years old, were clear-cut between 1972 and 1988 alone.

Given the pressures on lands surrounding and even containing old-growth forests in the
Pacific Northwest, the consequences of deforestation and forest fragmentation continue to be a
major issue in this region. Morrison (1988) estimated that 37% of the old growth in the national
forests of western Oregon and Washington occurs in fragmented landscapes (that is, stands < 162 ha surrounded by clear cuts, young plantations, or nonforested habitats). Today's forests are thus composed primarily of patches of older stands with much larger trees (average diameter greater > 102 cm, height > 70 m) intermixed with stands < 50 years old with small trees (average diameter at breast height < 51 cm) (Smith et al.). Road networks in some areas are also dense, and the proportion of the landscape occupied by old-growth coniferous forest beyond the influence of edge effects has continued to decline.

Summary

While contemporary patterns of species and forest ecosystems are clearly structured by abiotic conditions, they may also reflect the legacy of past land uses and disturbance history. In this chapter, we have tried to provide a historic perspective on natural and anthropogenic disturbance regimes in the United States, emphasizing the geographic progression of human settlement and logging effects and some corresponding effects on forest communities. In the next chapter, we examine recent efforts at quantifying regional and patterns of forest fragmentation in the United States.
Chapter 6: National Assessments of Forest Fragmentation Pattern

National and regional estimates of forest cover and its change through time have been produced using a range of tools, including General Land Office records, air photos, and satellite imagery (e.g., Greeley 1925; Loveland et al. 1999; USDA Forest Service 2002). Most of these surveys have documented changes in forest extent but few have addressed the concurrent changes in spatial configuration (i.e., fragmentation). Riitters (2003) notes that despite correlations with the amount of forest, fragmentation is a separate property of forest spatial distribution in the sense that it cannot be predicted by knowing only the amount of forest. He thus promotes the value of quantitative indices of fragmentation above and beyond those related to forest area and encourages the documentation of levels of fragmentation in much the same way that previous work has focused on changes in forest area.

In this chapter, we address the development of national forest fragmentation assessments by: (1) providing a brief overview of several national and international datasets that either have been or could be used in broad-scale fragmentation analyses, (2) summarizing the results of several initial assessments of fragmentation pattern conducted at the national level, and (3) discussing future directions for some of the ongoing efforts at mapping and analyzing patterns of fragmentation within the United States.

National Datasets for Assessing Forest Fragmentation

Numerous studies have examined patterns of forest fragmentation on relatively small scales (e.g., watershed, management unit) using remotely sensed imagery and analysis tools such as Fragstats. From a management and policy perspective, there is also interest in developing
national and international measures and methods that can be used to both map and monitor forest habitat loss and fragmentation (e.g., Heinz Center 2002). Such an undertaking at a national scale requires continuous and consistent data on land use and land cover and on any other features that act to fragment forest habitats. Only in the past decade have national and global maps derived from satellite imagery made it possible to consistently assess land cover at such broad scales (e.g., Loveland et al. 1999; DeFries et al. 2000) and thus to conduct preliminary assessments of forest loss and fragmentation in the U.S. (e.g., Riitters et al. 2002). These databases are discussed in brief below, with pertinent links to websites where more information is available and where each of the data sources can be acquired. However, land-cover maps indicate only the location and types of forest, and further processing is needed to quantify and map forest fragmentation. Therefore, we follow our discussion of these databases with synopses of several studies that have used these data sources to document patterns of fragmentation across the U.S.

National Land Cover Database

In 1992, a number of federal agencies formed the Multi-Resolution Land Characteristics (MRLC; http://www.epa.gov/mrlc/) consortium to acquire satellite-based, remotely-sensed data for their environmental monitoring programs. One of the projects sponsored by the MRLC consortium was the production of national land-cover data derived from early 1990’s Landsat 5 Thematic Mapper (TM) images and a number of ancillary data sources. The result, the National Land Cover Database (NLCD), was a 21-class land-cover classification scheme provided at a 30 m spatial resolution on a state-by-state basis and applied consistently over the United States (see the NLCD website for more information: landcover.usgs.gov/natlandcover.html).
The steps involved in the NLCD land-cover classification are found in detail elsewhere (Vogelmann et al. 1998, 2001) but are summarized here. First, multi-band Landsat TM mosaics were processed using an unsupervised clustering algorithm for a given region. The resulting clusters were interpreted and labeled using aerial photography and ground observations. In the case of clusters of pixels that included multiple land-cover types, models using ancillary data sets (e.g., elevation, population density) were developed to help assign land-cover categories. Finally, barren lands (e.g., quarries) and many grassy areas (e.g., parks, golf courses) are not easily distinguished from other land-cover classes using an automated process so a process of on-screen verifications was used as clarification (Heinz Center 2002).

The classification system used for the NLCD was modified from the Anderson land-use and land-cover classification system. Many of the Anderson classes, especially the Level III classes, are best derived using high-resolution aerial photography so no attempt was made in the NLCD to derive classes that were extremely difficult or “impractical” to obtain using Landsat TM data. In addition, some Anderson Level II classes were consolidated into a single NLCD class. The resulting classes are shown in Table 6.1 and discussed further at the NLCD website: http://landcover.usgs.gov/classes.asp.

The accuracy of any satellite-based classification is based on factors such as the amount of data available, the detail of the required land-cover classification (e.g., number of classes), and the classification method. Accuracy assessments of the NLCD have been conducted region-by-region, with results of these assessments indicating an accuracy of approximately 80% for the general land-cover classes (e.g., forest, agriculture). These results support the ability of the NLCD to meet data requirements for applications at the regional to continental scale, which is the primary objective of the mapping project. However, NLCD data users are encouraged to
Table 6.1. Classification schemes used in the 1992 and 2001 NLCD. Table is taken from the Multi-Resolution Land Characteristics website: http://www.epa.gov/mrlc/classification.html

<table>
<thead>
<tr>
<th>1992 Scheme</th>
<th>2001 Scheme (Under Development)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 - Open water</td>
<td>11 - Open water</td>
</tr>
<tr>
<td>12 - Perennial Ice/Snow</td>
<td>12 - Perennial Ice/Snow</td>
</tr>
<tr>
<td>21 - Low Intensity Residential</td>
<td>21 - Developed Open Space</td>
</tr>
<tr>
<td>22 - High Intensity Residential</td>
<td>22 - Developed Low Intensity</td>
</tr>
<tr>
<td>23 - Commercial/Industrial/Transportation</td>
<td>23 - Developed Medium Intensity</td>
</tr>
<tr>
<td>24 - Developed High Intensity</td>
<td>24 - Developed High Intensity</td>
</tr>
<tr>
<td>31 - Bare Rock/Sand/Clay</td>
<td>31 - Natural Barren</td>
</tr>
<tr>
<td>32 - Quarries/Strip Mines/Gravel Pits</td>
<td></td>
</tr>
<tr>
<td>33 - Transitional</td>
<td></td>
</tr>
<tr>
<td>41 - Deciduous Forest</td>
<td>41 - Deciduous Forest</td>
</tr>
<tr>
<td>42 - Evergreen Forest</td>
<td>42 - Evergreen Forest</td>
</tr>
<tr>
<td>43 - Mixed Forest</td>
<td>43 - Mixed Forest</td>
</tr>
<tr>
<td>51 - Shrubland</td>
<td>51 - Shrubland</td>
</tr>
<tr>
<td>52 - Short Shrubland</td>
<td>53 - Tall Shrubland</td>
</tr>
<tr>
<td>53 - Tall Shrubland</td>
<td>54 - Shrub/Herbaceous Mixed</td>
</tr>
<tr>
<td>54 - Shrub/Herbaceous Mixed</td>
<td></td>
</tr>
<tr>
<td>61 - Orchards/Vineyards/Other</td>
<td>61 - Orchards/Vineyards/Other</td>
</tr>
<tr>
<td>71 - Grasslands/Herbaceous</td>
<td>71 - Grasslands/Herbaceous</td>
</tr>
<tr>
<td>71 - Herbaceous</td>
<td></td>
</tr>
<tr>
<td>81 - Pasture/Hay</td>
<td>81 - Pasture/Hay</td>
</tr>
<tr>
<td>82 - Cultivated Crops</td>
<td>82 - Cultivated Crops</td>
</tr>
<tr>
<td>83 - Small Grains</td>
<td></td>
</tr>
<tr>
<td>84 - Fallow</td>
<td></td>
</tr>
<tr>
<td>85 - Urban/Recreational Grasses</td>
<td></td>
</tr>
<tr>
<td>91 - Woody Wetlands</td>
<td>91 - Woody Wetlands</td>
</tr>
<tr>
<td>92 - Emergent Herbaceous Wetlands</td>
<td>92 - Emergent Herbaceous Wetlands</td>
</tr>
</tbody>
</table>

utilize the data in a spatially aggregated form (e.g. 3x3 or 5x5 pixels blocks) whenever possible to alleviate the "salt and pepper" effect existing in the original full resolution product. Similarly, if a generalized land-cover classification scheme (e.g. Anderson level I) meets the application requirements, it is suggested that NLCD data be aggregated accordingly.

A second-generation MRLC consortium was formed in 1999 to purchase three dates of Landsat 7 imagery for the entire U.S. and to coordinate the production of a new comprehensive national land-cover database, NLCD 2001 (http://landcover.usgs.gov/natlandcover_2000.asp). This project entails re-mapping the conterminous U.S. plus Puerto Rico, Hawaii and Alaska using a modified process based on experience gained from the 1992 NLCD. As with the global
land-cover characteristics database (*discussed below*), NLCD 2001 utilizes a flexible, rule-based classification framework incorporating both spectral components (normalized tasseled cap transformations for three different time periods per scene, image derivatives of percent imperviousness and percent tree canopy per pixel, and image texture) and ancillary data layers such as DEM derivatives (elevation, slope angle, slope aspect) and soil derivatives from the STATSGO database. Land cover is then derived from the tasseled cap images, topographic derivatives and ancillary data. Classification schemes for the two rounds of classification are similar, but not identical: (*see: http://www.epa.gov/mrlc/definitions.html*). Areas in Utah and Virginia were selected for preliminary validation of the database, with cross-validation accuracies for land cover ranging from 65-82% and mean absolute error values of 10-15% for percent tree canopy cover and imperviousness (*http://landcover.usgs.gov/pdf/asprs_final.pdf*).

*Global Land Cover Characteristics Database (GLCC)*

At a broader spatial scale and coarser resolution than the NLCD, the Global Land Cover Characteristics (GLCC) database was released in 1997 and provides continent-by-continent land-cover data at a 1-km nominal spatial resolution (*except where cited, information in this section is from the GLCC website: http://edcdaac.usgs.gov/glcc/background.html*). The database was generated by the U.S. Geological Survey's (USGS) Earth Resources Observation System (EROS) Data Center, the University of Nebraska-Lincoln and the Joint Research Centre of the European Commission using Advanced Very High Resolution Radiometer (AVHRR) data spanning a 12-month period (April 1992-March 1993). Land-cover classes were defined using seasonal land-cover regions that are composed of relatively homogeneous land-cover associations (e.g., those with similar floristic and physiognomic characteristics) with distinctive phenology (i.e., onset,
peak, and seasonal duration of greenness) and common levels of primary production. Core attributes of each seasonal land-cover region include: (1) land cover descriptions, (2) seasonal characteristics, (3) site characteristics (elevation ranges, biome representation and other relevant descriptors), and (4) multi-temporal NDVI statistics (Loveland et al. 2000).

