



Conserving Forest Biodiversity

A Comprehensive Multiscaled Approach

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Critical Roles for the Matrix

The days are over when the forest may be viewed only as trees and the trees viewed only as timber.

—U.S. SENATOR HUBERT HUMPHREY (IN PATTON 1992)

The conservation of biodiversity is one of the fundamental guiding principles for ecologically sustainable forest management. Many existing conservation programs are limited to a primary or exclusive focus on lands contained in reserves for biodiversity conservation. Yet, most forest will be in off-reserve, or *matrix*, lands in the vast majority of forest regions and forest types. Comprehensive strategies for the conservation of forest biodiversity must include both reserves and matrix-based strategies. The importance of the matrix for the conservation of biodiversity in forests reflects its dominance in both temperate and tropical regions—most forest landscapes have been, or will be, actively used and managed. Therefore, many forest-dependent species will occur primarily in matrix lands—or not at all.

How the matrix is managed will influence the size and viability of populations of many forest taxa and thus biodiversity per se. Matrix conditions also greatly influence connectivity between reserves and the movement of organisms. In addition, by acting as buffers, matrix conditions strongly control reserve effectiveness. The matrix must sustain functionally viable populations of organisms that are fundamental to the maintenance of essential ecosystem processes such as nutrient cycling, seed dispersal, and plant pollination—processes that underpin the long-term productivity of ecosystems and their ability to produce goods and services for human use.

The conservation of biodiversity has become a major concern for resource managers and conservationists worldwide, and it is one of the foundation principles of ecologically sustainable forestry (Carey and Curtis 1996; Hunter 1999). This represents a major chal-

lenge for forest management because forests support approximately 65 percent of the world's terrestrial taxa (World Commission on Forests and Sustainable Development 1999). They are the most species-rich environments on the planet, not only for vertebrates, such as birds (Gill 1995), but also for invertebrates (Erwin 1982; Majer et al. 1994) and microbes (Torsvik et al. 1990).

Setting aside networks of dedicated reserves has been the traditional approach advocated by many conservation biologists to conserve the extraordinary biodiversity that characterizes forest ecosystems. Many books and vast numbers of scientific articles have been written on reserve design and selection (Shafer 1990; Noss and Cooperrider 1994; Margules et al. 1995; Anonymous 1996; Pigram and Sundell 1997). In this book, we argue that the conservation of a significant proportion of the world's forest biodiversity will require a far more comprehensive and multiscaled approach than simply partitioning forest lands into reserves and production areas, which we term the *matrix*. This book attempts to lay the foundations for such a comprehensive strategy. Although large ecological reserves are discussed (see Chapter 5), most of this book addresses management of the matrix.

Most temperate and subtropical forest landscapes are composed primarily (or even exclusively) of off-reserve forests, or matrix lands. It has been estimated that between 90 and 95 percent of the world's forests have no formal protection (Sugal 1997). This is particularly true in temperate regions where the most

productive (and species-diverse) forested lands have already been extensively modified by humans (Franklin 1988; Virkkala et al. 1994). Therefore, forests outside reserves are extremely important for the conservation of biodiversity—how they are managed will ultimately determine the fate of much biodiversity.

Our primary objective in this book is to illustrate the importance of the matrix for biodiversity conservation and to propose strategies for enhanced matrix management that can be the basis for a comprehensive approach to maintaining forest biodiversity. We begin in this first chapter by providing our definitions of biodiversity and the matrix. We then illustrate the importance of the matrix for conserving forest biodiversity.

Defining Biodiversity and Ecologically Sustainable Forest Management

There are many definitions of biodiversity. Ours is relatively simple:

Biodiversity encompasses genes, individuals, demes, metapopulations, populations, species, communities, ecosystems, and the interactions between these entities.

There are also many interpretations of ecologically sustainable forest management (Amaranthus 1997). Ours follows Lindenmayer and Recher (1998):

Ecologically sustainable forest management perpetuates ecosystem integrity while continuing to provide wood and non-wood values; where ecosystem integrity means the maintenance of forest structure, species composition, and the rate of ecological processes and functions with the bounds of normal disturbance regimes.

Two other terms widely used in this book are *stands* and *landscapes*. We define a stand as “a patch of forest distinct in composition or structure or both from adjacent areas.”

This definition is often inadequate, such as when modified cutting practices like retention at the time of harvest are employed (see Chapter 8); this means that

stands can actually be composed of structural mosaics (Franklin et al. 2002). However, the simple definition is widely used and understood (see Helms 1998) and, except where noted, we use it in this book.

Given that the focus of this book is on forests, we crudely define a landscape as “many sets of stands,” or patches, that cover an area ranging from many hundreds to tens of thousands of hectares. Drainage basins are a good landscape unit, but it often is necessary to consider much smaller areas or very large regional landscape units.

Defining the Matrix from a Conservation Biology and Landscape Ecology Perspective

In the technical language of landscape ecology, the *matrix* is defined as the dominant and most extensive “patch type” (Forman 1995; Crow and Gustafson 1997). Other criteria used in its definition include the portion of the landscape that is best connected and that has a controlling influence over key ecosystem processes such as water and energy flows (Forman 1995).

In conservation biology and forest planning literature, the “matrix” often refers to areas that are not devoted primarily to nature conservation. In temperate regions in particular, these areas are generally available for resource extraction and use, including the production of commodities, as well as for many other human uses. The definitions of “matrix” from both landscape ecology and conservation biology perspectives are congruent in many temperate regions where reserved lands are clearly in the minority. Conversely, in undeveloped regions, the matrix *sensu* landscape ecology (the dominant patch type) may not be equivalent to the matrix *sensu* conservation biology because the majority of the forested land is in a “natural” condition. For this book, we have adopted a very broad definition of the matrix:

The matrix comprises landscape areas that are *not* designated primarily for conservation of natural ecosystems, ecological processes, and biodiversity regardless of their current condition (i.e., whether natural or developed).

Much of our focus is on biodiversity conservation in wood production areas outside the dedicated reserve system because land allocation in many jurisdictions around the world has created a distinction between reserves and commodity landscapes. The term *matrix management* is used frequently throughout the book, and it refers to approaches to conserve biodiversity in forests outside the reserve system.

Critical Roles for the Matrix

There are four critical roles the matrix plays that relate specifically to biodiversity conservation: (1) supporting populations of species, (2) regulating the movement of organisms, (3) buffering sensitive areas and reserves, and (4) maintaining the integrity of aquatic systems.

Conditions in the matrix will determine the degree to which it contributes positively or negatively to these roles.

Conserving biodiversity for its own sake is only one of many possible goals of matrix management. Another is the production of commodities, such as wood, and services, such as well-regulated flows of high-quality water. Management practices in the matrix will determine whether these goods and services can be sustained, because such practices also influence whether elements of biodiversity critical to long-term sustainability, such as mycorrhizal-forming fungi, are maintained (Perry 1994). Such organisms need to be conserved at functionally effective levels to maintain ecosystem processes (Conner 1988). Hence, conservation of biodiversity in the matrix is fundamental to achieving intrinsic goals (e.g., sustainable production of wood products) and extrinsic goals (e.g., maintenance of regional biodiversity and regulation of streamflow).

Supporting Populations of Species

The matrix can be managed to support broadly distributed populations of many species (deMaynadier and Hunter 1995) (Figure 1.1). Such populations have a lower risk of extinction through demographic stochasticity (Pimm et al. 1988; McCarthy et al. 1994) and environmental variability (Thomas 1990;



FIGURE 1.1. The matrix will be the primary habitat for populations of most temperate forest organisms—or not. The matrix can be managed to provide significant and well distributed populations of many forest species and is essential for maintenance of some species. The conservation of biodiversity in the matrix can have significant positive implications for the maintenance of key ecosystem processes. The conservation of the Australian arboreal marsupial, the mountain brushtail possum (*Trichosurus caninus*), is a classic example. The species is known to consume a wide range of food resources, including hypogaeal fungi that form a mycorrhizal association with the root systems of eucalypt trees. Photo by E. Beaton.

Tscharntke 1992) (Figure 1.2). Large populations also have greater levels of genetic variation (e.g., Billington 1991; Madsen et al. 1999b) and are less likely to suffer extinction as a result of genetic stochasticity (Lacy 1987, 1993a; Young et al. 1996) (Figure 1.3). For example, Saccheri et al. (1998) demonstrated that low levels of genetic variation and subsequent in-

breeding depression significantly increased the risk of extinction of fragmented populations of the Glanville fritillary butterfly (*Melitaea cinixia*) in Finland.

The maintenance of large, well-distributed populations also reduces the risks that an entire population will be extinguished in a single catastrophic event such as a wildfire (Gilpin 1987; McCarthy and Lindenmayer 1999a). In the forests of southeastern Australia, the maintenance of populations of Leadbeater's possum (*Gymnobelideus leadbeateri*) in many habitat

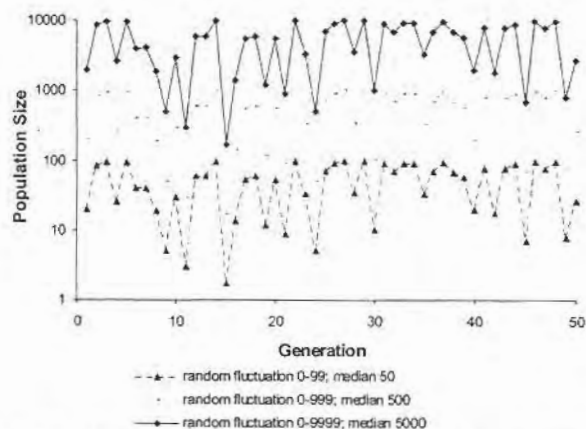


FIGURE 1.2. Larger populations have a lower risk of extinction as a result of environmental variability as indicated in this diagram (redrawn from Thomas 1990). Larger populations distributed across reserves and the matrix have a greater chance of long-term persistence.

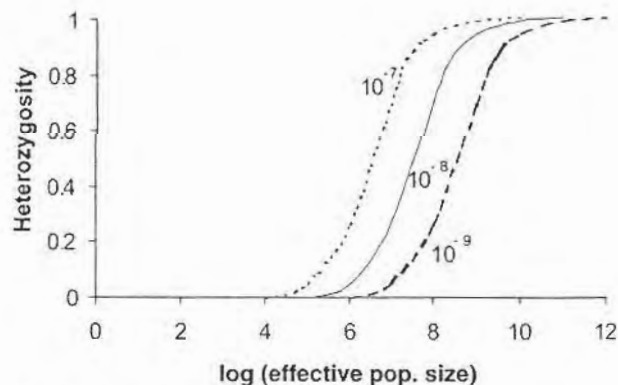


FIGURE 1.3. Relationships between effective population size and genetic variability as reflected by higher levels of heterozygosity in larger populations (redrawn from Frankham 1996). Larger populations distributed across reserves and the matrix should retain higher levels of genetic variability and, in turn, have a greater chance of long-term persistence.

patches is predicted to reduce extinction risks as a result of wildfire (Lindenmayer and Possingham 1995a).

Maintaining populations of species in the matrix can supplement populations in reserves. Species that persist in the matrix will also be those most likely to reside in reserves or remnant patches (Diamond et al. 1987; Laurance 1991a; Ås 1999; Renjifo 2001). The contribution of matrix populations to the persistence of populations within reserves is illustrated by the bald eagle (*Haliaeetus leucocephalus*) in Yellowstone National Park. Although Yellowstone is a large reserve (more than 1 million hectares), the long-term persistence of the species within the park is dependent on dispersal by animals from off-reserve populations (Swenson et al. 1986) (Figure 1.4).