Unlike more traditional approaches that derive a single map of land cover based on the spectral properties of a predefined set of classes, the GLCC is a multi-attributed and multi-layered database that shifts the focus away from a conventional mapping effort to a process of description, documentation and data fusion (Loveland et al. 2000). The methods used to develop the land-cover types in the GLCC database are described in greater detail at the GLCC website, but they can best be described as a multi-temporal unsupervised classification of NDVI data with post-classification refinement using ancillary data. Monthly AVHRR NDVI maximum value composites for April 1992 through March 1993 were used to define seasonal greenness classes. These classes were translated into seasonal land-cover regions through post-classification refinement with the addition of digital elevation data, ecoregions data, and a collection of other land cover/vegetation reference data. Although the interpretation was based on extensive use of computer-assisted image processing tools, this classification process was not automated and more closely resembled a traditional manual image interpretation philosophy.

The final land-cover characterization involved generating a suite of attributes that described the characteristics of each seasonal land-cover region. Both statistics and contingency tables were created between the final seasonal land-cover regions layer and the respective ancillary variables (e.g., NDVI, AVHRR channels, elevation, ecoregions). The seasonal land-cover regions were then translated into land-cover types for a number of different systems, including the Global Ecosystem framework (Olson 1994a, 1994b). This system has 94 defined
ecosystem classes that are based on their land-cover mosaic, floristic properties, climate and physiognomy. The Global Ecosystem types have in turn been cross-referenced to land-cover classes from other classification systems, including the Simple Biosphere Model, Simple Biosphere 2 Model, the Biosphere Atmosphere Transfer Scheme, the International Geosphere Biosphere Programme, and the USGS/Anderson scheme.

There are currently two available versions of the GLCC database. Version 1.2 was produced as an International Geosphere Biosphere Programme-Data and Information System (IGBP-DIS) initiative. Accuracy statistics for the IGBP- DISCover data set were calculated by Scepan (1999). For the 15 DISCover classes validated, the average class accuracy was 59.4%, with accuracies ranging between 40-100%. The overall area-weighted accuracy of the data set was determined to be 67%. When only samples that had a majority interpretation for errors as well as for correct classification were considered, the average class accuracy of the data set increased to 73.5%. A revised version of the GLCC database (Version 2.0) has recently been released, but a formal accuracy assessment is still pending (http://edcdaac.usgs.gov/glcc/globdoc2_0.html).

Global Land Cover Facility (GLCF) Databases

The Global Land Cover Facility (GLCF) at the University of Maryland is a funded member of NASA’s Earth Science Information Partnership that develops and distributes remotely sensed satellite data and products. Several of the GLCF’s land-cover mapping products are well suited for broad-scale assessments of forest habitat loss and fragmentation (e.g., the Deforestation Mapping Group’s webpage: http://dmg.umiacs.umd.edu/), although their use for this task in the U.S. has been limited. In this section, we present a brief synopsis of some relevant

133
Figure 6.1. A prototype dataset derived from satellite data estimating the percentage of tree cover with evergreen (left) and deciduous (right) woody vegetation. Figures adapted from DeFries et al. (2000).

GLCF databases; more information is available from related publications (DeFries et al. 1999; DeFries et al. 2000; Hansen et al. 2002; Hansen and DeFries 2003; Hansen et al. 2003) and the GLCF website (http://glcf.umiacs.umd.edu/data/).

Most efforts to characterize land cover using satellite data classify the vegetation according to a discrete number of classes. DeFries et al. (1999, 2000) instead combined datasets previously derived from the Advanced Very High Resolution Radiometer (AVHRR) to represent global land cover as continuous fields of vegetation characteristics at 1km spatial resolution (see the website for this project at: http://glcf.umiacs.umd.edu/data/treecover/index.shtml). Prototype global maps depicting leaf form (% woody vegetation, % herbaceous vegetation, % bare ground), leaf type (% needleleaf, % broadleaf) and leaf longevity (% deciduous, % evergreen) were developed using linear mixture models as described in DeFries et al. (1999) (Fig. 6.1).

A preliminary classification of cover types was then obtained by using a decision tree algorithm employing 41 metrics derived from the annual temporal profile of the Normalized Difference Vegetation Index (NDVI) and the five individual bands acquired by the AVHRR. The classification contained 12 cover types based on requirements for land-cover data identified by the IGBP. Each of these cover types was defined in terms of dominant life form, percentage
canopy cover of trees, height of woody vegetation, and seasonality. Details of the methodology for this classification are described at http://glcf.umiacs.umd.edu/data/landcover/index.shtml and in Hansen et al. (2000). A similar procedure was used to develop a global land-cover classification product based on the National Aeronautics and Space Administration/National Oceanic and Atmospheric Administration Pathfinder Land (PAL) data at a spatial resolution of 8 km (DeFries et al. 1998).

The same basic methodology used to develop the 1km global land-cover dataset has since been extended to the creation of the GLCF’s finer scale MODIS 500m Vegetation Continuous Fields (VCF) product. Released in 2002, this dataset was generated from monthly composites of 500m resolution MODIS data taken from October 2000 to December 2001 (all information on the MODIS 500m VCF database is from: http://modis.umiacs.umd.edu/vcf.htm; more information on the derivation of the dataset can be found in Hansen et al. 2002). Like its predecessor, the MODIS 500m VCF database includes proportional estimates of forest canopy cover that were developed from global training data derived from high-resolution imagery. Training data and phenological metrics were used with a regression tree to derive percent cover globally (Fig. 6.2), and models were then used to estimate aerial proportions of life form, leaf type and leaf longevity. At the time of this publication, MODIS 500m Global VCF data were available for only the 3 layers associated with aerial proportions of life form (% tree canopy cover, % herbaceous cover, % bare ground). Initial validation efforts show “a reasonable relationship between the MODIS estimated tree cover and tree cover from validation sites” (Hansen et al. 2003), but validation is ongoing.
The National Gap Analysis Program

The gap analysis process was conceived in the 1980s as a means for assessing the level of protection given to areas rich in biodiversity. Specifically, gap analysis is a scientific method for identifying the degree to which native animal species and natural communities are represented in our present-day mix of conservation lands (note: except where cited, all information in this section is from the National Gap Program website: http://www.gap.uidaho.edu/). Those species and communities not adequately represented in the existing network of conservation lands constitute conservation "gaps." The purpose of the National Gap Analysis Program (GAP) is to provide broad geographic information on the status of ordinary species (those not threatened with extinction or naturally rare) and their habitats in order to provide land managers, planners, scientists and policy makers with the information they need to make better-informed decisions.
The Gap Analysis Program assumes that a standardized land-cover classification system is critical to the development of data sets that cover more than one state. The following land-cover classification criteria were assumed as basic requirements: (a) an ability to distinguish areas of different actual dominant vegetation; (b) a utility for modeling vertebrate species habitats; (c) a suitability for use within and among biogeographic regions; (d) an applicability to Landsat TM imagery for both rendering a base map and from which to extract basic patterns; (e) a framework that can interface with classification systems used by other organizations (e.g., MRLC, NLCD) and nations to the greatest extent possible; and (f) a capability to fit, both categorically and spatially, with non-natural areas such as agricultural and built environments. The program thus worked with its partners to develop the National Vegetation Classification System (FGDC 1996), which then served as the basis for vegetation mapping.

The GAP data sets are produced at a nominal scale of 1:100,000. They do not show habitats or features smaller than the minimum mapping unit (MMU), which varies from 900 m² (the size of a Landsat pixel) to 100 ha in some states involved in the earliest generation of maps. Each homogeneous area equal to or larger than the MMU is categorized according to the land-cover classification system by its dominant vegetation type or, in the absence of vegetation, by the dominant land-cover feature. The GAP data sets in some states serve as a spatial framework for finer-level habitat characteristics, which can be mapped as needed with a greater level of effort. Subdominant features of known occurrence can be listed in the database as an attribute of a given mapped polygon. An example of GAP land-cover data are shown in Fig. 6.3.
Figure 6.3. Arizona land cover map produced as part of the Gap Analysis Program. Source: ftp.gap.uidaho.edu/products/arizona/gis/vegcovs

Roads

There are two primary sources of data on road networks. TIGER/Line files are extracts from the TIGER (Topologically Integrated Geographic Encoding and Referencing) database produced by the U.S. Census Bureau. The Census 2000 TIGER/Line file dataset contains statewide road data, including not only road locations but also attribute information on the type of road (e.g., primary highway with limited access; primary road without limited access; secondary and connecting roads; local, neighborhood and rural roads). Websites of the Census Bureau (http://www.census.gov/geo/www/tiger/) and Environmental Systems Research Institute (ESRI) (http://www.esri.com/data/download/census2000_tigerline/index.html) contain more
National Fragmentation Patterns

Within the last 5 years, several national assessments of forest ecosystem conditions have included some measure of fragmentation in their criteria. Several other studies have taken advantage of the growing availability of national datasets such as the NLCD and GLCC dataset to examine various aspects of fragmentation pattern across the U.S., including the prevalence of roads as fragmenting agents. Results from several of these studies are summarized below.

Roundtable on Sustainable Forests

In 1994, the U.S.D.A. Forest Service and the U.S. State Department conducted an extensive national outreach effort to assemble a group of forest stakeholders to provide an ongoing forum for sharing information and perspectives on sustainable forest management (note:}
The initial focus of discussion for the stakeholder group concerned development of a set of criteria and indicators (C&I) that would describe the basic elements of sustainable forest management and be used to measure national progress toward this goal. Results of stakeholder discussions were used in international deliberations on C&I, resulting in the adoption in 1995 of a set of C&I by the U.S. and several other countries in what is known as the Montréal Process Working Group on C&I. The C&I are meant to provide a common understanding of the essential components of sustainable forest management and a common framework for describing, assessing and evaluating a country’s progress toward this goal at the national level.

Participants in the stakeholder forum have continued to meet periodically to review progress in the use of the endorsed C&I, with the forum evolving into what is now known as the Roundtable on Sustainable Forests. Participants in this forum, first convened in 1999, have included individuals from federal and state government agencies, forest products companies, conservation and environmental groups, tribal governments, regional and community-based organizations, private forest landowner organizations, professional societies, academic institutions, and other citizens. The focus of the Roundtable has been to advance the use of the endorsed C&I and share other opportunities for sustainable forest management. The preparation of the group’s first full report started with a series of three workshops for technical experts to assess potential sources of data. The authors used the results of these workshops in gathering and analyzing data for the report.

As part of this effort, Riitters (2003) and Riitters et al. (2004) used land-cover maps from the National Land Cover Dataset (NLCD) to create and analyze four preliminary indicators of
fragmentation: patch size, edge amount, inter-patch distance and patch contrast. The analyses were conducted within 137,444 non-overlapping 5625ha analysis units, and results included both maps of the indicators values as well as regional comparisons (see Figs. 6.4-6.8 for sample results). The authors found that most analysis units contained a large number of small patches (< 1 ha) while only 10% contained one or more forest patches > 2000-5000ha. The perimeter of a typical forest patch was only about 100m from the perimeter of its nearest neighbor, except in areas of sparse forest where it was farther (200-300m). Forest patch contrast, which addressed the amount of similarity in physiognomic structure between patch types, was either generally very high or very low in the eastern U.S. and intermediate in western regions. The primary conclusion was that while most forestland in the U.S. was reasonably well connected over large regions, especially in places where forest was generally dominant, much of it was highly fragmented and in close proximity to roads at local scales. A limitation of these analyses, noted by Riitters et al. (2004), is that at least three of these three metrics, patch size, patch contrast and edge amount, show a high degree of intercorrelation (Pearson r > 0.80 or < -0.80), meaning that these indices likely capture similar aspects of landscape pattern while possibly ignoring others.

*Forest Intactness Database*

To address not only the effects of land-cover change in fragmenting forest ecosystems but also road systems, Heilman et al. (2002) developed a “Forest Intactness Database” using the National Land Cover Database (NLCD) and 1:100,000 scale USGS road data sets. For 39 forested ecoregions in the continental U.S., they defined “land units” based on highways and urban areas that contained more than 50,000 people (Table 6.2). For each land unit, they calculated road density and a broad range of landscape metrics. These were used to create a
Figure 6.4. Percent forest land-cover in 5625 ha analysis units (n = 137,744), with darker colors indicating higher values. Adapted from Riitters (2003).

Figure 6.5. Area-weighted average forest patch size (pixel units; 1 pixel unit = 0.09 ha; n = 127,012). Adapted from Riitters (2003).
Figure 6.6. Average minimum inter-patch distance in pixel units (1 pixel unit = 30 m; n = 84,124) for forest patches in analysis units with > 5% forest cover. Adapted from Riitters (2003).

Figure 6.7. Number of forest edges per unit forest area (n=127,012). Adapted from Riitters (2003).
Figure 6.8. Relative frequency of number of forest edges per unit forest area in analysis units with forest by RPA. Region abbreviations: NO = North; PC = Pacific Coast; RM = Rocky Mountains, and; SO = South. Figure adapted from Riitters (2003).
flexible, composite score system based on ordinal ranks to characterize fragmentation of each unit. For example, road density, class area, percentage of landscape in forest, total core area index, and mean nearest neighbor results could be assigned ordinal scores from which a cumulative score was calculated to create an overall relative forest intactness score (Fig. 6.9). By assigning all land units a quantitative measurement of relative forest intactness based on a uniform dataset, they were able to identify remaining areas of comparatively intact forest (e.g. the eastern forest/boreal transition ecoregion that includes the Boundary Waters area or the Central Pacific Coastal Forest ecoregion), highlight land units that may make good restoration candidates from a regional context, and examine forest fragmentation due to roads, which had been omitted from other recent national assessments. More information on this dataset can be found at: http://www.consbio.org/cbi/applied_research/intactness/intactness.htm.
Table 6.2. Summary of selected fragmentation metrics for the conterminous United States by ecoregion. Data from Heilman et al. (2002)

<table>
<thead>
<tr>
<th>Ecoregion</th>
<th>Area (ha)</th>
<th>Number of land units</th>
<th>Percent forest(^a)</th>
<th>% core area(^b)</th>
<th>Number of forest patches</th>
<th>Mean forest patch size (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allegheny Highland Forest</td>
<td>7,675,748</td>
<td>602</td>
<td>69.7</td>
<td>46.5</td>
<td>66,514</td>
<td>90</td>
</tr>
<tr>
<td>Appalachian Mixed Mesophytic Forest</td>
<td>17,854,294</td>
<td>1,602</td>
<td>76.7</td>
<td>52.8</td>
<td>125,894</td>
<td>123</td>
</tr>
<tr>
<td>Appalachian/Blue Ridge Forest</td>
<td>14,827,932</td>
<td>1,301</td>
<td>72.5</td>
<td>50.8</td>
<td>142,238</td>
<td>97</td>
</tr>
<tr>
<td>Arizona Mountain Forest</td>
<td>10,330,107</td>
<td>101</td>
<td>48.5</td>
<td>29.9</td>
<td>76,303</td>
<td>65</td>
</tr>
<tr>
<td>Atlantic Coastal Pine Barren</td>
<td>825,117</td>
<td>113</td>
<td>54.6</td>
<td>27.0</td>
<td>19,918</td>
<td>28</td>
</tr>
<tr>
<td>Blue Mountain Forest</td>
<td>5,898,031</td>
<td>47</td>
<td>48.3</td>
<td>28.6</td>
<td>71,800</td>
<td>83</td>
</tr>
<tr>
<td>Cascade Mountain Leeward Forest</td>
<td>1,456,954</td>
<td>17</td>
<td>62.3</td>
<td>39.9</td>
<td>14,914</td>
<td>142</td>
</tr>
<tr>
<td>Central and Southern Cascade Forest</td>
<td>4,090,056</td>
<td>65</td>
<td>68.0</td>
<td>46.5</td>
<td>31,894</td>
<td>163</td>
</tr>
<tr>
<td>Central Pacific Coastal Forest</td>
<td>3,745,165</td>
<td>88</td>
<td>84.0</td>
<td>62.4</td>
<td>15,401</td>
<td>268</td>
</tr>
<tr>
<td>Central US Hardwood Forest</td>
<td>27,580,236</td>
<td>1,886</td>
<td>50.3</td>
<td>28.3</td>
<td>327,957</td>
<td>49</td>
</tr>
<tr>
<td>Colorado Rockies Forest</td>
<td>12,283,430</td>
<td>134</td>
<td>58.9</td>
<td>38.5</td>
<td>69,452</td>
<td>105</td>
</tr>
<tr>
<td>East Central Texas Forest</td>
<td>5,119,185</td>
<td>445</td>
<td>29.5</td>
<td>10.9</td>
<td>98,364</td>
<td>22</td>
</tr>
<tr>
<td>Eastern Cascade Forest</td>
<td>5,045,576</td>
<td>103</td>
<td>37.8</td>
<td>22.9</td>
<td>76,509</td>
<td>75</td>
</tr>
<tr>
<td>Eastern Forest/Boreal Transition</td>
<td>2,659,400</td>
<td>78</td>
<td>82.3</td>
<td>68.1</td>
<td>11,236</td>
<td>242</td>
</tr>
<tr>
<td>Eastern Great Lakes Lowland Forest</td>
<td>2,374,371</td>
<td>224</td>
<td>66.5</td>
<td>47.4</td>
<td>32,640</td>
<td>93</td>
</tr>
<tr>
<td>Florida Sand Pine Scrub</td>
<td>386,176</td>
<td>90</td>
<td>34.0</td>
<td>16.5</td>
<td>21,452</td>
<td>33</td>
</tr>
<tr>
<td>Great Basin Montane Forest</td>
<td>534,324</td>
<td>27</td>
<td>48.3</td>
<td>24.5</td>
<td>3,942</td>
<td>63</td>
</tr>
<tr>
<td>Klamath-Siskiyou Forest</td>
<td>4,610,238</td>
<td>110</td>
<td>77.1</td>
<td>52.1</td>
<td>32,762</td>
<td>182</td>
</tr>
<tr>
<td>Madrean Sky Island Montane Forest</td>
<td>1,097,147</td>
<td>31</td>
<td>21.3</td>
<td>10.1</td>
<td>7,756</td>
<td>28</td>
</tr>
<tr>
<td>Middle Atlantic Coastal Forest</td>
<td>12,624,046</td>
<td>1,055</td>
<td>58.2</td>
<td>33.4</td>
<td>126,351</td>
<td>62</td>
</tr>
<tr>
<td>Mississippi Lowland Forest</td>
<td>10,690,623</td>
<td>675</td>
<td>25.4</td>
<td>14.5</td>
<td>86,938</td>
<td>42</td>
</tr>
<tr>
<td>New England/Acadian Mixed Forest</td>
<td>10,741,731</td>
<td>611</td>
<td>83.2</td>
<td>64.2</td>
<td>41,023</td>
<td>231</td>
</tr>
<tr>
<td>North Cascade Forest</td>
<td>1,304,363</td>
<td>9</td>
<td>72.1</td>
<td>49.8</td>
<td>14,775</td>
<td>188</td>
</tr>
<tr>
<td>North Central Rockies Forest</td>
<td>9,313,772</td>
<td>71</td>
<td>66.1</td>
<td>46.3</td>
<td>52,617</td>
<td>180</td>
</tr>
<tr>
<td>Northeastern Coastal Forest</td>
<td>8,217,277</td>
<td>1,185</td>
<td>69.4</td>
<td>46.5</td>
<td>101,060</td>
<td>77</td>
</tr>
<tr>
<td>Northern California Coastal Forest</td>
<td>1,223,314</td>
<td>85</td>
<td>75.5</td>
<td>50.5</td>
<td>13,690</td>
<td>160</td>
</tr>
<tr>
<td>Okanogan Forest</td>
<td>1,303,530</td>
<td>38</td>
<td>55.5</td>
<td>32.7</td>
<td>13,359</td>
<td>93</td>
</tr>
<tr>
<td>Ozark Mountain Forest</td>
<td>5,836,909</td>
<td>253</td>
<td>67.2</td>
<td>46.9</td>
<td>44,875</td>
<td>105</td>
</tr>
<tr>
<td>Piney Wood Forest</td>
<td>13,523,604</td>
<td>957</td>
<td>69.0</td>
<td>46.3</td>
<td>101,365</td>
<td>102</td>
</tr>
<tr>
<td>Puget Lowland Forest</td>
<td>1,496,320</td>
<td>163</td>
<td>71.7</td>
<td>48.2</td>
<td>31,865</td>
<td>136</td>
</tr>
<tr>
<td>Sierra Nevada Forest</td>
<td>4,889,313</td>
<td>166</td>
<td>46.4</td>
<td>25.4</td>
<td>55,452</td>
<td>71</td>
</tr>
<tr>
<td>South Central Rockies Forest</td>
<td>14,530,308</td>
<td>107</td>
<td>37.7</td>
<td>23.4</td>
<td>121,234</td>
<td>77</td>
</tr>
<tr>
<td>South Florida Rockland</td>
<td>219,994</td>
<td>17</td>
<td>34.1</td>
<td>12.3</td>
<td>12,573</td>
<td>29</td>
</tr>
<tr>
<td>Southeastern Conifer Forest</td>
<td>23,103,750</td>
<td>1,695</td>
<td>53.5</td>
<td>31.0</td>
<td>229,194</td>
<td>59</td>
</tr>
<tr>
<td>Southeastern Mixed Forest</td>
<td>32,933,256</td>
<td>2,606</td>
<td>68.4</td>
<td>42.3</td>
<td>268,860</td>
<td>92</td>
</tr>
<tr>
<td>Southern Great Lakes Forest</td>
<td>20,178,698</td>
<td>2,777</td>
<td>25.4</td>
<td>9.8</td>
<td>255,440</td>
<td>21</td>
</tr>
<tr>
<td>Upper Midwest Forest/Savanna Transition</td>
<td>15,150,620</td>
<td>1,602</td>
<td>31.5</td>
<td>14.4</td>
<td>204,508</td>
<td>28</td>
</tr>
<tr>
<td>Wasatch and Uinta Montane Forest</td>
<td>3,817,489</td>
<td>79</td>
<td>54.5</td>
<td>27.8</td>
<td>33,129</td>
<td>62</td>
</tr>
<tr>
<td>Western Great Lakes Forest</td>
<td>18,232,102</td>
<td>861</td>
<td>72.0</td>
<td>49.6</td>
<td>106,790</td>
<td>135</td>
</tr>
<tr>
<td>Western Conterminous U.S.</td>
<td>86,969,605</td>
<td>1,294</td>
<td>50.9</td>
<td>31.9</td>
<td>595,252</td>
<td>92</td>
</tr>
<tr>
<td>Eastern Conterminous U.S.</td>
<td>250,755,098</td>
<td>18,659</td>
<td>56.5</td>
<td>35.3</td>
<td>2,100,742</td>
<td>67</td>
</tr>
<tr>
<td>Entire Conterminous U.S.</td>
<td>337,724,703</td>
<td>19,953</td>
<td>54.8</td>
<td>34.3</td>
<td>2,695,994</td>
<td>72</td>
</tr>
</tbody>
</table>

\(^a\) Percent forest is the amount of the entire land unit area that is composed of forest.