Evidence of rapid species turnover within protected areas (e.g., Margules et al. 1994a) also suggests that individuals dispersing from populations in the

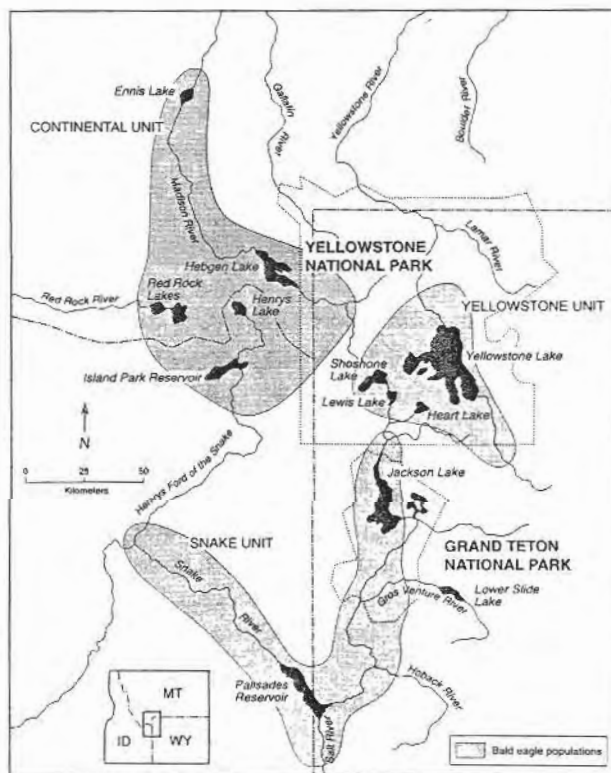


FIGURE 1.4. Populations even in some of the largest national parks often need to be supplemented by populations in matrix lands. This is illustrated by movement patterns among bald eagle populations in the Greater Yellowstone Ecosystem in the central United States (redrawn from Swenson et al. 1986).

matrix can help reverse localized extinctions within reserves (Thomas et al. 1992a; Hanski et al. 1995). Many studies show that the occupancy of reserves and habitat patches by biota is strongly related to their abundance at larger spatial scales (i.e., throughout regions) (e.g., Askins and Philbrick 1987; Askins et al. 1987; Freemark and Collins 1992; McGarigal and McComb 1995; Schmiegelow et al. 1997; Arnold and Weeldenburg 1998; Boulinier et al. 2001).

Regulating the Movement of Organisms

The matrix has a significant effect on connectivity in forest landscapes (Figure 1.5). In most temperate forest landscapes, the matrix will be the most important factor influencing connectivity—the movement of organisms

and genes will be either facilitated or obstructed by the conditions in the matrix (Taylor et al. 1993).

Noss (1991) defined connectivity as “linkages of habitats . . . communities and ecological processes at multiple spatial and temporal scales.”

Connectivity in forest landscapes embodies concepts such as

- Persistence of species in cutover areas
- Species recolonization of cutover areas
- Exchange of individuals and genes among subpopulations in a metapopulation
- The role of suboptimal habitat (which may or may not be logged) in maintaining links with optimal habitat for particular species



FIGURE 1.5. Matrix conditions are the primary controllers of connectivity in landscapes, either facilitating or impeding movement of organisms. In these contrasting views (H. J. Andrews Experimental Forest, western Cascade Range, Oregon, United States): (A) Dispersed retention of 15 percent of dominant trees and woody debris on this cutover facilitates movement of many organisms. (B) Clearcutting provides hostile conditions for movement of many organisms. Photos by J. Franklin.

Facilitating connectivity in the matrix may prevent populations of species in reserves from becoming isolated and fragmented (Burkey 1989). It also can allow populations to maintain or increase their demographic and genetic size (Lacy 1993a; Saccheri et al. 1998), thereby enhancing chances of long-term persistence (Scotts 1994). Connectivity is also important because of the role of movement in shaping distribution and abundance patterns (Stenseth and Lidicker 1992)—it underpins processes such as localized extinction and recolonization dynamics (Brown and Kodric-Brown 1977) and influences patterns of gene flow (Leung et al. 1993; Mills and Allendorf 1996).

For plants, connectivity may include not only movements of species and populations, but also the movement of propagules such as spores, pollen, and seeds. In the case of animals, connectivity involves five broad types of movement (modified from Hunter 1994):

1. Day-to-day movements, such as those within home ranges or territories. These can be small for species such as adult frogs, or large in the case of wide-ranging animals like bats (e.g., Lumsden et al. 1994) or large vertebrates like the black bear (*Ursus americanus*; Klenner and Kroecker 1990).
2. Dispersal events between the natal territory and suitable habitat patches (Wolfenbarger 1946). These are typically made by juvenile or sub-adult animals attempting to establish new territories (Stenseth and Lidicker 1992).
3. Annual patterns of long-distance migration, which can span continents and/or hemispheres (Keast 1968; Flather and Sauer 1996).
4. Nomadic movements made in response to temporal and spatial variability of important resources (e.g., food; Price 1999).
5. Large shifts in distribution patterns in response to climate change. These have typically been slow in the past (Keast 1981), but more-rapid and extreme changes are expected in response to global climate change (Peters and Lovejoy 1992; see Chapter 5).

Connectivity is controlled by conditions such as appropriate vegetation cover or key structures (e.g., logs) in the matrix. Connectivity relates, in part, to the extent of matrix hostility, or "permeability," for movement

(Wiens 1997a; Hokit et al. 1999). Matrix hostility and an associated lack of connectivity may result in suitable habitat remaining unoccupied, meaning that the spatial distribution of a species may not directly correspond to the spatial distribution of available habitat (Wiens et al. 1997). The connectivity role of the matrix is illustrated by a lack of gap-crossing ability among some forest birds (Dale et al. 1994; Desrochers and Hannon 1997), resulting in habitat fragmentation. The reluctance of some species of forest birds to move through open areas has been documented in many studies (e.g., Martin and Karr 1986; van Dorp and Opdam 1987; Bierregaard et al. 1992). Conversely, fragmentation-tolerant species will typically be those that can readily cross matrix lands and colonize isolated patches (Villard and Taylor 1994; Robinson 1999).

A matrix that provides a high degree of connectivity is critical, because habitat loss and habitat fragmentation are major contributors to biodiversity loss (Wilcove et al. 1986; Groombridge 1992). For example, Angermeier (1995) showed that a lack of connectivity contributed to extinction proneness in fish. Because natural forest landscapes are typically characterized by high levels of connectivity (Noss 1987; Lindenmayer 1998), the connectivity role of the matrix assumes even greater importance. Species that were abundant and well distributed in such well-connected landscapes may not have evolved well-developed dispersal mechanisms. Such taxa with relatively low mobility may be vulnerable to landscape change and fragmentation because their dispersal systems are maladapted to reduced levels of connectivity.

Buffering Sensitive Areas and Reserves

Completely open conditions in the matrix produce significant biotic and abiotic edge effects in adjacent forest patches (e.g., Lovejoy et al. 1986; Murcia 1995) with substantial negative implications for biodiversity conservation (Paton 1994; Richardson et al. 1994). The intensity of the edge interactions between two landscape units (e.g., a patch and the surrounding matrix) is typically directly related to their level of structural contrast. Matrix management strategies that reduce the contrast in structural and biophysical conditions between neighboring areas can, therefore, significantly reduce the intensity and depth of edge effects (Parry 1997; Matlack and Litvaitis 1999) (Figure

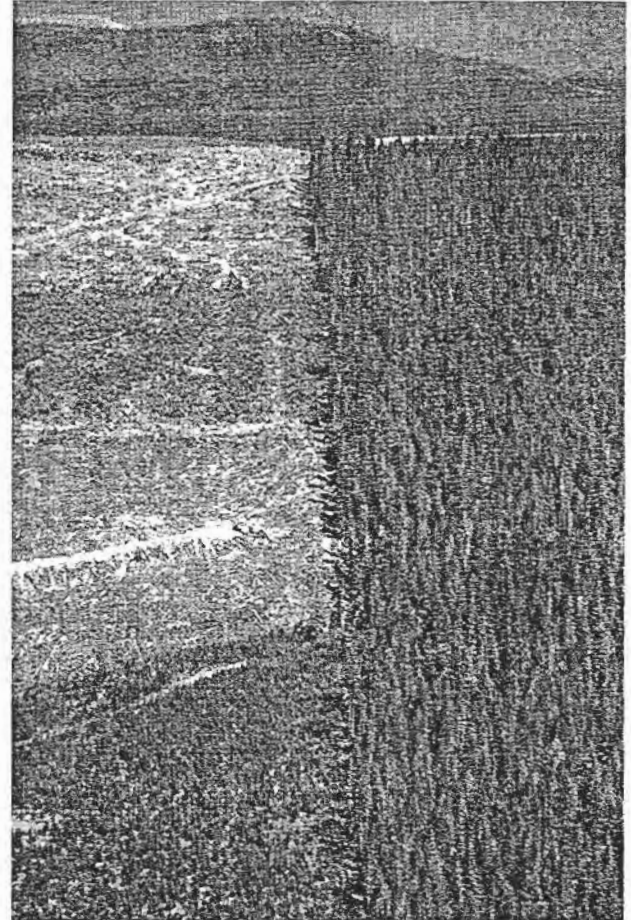


FIGURE 1.6. Matrix conditions determine the degree to which reserves and other sensitive areas are buffered. (A) Retention of tree aggregates in this cutover buffer conditions in an adjacent forest patch (Weyerhaeuser Company lands, eastern Vancouver Island, British Columbia, Canada). (B) Sharply defined boundary between reserved federal lands (right) and industrial forest lands (left) (Cascade Range, Washington, United States). Photos by J. Franklin.

1.6). Managing the matrix-to-buffer edges can substantially increase the effective size of small or medium-sized reserves and other protected areas embedded within the matrix (Janzen 1983; Schonewald-Cox 1988; Nelson 1991; see Chapter 6); processes that can negatively influence reserves can be reduced and the area available for species requiring forest-interior habitats expanded.

To illustrate the magnitude of buffering, Harris (1984) believed that an old-growth patch bounded by a recent clearcut would need to be ten times larger than one surrounded by mature forest to achieve the same area of interior forest habitat (Figure 1.7). In the case of fire risks and edge effects, mature forest buffers may reduce the chance of a fire burning into an old-growth

patch (Harris 1984) because the probability of ignition and spread declines with increasing age in some forest types (Agee and Huff 1987). Similarly, an old-growth forest surrounded by a mature stand may support different species or larger populations of a given taxon than the same stand bordered by a recently clearcut forest (Lindenmayer et al. 1999a,b).

Maintaining the Integrity of Aquatic Systems

Aquatic ecosystems support much of the biodiversity in forest landscapes. Aquatic ecosystems include surface water bodies (rivers, streams, ponds, lakes, and swamps) as well as saturated subterranean habitats such as the hyporheic zone (the zone below and

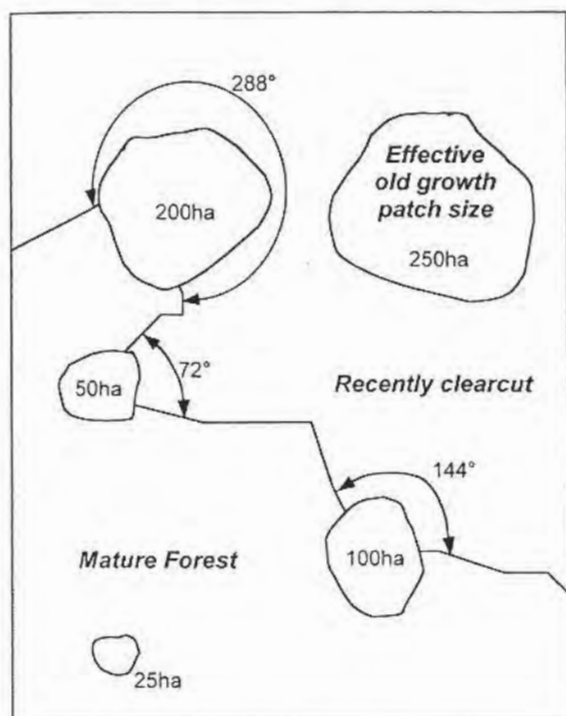


FIGURE 1.7. The buffering effect of the matrix on old-growth forest—the diagram shows the size of an area of old-growth forest needed to maintain interior conditions in a matrix dominated by recently cut forests (250 hectares in size) contrasted with one surrounded by mature forest (25 hectares in size). Redrawn from Harris 1984.

adjacent to the surface stream; Stanford and Ward 1993; Stanford et al. 1994). Aquatic ecosystems and their associated biodiversity have not received as much attention as terrestrial ecosystems in conservation biology, even though they can be heavily, and sometimes permanently, impacted (Michaelis 1984; Forest Ecosystem Management Assessment Team 1993). Maintaining and/or restoring the integrity of aquatic ecosystems must, therefore, receive high priority.