\(^b\) Percent core area is the amount of forest cover composed of core forest area using a 90 m edge effects distance.
The H. John Heinz III Center for Science, Economics and the Environment was established in 1995 as a nonprofit, nonpartisan institution dedicated to improving the scientific and economic foundation for environmental policy through multisectoral collaboration (www.heinzctr.org). The Center creates and fosters collaboration among industry, environmental organizations, academia, and government in each of its program areas and projects, and results of these collaborations are disseminated, in part, through publications, reports and workshops.

One of the primary publications produced by the Heinz Center is *State of the Nation's Ecosystems* (Heinz Center 2002; http://www.heinzctr.org/ecosystems/report.html). Published in 2002 with input from dozens of experts from businesses, universities, environmental organizations, and federal, state, and local government agencies, *State of the Nation's Ecosystems* laid out a blueprint for periodic reporting on the condition and use of ecosystems in the U.S. by identifying major characteristics of ecosystems that should be tracked through time and, where possible, providing information on both current conditions and historic trends. It also highlighted situations where data did not exist or had not been assembled to support national reporting. Separate ecosystem-specific indicators were reported for coasts and oceans, farmlands, forests, fresh waters, grasslands and shrublands, and urban and suburban areas, and ten core national indicators were provided as aggregate measures of overall conditions.

Fifteen indicators were proposed for monitoring aspects of forest conditions, including indicators addressing biological conditions (at-risk native species; area covered by non-native plants; forest age; forest disturbance: fire, insects, and disease; fire frequency; forest community types with significantly reduced area), chemical and physical conditions (nitrate in forest streams; carbon storage), human usage (timber harvest; timber growth and harvest; recreation in
forests) and system dimensions (forest area and ownership; forest types; forest management categories; forest pattern and fragmentation). Forest pattern and fragmentation was also proposed as a core national indicator, although no specific indicator was agreed upon.

The proposed forest fragmentation indicator described a forested pixel’s neighborhood according to the amount of forest cover within moving windows of varying sizes. Three moving window sizes were used to analyze NLCD data: 2.3 ha (the “immediate neighborhood”), 66 ha (the “local neighborhood”) and 5310 ha (the “larger neighborhood”). These sizes corresponded to windows of 25 pixels (a square of 5 x 5 pixels); 729 pixels (a square of 27 x 27 pixels) and 59,049 pixels (a square of 243 x 243 pixels), respectively. Two other window sizes (7.3 ha, 590 ha) were also analyzed, with results reported in Riitters et al. (2002) but not in the body of State of the Nation’s Ecosystems. The analyses for each pixel and window size were conducted for three different forested criteria, whether the pixel was surrounded by at least 60% forest (“% connected”), at least 90% forest (“% interior”), or exactly 100% forest (“% core”).

In short, most forest was found to be in fragmented landscapes (Table 6.3). For example, with a 66 ha landscape (i.e., window size), only 9.9% of all forest was contained in a fully forested landscape, and only 46.9% was in a landscape that was more than 90% forested. Nevertheless, where forest existed, it was usually dominant, with at least 73% of all forest in landscapes that were at least 60% forested for all landscape sizes. Small (< 7.29 ha) perforations in otherwise continuous forest cover accounted for about half of the fragmentation, and in general, western forests had lower amounts of surrounding forest. These results led Riitters et al. (2002) to conclude that forests were connected over large regions but also to note that fragmentation was so pervasive that edge effects potentially influenced ecological processes on most forested lands.
Table 6.3. Percentage of forested pixels surrounded by 100% forest cover (“core”), 90% forest cover (“interior”) and 60% forest cover (“connected”) in surrounding windows of varying size. Data from: http://www.heinzctr.org/ecosystems/forest_technotes/forest_ptrn_frag.shtml.

<table>
<thead>
<tr>
<th>Window area (ha)</th>
<th>West</th>
<th></th>
<th></th>
<th>East</th>
<th></th>
<th></th>
<th>East &amp; West</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% core</td>
<td>% interior</td>
<td>% connected</td>
<td>% core</td>
<td>% interior</td>
<td>% connected</td>
<td>% core</td>
<td>% interior</td>
</tr>
<tr>
<td>2.3</td>
<td>51.0</td>
<td>64.1</td>
<td>85.4</td>
<td>59.0</td>
<td>70.7</td>
<td>88.6</td>
<td>56.5</td>
<td>68.7</td>
</tr>
<tr>
<td>7.3</td>
<td>32.7</td>
<td>55.7</td>
<td>83.3</td>
<td>40.7</td>
<td>62.4</td>
<td>86.3</td>
<td>38.2</td>
<td>60.4</td>
</tr>
<tr>
<td>66</td>
<td>7.1</td>
<td>44.0</td>
<td>78.5</td>
<td>11.1</td>
<td>48.2</td>
<td>80.0</td>
<td>9.9</td>
<td>46.9</td>
</tr>
<tr>
<td>590</td>
<td>0.2</td>
<td>33.1</td>
<td>75.0</td>
<td>0.9</td>
<td>34.8</td>
<td>75.2</td>
<td>0.7</td>
<td>34.3</td>
</tr>
<tr>
<td>5310</td>
<td>0.0</td>
<td>22.4</td>
<td>70.5</td>
<td>0.0</td>
<td>25.1</td>
<td>72.6</td>
<td>0.0</td>
<td>24.2</td>
</tr>
</tbody>
</table>

**Forest and Rangeland Renewable Resources Planning Act**

In the belief that reliable information was necessary to properly manage the Nation's renewable resources and make informed policy decisions, Congress passed the Forest and Rangeland Renewable Resources Planning Act (RPA) in 1974. The RPA required the Secretary of Agriculture, through the Forest Service, to periodically prepare a Renewable Resource Assessment that, among other things, includes “an analysis of present and anticipated uses, demand for, and supply of the renewable resources, with consideration of the international resource situation, and an emphasis of pertinent supply, demand, and price relationship trends”.

The Act further directs the Secretary of Agriculture “to make and keep current a comprehensive survey and analysis of the present and prospective conditions of and requirements for the renewable resources of the forest and range lands of the United States….”

The data for the national assessment of forests are collected under the guidance of the USDA Forest Service and compiled by the agency’s Forest Inventory and Analysis (FIA) program (http://www.fia.fs.fed.us/). In operation since the 1930’s, FIA is managed by the Research and Development arm of the Forest Service in cooperation with the State and Private Forestry and National Forest systems. The FIA program monitors a grid of approximately 6.5
million photo points and over 400,000 sample locations on private and public land across the United States, and reports on status and trends in: forest area and location; the species, size, and health of trees; total tree growth, mortality, and removals by harvest; wood production and utilization rates by various products; and forest land ownership. Selected data are then organized and presented nationally as part of the Resources Planning Act.

The original language of the RPA emphasized resource availability in an economic context (note: this paragraph is based on information from the RPA website: http://svinet2.fs.fed.us/pl/rpa/what.htm). However, it is clear that the ability of the resource base to produce both tangible and intangible outputs for society is dependent on the condition of the resource base. As a result, more attention was directed to assessing resource conditions for the most recent RPA Assessment (http://www.fs.usda.gov/pl/rpa/rpaasses.pdf). Further, national policies and international agreements on global warming and biological diversity have increased the visibility of international resource issues, including the signing of the Santiago Declaration in 1995, which committed the U.S. to a process of developing and evaluating national indicators of sustainable forest management. The Forest Service has subsequently decided to use the set of seven criteria and 67 indicators endorsed for use by the Montréal Process Working Group on C&I as the organizing framework for the RPA Process. These criteria include various indicators addressing conservation of biological diversity, maintenance of productive capacity of forest and range ecosystems, maintenance of forest ecosystem health and vitality, maintenance of forest contribution to global carbon cycles, and maintenance and enhancement of long-term multiple socioeconomic benefits to meet the needs of societies. The effects of fragmentation on biodiversity are included and addressed briefly in the 2000 RPA Assessment, and the important
landscape metrics that are mentioned include patch size, edge, distances between habitat areas, and interconnectedness.

We should add that there is also the potential for greater information on fragmentation effects via the Forest Inventory and Analysis (FIA) ground plots, at least at the regional scale. FIA data are not well suited for addressing fragmentation because the plot design is such that a given ground plot is meant to represent ca. 2400 ha. Thus, the plots are considered to be too sparsely distributed to characterize landscape features at finer scales. Also, no data directly related to forest patch size or other measures of fragmentation are collected on the plots so any attempt to make inferences about forest fragmentation based on the plot data alone is difficult. However, efforts by FIA personnel on regional scales are beginning to provide the kinds of information regarding the proximity of forested areas to human development that could be gathered on a national level. Examples include: (1) the Pacific Northwest unit has been measuring the proximity and density of development (number of buildings or other man-made structures) around each FIA ground plot, (2) both the Pacific Northwest and North Central units have been measuring the percentage of each of six cover types within fixed areas around each ground plot (10, 40, 160 and 640 ha areas in PNW; 5 and 50 ha areas in NC), (3) the North Central unit has also been looking at forest fragmentation using a combination of ground inventory and photointerpreted information (e.g., stand area, size of ownership, disturbance, distance to nearest road), and (4) the Northeast unit has been recording the size of the forested patch at each photointerpretation point location, the distance from that point to the nearest developed land use, and the nearest land use for each photointerpretation point (Schmidt and Raile 1998; Riemann and Tillman 1999).
Riitters’ Fragmentation Index

While the previously mentioned studies generally relied on traditional habitat metrics (e.g. patch size, edge factors, interpatch distance), Riitters et al. (2000) developed a more complex fragmentation index and implemented the index using 1 km resolution land-cover maps (the Global Land Cover Characteristics database) to characterize global patterns of forest fragmentation. Their fragmentation index was based on the amount of forest and a measure of forest connectivity within fixed-area moving windows ranging in size from 81 km² to 59,049 km². Each window was classified based on two measures: Pf, the proportion of pixels within the moving window that were forested, and Pff, the proportion of adjacent pixel pairs in the window that were both forested, given that at least one of the pair was forested. Based on these values, each window was assigned a forest fragmentation class: interior (Pf = 1.0); patch (Pf < 0.4); transitional (0.4 < Pf < 0.6); perforated (Pf > 0.6 and Pf - Pff > 0); edge (Pf > 0.6 and Pf - Pff < 0), and undetermined (Pf > 0.6 and Pf = Pff) (Fig. 6.10). The difference (Pf – Pff) characterizes a gradient from forest clumping to nonforest clumping. Results of the classification using the 81 km² window for the U.S. are shown in Figure 6.11, but the findings are highly sensitive to scale of the window used (i.e., results changed significantly with size of surrounding landscape considered). A modified version of this index was also developed for quantifying and describing urbanizing landscapes in the northeastern U.S. (Civco et al. 2002) but has not implemented using national data.

How Far to the Nearest Road?

To more directly emphasize the prevalence of roads as fragmenting agents, Riitters and Wickham (2003) measured the proportion of land area that was located within nine distances
Figure 6.10. Model used by Riitters et al. (2000) to assign forest fragmentation categories from local measurements of \( P_f \) and \( P_{ff} \) in a fixed-area moving window. \( P_f \) represents the proportion of forested cells within the window while \( P_{ff} \) roughly estimates the probability that, given a forested pixel, its neighbor is also forest.

Figure 6.11. Fragmentation types for the continental United States and adjacent areas based on measurements of \( P_f \) and \( P_{ff} \) in an 81 km² fixed-area moving window. Figure adapted from Riitters et al. (2000).
from the nearest road of any type and mapped the results for 164 ecoregions and 2108
watersheds nationwide. Overall, 20% of the total U.S. land area was within 127 m of a road (Fig.
6.12), although the authors did not distinguish among different road types (e.g., dirt roads vs.
interstate highways). The proportion increased rapidly with distance, so that 83% of the total
U.S. land area was within ca. 1 km of a road. Conversely, only 3% of the U.S. land area was more
than 5 km away from the nearest road. When only forest lands were considered, the proportions
differed by less than 2% for all distances.

Because they used the same road database, Riitters and Wickham (2003) also compared
their results to those of Heilman et al. (2002) to assess the relative importance of roads vs. land-
cover differences as fragmenting agents. Specifically, Heilman et al. (2002) looked at
fragmentation by all land-cover types as well as by roads and estimated that 66% of forest land
within large forested regions was within 90 m of a road or a forest edge. In comparison, Riitters
and Wickham (2003) found that 11% of all forest land was located within 85 m of a road,
suggesting that much of the overall fragmentation measured in the previous was the result of the
juxtaposition of forest and non-forest land-cover types rather than roads or road-mediated land-cover change. However, the relative contribution of roads to fragmentation is much higher in mostly forested regions with high road density, such as the Pacific Northwest coast and the Appalachian Mountains. Because the juxtaposition of forest and non-forest land-cover types can involve not only human-created changes (e.g., logging, urbanization) but also natural heterogeneity in land cover, these results underscore the importance of addressing and separating the effects of various agents of fragmentation.

**Summary of National Assessments and Conclusions**

Results of these recent assessments reinforce that forest fragmentation is an issue of concern in national studies of forest conditions. Further, they illustrate that it is possible to assess forest fragmentation using fairly high-resolution maps (often with relatively coarse thematic resolution) in a consistent manner over large scales, even if the results of such analyses are preliminary and contingent on the quality of the data. In terms of mapping, analyzing and monitoring fragmentation effects, these assessments all generally rely on traditional and easily interpretable habitat metrics that are simple to implement at the national scale (e.g. patch size, edge factors, interpatch distance). Further, the primary motivation and rationale for the data and metrics being used as well as their interpretation is generally the same: to serve as an indicator of the effects of fragmentation on biodiversity. Specifically, habitat capacity and thus biodiversity is thought to be not only a function of forest area but also the arrangement of that forest and the presence of agents of fragmentation (e.g., non-forested cover types, roads).

While the assessments have much in common, they vary considerably in terms of: 1) their incorporation of roads vs. land use, 2) the spatial resolution of the data (e.g., 30m vs. 1km),...
3) the scale of analysis (e.g., the size of the surrounding landscape considered in analyses), and
4) their consideration of not only landscape structure but also ecosystem context and contrast
(e.g., forest type, age class, protected status). In all of the studies described, there is little analysis
of temporal change, largely due to a lack of consistent long-term datasets at the national scale.
Further, there is little treatment of natural levels of fragmentation and spatial heterogeneity and
little discussion of endpoints of the analyses other than for biodiversity.

Some of these shortcomings are major themes for the next round of ongoing national
assessments. Specifically, all three of the “organized” national forest assessments discussed
above are in the process of being updated, and fragmentation has a role in all of them. Major
themes for the 2005 U.S. Forest Service RPA Assessment Update include the incorporation of
road-mediated fragmentation, the inclusion of parcelization in the context of urbanization (as
opposed to biodiversity), and a demonstration of the localization of national statistics. For
example, the 2005 RPA update will have an example of overlaying forest type maps based on
GAP data with the moving window national fragmentation maps developed by Riitters et al.
(2000) to “localize the information” (sensu Riitters et al. 2003). For the update of the Heinz
Center’s *State of the Nation’s Ecosystems* (scheduled to be released in 2007), a landscape pattern
taskgroup is currently working on potential new indicators of forest pattern and fragmentation
involving the interspersion of different ecosystem types and the harmonization of landscape
pattern measures across ecosystem types to develop a core national indicator of fragmentation
and pattern. Finally, for the 2008 Montréal Process / US Roundtable on Sustainable Forests,
major themes likely to be included will be the local application and interpretation of national
statistics, a reevaluation of proposed fragmentation metrics, the incorporation of trend analyses
(if new land-cover maps become available) and possible harmonization of indicators with the Range Roundtable and Water Roundtable.

Finally, it is important to recognize not only the contributions of national assessments of fragmentation pattern but also their limitations. It is becoming widely accepted that some measure of fragmentation or landscape pattern is needed in national evaluations of forest condition because of perceived relationships between biodiversity and fragmentation. National (and regional) studies provide valuable information that can be used to both map and monitor forest habitat loss and fragmentation, which can be valuable from a management and policy perspective. However, it is important to understand that while such efforts are useful for characterizing and even monitoring changes in fragmentation (within the constraints of data quality), their interpretation with respect to effects on biodiversity and ecological pattern and process remains open-ended. In particular, the tradeoffs between developing simple yet elegant fragmentation metrics that can be implemented at a national scale must be balanced against the need to link quantitative measures of fragmentation to specific ecological effects.
Chapter 7. Forest Fragmentation: Research Needs

While natural processes can cause habitat loss and the fragmentation of landscapes and habitats, human landscape modification is by far the most significant factor resulting in deforestation and fragmentation in many, if not most, forest ecosystems (Saunders et al. 1987; Groombridge 1992). Throughout this paper, we have tried to stress that an understanding of the effects of fragmentation on biodiversity and ecosystem processes requires consideration of both the ways in which fragmentation alters spatial configuration and habitat suitability in the remnants and the surrounding matrix as well as the ways in which species respond to these changes (Lindenmayer and Franklin 2002). The degree of deforestation and fragmentation varies widely from place to place as a function of the intensity of human activities and landscape history, and fragmentation by different activities (e.g., urban development vs. timber harvesting) or even between different forms of the same disturbance (e.g., dispersed vs. aggregated structural retention logging) may have very different effects on habitat quality and species movement. Further, because organisms perceive and respond to the environment in different ways and at different spatial and temporal scales, the effects of fragmentation are impossible to generalize across all species; an agricultural landscape that may be un-crossable for a small rodent may pose no restrictions to the movement of an avian species, or vice-versa.

In the preceding chapters, we discussed the ways in which fragmentation affects biodiversity and ecological processes and discussed metrics that have been used both to assess and monitor forest fragmentation and to better understand the effects of changing landscape structures in fragmented landscapes. We also presented a working conceptual model of forest fragmentation effects, focusing especially on the effects of habitat loss, remnant isolation, and edge creation. Our objective has been to present an overview of the current status of knowledge
of fragmentation effects while also calling attention to what we see as some of the shortcomings of past (and in some cases, current) approaches to the study of fragmentation. In this final section, we present and discuss in more depth some issues that we believe need to be addressed in future fragmentation research. In particular, we focus on two major areas: the relationship between forest fragmentation and issues of spatial heterogeneity (including discussions of landscape representation, the effects of corridors, the importance of natural spatial heterogeneity, the roles of forest edges in fragmented landscapes, and the usefulness of landscape metrics), and the linkage of fragmentation research and findings to applied management situations.

Fragmentation and Spatial Heterogeneity

Over the last decade, the overriding change in the conceptualization of how fragmentation alters landscape structure has been a shift away from the view of remnants as discrete habitat islands surrounded by areas of unsuitable land use toward one that recognizes the wide range of changes in habitat quality that take place in all components of the fragmented landscape. This realization underscores the importance of studying and understanding how fragmentation alters the flows of energy, matter and species across the modified landscape and thus affects a range of key community and ecosystem processes (e.g., succession, sediment fluxes, nutrient cycling, carbon sequestration). Throughout this paper, and most explicitly in our conceptual model of forest fragmentation effects, we have identified and discussed the singular and interactive importance of habitat loss, patch isolation, and edge effects on biodiversity and ecological processes in fragmented landscapes. The nature and consequences of each one of these effects is very different depending on how the landscape is conceptualized, including how spatial heterogeneity is represented. Changing attitudes toward the nature of fragmented
landscapes in turn result in a changing understanding of fragmentation effects, as we will demonstrate below.

**Spatial Heterogeneity and Models of Landscape Representation**

Island biogeography theory influenced much of the early work on forest fragmentation effects, resulting in a binary conceptualization involving suitable (the remnants) and unsuitable (the matrix) habitat. Within this context, biodiversity declines in forest fragments were seen to be solely a function of reduced patch areas and increased distance among remnants. Island biogeography did not address nor provide insights into either edge effects or the effects of fragmentation on ecological processes (e.g., disturbances, succession, trophic fluxes). Further, the effects of fragmentation on specific species, often a primary management issue for forest managers, were not predictable because island biogeography only explicitly addressed species richness.

While the utility of island biogeography theory *per se* for examining forest fragmentation issues has largely been dismissed, concepts such as species-area curves and the importance of patch isolation have survived and been incorporated into more contemporary theories. Island biogeographic representations of the landscape have been gradually transformed into the corridor-patch-matrix model (Forman and Godron 1986; Forman 1995), in which landscapes are conceived as mosaics of discrete landscape elements (corridors, patches) within a more extensive, better-connected landscape matrix. The non-forested cover types are neither the matrix by default (e.g., in the case of forest perforation) nor completely inhospitable by definition, although this has been a common representation in fragmentation studies (e.g., forest remnants within an agricultural matrix). Changes in remnant biodiversity are still seen as being a
function of forest habitat loss and changes in forest connectivity, but habitat diversity, other
disturbances, matrix heterogeneity and boundary discreteness are also viewed as being important
(Forman and Godron 1986). Recent developments in population dynamic models (e.g.,
metapopulation models) have fit easily within the patch-corridor-matrix model (Kupfer 1995),
with patches of forested habitat serving as the basic unit of interest. Corridors are seen as
important elements for their value as both habitat and landscape connections, and edge effects
are acknowledged and studied. The patch-corridor-matrix model approach has also been helped
by the growth of remote sensing and GIS, which allow scientists and managers to classify
landscapes into discrete and relatively homogeneous landscape elements and facilitate the
quantitative analysis of landscape patterns.