As the dominant patch type in most temperate landscapes, the matrix strongly influences the condition of aquatic ecosystems and water quality (Doeg and Koehn 1990; Naiman 1992) (Figure 1.8). Vegetation conditions in a watershed, especially the type and density of forest cover, directly influence the structure, environment, and diversity of associated aquatic ecosystems (Naiman 1992). Terrestrial vegetation also



FIGURE 1.8. Matrix conditions determine the degree to which the integrity of aquatic ecosystems are maintained. (A) Valley of the south fork of the Hoh River, which is buffered by federal park lands (Olympic National Park, Washington, United States). (B) Steep mountain slopes that have been roaded and clearcut (eastern Vancouver Island, British Columbia, Canada). Photos by J. Franklin.

regulates the paths and rates of water movement, erosion, and sediment transport through a watershed.

Natural forests typically provide a stable landscape context for the development of aquatic ecosystems and organisms (Likens 1985; Naiman and Bilby 1998). Forest cover mutes environmental extremes, such as in-stream temperature fluctuations; provides energy and nutrient inputs; filters sediments; and provides large woody debris, which is an essential structural element of many aquatic ecosystems (Harmon et al. 1986; Maser et al. 1988). Forest cover can influence storm response such as by reducing peak flood flows. Forests also can extend runoff in watersheds, such as those dominated by spring snowmelt. Erosion is also minimized in natural forest landscapes, resulting in high-quality water with low levels of sediment and dissolved and suspended materials (e.g., Ghassemi et al. 1995).

Harvesting practices, rotation lengths, and the density and quality of road systems are significant variables influencing the integrity of associated aquatic ecosystems (e.g., Vos and Chardon 1998; see Chapter 7). Decisions about what constitutes a significant watercourse, the extent of stream or riparian buffers (e.g., width and lineal extent), and forestry practices allowed within the buffers (e.g., levels of tree harvest) are also critical (Haycock et al. 1997). Clearcutting on short rotations, extensive and poorly constructed and maintained road systems, and the limited use of stream buffers can lead to the degradation of associated aquatic ecosystems (e.g., Silsbee and Larson 1983; Graynoth 1989). Conversely, extensive buffering, restrictions on harvesting on steep slopes and unstable soils, and limited road densities of well-constructed and well-maintained roads are practices that contribute to the diversity and integrity of aquatic ecosystems (Clinnick 1985; O'Shaughnessy and Jayasuriya 1991; Barling and Moore 1994). One difficulty in assessing linkages between terrestrial and aquatic ecosystems is that cause and effect are often highly displaced in time and place with regard to sources, sinks, and movement of sediment and coarse woody debris (e.g., Bormann and Likens 1979; Langford et al. 1982). However, long-term assessments of material flows in watersheds are an essential part of a forest planning process.

Providing for the Production of Commodities and Services

The environment returns an estimated \$US33 trillion in goods and services to human society each year (BirdLife International 2000). In temperate forest regions, the matrix is the primary zone for the production of goods and the provision of services (Franklin 1993a). Management practices and conditions in the matrix will determine the quality, quantity, and sustainability of goods and services obtained from forests (Chapin et al. 1998) (Figure 1.9). Humans derive a variety of goods from forests (Costanza et al. 1997). Production of wood fiber is a major one—wood products contribute \$US400 billion annually to the world market economy (or about 2 percent of total gross domestic product) (World Commission on Forests and Sustainable Development 1999). Services from forests include the regulation of streamflow, soil protection, and nutrient retention and cycling. Forests are also recognized as a major carbon sink—another important ecosystem service (Harmon et al. 1990; Brown et al. 1997; Pinard and Putz, 1997; Wayburn et al. 2000; Harmon 2001).

Many elements of biodiversity need to be conserved within the matrix to sustain the long-term production of wood and other products, as well as ecosystem services (Pimentel et al. 1992, 1997). Losses of elements of forest biodiversity may impair essential ecosystem functions. Examples include organisms that play key roles in the decomposition of organic matter (McGrady-Steed et al. 1997), pollination (e.g., Prance 1991; Robertson et al. 1999), seed dispersal, and the formation of mycorrhizal associations (Maser et al. 1978). Changes in biodiversity could influence the long-term floristic composition and stand architecture of forests (Claridge 1993), which could have negative ramifications for the sustained production of commodities. This is related to the "insurance hypothesis," which suggests that higher levels of biodiversity should lead to the maintenance of more reliable ecosystem functions, particularly when environmental conditions change (Naeem 1998).

Matrix management is also important for conserving ecosystem processes by emphasizing the importance of biodiversity conservation in the matrix as well as conservation of genes, species, and populations for

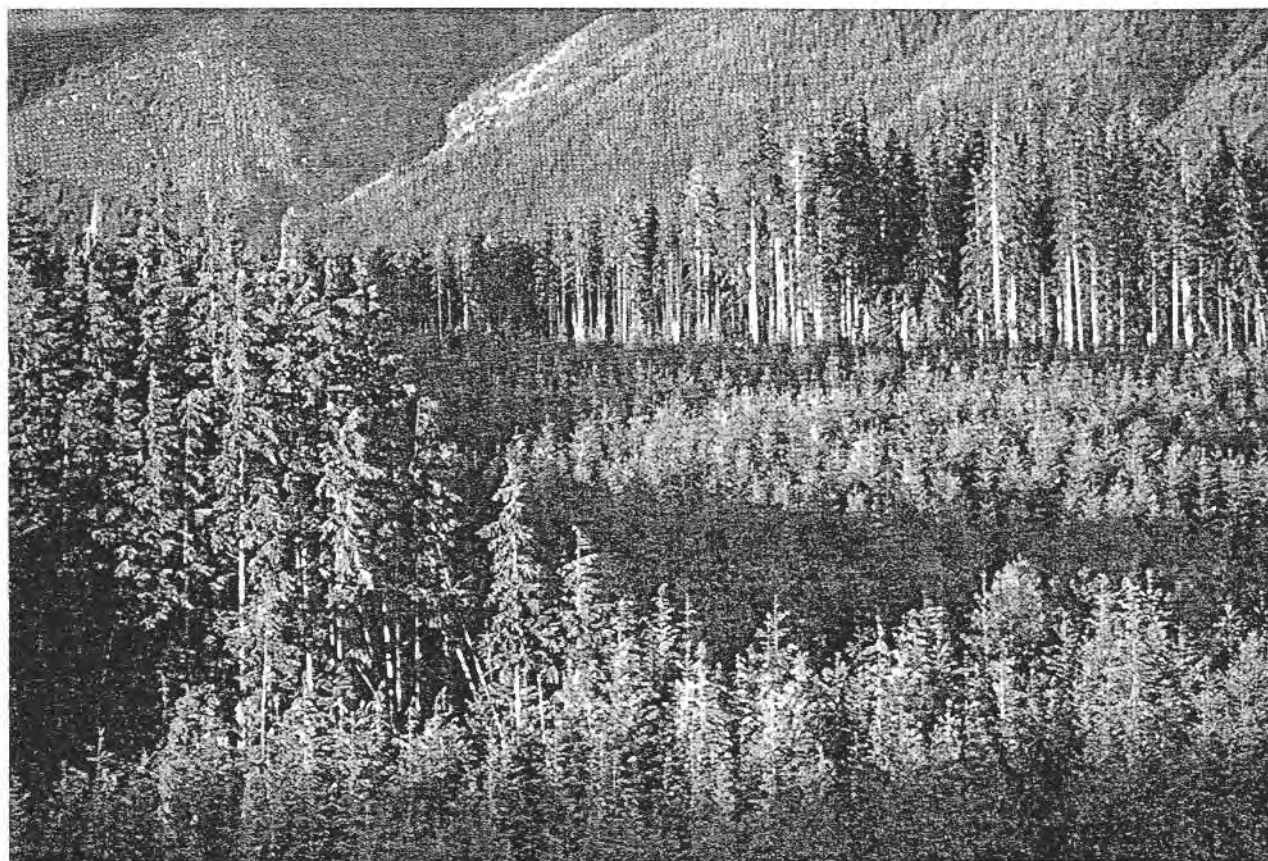


FIGURE 1.9. The matrix is the source of most commodities, such as wood, and services, such as well-regulated flows of high-quality water. Maintaining long-term productivity of such lands and their ability to maintain natural levels of hydrologic and geomorphic processes is critical (managed forest landscape in Olympic State Experimental Forest, Washington, United States). Photo by J. Franklin.

their own sake (Simberloff 1998). This is why Conner (1988) recommended that organisms be conserved at functionally viable numbers to ensure their ecological "effectiveness" in the maintenance of ecosystem processes.

Many of the components of forest biodiversity that play important roles in ecosystem processes are inconspicuous invertebrates (Recher et al. 1996), microbes (Torsvik et al. 1990), and cryptogams (Ashton 1986; Vellak and Paal 1999). These taxa have received limited attention in conservation programs, and even when they are considered (e.g., Taylor 1991; Brown et al. 1994) they can be difficult to assess and manage (Forest Practices Board 1998). Such species play pivotal roles in such processes as nutrient cycling and pollination (Goldingay et al. 1991). Lichens, for example, are valuable nitrogen-fixing organisms in many

forest ecosystems as are vascular epiphytes in Australian rainforests and wet sclerophyll forests (Lamb 1991). Similarly, fungi that form mycorrhizae promote the regeneration and growth of trees in most forests, as has been demonstrated in the Douglas-fir forests of the northwestern United States (Perry 1994). Retained patches of vegetation within harvested forests can provide a reservoir of mycorrhizal fungi and soil microbes that subsequently inoculate regenerating forests on a cutover site (Perry and Amaranthus 1997).

Vertebrates also may facilitate ecosystem processes that sustain forest productivity. Hummingbirds pollinate many forest plants (Pauw 1998). Pollen from numerous plant species is carried in the fur of some arboreal Australian animals such as the sugar glider (*Petaurus breviceps*); these animals can be significant

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plant pollinators (Carthew and Goldingay 1997; Goldingay 2000a). Some species of rodents (e.g., voles, shrews, and squirrels) and small and medium-sized forest mammals (e.g., Australian rodents and marsupials) disseminate spores of mycorrhizal-forming hypogaeal fungi (Maser et al. 1977; Claridge and Lindenmayer 1993; Mills et al. 1993). In the case of symbiotic small mammal-fungal interrelationships, activities such as poisoning rodents to enhance tree survival can negatively affect forest growth and ecosystem processes (Maser et al. 1978).

Reduced production of goods and services in the matrix due to impaired ecosystem processes has substantial social and economic costs (Costanza et al. 1997; Pimentel et al. 1997). For example, populations of natural parasites and predators are estimated to accomplish the equivalent of \$100–200 billion worth of pest control—compared to \$20 billion expended on artificial control measures such as spraying (Pimentel et al. 1992). Thus, the loss of natural populations of parasites and predators has massive financial implications for timber and pulp production from native and plantation forests (Pimentel et al. 1992). A useful example of the intersection of pest control and matrix management comes from exotic eucalypt plantations that cover 5 million hectares in Brazil. Strips of native vegetation left within eucalypt plantations support a diverse insect biota, including many natural predators of defoliating lepidopteran caterpillars. These predators may reduce pest populations in the surrounding eucalypt plantations (Zanuncio et al. 1997).

Synergies among Roles of the Matrix

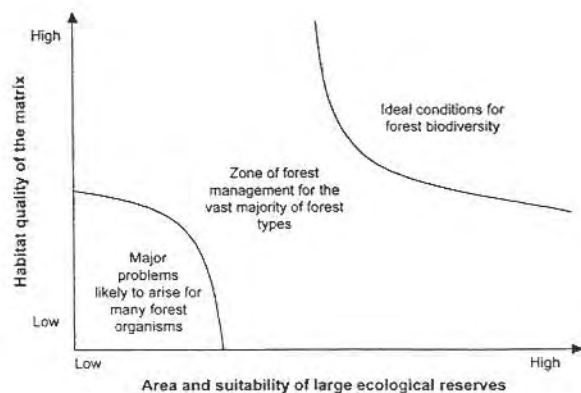
The five roles of the matrix are interrelated. For example, managing the matrix to buffer sensitive areas, such as riparian zones, promotes the conservation of aquatic ecosystems, contributes to improved connectivity for wildlife, and increases the ability of the matrix to support populations of species. This is illustrated in the forests of southeastern Australia, where stream buffers promote the protection of aquatic ecosystems (Clinnick 1985) and its associated biodiversity (Doeg and Koehn 1990) and act as conduits for the movement of terrestrial vertebrates (Hewittson 1997). They also provide habitat for resident animals (Recher et al. 1987; Fisher and Goldney 1997), which may subsequently reinvade post-logging regrowth

stands (Kavanagh and Turner 1994). Some of the species inhabiting riparian buffers may help control populations of forest pests, such as the large, defoliating phasid “stick” insects.

Limitations of a Reserve-Only Conservation Strategy for Biodiversity Conservation

Despite the critical roles of the matrix for forest biodiversity outlined above, the traditional emphasis of conservation biology and forest management has been the establishment of large ecological reserves. Reserves are unquestionably important where particular ecosystem types, vegetation communities, or forest age classes are being rapidly modified or eliminated (McNeely 1994a), or where only small amounts of the original cover of forest types remain (Pressey et al. 1996; Lindenmayer and Franklin 2000). The establishment of reserves is also critical for species intolerant of even limited levels of human disturbance and for those that can only be conserved in large ecological reserves. For example, even limited levels of human-related forest disturbance can lead to marked changes in stream conditions (McIntosh et al. 2000) with concomitant negative impacts on some aquatic biota, such as fish (Baxter et al. 1999). However, as important as reserves are, we feel that a conservation strategy based primarily or exclusively on reserves will fail because of its inherent limitations (as discussed in Chapter 5). As proposed by Soulé and Sanjayan (1998), 50 percent of tropical taxa would be extinct within the next few decades, even if more than 10 percent of tropical forests were protected in well-designed reserve systems.

We are greatly concerned that approximately half the world's native forests have been cleared in the past forty years—slowing the rate of clearing is critical for forest biodiversity conservation. Hence, the establishment of reserve systems is essential despite their limitations. However, large ecological reserves and matrix-based efforts to conserve forest biodiversity need to be implemented simultaneously. We do not propose to replace large ecological reserves with matrix management, but rather we emphasize the complementarity of the two broad strategies (Figure



1.10). We stress the need for both reserves and matrix management as part of a comprehensive strategy for biodiversity conservation across multiple spatial and temporal scales.

FIGURE 1.10. Forest biodiversity will require multiscaled strategies that encompass large ecological reserves and management of matrix lands. This is highlighted in this conceptual diagram, which shows the complementarity between the two broad approaches (from D. Perry personal communication).

The Matrix and Major Themes in Landscape Ecology and Conservation Biology

[A] species or system may simply not operate in the way envisioned by the theories applied to it.

DOAK AND MILLS (1994)

Landscapes have been conceptualized using two main models—the *corridor-patch-matrix model* of Forman (1995) and the *landscape continuum model* developed by McIntyre and Hobbs (1999). The two models differ in their relative emphasis. In the corridor-patch-matrix model, landscapes are viewed as varying mosaics of different types of patches and corridors. In the landscape continuum model, landscapes are characterized by having different levels of vegetation cover with a continuum or gradient of possible conditions that range from an intact cover of native vegetation through to relictual levels of cover. The focus of the corridor-patch-matrix model is on the form or structure of landscapes, whereas the landscape continuum model emphasizes the function of a landscape across varying structural gradients of vegetation cover. Simultaneous consideration of both models is useful because it can lead to greater awareness of the range of conditions that occur in real landscapes and, in turn, the diversity of responses to such varying conditions by different biota. Both models have limitations. In particular, landscapes are usually treated (intentionally or otherwise) in very simple terms as having two components—patches (habitat) and remaining land (non-habitat). Real landscapes are more complex than this. Such complexity matters—particularly when attempting to predict the response of species to landscape modification.

The simplification of landscape conditions pervades many major themes in conservation biology in which the importance of the matrix has received little or no consideration. Ecological theories such as island biogeography, nested subset theory, and metapopulation biology often take a highly reductionist approach and largely ignore the

complexity found in real landscapes. This limits the explanatory and predictive value of such theories because

- Habitat fragments and reserves are treated as islands and the matrix is often considered as either totally unsuitable habitat or neutral habitat.
- There is no recognition that the matrix is inherently heterogeneous in both form and function and thus variable, for example, in habitat quality.
- Interrelationships between fragment-matrix dynamics are disregarded or greatly oversimplified.

Conditions in the matrix are pivotal to studies of habitat fragmentation, metapopulation dynamics, extinction proneness, edge effects, and reserve design. The responses of biota in habitat fragments are not isolated from conditions in the surrounding matrix. Matrix conditions may even be more important in determining the survival of some species than factors that are traditionally examined, such as fragment size and patch isolation. Consideration of the matrix can highlight fundamental differences in species responses between fragmented forest landscapes versus fragmented agricultural landscapes, such as the magnitude of edge effects and threshold vegetation cover impacts on species loss.

In order to develop more useful ecological theory and to advance biodiversity conservation efforts, it is important to

shift the emphasis from the fragments to the management of the matrix in which they are embedded. If the biota in the fragmented landscape is to persist then the management of the matrix becomes all important. Ameliorating the matrix may be the most important way to manage fragments. (Crome 1994)

In this chapter, we address two main themes. First, we describe two models that have been developed to classify patterns of landscape cover: Forman's 1995 *corridor-patch-matrix model* and McIntyre and Hobbs' (1999) *landscape continuum model*. We discuss why it is useful to consider both models and also how both are often (mis)interpreted in ways that oversimplify the complexity and range of habitat conditions within real landscapes. Such oversimplification is not confined to these two landscape models—it pervades many themes in conservation biology. In the second part of this chapter, we explore interrelationships between the role and importance of the matrix and major themes in conservation biology. Such conservation-related topics as island biogeography, extinction proneness, habitat fragmentation, metapopulation dynamics, connectivity, reserve selection, and edge effects have developed in recent decades. Their frequent omission of a key element—conditions in the matrix—has often limited the comprehensiveness of some of these concepts and curtailed their predictive value in real landscapes.

Models of Landscape Cover

The matrix is often the most extensive patch type in a landscape (Forman 1995; see Chapter 1). It is considered in both the general conceptual models of landscape cover discussed below—the corridor-patch-matrix model and the landscape continuum model. The aim of both models is to incorporate the range of conditions in a landscape.

The Corridor-Patch-Matrix Model

Forman (1995) developed the corridor-patch-matrix model, in which landscapes are conceived as mosaics of three components: patches, corridors, and the matrix (Figure 2.1). Forman defined these landscape units as follows:

- Patches are . . . relatively homogeneous nonlinear area[s] that differ from their surroundings.

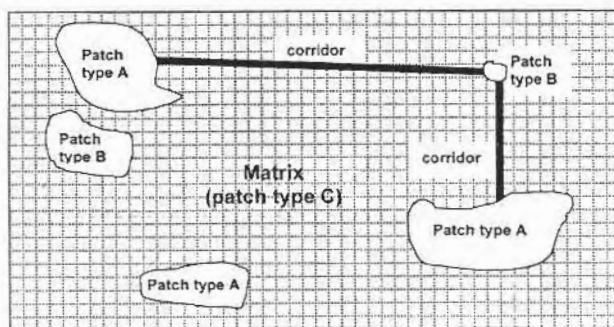


FIGURE 2.1. A landscape perspective based on the corridor-patch-matrix model (sensu Forman 1995). The model has a number of patch types, including the most extensive background matrix (patch type C).

- Corridors are narrow, linear patches of a patch type that differ from those on either side.
- The matrix is the dominant patch type in a landscape. It is characterized by extensive cover, high connectivity, and/or a major control over dynamics.

The matrix is often intersected by corridors or perforated by smaller patches (Forman 1995). In Forman's model, patches and corridors are two types of readily identifiable landscape components distinguished from the background matrix (Forman and Godron 1986; Kotliar and Wiens 1990) (Figure 2.1).

Forman (1995) noted that "every point in a landscape was either within a patch, corridor, or the background matrix," and in allowing for the complexity of many landscapes he states that patches within the matrix can be "as large as a national forest or a single tree" (Dramstad et al. 1996). Similarly, the matrix can be "extensive to limited, continuous to perforated, and variegated to nearly homogenous" (Forman 1995).

The Landscape Continuum Model

In some landscapes, the boundaries between patch types are not obvious, and differentiating them from the background matrix may not be straightforward. The landscape continuum model was developed in response to this problem (McIntyre 1994; McIntyre and Hobbs 1999) (Figure 2.2). The model was originally

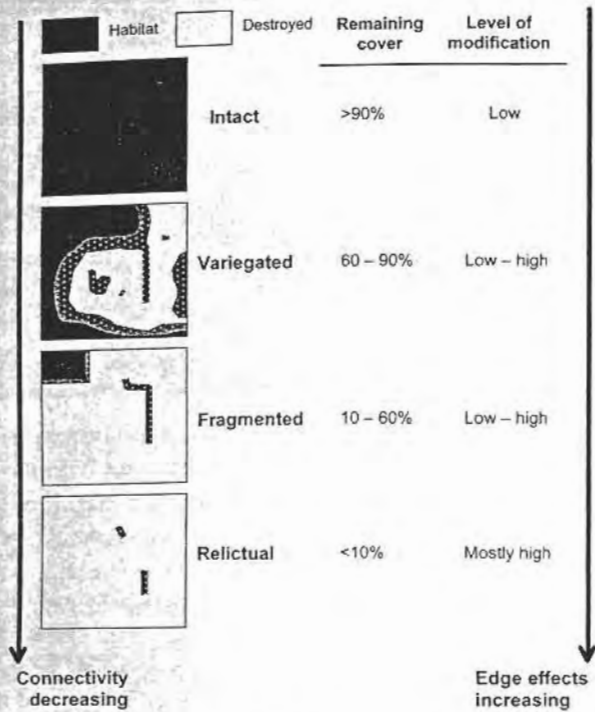


FIGURE 2.2. States of landscape condition in the landscape continuum model. Redrawn from McIntyre and Hobbs 1999.

proposed for semi-cleared grazing and cropping landscapes in parts of rural eastern Australia characterized by small fragments of woodland habitat and relatively isolated native trees scattered throughout grazing lands (McIntyre and Barrett 1992; McIntyre et al. 1996) (Figure 2.3). Here, from a human perspective, “patches” and “corridors” are difficult to identify among the loosely organized and spatially dispersed arrays of trees (or other vegetation cover such as native grassland). Although single paddock trees in isolation may not provide habitat or act as micropatches for many taxa (but see Fischer and Lindenmayer 2002), numerous trees scattered across a landscape will *collectively* provide habitat for some species (e.g., for some woodland birds; Barrett et al. 1994). In this way, the landscape continuum model takes account of small habitat elements that might otherwise be classified as “unsuitable habitat” in the background matrix (Tickle et al. 1998). More recently, McIntyre and Hobbs (1999) extended their model to include other

types of landscapes, such as tropical and temperate forests.