More recently, McIntyre and Hobbs (1999) have proposed the landscape continuum
model, which focuses on variation in habitat quality so that boundaries among landscape
elements are not recognized. Landscapes are represented as continuous surfaces of a habitat
variable (e.g., forest cover) so that small elements of habitat that might otherwise be classified as
unsuitable in a larger matrix can be accounted for (e.g., individual clumps of savanna trees
within a grassland matrix). This model is well suited to forests where habitat patches are
indistinct, although the basic approach of quantifying gradients rather than classes is applicable
to a broad range of forest types and attributes (McIntyre and Hobbs 1999).

Lindenmayer and Franklin (2002) note that these two models are congruent on several
levels, with the primary distinctions being differences in their relative perspectives on landscapes
and the importance that each inherently places on landscape form vs. function. Specifically, the
patch-corridor-matrix model focuses on the pattern and form of the different landscape elements
comprising a landscape mosaic; in the context of forest fragmentation, the emphasis is on
quantifying changes in landscape structure as a means of determining how such changes relate to ecological effects. The landscape continuum model recognizes that distinct patch boundaries may not be identifiable (although sharp edges can be represented as areas of rapid changes in gradients: Jones and Kupfer, in review) so the focus is on how variability across a structural gradient such as forest cover affects specific functions in the landscape. The two models are thus analogous to the two major GIS data structures, vector (patch-corridor-matrix) and raster (landscape continuum). Because the patch-corridor-matrix model treats landscape elements as discrete units, the landscape continuum model is likely better able to capture heterogeneity that is present in both forest remnants and other habitats and is thus a more realistic characterization for many fragmented landscapes. However, examining fragmented landscapes from the context of both models helps to emphasize the relationship between how changes in landscape structure (e.g., deforestation, patch isolation) are related to the underlying functional changes (e.g., in dispersal or migration).

The differences between the corridor-patch-matrix model and the continuum model are evident when looking at real world landscapes. Figure 7.1 shows an area of ponderosa pine and mixed conifer forest at Valles Caldera National Preserve in northern New Mexico that has been subjected to different harvesting techniques at different times. It is possible to classify the areas, as we have done in the photo, into discrete patches as a function of logging history (or for that matter, vegetation cover type, or even classes including both logging history and vegetation type). However, it is clear that there is considerable variability in forest structure even within the “homogeneous” patches (this also underscores the importance of scale, since the resolution of the
data and the scale at which patches are being delineated will greatly influence the definition of the landscape structure).

This example illustrates an important practical tradeoff that is worth discussing briefly: it is functionally much easier (though not necessarily more correct) to characterize landscapes into discrete patches, but there is a greater resulting loss of information on variability and heterogeneity. Further, methods of quantifying landscape attributes are much easier for the corridor-patch-matrix model and analytical techniques are better developed and much more familiar to most ecologists (e.g., using multivariate parametric or non-parametric statistics to link ecological response variables to independent variables describing landscape structure).
Conversely, quantifying elements of landscape structure in a continuum representation will likely involve the use of less common techniques, both to derive the surfaces (e.g., linking remotely
detected values of NDVI to forest biomass: Gemmell et al. 2002) and to quantify patterns of heterogeneity (e.g., geostatistics, wavelets; e.g., Li and Reynolds 1995; Csillag and Kabos 2002). Further, the linkage to ecological responses will be less intuitive for many scientists and managers. Thus, as is always the case with classification and clustering, this raises the question of how much additional benefit is provided to a scientist or manager by investing in a more spatially-explicit representation. Common sense would dictate that as heterogeneity (either structural, compositional or spatial) increases in either the forest remnants or the matrix (or both), the value of a continuum approach would likely increase because it would capture potentially significant variation in the landscape elements. In cases of low heterogeneity (e.g., a row cropped Iowa cornfield), the additional effort required to document heterogeneity may yield little information over and above assuming a homogeneous surface. Finally, it is worth noting that just because a landscape continuum may capture habitat heterogeneity, it is still up to ecologists to determine its ecological significance (if any). Studies examining the importance of landscape heterogeneity (and how it is represented) are only just beginning to be undertaken (e.g., Malanson 2002a,b).

The importance of spatial heterogeneity within remnants and the matrix has significant implications on the design and implementation of new silvicultural systems. Different systems (e.g., clear cutting, shelterwood cutting, selection cutting) create very different forest patterns across the landscape and may be expected to have different area effects, isolation effects and edge effects. Systems that reduce the impact of one fragmentation effect may increase the effect of another (e.g., selection cutting may result in less area effect but increase isolation effects through the creation of a larger transportation network). Of particular recent interest has been the use of structural retention harvesting strategies, which involve retaining structures from the
original stand at the time of harvest (Franklin et al. 1997). Structural retention may make substantial contributions to biodiversity conservation by: 1) maintaining biota on a harvested site by conserving essential habitat (e.g., snags or logs), 2) adding structural heterogeneity to the stand and allowing organisms to return more quickly, 3) modifying post-harvest conditions (e.g., microclimate), making it more suitable for certain species, 4) facilitating movement of species through the harvested areas, and 5) buffering protected zones such as riparian areas within the matrix (Lindenmayer and Franklin 2002). In the context of our research on forest fragmentation, retention can be used to increase the habitat quality of the matrix (reducing the area effect), facilitate movement through the matrix (reducing the isolation effect), and limit the number of hard edges in a landscape (potentially reducing the importance of the edge effect). The extent to which these functions are enhanced, however, depends on what structures are retained, how much is retained, and in what spatial pattern the retentions are left.

The effectiveness of various silvicultural strategies are not well known, and there is an urgent need for carefully designed research to: 1) identify and quantify relationships between structural or floristic features of stands and the requirements of forest dependent biota, and 2) evaluate the effectiveness of specific retention and stand management prescriptions in achieving goals (Wilson and Carey 2000; Lindenmayer and Franklin 2002; Crow et al. 2002; Drever and Lertzman 2003). Perhaps one of the best models for such research is the Demonstration of Ecosystem Management Options (DEMO) Study, an ongoing large-scale experiment on structural retention harvests in Pacific Northwestern forests (all information on the DEMO Project is from: http://www.cfr.washington.edu/Research.demo/index.htm). In 1992, the Pacific Northwest Region of the USDA Forest Service received Congressional direction to establish a major silvicultural experiment in Washington and Oregon “using new forestry and landscape
management techniques”. The DEMO Study evolved as a regional interdisciplinary experiment to examine the responses of diverse groups of forest organisms and processes to variation in the amount and/or pattern of live-trees retained through harvest. The study consists of a randomized complete block design, consisting of six, 13-ha structural retention treatments, including a control, replicated at each of six blocks (geographic locations). The six treatments include:

1) 100% retention, a 13-ha control that provides a baseline for assessing the effects of harvest treatments on ecosystem composition, structure, and function.

2) 75% aggregated retention, in which three circular, 1-ha patches are harvested in a triangular array, removing 25% of the original stand area. The pattern and distances between "gaps" are consistent among experimental blocks.

3. 40% dispersed retention: a proportion of the dominant and co-dominant trees are retained in a relatively even distribution throughout the treatment unit. The total basal area retained is equivalent to that of the corresponding aggregated retention treatment (40% aggregated retention).

4. 40% aggregated retention: five undisturbed, 1-ha circular aggregates are retained at fixed distances from each other; all merchantable trees in the surrounding area are cut and removed.

5. 15% dispersed retention: a proportion of the dominant and co-dominant trees are retained in a relatively even distribution throughout the treatment unit. The total basal area retained is equivalent to that of the corresponding aggregated retention treatment (15% aggregated retention).

6. 15% aggregated retention: two undisturbed, 1-ha circular aggregates are retained at fixed distances from each other; all merchantable trees in the surrounding area are cut and removed.

In conclusion, we echo the conclusions of previous authors who have emphasized the importance of understanding how biota use all elements of the landscape, including the matrix (e.g., Åberg et al. 1995; Flather and Sauer 1996). As Wiens (1989) has noted:

“(A) focus exclusively on fragmentation of habitats misses the point that it is often the structure of the entire landscape mosaic rather than the size or shape of individual patches (that matters)….”
Figure 7.2. A wildlife corridor in logged forest that provides a connection from a stream to ridgeline. Photo by R. Meggs, in Lindenmayer and Franklin (2002).

Corridors and connectivity

Because one of the primary effects of fragmentation is to isolate forest patches through the creation of an intervening non-forested habitat, structural and functional connectivity of the landscape may be altered. One of the primary means that has been advocated for promoting connectivity has been the creation of corridors, narrow patches of land that connect similar patches but that differ from the surrounding matrix (Fig 7.2). Corridors are thought to increase the movement of individuals among habitat patches, promote genetic exchange, and facilitate the recolonization of suitable habitat patches (Tewksbury et al. 2002). Corridors may also reduce mortality during interpatch movement (Beier 1993) and direct the movement of a broad range of taxa across the landscape (Haddad et al. 2003). Species that seem to benefit most from corridors are those that avoid dispersing through open habitat and species for which habitat suitability is the primary factor influencing dispersal (e.g., Baur and Baur 1992). They can also provide additional habitat area (Bennett 1998), increase the foraging area for wide-ranging species, and
serve as refugia from large disturbances (Noss 1987). Despite such evidence and the widespread acceptance of corridors as management tools, debate continues over the ability of corridors to increase connectivity for many species, and their effectiveness for conserving biodiversity continues to be questioned by some scientists due to a lack of randomized and replicated field experiments (Simberloff and Cox 1987; Simberloff et al. 1992; Beier and Noss 1998). Corridor benefits are also species-specific (Mabry et al. 2003), making general guidelines for corridor implementation imperfect at best. Nonetheless, a few generalizations can be made about the effectiveness of corridors.

Given that fragmentation is associated with the loss of forest area and decreased connectivity, the most effective corridors will be those that support breeding populations and dispersal of their offspring as well as facilitate the general movement of biota (Sieving et al. 2000; Lindenmayer and Franklin 2002). For example, Hudgens and Haddad (2003) found that emigration and habitat specific mortality rates were key determinants of the effects of simulated corridors on population sizes. The value and effectiveness of corridors, however, will also likely depend on interactions between habitat quality in the matrix and the extent of deforestation. In landscapes with an inhospitable matrix, the value of corridors will vary non-linearly as a function of deforestation levels. At low levels of deforestation, structural and functional connectivity both remain initially high. As deforestation increases, structural connectivity changes most rapidly around a threshold value (e.g., 60% forest cover in random landscapes), with lower changes in structural connectivity at high levels of forest loss. Functional connectivity, however, is the key to understanding species movement in fragmented landscapes, and it varies as a function of many traits other than structural connectivity (e.g., the distribution of stepping stones, species-specific responses to landscape characteristics). For some species, landscapes remain effectively
connected at even very low forest cover (<10%) while functional connectivity for other species may be reduced with even relatively minimal forest loss. Corridors would be most valuable, at least in terms of linking disjunct habitat patches, at levels where functional connectivity exhibits the most rapid decreases with small changes in landscape structure.

The relationship between connectivity and corridor value is further complicated when the complexity of matrix heterogeneity is factored in. As With (1997) noted, corridors are particularly appealing within a patch-based landscape framework in which habitat is considered to be either suitable or unsuitable (the binary landscape representation discussed earlier) because they provide a physical (and theoretically functional) linkage between areas of suitable habitat. As the matrix becomes more permeable or of higher quality, the value of corridors should decrease. Robichaud et al. (2002), for example, found that songbird use of a riparian buffer strip decreased over a four-year period as birds increasingly used the adjacent, regenerating clear cut.

Thus while generalizations concerning corridor effectiveness may be useful, the complexity of factors involved suggests that corridors should not automatically be assumed to be a part of every conservation strategy (Lindenmayer and Franklin 2002). Whether corridors are effective depends on a wide range of factors that are specific to individual cases, including: corridor characteristics (e.g., length and width: Andreassen et al. 1996), habitat suitability within the corridor (Bowne et al. 1999) and the adjacent matrix (Perault and Lomolino 2000), remnant patch demography (Andreassen and Ims 2001), and characteristics of the target species, including its dispersal method and behavior (Murphy and Noon 1992). What is clearly needed are more studies that document not only whether corridors facilitate the movement of species across the landscape but how such movement differs from that in the absence of corridors, recognizing that matrix characteristics are important. Studies addressing the willingness of
species to use corridors (e.g., Sieving et al. 2000), cross gaps (e.g., Bélisle and Desrochers 2002; Bowman and Fahrig 2002), and cross different matrix structures (e.g., Mabry and Barrett 2002; Berggren et al. 2002) are especially needed. It may be that in some cases the best general strategy to enhance connectivity for some biota is to manage for or improve structural conditions in the matrix rather than investing in corridors (Lindenmayer and Franklin 2002).

Natural heterogeneity

Patchiness and spatial heterogeneity have been a factor for centuries in many forested landscapes due to natural disturbance regimes, including gap phase dynamics (Watt 1947), fires (Arno 1980), and blowdowns (Veblen et al. 2001). Many species have even developed adaptations to the common disturbances in their ecosystems (e.g., Barton 1999). Evaluations of current fragmentation levels and effects thus need to address not only the question of how fragmented landscapes currently are, but also how different landscape structures are from some temporal frame of reference (e.g., pre-European settlement conditions). For example, pre-European settlement forests of the Southeast as well as ponderosa pine forests in the western United States have been generally described as open or park-like. Changes in the disturbance regime (specifically, the suppression of fire) have actually led to less fragmented conditions and less spatial heterogeneity, favoring different species as a result. Conversely, other human activities such as logging may result in a decline in stand structural complexity (e.g., Kupfer and Kirsch 1998), with other implications for plant and animal species.

The relationship between natural heterogeneity and fragmentation has usually been addressed within the context of whether human disturbances such as logging can be designed to replicate or mirror the natural disturbance regime, often with a goal of reducing the total impact
of the treatment. However, human disturbance regimes will never be exact replicates of natural disturbances; logging, for instance, differs from most natural disturbances in its frequency and regularity, the species it favors, its effects on ecosystem function, the complexity of the remaining forest structure, and the spatial distribution of structural attributes (e.g., Mladenoff et al. 1993; McCarthy and Burgman 1995). Further, as traditionally practiced, existing silvicultural systems do not incorporate the landscape-level complexity that is characteristic of natural disturbance regimes (Franklin et al. 1997). Rather than trying to emulate natural disturbance regimes, the objective, argue Lindenmayer and Franklin (2002), should be to use information on natural disturbances to aid in the development of silvicultural systems that encourage the maintenance of biodiversity in the affected landscapes, including not only uncut remnants but also the matrix.

Hunter (1993) has suggested three properties of natural disturbance regimes that can guide management plans: frequency, spatial pattern, and levels of biotic legacies. Buskirk et al. (2000) also suggest that aspects of human fragmentation can be evaluated with respect to natural heterogeneity on the basis of: 1) novelty, which relates to how often a similar perturbation has been experienced over the evolutionary history of a forest community, and 2) distinctness, meaning how different a perturbed site is from the structure and function of the unaffected area around it. Using the southern Rocky Mountains as an example, a primitive trail is neither new nor very distinct, a single tree removal is not distinct but it is novel because the scale of the natural disturbances in that area are very different, and an interstate highway is both distinct and novel (Fig. 7.3). Knight and Reiners (2000) expand on these ideas and propose that harvesting regimes should be evaluated in light of the surrounding natural heterogeneity. They argue that landscapes with an intermediate level of natural heterogeneity (near the thresholds discussed
Figure 7.3. Aspects of human fragmentation can be evaluated with respect to natural heterogeneity on the basis of: 1. novelty, which relates to how often a similar perturbation has been experienced over the evolutionary history of a forest community, and 2. distinctness, meaning how different a perturbed site is from the structure and function of the unaffected area around it. Figure from Buskirk et al. (2000).

Figure 7.4. Hypothetical relationships between the potentially adverse effects of further fragmentation, such as by clear-cutting, and the natural heterogeneity of patchiness of the landscape. Figure from Knight and Reiners (2000).
above) may often be those that are most susceptible to further fragmentation (Fig 7.4), but that substantial additional work is still needed in this area.

We believe that the relationship between natural heterogeneity and logging is a tremendous area for additional research. The potential effectiveness of various alternative silvicultural strategies such as structural retention is based on the principles discussed throughout this paper but is largely undocumented, which is somewhat surprising given the numerous calls for more basic information on the effects of natural and human disturbances in forested ecosystems (e.g., National Research Council 1990). Lindenmayer and Franklin (2002), for example, argue that silvicultural research needs to consider the ways that various aspects of forestry operations (e.g., transportation networks and logging methods) can be modified to enhance biodiversity and ecosystem operation or at least minimize negative effects. We would emphasize that these types of studies need to be replicated and interpreted within the context of different ecoregions because of the unique disturbance regimes and resulting natural heterogeneity that are inherent to each.

*Edge-mediated dynamics*

Many of the most severe impacts of forest fragmentation are related to the increased susceptibility of forest remnants to edge effects, which have thus become a topic of interest for conservation biologists and forest managers studying forest fragmentation. Extensive work has focused on documenting changes in microclimate and biotic assemblages along edges and determining the depth to which such changes penetrate into the forest interior (*see Murcia 1995 and Baker and Dillon 2000 for recent reviews*). Research on these “traditional” edge effects is crucial and has provided a wealth of information about the consequences of edge creation in a
range of forest types, but such studies often focus on a relatively narrow band (e.g., 10-100 m) of affected forest at or near the interface with a non-forested ecosystem.

It is clear that studies of forest edges must not only document the characteristics of the edges themselves but also seek to uncover the dynamic manners by which edges alter key ecological processes in forest remnants and across the landscape as a whole (boundary dynamics: Wiens et al. 1985; edge-mediated effects: Fagan et al. 1999). This conceptual shift necessitates the utilization of stand- and landscape-level approaches to the study and understanding of the diverse nature of edge effects (e.g., Kupfer 1995; Laurance 2000). Researchers are now beginning to address questions concerning the role of such edge-mediated effects in fragmented landscapes, including the importance of forest edges in influencing the flows of energy, matter and species both within and between landscape elements and the effects of such changes on species interactions (e.g., Fagan et al. 1999; Cadenasso and Pickett 2000).

In addition to serving as habitat for edge-adapted species, Forman and Moore (1992) posited that edges can: 1) function as conduits for the flow of objects (defined here as matter, plant propagules or animals) across a landscape, 2) act as filters or barriers controlling the flow of objects between adjacent ecosystems, 3) serve as a source of objects which are exported to the adjacent ecosystems, and 4) absorb or accumulate objects originating in the surrounding ecosystems. Evidence for each of these roles is accumulating (Alexander and Waters 2000; Develey and Stouffer 2001; Weathers et al. 2001; Bhattacharya et al. 2003), and such studies are important because they begin to shift the focus of edge communities away from edge structure to function (Cadenasso and Pickett 2000; Cadenasso et al. 2003).

Perhaps one of the best-documented cases of edge-mediated effects involves the function of edges as seed sources. Studies have shown that edge individuals may serve as an important
source of seeds dispersed into both the adjacent non-forested habitat (Greene and Johnson 1996) as well as the forest remnant itself (Cadenasso and Pickett 2001). Ranney et al. (1981) argued that edges provide propagules of a different species composition than might otherwise be available to tree replacement processes in the forest interior because of their unique compositions. By reducing forest patch size, humans effectively increase the dissemination of seeds from edge habitats to the forest interior as the reduction in forest patch area brings a greater percentage of interior forest within the dispersal range of edge propagules. Because species that are well adapted to the microenvironmental conditions that occur at edges are also well adapted to conditions in canopy gaps, such effects have been shown to have an important influence on gap successional processes (Kupfer and Runkle 1996, 2003; Kupfer et al. 1997).

Treating edges as dynamic, functioning habitats with interactive ties to the forest patch as a whole is a drastic change from the traditional view of edge effects. It reinforces the need to: 1) re-evaluate our view of edges and strive for a more complete understanding of their roles in landscape functioning, and 2) explore the importance of reserve boundaries in affecting reserve functioning and viability. Knowledge of boundary dynamics would, for instance, aid in the design of buffer areas around reserves to help maintain interior processes and may help to inform decisions concerning the amount of edge that is created during silvicultural treatments. In particular, the manner in which forest boundaries may affect patterns of dispersal, growth, establishment and death throughout a reserve and across a landscape is still poorly known.

*Landscape Metrics: Future Research Needs*

Landscape metrics have become a ubiquitous tool in the study of forest fragmentation (Haines-Young and Chopping 1996; Lindenmayer et al. 2002a), both as a means of
characterizing the pattern and composition of a landscape at a given time (e.g., as part of an inventory and monitoring process) and as a means of better understanding ecological responses to changes in landscape structure (e.g. by statistically linking measures of forest fragmentation to population dynamics). Understanding and clarifying the responses of forest-dependent organisms to fragmentation and changes in the spatial pattern and heterogeneity of ecosystems continues to be an important area for future research.

As was discussed earlier, results of studies using landscape metrics to examine wildlife responses to fragmentation have generally been equivocal (Tischendorf 2001). Cale and Hobbs (1994) and Lindenmayer et al. (2002a) suggest that this may be because the metrics used to characterize heterogeneity are not always meaningful for assessing species responses. Part of the problem may be that metrics capture landscape features that are irrelevant to how species perceive and utilize the landscape. One proposed answer to this problem is to develop ecologically scaled landscape indices (ESLI) (Vos et al. 2001). In other cases, species responses may be more dictated by factors such as time since fragmentation or within-patch spatial heterogeneity that are typically not captured effectively by most metrics (Lindenmayer et al. 2002b). Some progress has been made in understanding the relations among different metrics and their relations to landscape structure (Hargis et al. 1998; Trani and Giles 1999). However, current metrics still suffer from issues such as redundancy and potential sensitivity to threshold effects, and the statistical properties and sensitivity of most metrics to changing landscape patterns continues to be poorly understood (Turner et al. 2001; Lindenmayer et al. 2002a). Despite the widespread interest in the use of metrics as ecological indicators, a considerable amount of research is still needed before metrics can serve as anything more than a rough tool in forest management practices.
A second shortcoming of most widely used metrics is that they are based on the definition of discrete patches (e.g., patch area, edge density) and thus sensitive to issues such as class number and scale effects (e.g., grain and extent of the data). If landscape management is to move toward a framework that embraces the existence of spatial heterogeneity within all elements of the landscape, new metrics perhaps involving neighborhood functions that are scaled to specific species will need to be developed and tested. Such metrics will need to focus on capturing spatial heterogeneity (which raises problems of its own, as discussed above), yet will still need to capture relevant aspects of habitat suitability and habitat contrast because species do not respond to heterogeneity per se but rather the heterogeneity of specific habitat elements. Further, these metrics will still face the same ultimate question as patch-based metrics: do they capture the effects of spatial pattern on biodiversity and ecological process in fragmented landscapes?