The landscape continuum model developed by McIntyre and Hobbs (1999) recognizes four broad cover classes. At opposite ends of the continuum are the intact landscape and the relictual landscape. Intermediate between these conditions are the variegated landscape and the fragmented landscape (Figure 2.2):

In variegated landscapes, the habitat [not necessarily an unsuitable environment] still forms the matrix, whereas in fragmented landscapes, the matrix comprises “destroyed habitat.” (McIntyre and Hobbs 1999)

McIntyre and Hobbs (1999), and other workers before them (e.g., Wiens 1994; Pearson et al. 1996), believed that landscapes were more complex than could be described by the corridor-patch-matrix model. Furthermore, they contended this approach to be anthropocentric because human disturbances give rise to a greater range of landscape conditions. McIntyre and Hobbs (1999) argued their model was needed because the corridor-patch-matrix model did not “capture the richness of possible landscape configurations, since it always assumes that the matrix is ‘nonhabitat’ . . .” (McIntyre and Hobbs 1999). They equated the corridor-patch-matrix model to only one landscape condition—fragmentation—a condition in which they considered patches and corridors to be habitat “islands” embedded within a hostile background matrix (McIntyre and Hobbs 1999).

McIntyre and Hobbs (1999) believed that by recognizing different landscape conditions, conservation strategies could be better focused. In their view, many forest landscapes will conform to an intact or variegated condition for numerous elements of the biota if the matrix is managed appropriately. Failure to embrace matrix management means that the background matrix can be readily distinguished from the patches and corridors it contains (McIntyre et al. 1996) and the system will degenerate from a variegated to a fragmented or even relictual one (*sensu* McIntyre and Hobbs 1999). By recognizing that some landscapes were variegated, matrix management strategies would attempt to prevent landscapes deteriorating into a “fragmented” condition that is significantly less suitable for biota (McIntyre et al. 1996). Conversely, by

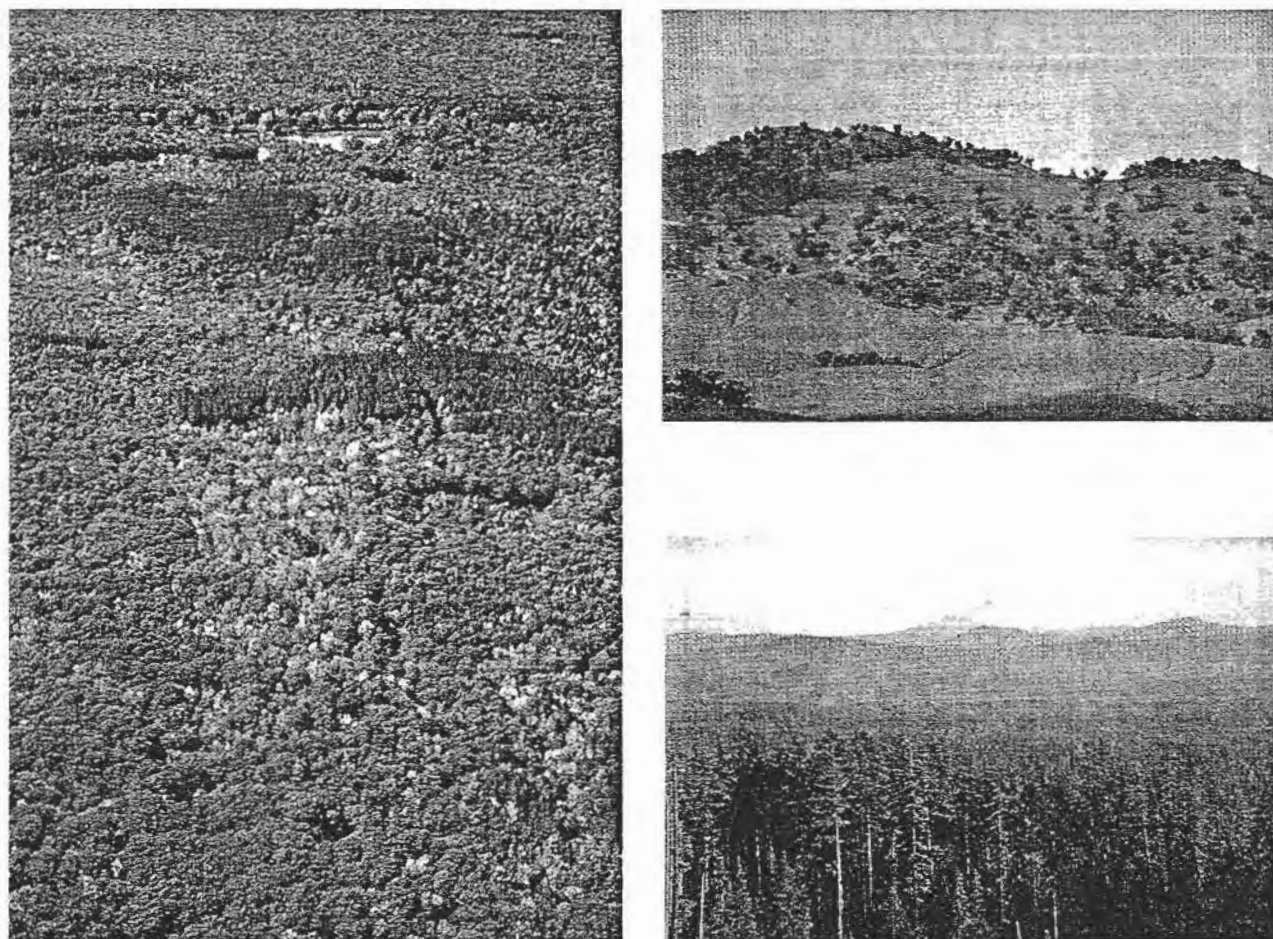


FIGURE 2.3. Variation in vegetation cover in different landscapes. (A) A strongly patchy landscape composed of forest stands of different ages and composition (conifers, hardwoods, and mixtures of the two groups) (Harvard Forest in central Massachusetts, United States) (photo by J. Franklin). (B) A variegated landscape (*sensu* McIntyre and Barrett 1992) of scattered paddock trees in southeastern Australia (photo by D. Lindenmayer). (C) A landscape dominated by a matrix of old-growth forest of Douglas-fir and other coniferous species (Mount Hood National Forest, Oregon, United States) (photo by J. Franklin).

distinguishing fragmented landscapes from variegated ones, appropriate matrix management protocols would “re-variegate” fragmented landscapes through steps such as restoring connectivity and halting degrading processes (Hobbs et al. 1993; McIntyre and Hobbs 1999).

We believe that some of the assertions about the advantages of the landscape continuum model fail to recognize aspects of Forman’s (1995) original corridor-patch-matrix model. The interpretation of this model by McIntyre and Hobbs (1999) is often a landscape composed of patches and corridors of suitable habitat embedded within a hostile (nonhabitat) ma-

trix. However, Forman (1995) stated that the matrix was often the largest and most dominant landscape component “characterized by extensive cover, high connectivity, and/or a major control over dynamics” (see definition given in Chapter 1). The corridor-patch-matrix model is actually “interpretation-free” in terms of the response of a given species to particular landscape components (Forman 1995). The corridor-patch-matrix model does not rely on a single patch and corridor type or matrix condition of uniform quality and also allows for a continuum of conditions by recognizing that landscapes are a mosaic of many

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types of patches and corridors that cover different landscapes to varying extents.

Congruence between the Corridor-Patch-Matrix and Landscape Continuum Models

The corridor-patch-matrix model and the landscape continuum model are congruent on many levels. Both clearly recognize a gradient in the complexity of landscape conditions and a continuum of landscape "naturalness." Also, the matrix will usually be the dominant landscape component irrespective of whether the corridor-patch-matrix model or the landscape continuum model is applied.

The primary distinctions between the two models are differences in their relative perspectives on landscapes. The focus of the corridor-patch-matrix model is on the *pattern* or *form* of different landscape units (i.e., the size and shape of different patches and patch types) that compose a landscape mosaic. McIntyre and Hobbs (1999) have recognized that distinct patch boundaries may not always be identifiable in some landscapes (particularly those classified as "variegated"). Therefore, the emphasis of their landscape continuum model is on the specific *function* of a given landscape across a structural gradient of vegetation cover—a focus that requires stipulating the organism or assemblage of interest and specifying the processes influencing species' responses.

Using both models leads to a better appreciation of landscapes and how species respond to them. This is important because landscape changes, such as habitat fragmentation, are both a pattern (e.g., subdivision of habitat cover) and a process (e.g., altered population dynamics) (Wiens 1994; Cale 1999). Looking at attributes of both models encourages landscape ecologists, conservation biologists, and land managers to think not only about the form and the function of a landscape but also about the interrelationships *between* form (or structure) and function. It is also useful because patterns of landscape cover seen from a human perspective may or may not provide a useful framework for interpreting biotic response to landscape conditions (Ingham and Samways 1996). Strips of

vegetation may provide conduits for movements between patches for some animals that avoid the surrounding matrix because of its unsuitability (e.g., kangaroo populations in the wheatbelt of Western Australia; Arnold et al. 1993). In other cases, some taxa will live in, and move readily through, the matrix (e.g., bird taxa in rural northern New South Wales, Australia; Barrett et al. 1994).

A limitation of all landscape models is recognizing that species will have unique responses to the same landscape (Kotliar and Wiens 1990; Villard et al. 1999). Interspecific variation in response will depend on (1) the scale at which species perceive the environment (Andr  n 1996), (2) the habitat requirements of a particular species, (3) where suitable habitat occurs in a landscape, and (4) how animals move across (and disperse between) areas of suitable habitat (Tickle et al. 1998). Such an organism-centered view of landscape cover means there is no single most appropriate perspective or scale from which to view landscapes (Haila 1999). Aerial photography interpretation—which both models use to conceptualize landscapes—is only able to represent species-specific responses in a limited sense.

Limitations in the Application of the Landscape Models

Irrespective of the original intentions of the architects of the corridor-patch-matrix model and the landscape continuum model, both models have often been misinterpreted by practicing landscape ecologists and conservation biologists. The models are sometimes simplified to represent landscapes as patches or corridors of habitat, which contrast markedly with remaining areas of nonhabitat. This is a reductionist approach based on a human interpretation of the perceived function of a landscape. Too often, mapping tools (such as geographic information systems, or GIS) have been used to define patches, assuming that species would perceive "patches" in the same way and at the same scale as humans do (Bunnell 1999a). However, the determination of what constitutes a suitable patch and what does not must be based on the habitat

requirements, movement patterns, and other attributes of the organism of interest.

The binomial classification of landscapes into habitat and nonhabitat is problematic for other reasons not accounted for by either landscape model (as traditionally interpreted). First, habitat quality for a particular species is often a graded, rather than an either/or, measure. In effect, there can be a gradient of conditions that are suitable to varying degrees (Whittaker et al. 1973; Austin 1999) with some areas of habitat being more important than others (Block and Brennan 1993; Lindenmayer and Cunningham 1996). This is not unlike the source-sink concept of Pulliam et al. (1992) and others (e.g., Howe et al. 1991). Second, patches and corridors (as traditionally defined) are never uniform but rather are always characterized by within-patch heterogeneity (Forman 1995). Such heterogeneity matters (Fox and Fox 2000)—as demonstrated in many studies that have found that within-patch quality can have a significant influence on species occurrence as well as (or instead of) attributes like patch size (e.g., Lindenmayer et al. 1993a, 1999b; Mac Nally et al. 2000; Sieving et al. 2000). In these cases, within-patch processes as well as between-patch processes can be important (Harrison and Taylor 1997).

The simplifications in landscape models are understandable given the complexity of real landscapes and the difficulty ecologists face in tackling such complexity. However, it is important to know the assumptions underlying these models and the limitations in their application.

Landscape Models and the Terminology Used in This Book

Although this book is largely about the function (rather than the pattern or form) of landscapes for forest biodiversity conservation, we have not adopted the terminology used by McIntyre and Hobbs (1999). Instead, we use the terms *patches*, *corridors*, and *matrix* because they will be more familiar to readers responsible for implementing matrix-based management. It is crucial to emphasize that the "matrix" in the corridor-patch-matrix and landscape continuum models can range from a very small entity, such as the area around

a clump of vegetation (e.g., for beetles; Wiens et al. 1997), to a large one, such as an entire national forest (Forman 1995) or an entire geographic region such as the area surrounding Yellowstone National Park (the Greater Yellowstone Ecosystem). This means that the scale of the matrix will vary according to the organism or ecological process under scrutiny and that strategies for biodiversity conservation within the matrix also will be variously scaled from single trees to entire landscapes (see Chapters 3, 6, 7, and 8).

The Matrix and Major Themes in Conservation Biology

Reductionist approaches to the complexity of real landscapes are not confined to models of landscape cover. It is commonplace in many aspects of conservation biology where the importance of the matrix has often been overlooked. Failure to recognize the richness of the matrix concept has the potential to limit the applicability of some theoretical constructs of conservation biology to practical resource management and conservation problems.

Island Biogeography

An observation made early in the study of ecology was that large areas support more species than smaller ones do (e.g., Arrhenius 1921; Preston 1962)—a fact that was later often referred to as the *species-area relationship* (Rosenzweig 1995). Species-area relationships are common for some groups, such as birds (Newton 1998). The *theory of island biogeography* (MacArthur and Wilson 1963, 1967) was developed, in part, to explain the species-area phenomenon, particularly for island biotas. Part of this theory considers aggregate species richness on islands of varying size and isolation from a mainland source of colonists (Shafer 1990). The balance between extinction and recolonization is predicted to produce an equilibrium number of species on a given island, which is a derivative of island size and island isolation. Larger and less-isolated islands

are predicted to support more species. Diamond (1975) (among many others) likened oceanic islands to reserves and extended the theory of island biogeography as a basis for generic design principles for protected areas. This became a highly controversial topic in conservation biology for several decades (see reviews by Gilbert 1980; Burgman et al. 1988).

Island biogeography theory does not account for conditions and processes in the matrix, such as disturbance regimes (Baker 1992), the magnitude of edge effects (that are, in turn, related to patch-matrix contrasts), and matrix suitability for habitat and movement—all of which strongly influence the distribution of species in forest landscapes (Gascon and Lovejoy 1998). Uncritical adoption of "general rules" for reserve design derived from island biogeography theory can even have a negative effect on conservation values (Simberloff 1988). The theory is too simplistic to have practical application in most real-world landscape mosaics (Zimmerman and Bierregaard 1986; Doak and Mills 1994; see Chapter 5).

Island Biogeography Theory and General Reserve Design Principles

As reserves and habitat fragments have been likened to oceanic islands, some elements of the theory of island biogeography have been proposed as general principles to guide the design of nature reserves (e.g., Terborgh 1974; Diamond 1975; Diamond and May 1976; Shafer 1990; Noss and Cooperrider 1994). The IUCN's 1980 World Conservation Strategy (IUCN 1980) adopted these principles, and in Australia they were recommended for wildlife management in forests (Davey 1989).

Six general principles (based on the unrealistic assumption that there are identical places from which protected areas can be selected) are derived largely from island biogeography theory:

Principle 1. Large reserves are better than small reserves.

Principle 2. A single large reserve is better than a group of small ones of equivalent total area (the basis for the so-called SLOSS [Single Large Or Several Small] debate; see Gilbert 1980; Burgman et al. 1988).

Principle 3. Reserves close together are better than those far apart.

Principle 4. A compact cluster of reserves is better than a line of reserves.

Principle 5. Circular reserves are better than long, thin ones.

Principle 6. Reserves connected by a corridor are better than reserves not connected by a corridor.

Effects of the matrix on biodiversity are ignored, whether positive or negative. Yet, matrix conditions can significantly influence biodiversity conservation. For example, the outcomes of Principles 2, 3, and 4 (reserve size and spatial location) depend upon interacting factors that include

- *Demographic interactions between populations in reserves and populations from the surrounding matrix lands.* These may include the dispersal capabilities of those taxa targeted for conservation and their ability to colonize reserves from the matrix (Swenson et al. 1986).
- *Disturbance regimes in both the matrix and those parts of a landscape set aside for reservation.* Where disturbance regimes do not impact landscapes or are not fundamental to persistence or regeneration, the outcome of Principle 2 may be quite simple—a single large reserve will often function more effectively than a number of smaller ones of equivalent size. More-complex trade-offs occur in environments where disturbance regimes are important (Baker 1992). For example, a single large reserve may be more susceptible to destruction by a single catastrophic event than a set of smaller, spatially separated ones (Quinn and Hastings 1987; Quinn et al. 1989; Lindenmayer and Possingham 1995b). Organisms in patches unaffected by a disturbance may be able to recolonize patches where localized extinctions have resulted from a catastrophic event. Such a lack of correlation in disturbance regimes between different patches has promoted the persistence of a number of species (Berger 1990; Murphy et al. 1990; Stacey and Taper 1992).

Conditions in the matrix, including the level of structural contrast between reserves and matrix lands, also influence the effect of reserve shape (Principle 5).

If negative edge effects emanating from the matrix are limited, a long, narrow reserve system might better capture sensitive areas, particularly those characterized by a linear spatial configuration like a riparian system (Burgman and Ferguson 1995).

Island Biogeography and Other Issues Associated with Matrix Conditions

One significant issue ignored in island biogeography theory is that the *composition* of a faunal community can be more important than species richness (Noss 1983). The contribution of the matrix to patterns of species diversity and the response of individual species and species assemblages to landscape change are not taken into account. The theory may fail where the matrix provides even temporarily suitable habitat (Zimmerman and Bierregaard 1986; Ricketts 2001). It also has limited predictive ability when the importance of fragment size is outweighed by other factors such as (1) disturbance regimes or habitat conditions within and outside patches (e.g., Fitzgibbon 1997; Fox and Fox 2000), (2) edge effects at the patch-matrix interface (Saurez et al. 1998), and (3) levels of heterogeneity and connectivity across entire landscapes (Brereton 1997; Metzger 1997).

Examples that illustrate the shortcomings of island biogeography theory include the Biological Dynamics of Forest Fragments Project in Brazil, where edge effects and matrix conditions had a substantially greater influence than fragment size for some animals (Brown and Hutchings 1997; see Chapter 14). In that study, there was an *increase* in frog, small mammal, and butterfly species richness following the isolation of rain-forest patches—a result opposite to predictions from island biogeography theory (Gascon and Lovejoy 1998). Species richness was elevated by an influx of taxa capable of using the changed matrix. Estades and Temple (1999) similarly recorded increased bird species richness in small rather than large *Nothofagus* spp. remnants embedded within an exotic radiata pine (*Pinus radiata*) plantation in Chile. An increase in species number in fragments may be due to the influx of organisms displaced from the adjacent matrix (Bierregaard and Stouffer 1997; Darveau et al. 1995) or a predominance of edge or generalist taxa from the surrounding matrix (Gascon and Lovejoy 1998; Ås

1999)—taxa that are sometimes called *invaders* (see also Halme and Niemelä 1993; Saurez et al. 1998).

In summary, some of the influences of the matrix that limit island biogeography theory are that (after Davies et al. 2001): (1) the matrix can influence dispersal and recolonization rates (Ricketts 2001; Vandermeer et al. 2001); (2) the matrix can provide suitable habitat for some of the original taxa (Laurance 1991a; Gascon et al. 1999); (3) invading species can use the matrix as habitat and colonize habitat fragments (Aldrich and Hamrick 1998; Saurez et al. 1998); and (4) the matrix can affect the type and magnitude of edge effects (see the section that follows).

Given the problems with the six general principles from island biogeography theory outlined above, Margules et al. (1982) warned against their widespread application. This was because their uncritical adoption without consideration of matrix conditions and other factors can have negative implications for biodiversity conservation.

A problem for reserve design that stems from the uncritical application of island biogeography theory has been excessive emphasis on large reserves (for a detailed discussion, see Chapter 5). While large reserves are unquestionably important, small remnants also can have considerable value for biodiversity (Gascon 1993; Powell and Björk 1995; Turner 1996; Angelstam and Pettersson 1997; Semlitsch and Bodie 1998; McCoy and Mushinsky 1999; Palmer and Woinarski 1999; Schwartz 1999; Abensperg-Traun and Smith 2000; Mac Nally and Horrocks 2000). Indeed, sometimes the protection of small reserves is the only conservation option, particularly in highly productive landscapes subject to significant human alteration.

Nested Subset Theory

Ignoring the matrix and treating reserves and habitat fragments as equivalent to oceanic islands not only limits the validity of island biogeography theory, but also affects the broadly related concept of *nested subset theory* (Patterson and Atmar 1986). This theory attempts to extend the species-area relationship underpinning island biogeography theory by tracking both

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the numbers of species and their identities on islands. The premise is that species-poor small islands should support assemblages that are subsets of larger species-rich islands (Patterson 1987; Cutler 1991). The concept has been (often uncritically) extended to reserves and habitat fragments, where it is implied that species-poor small fragments should support assemblages that are subsets of larger species-rich fragments—assuming that islands (including habitat fragments) are unaffected by matrix conditions (Doak and Mills 1994). Nested subset theory would not predict, for example, the results of empirical studies such as those from the Biological Dynamics of Forest Fragments Project in Brazil (see Chapter 14), or the outcomes for birds in the Tumut Fragmentation Experiment in southeastern Australia (see Chapter 13). Advocates of nested subset theory often fail to test the null hypothesis that small patches merely sample organisms from a larger regional pool of taxa (but see Haila et al. 1993).

Constructs such as island biogeography theory and nested subset theory that assume that reserve “islands” are located in a sea of “unsuitable [matrix] lands” (Gascon and Lovejoy 1998; Gascon et al. 1999) may be too pessimistic in their predictions of species loss and fail to recognize the importance of matrix-based conservation strategies and/or the recovery of forests following disturbance. This led Wiens (1994) to conclude that

fragments of habitat are often viewed as islands and are managed as such; however, habitat fragmentation includes a wide range of spatial patterns. . . . Fragments exist in a complex landscape mosaic and dynamics within a fragment are affected by external factors that vary as the mosaic structure changes and/or the recovery of forests following disturbance. The simple analogy of fragments to islands, therefore, is unsatisfactory.

Habitat Loss, Habitat Fragmentation, and Landscape Composition

Natural processes can cause habitat loss and the fragmentation of landscapes and habitats. Geological events (e.g., volcanic eruptions; Croizat 1960;

Franklin et al. 1985), long-term climatic change (Cunningham and Moritz 1998), and wildfires (Williams and Gill 1995; Agee 1999) are some examples. But human landscape modification, including vegetation clearing, is by far the most significant modern factor resulting in habitat loss and habitat fragmentation (Saunders et al. 1987; Groombridge 1992) and is often a significant threat to the persistence of forest fauna worldwide (Wilcox and Murphy 1984; Wilcove et al. 1986).

Proper interpretation of fragmentation effects requires consideration of habitat fragments and conditions in the matrix *and* the use of both by the organisms targeted for investigation (Wiens 1994; Gascon et al. 1999). Fragmentation effects and metapopulation dynamics (see the following section) only become relevant when habitat suitability in the matrix undergoes changes that creates patch-matrix differences that significantly influence the species of interest (Fahrig and Merriam 1994). Crome's (1997) recommendation is most apt here: “[A]s much, if not more emphasis [should be] placed on the matrix as on the fragments in research.”

Processes Associated with Habitat Loss and Habitat Fragmentation

The dynamics of populations are influenced by four interrelated processes associated with habitat loss and subsequent habitat fragmentation: habitat loss, subdivision of habitat, patch isolation, and edge effects (Figures 2.4 and 2.5).

- **Habitat loss.** After habitat loss occurs, habitat fragments become “samples” of the original

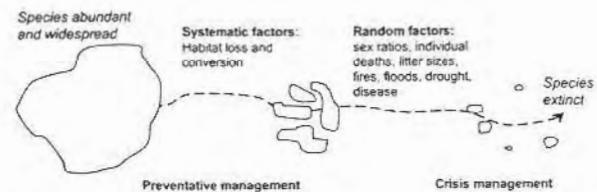


FIGURE 2.4. Interrelationships between the loss of a species and habitat loss (as a systematic threatening process) and subsequently cascading (often random) fragmentation effects that operate in addition to habitat loss and low levels of habitat cover (modified from Clark et al. 1990).