Finally, in addition to tools and metrics that can be used for mapping and monitoring landscape change, forest managers need tools for projecting fragmentation and habitat change into the future (e.g., Cissell et al. 1999; Lindner and Cramer 2002; Pennanen and Kuuluvainen 2002). Landscape projection models and spatial decision support systems are rapidly becoming important tools in forest management planning, and they hold great promise as a means of bringing landscape ecologists and forest managers together (e.g., Hjortso and Strade 2001; He et al. 2002; Turner et al. 2002). As Boutin and Hebert (2002) noted:

“The ability to produce future landscapes under different management scenarios and to compare these to landscapes produced by natural disturbance regimes will help to focus both managers and scientists on understanding the key interactions among human activities, landscape features, and ecological processes.” (p. 396)
One such example is the HABPLAN model, a computer program developed for creating spatial configurations on the landscape while simultaneously incorporating objectives associated with harvest scheduling (Van Deusen 1999, 2001). This method makes it possible to include goals such as the protection of habitats for endangered species, the protection of water quality through the implementation of buffer zones, and the maintenance of forest connectivity while still meeting pre-specified harvest goals (Fig. 7.5). Such models also underscore the need to incorporate not only environmental factors into understanding fragmentation effects but also socio-economic drivers (e.g., Kangas et al. 2000; Rohner and Boswald 2001).

**How can ongoing work on fragmentation effects be linked to forest management?**

It has been said that: “Forest management isn’t rocket science – it’s far more complex” (e.g., Bunnell 1999b). This certainly applies to the study of forest fragmentation, which is
complicated by the existence of thresholds and non-linearities, the interaction of various fragmentation effects, and the species-specific nature of many biotic responses to fragmentation. Nonetheless, scientists are increasingly being called upon to make contributions that can assist forest and land managers in their decision-making process (e.g., Villard 2002).

With respect to forest fragmentation, an extensive literature has been developed over the last thirty years from which we can draw to create guiding principles for developing comprehensive forest management plans that recognize the effects of fragmentation on forest biodiversity and ecological processes. Such plans need to address the maintenance of suitable habitat for species at a range of scales because individual taxa respond to factors at different spatial and temporal scales. Further, we urge against basing management plans solely (or even primarily) on notions of species richness (or “biodiversity”), which may not be a reliable indicator of community dynamics or ecosystem function. Rather, as has been suggested by Huston (1997), Tilman et al. (1997b) and Grime (1998), compositional changes may be better indicators of functional changes. We use the objectives and principles for developing comprehensive plans for forest biodiversity conservation that are presented by Lindenmayer and Franklin (2002) as our basis for three principles more specifically associated with forest fragmentation.

**Principle 1: Promote connectivity using a variety of approaches.** By altering the degree of structural and functional connectivity in a landscape, deforestation and fragmentation influence population dynamics and persistence in landscapes in a range of ways. The effects of such changes are interactive and non-linear such that the degree of functional connectivity in a landscape is a function of not only inter-patch distance or other measures of isolation but also the
degree of forest loss. Because connectivity is the ease with which species move across a landscape, it can be improved in a range of ways, including not only the creation or reservation of habitat corridors to maintain structural connectivity but also the implementation of stepping stones and other features that help to facilitate the movement of species across the landscape (e.g., Dramstad et al. 1996; Collingham and Huntley 2000). In many landscapes, managing the matrix to increase its suitability as habitat and increase its permeability to movement may be one of the best options for increasing connectivity because connectivity is fundamentally controlled by the degree to which the matrix is hostile or habitable (Wiens 1997). A matrix-based approach may especially benefit poorly dispersing but more competitive species that are at a disadvantage in fragmented landscapes (e.g., Malanson 2002b). These concepts are directly relevant to the development and implementation of silvicultural systems that can be used to help maintain connectivity in logged areas while still meeting pre-define harvest goals.

**Principle 2: Maintain stand structural complexity and landscape heterogeneity.** Two of the primary effects of logging are reductions in the structural complexity of stands and alterations of the landscape’s natural heterogeneity. Structural complexity pertains to: 1) the variety of stand structural attributes that are present in natural forests in an area (e.g., the stand age and size class structure, presence of standing snags and downed woody debris, variation in canopy gap structure, vertical heterogeneity associated with different canopy layers), and 2) how these features are arranged across a landscape (i.e., spatial heterogeneity). Maintaining such structures can be valuable in four ways (Lindenmayer and Franklin 2002): 1) it may allow organisms to persist in logged areas from which they would otherwise be eliminated; 2) it may allow logged and regenerated stands to more quickly return to suitable habitat; 3) it may enhance
the dispersal of animal species through the logged matrix and also enhance plant dispersal by serving as seed sources; and 4) it may be essential to providing within-stand habitat heterogeneity that is needed for some species. Perhaps even more so than with connectivity, research on how alternative harvesting regimes can be used to maintain vertical (structural) and horizontal (spatial) heterogeneity within the logged matrix are needed. Further, because structural and spatial heterogeneity inherently vary among forest types and ecoregions, ecologists can help to inform forest management plans by documenting conditions in a range of forest types that have a range of disturbance histories (e.g., to help understand the effects of biotic legacies).

**Principle 3. Embrace risk spreading and recognize the importance of different conservation strategies at different spatial scales.** Lindenmayer and Franklin (2002) note several advantages to adopting management techniques associated with the principles above, especially when management plans are implemented at multiple scales. First, identifying how changes in forest extent or connectivity associated with fragmentation affect even a single species can be a monumental task (see the literature on the northern spotted owl, as an example) so the adoption of multiple strategies at multiple scales increases the likeliness that suitable habitat, connectivity, heterogeneity, and stand complexity will be provided in at least some parts of the landscape. Second, if one strategy is found to be ineffective (e.g., the establishment of wildlife corridors), others such as structural retention will be in place that might help to protect important elements of the landscape or help to perform the functions intended by the unsuccessful strategy. Using a multi-faceted approach thus reduces the over-reliance on any single strategy that may be found to be of limited value. As Lindenmayer and Franklin (2002) admit, this risk-spreading approach (which focuses on ensuring a range of conditions at all spatial scales) contrasts fundamentally
with the norm of strict production forestry, which tries to limit heterogeneity at both the stand and landscape level, posing potential hurdles to the acceptance and implementation of such an approach. Investment in some strategies may also preclude the implementation of other alternatives – for example, money spent (or revenues forgone) to protect habitat corridors may be money that can’t be spent on protecting other features. Research that continues to clarify the importance of fragmentation at various levels of deforestation can help to inform managers when strategies to maintain connectivity may be especially important. Further, research on the importance of habitat quality (e.g., of the matrix or corridors) may help to show the value of sometimes improving the quality of existing habitat over setting aside other areas.

Recent attempts to address the effects of fragmentation in forest management plans and incorporate some of these principles have been made. Cissell et al. (1999), for example, present the development of management plans in western Oregon based on natural disturbance regimes in the area. Their approach involved: 1) stratifying the area based on the dominant fire regimes, 2) identifying special reserve areas, and 3) developing silvicultural prescriptions for each of the non-reserve areas based on the historic patterns of disturbance. Projects in the Chequamegon National Forest in Wisconsin provide another example (Parker 1997). Three alternative management plans were proposed and analyzed that: 1) emphasized the creation of large units of habitat for plant and animal species, 2) emphasized human recreation and creating large habitat units for nongame wildlife species, and 3) emphasized harvesting timber in small (<15 ha) clear cuts (Fig. 7.6 and Table 7.1).
Table 7.1 Landscape attributes under three management alternatives proposed for the Sunken Camp area of the Chequamegon National Forest, WI. Alternatives 1 and 2 were designed to create larger habitat units while Alternative 3 was designed to create dispersed timber harvest activity in small (< 15 ha) clear cuts. Edge effects were calculated using a depth of edge influence of 100 m. Data from Lindenmayer and Franklin (2002).

<table>
<thead>
<tr>
<th>Alternative</th>
<th>Edge (km)</th>
<th>Area of newly created edge (% of landscape)</th>
<th>Area of contiguous interior forest (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>185</td>
<td>18.9</td>
<td>4884</td>
</tr>
<tr>
<td>2</td>
<td>156</td>
<td>15.9</td>
<td>5670</td>
</tr>
<tr>
<td>3</td>
<td>238</td>
<td>24.3</td>
<td>4788</td>
</tr>
</tbody>
</table>

Figure 7.6. Spatial arrangement of timber harvest activities under two alternatives proposed for the Sunken Camp area of the Chequamegon National Forest, WI. (a) Alternative designed to create large habitat units for nongame wildlife species, (b) Alternative to create dispersed timber harvest activity in small (< 15 ha) clear cuts. Figure from Kick (1990) in Lindenmayer and Franklin (2002).
Summary

Due to the rapidly changing state of knowledge concerning forest fragmentation and the importance of addressing fragmentation issues in forest management planning, we have assembled this paper as a way of synthesizing the manners in which fragmentation influences biodiversity and ecological processes. We have done so, in part, by critically contrasting the long-held “fragments as islands” depiction of forested landscapes as forest (areas of uniformly “suitable” habitat) and non-forest (areas of uniformly “unsuitable” habitat) with an approach focused more specifically on issues of habitat heterogeneity in not only forested stands but also in the surrounding non-forested ecosystems. Because evidence suggests that a binary “forest/non-forest” conceptualization of forested landscapes is unrealistic for many applications, we believe that future research needs to continue to address: 1) the importance of variability in habitat quality in fragmented landscapes, 2) the importance of feedbacks and thresholds, and 3) manners by which heterogeneity has been and may be measured and captured. This approach implicitly recognizes the importance of studying and understanding how fragmentation alters flows of energy, matter and species across the modified landscape (including the matrix) and thus a range of key community and ecosystem processes. Such work has important implications in the development of sustainable silvicultural systems as well as the implementation of features meant to foster connectivity in the fragmented landscape (e.g., corridors). Although the individual contributions of area, isolation and edge effects can be conceptually separated, they are inextricably linked in nature and more emphasis is needed on understanding their interaction across the range of deforestation and fragmentation levels.
Suggested References


Evans, T.P., Manire, A., de Castro, F., Brondizio, E., and McCracken, S. 2001. A dynamic model of household decision-making and parcel level landcover change in the eastern Amazon. Ecological Modelling 143: 95–113


McGarigal, K., Cushman, S.A., Neel, M. C. and Ene, E. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html


Rudis, V.A.; Jacobs, D.M. In review. Regional status and change in selected nonnative invasive plants of southeastern United States forests.


Seagle, S.W. Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets? In press, Oikos.


Sumner, J., Moritz, C. and Shine, R. 1999. Shrinking forest shrinks skinks: morphological change in the response to rainforest fragmentation in the prickly forest skink (Gnypetoscincus queenslandiae). Biological Conservation 91: 159-167.