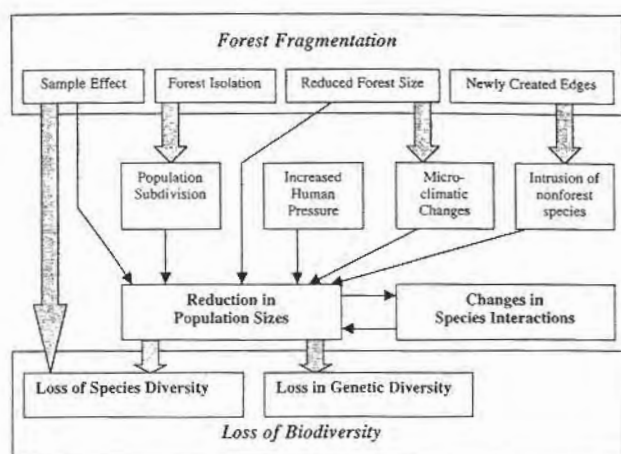


FIGURE 2.5. Graphical summary of the interacting effects of habitat loss and habitat fragmentation (modified from Zuidema et al. 1996).

(pre-fragmentation) vegetation cover (Connor and McCoy 1979; Zuidema et al. 1996). Recent studies indicate the total amount of forest habitat (and hence also the amount of suitable habitat in the matrix) can be a more important factor influencing the distribution of forest organisms than the spatial configuration of habitat (Delin and Andrén 1999; Fahrig 1999; Trzcinski et al. 1999; Villard et al. 1999). For some generalist species, which can use disturbed environments, the amount of suitable habitat may increase with habitat loss as the area between patches expands (Saunders and Ingram 1995; Lindenmayer et al. 2001a).

- *Subdivision of habitat.* Greater levels of habitat loss can lead to increased subdivision of remaining habitat, resulting in smaller habitat patches—the habitat-fragmentation process (Fahrig 1997; Bender et al. 1998). This may reduce populations of some species to nonviable levels (Shaffer 1981; Shaffer and Samson 1985; Armbruster and Lande 1993).
- *Patch isolation.* Increasing habitat loss and habitat fragmentation can lead to larger distances between remnant patches and, therefore, to greater levels of patch isolation (Fritz 1979; Smith 1980; Hanski 1994a). This may impede interfragment movement (Powell and Powell 1987; Bierregaard and Lovejoy 1989; Desrochers and Hannon 1997). The relation-

ship between forest habitat loss and patch isolation is not necessarily linear. A modeling study by Franklin and Forman (1987) forecast that patches of old-growth forest can become fragmented even when approximately 70 percent of the landscape cover remains. Percolation models (e.g., Gardner et al. 1987) predict that habitat fragmentation begins to occur when about 60 percent of original vegetation cover remains. Below some threshold level of habitat loss, distances between habitat patches can increase exponentially (Gustafson and Parker 1992).

- *Edge effects.* The ratio of patch perimeter to interior area increases in fragmented environments. This can result in edge effects within remaining patches. Such edge effects can include weed invasion (Brothers and Spingarn 1992; Burdon and Chilvers 1994), altered microclimatic conditions (e.g., modification of wind speeds, light fluxes, and temperature regimes; Chen et al. 1992; Matlack and Litvaitis 1999), increased nest predation and brood parasitism (Paton 1994; Robinson et al. 1995), and lowered rates of fledging success among birds with territories located at habitat edges (Hutha et al. 1998).

Theoretically, habitat loss can occur without habitat fragmentation, as shown by Forman's (1995) landscape modification models (such as perforation, dissection, and shrinkage) that were tested empirically on the use of an artificial ecosystem by grassland insects (Collinge and Forman 1998). However, in the majority of cases it will be extremely difficult to separate the effects of habitat fragmentation from the effects of habitat loss (Andrén 1997; Harrison and Bruna 2000). The two processes are nearly always confounded. Although theoretical models associated with landscape-levels of vegetation cover and patterns of species loss attempt to tackle this problem (Fahrig 1997, 1999), from a practical perspective it is essential to be aware that several processes accompany landscape modification (Bunnell 1999a; Fahrig 1999).

Determining the relative importance of habitat loss versus habitat fragmentation (i.e., the amount of habitat left versus the spatial configuration of remaining habitat) is an important area of research in forest landscapes. If habitat loss is the primary factor influencing

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the persistence and occurrence of species (which appears to be true for the majority of taxa; Fahrig 1997), then a thrust of forest management must be to maintain suitable habitat at multiple spatial and temporal scales—which is what, in our view, the overarching objective of matrix management should be (see Chapter 3).

Habitat Loss and Species Loss

Over 80 percent of the world's endangered birds are threatened by habitat loss (Temple 1986). In central Amazonia, for example, habitat loss has caused an immediate and obvious decrease in species richness (Zimmerman and Bierregaard 1986; Klein 1989). Habitat loss is also considered to be the chief factor in invertebrate extinctions (Thomas and Morris 1995). The total amount of habitat lost can be a better predictor of species loss than the spatial arrangement of habitat in many landscapes, especially those with relatively high levels of remaining cover (Fahrig 1998; see the section that follows). The loss of species is believed to track the loss of habitat in these cases.

Cascading Fragmentation Effects below Threshold Habitat Cover Levels

With and King (1999) defined critical thresholds as abrupt, nonlinear changes (such as the rate of loss of species) that occur in some measure across a small amount of habitat loss. Below threshold levels of habitat cover, the loss of species and population declines of individual taxa are more substantial than predicted from habitat reduction alone (Andrén 1994; With and Crist 1995; With 1997; McCarthy and Lindenmayer 1999b). Empirical studies of the capercaillie grouse (*Tetrao urogallus*) identified threshold habitat cover responses, with populations of this species declining faster than by habitat tracking alone when less than 30 percent habitat cover remained (Rolstad and Wegge 1987). Other studies of birds support these findings (Enoksson et al. 1995). However, Mönkkönen and Reunanen (1999) recognized that threshold responses to vegetation cover will vary on a species-by-species basis.

In a review of studies on birds and mammals, Andrén (1994) calculated that threshold levels for remaining habitat were 10–30 percent of original levels of vegetation cover. That is, populations declined

more rapidly than expected by habitat loss alone when less than 10–30 percent of habitat cover remained. Threshold levels will vary among landscape types and species (Andrén 1999), from 60 percent for some taxa to 10 percent for others (Bennett and Ford 1997). They will also vary according to the number and spatial arrangement of patches in fragmented environments (Thomas et al. 1990; Lamberson et al. 1994), the movement capabilities of the species targeted for investigation (Andrén 1994, 1999), and the spatial scale at which organisms use the landscape (Cale and Hobbs 1994; Pearson et al. 1996). It is important to recognize that 10–30 percent threshold levels in habitat availability will be an underestimate for many species (Mönkkönen and Reunanen 1999), and that some species could be lost above particular threshold cover levels, simply as a function of habitat loss per se.

As levels of habitat cover drop below critical threshold levels, a wide range of factors in addition to continued habitat loss can influence both the reduction in species diversity and the decline of populations of individual taxa. These are sometimes called *cascading fragmentation effects* and are summarized in Table 2.1. They include demographic stochasticity, genetic stochasticity, and environmental variability. Additional factors that become important below threshold levels of habitat cover are altered ecosystem processes (e.g., pollination; Cunningham 2000), disrupted species interactions (e.g., aggressive interspecific behavior), and altered intraspecific dynamics (e.g., Allee effects; Allee et al. 1949). For example, Ims et al. (1993) found that with increasing habitat loss and habitat fragmentation, the social system of the capercaillie grouse changed from a lekking system to one of solitary displaying males.

Threshold Habitat Levels, Species Loss, and Matrix Conditions

Conditions in the matrix substantially influence threshold responses, for example, through their impacts on permeability to movement (Taylor et al. 1993), and thus colonization probabilities for habitat fragments (Andrén 1999). A reappraisal of the seminal paper by Andrén (1994) showed that threshold values depended significantly on landscape context—in other words, whether the matrix surrounding habitat fragments was an agricultural one or one composed of re-

TABLE 2.1.
Potential "cascading" impacts of habitat loss and habitat fragmentation
that occur below threshold habitat cover levels.

IMPACT AND EXAMPLES	SOURCE
Destabilized population dynamics (e.g., disrupted sex ratios and Allee effects)	McCarthy et al. 1994; Allee 1931
Altered movement patterns (e.g., modified home ranges)	Barbour and Litvaitis 1993
Altered social systems	Ims et al. 1993
Food shortages in fragments	Robinson 1998; Zanette et al. 2000
Altered breeding success (e.g., smaller young)	Hinsley et al. 1999
Increased short-term population densities in habitat fragments	Darveau et al. 1995
Altered vulnerability of populations to catastrophic events	Burgman et al. 1993
Increased human hunting pressure	Redford 1992
Altered gene frequencies in populations	Lacy 1993a; Sarre 1995
Altered interactions between species (e.g., interspecific aggression) or weed/parasite invasions	Catterall et al. 1991; Lavorel et al. 1999
Disrupted ecological processes (e.g., pollination)	Kapos 1989; Klein 1989
Increased potential for some types of disturbance (e.g., windthrow)	Lovejoy et al. 1986
Altered evolutionary processes (e.g., morphological changes in organisms)	Hill et al. 1999; Weishampel et al. 1997

growth forest regenerated after timber harvesting (Mönkkönen and Reunanen 1999).

Although the threshold concept is an appealing one and has some empirical evidence to support it (e.g., Jansson and Angelstam 1999), the concept is not free of problems.

First, threshold theory (like most fragmentation paradigms) treats landscape cover as a categorical variable with only two states—habitat and nonhabitat. This is too simplified. Not all habitat patches are alike, and internal differences between them can have significant effects on species occurrence (Lindenmayer et al. 1999b). Similarly, not all human-perceived nonhabitat is alike—even limited suitability of conditions in some parts of the matrix can influence the ability of some species to persist in a landscape.

Second, threshold levels for habitat loss will vary for each species and will depend on the scale at which it interacts with the patch mosaic in a landscape (With 1999). For some taxa there may not be distinct thresholds at all but rather responses might be linear, curvilinear, or some other form.

Third, there are often interactions between matrix conditions and habitat loss—habitat loss does not occur in isolation from other processes in the land-

scape. This is highlighted in the biotic interactions model developed by Ambuel and Temple (1983) and empirical studies such as those on fragmented populations of small mammals (Dunstan and Fox 1996) and birds (Mac Nally et al. 2000). In these cases, species composition is influenced as much by matrix conditions and habitat suitability within fragments as it is by fragment size per se.

Finally, patterns of habitat loss rarely occur in a random fashion across a landscape that results in a given level of habitat cover of uniform quality. Rather, fragmentation is a nonrandom process driven by human land-use practices—vegetation remnants are not therefore representative of the pre-fragmentation landscape (Saunders et al. 1987). The most productive parts of a landscape are almost always those modified first (Woolley and Kirkpatrick 1999; Smith et al. 2000; Scott et al. 2001a,b). In these cases, the response of some individual taxa (and the number of species persisting) will be strongly affected by the quality of *what* remains as well as *how much* remains. Threshold theory ignores the critical role of some (often small) areas of a landscape for the persistence of biodiversity. For example, the limited area of riparian systems can be essential for a large amount of the bio-

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diversity in some ecosystems (e.g., Mac Nally et al. 2000), and degradation of this habitat can have impacts highly disproportionate to their areal extent (see Chapter 6). Similarly, specialized habitats like cave systems can be small but support an important and often unique component of the endemic biota of a region (Culver et al. 2000; see Chapter 6).

In summary, there are no generic rules for threshold levels of vegetation or habitat cover (e.g., 10, or 30, or 70 percent). Rather, thresholds will depend on the landscape in question (a forest-forest or forest-agriculture system), the species of interest, and the ecological processes in question (the extent of tree health or the hydrological impacts of rain-on-snow events as a function of the extent of landscape-wide clearcutting).

A useful illustration of the effects of different processes in different systems and different species comes from Australian forest and woodland systems. There can be extensive loss of an array of small and intermediate-sized mammals from forest ecosystems whose vegetation appears to be relatively intact. The wide distribution of feral predators (the red fox [*Vulpes vulpes*] and feral cat [*Felis catus*]) in these landscape

(and their use of the road system) could be important factors driving species loss despite limited apparent habitat loss (May 2001). Threshold cover levels and species decline and loss do not appear to be related in this case. Conversely, threshold levels of cover of native woodlands of 30 percent or more have been found to be important for limiting the effects of tree dieback and death (McIntyre et al. 2000).

Compositional Studies, Habitat Fragmentation, and Matrix Conditions

Many compositional and modeling studies clearly demonstrate that matrix conditions have a significant bearing on species occurrence in fragmented ecosystems (Szaro and Jakle 1985; Fahrig and Merriam 1994; Fitzgibbon 1997; Saari et al. 1998; Saab 1999; Renjifo 2001). A species for which the matrix is suitable or even partially suitable will be significantly less affected by fragmentation than one for which the matrix is totally lacking in value (Davies and Margules 1998; Ås 1999; Ricketts 2001) (Table 2.2).

Landscape composition and patch-matrix contrasts also influence the effects of disturbance regimes. For example, the spatial juxtaposition of fire-prone pastures

TABLE 2.2.

Examples of matrix effects on species responses.

ORGANISM, STUDY SITE	DESCRIPTION	REFERENCES
Hazel grouse (<i>Bonasa bonasia</i>), Scandinavia	In areas where the matrix was dominated by agricultural land, hazel grouse were absent from suitable habitat patches >100 m from a population source area; hazel grouse occupied patches up to 2 km from a population source if the matrix was an intensively managed plantation forest	Åberg et al. 1995
Small mammals, Brazil	The response of small mammals in rainforest fragments was different if the matrix was cleared pasture compared with regrowth rainforest	Malcolm 1997
Birds, North America	Up to 65% of the variation in the distribution of some taxa could be explained by matrix conditions	Pearson 1993
Invertebrates, English heathlands	Populations changed according to the nature of the surrounding landscape matrix	Webb et al. 1984; Webb and Hopkins 1984
Red-listed fungi, Norway	The occurrence of fungi at the stand level was strongly related to its occurrence in the surrounding forest. Where there was long-term (>140-year) persistence of host logs in a landscape, fungi were likely to occur in a stand.	Sverdrup-Thygeson 1999

can significantly increase wildfire risk in adjacent rain-forest fragments (Kauffman and Uhl 1991). Similarly, relatively nonflammable patches in Yellowstone National Park burned when the surrounding matrix supported high-intensity fires (Romme and Despain 1989).

The preceding examples clearly illustrate that matrix conditions are fundamental to interpreting fragmentation effects. This can help explain why two patches of similar shape and size, but with different landscape contexts, may have very different levels of biodiversity (Lindenmayer et al. 1999b,c; Vandermeer et al. 2001). Even if the matrix is suitable only for foraging (Landers et al. 1979; Loman and von Schantz 1991; Yahner 1983; Rodenhouse and Best 1994; McAlpine et al. 1999), or allows for the extension of home ranges, it may facilitate the occupancy of (other) breeding sites (McCarthy et al. 2000).

History of the Matrix and Fragmentation Effects

Historical factors in the matrix also can be very useful for interpreting fragmentation effects and associated population phenomena (Thomas et al. 1992a; Díaz et al. 2000). For example, forest fragmentation effects can appear and then disappear depending on regeneration dynamics in the surrounding matrix (Fahrig 1992). In other cases, the length of isolation of remnants created by a high contrast with conditions in the surrounding matrix is a significant predictor of species occurrence in some fragments (Suckling 1982; Bennett 1990b). Loyn (1987) showed that one bird species was lost from habitat fragments for every decade of isolation in a modified landscape in eastern Victoria, southeastern Australia. Forest fragmentation, therefore, has both a temporal and a spatial domain (Lord and Norton 1990), and it is dependent on matrix conditions and the length of time the matrix has been characterized by a particular condition.

The Use of the Matrix and Fragmentation Effects

Several studies have shown that a species' ability to exploit the matrix can strongly influence the nature and strength of fragmentation effects (Mills 1995; Sisk et al. 1997). In some cases, new species will occur in the matrix when it is modified, which may affect the dy-

namics of populations residing within habitat fragments. For example, clearing of moist forest in Brazil led to the colonization of the matrix by new species (Brown and Hutchings 1997; Tocher et al. 1997). These included both predators and competitors of the original inhabitants of the fragments (Gascon and Lovejoy 1998).

In places where there is high contrast in suitability between a patch and the surrounding matrix, a *fence effect* can occur—levels of patch occupancy and within-patch population density may be considerably higher than expected. Here, animals are reluctant to disperse from a patch of suitable habitat into neighboring areas of unsuitable habitat; that factor can inflate levels of abundance (e.g., "crowding") and/or patch occupancy (Wolff et al. 1997; Bayne and Hobson 1998). Animals restricted to areas of favorable habitat when dispersing (e.g., Garrett and Franklin 1988; Merriam and Lanoue 1990) may be particularly prone to this effect.

Many fragmentation studies (e.g., Sieving et al. 2000) have focused almost exclusively on species use of remnants or corridors and ignored the role of the surrounding landscape matrix (see critiques by Simberloff et al. 1992; Laurance and Bierregaard 1997). This is because the vegetation that characterizes the landscape matrix is often different from that in habitat remnants. However, such matrix areas may support populations of species also found in the remnant patches, and they may make a substantial contributions to population persistence (Gascon et al. 1999). On this basis, Wiens (1989) noted that

a focus exclusively on fragmentation of habitats misses the point that it is often the structure of an entire landscape mosaic rather than the size or shape of individual patches [that matters]. . . . The likelihood that dispersal can occur between fragments and forestall the extinction of sensitive species on a regional scale is influenced by the configuration of the fragments and the landscape mosaic in which they are embedded.

Sampling of the landscape matrix may reveal that some areas considered to be "remnants" are, in fact, part of a habitat continuum and may not be acting as discrete habitat patches at all. Studies in the Biological Dynamics of Forest Fragments Project showed that

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ffects on interpatch dispersal by the red squirrel (*Sciurus vulgaris*). Thus, conditions in the matrix can strongly influence the degree of isolation of patches, which may be more or less than typically revealed by simple euclidean distances in landscape models of population dynamics (Ricketts 2001). Most existing computer models for metapopulation dynamics assume that the matrix is totally unsuitable breeding and foraging habitat and does not influence the success of interpatch dispersal and that taxa have random dispersal patterns. Nonrandom dispersal patterns and the effects of matrix conditions on dispersal were found to be significant in the dynamics of butterfly populations (Conradt et al. 2000). Lindenmayer et al. (2000a) found greater congruence between the predictions of a metapopulation model and actual field data for patch occupancy when the effects of matrix conditions on dispersal were included in the model specifications. Most metapopulation models do not consider movement in the context of the mosaic nature of most real landscapes (Cale 1999). Linear distance may actually be a poor measure of connectivity and/or isolation (Wegner and Merriam 1979). Two fragments far apart with high connectivity will be less isolated than closely spaced ones with low interpatch connectivity (Haila 1999).

Forecasts from metapopulation models will also be very poor for animals that cannot use the matrix but can readily disperse through it. Metapopulation models generally do not accommodate changes in home range sizes that can occur with habitat fragmentation (e.g., Barbour and Litvaitis 1993), changed landscape mosaics (Milne et al. 1992), or frequent movements between many patches to gather spatially separated food resources (e.g., Boone and Hunter 1996). Concepts such as the *central place foraging theory* are relevant to how matrix conditions and their relationships with patch configuration influence patchily distributed organisms (Recher et al. 1987; Lindenmayer et al. 1993a). For example, modeling of an Australian kingfisher, the laughing kookaburra (*Dacelo novaeguineae*), produced inaccurate estimates of patch occupancy because birds appear to alter home range movements in response to landscape change, and to move between many different patches to gather

food—in other words, classic metapopulation models did not fit (Lindenmayer et al. 2001b).

Spatial and Temporal Changes in Matrix Suitability

Most metapopulation models assume that the matrix and the patches it contains are homogeneous (Wiens 1997a) and that the habitat suitability of both landscape elements will not change on a spatial or temporal basis. Yet, in wood production forests the reverse will often occur and habitats will become suitable for many taxa with increasing time after harvesting, especially if matrix-based management strategies are adopted. Spatially explicit models like the one developed by Possingham and Davies (1995) can be useful in this regard. Different habitat-quality values can be assigned to any number of patches in this model. These habitat-quality values can, in turn, have varying temporal trajectories depending on, for example, regrowth of cutover stands in the matrix (Lindenmayer and Possingham 1995a).

All models invariably simplify the systems they attempt to portray (Burgman et al. 1993). Metapopulation models are no different in this regard (Hanski 1999a), and models like Hanski's (1994b) incidence function model consistently favor simplicity above model complexity (Ludwig 1999). However, it is essential to consider temporal and spatial variation in matrix conditions when applying metapopulation modeling to dynamic managed landscapes. It is also vital to check model assumptions before models are applied to real landscapes and real conservation problems (Wiens 1994; Pope et al. 2000). In some patchily distributed populations there will be no conformity to a metapopulation structure (1) where the matrix is so hostile that it precludes movement and relict populations are confined only to totally isolated habitat patches, (2) where the matrix is sufficiently suitable to facilitate frequent movements between habitat patches, and (3) where conditions in the matrix are suitable enough to allow organisms to forage or live there.

The incorporation of these sorts of considerations into modeling frames may ultimately lead to new generations of spatially explicit population models that include some of the complexity that characterizes real

landscapes and the responses of biota to it (e.g., Gustafson and Gardner 1996; Hokit et al. 1999).

Connectivity and Corridors

Determining what constitutes connectivity for a given species or group of organisms is a critical issue in conservation biology. Much work has focused on corridors, yet connectivity in forests involves much more than just the establishment of wildlife corridors (Wiens 1997a), and the connectivity role of the matrix (see Chapter 1) has often been overlooked. This is particularly true in forest environments—the majority of corridor studies have been in agricultural landscapes (Saunders and Hobbs 1991; Gustafsson and Hansson 1997). Dynamic matrix conditions can have a fundamentally important influence on connectivity in forest ecosystems (Lindenmayer 1998).

Although the establishment of wildlife corridors is common in wood production forests (reviewed by Lindenmayer 1998), assessments of their effectiveness in contributing to connectivity cannot be made without consideration of the matrix (Noss 1987; Simberloff and Cox 1987; Beier and Noss 1998). Moreover, if there is continued habitat loss in the surrounding matrix, the establishment of corridors may make only a limited contribution to biodiversity conservation (Rosenberg et al. 1997; Harrison and Bruna 2000).

If conditions in the matrix are hostile, then large corridors linking large retained patches may be required to retain connectivity for some species. Conversely, given suitable matrix conditions, reliance on corridors to provide connectivity may be minimized (Rosenberg et al. 1997) and corridor widths reduced (Forman 1995; Lindenmayer 1998). Only a limited amount of movement may then be required to “rescue” populations in reserves or habitat remnants and limit losses of genetic variability or limit population decline (Stacey and Taper 1992; Mills and Allendorf 1996). For example, an average of only one migrant per generation (every three to four years) was predicted to stem losses of expected heterozygosity from patchy populations of arboreal marsupials (Lindenmayer and Lacy 1995a).

The matrix will be a filter rather than a complete barrier to movement for many organisms (Gascon and Lovejoy 1998). Forman (1995) termed the control of the matrix over connectivity as “resistance” and hypothesized that barriers to movement across the matrix will be reduced if patch conditions resemble those in the matrix (see Stouffer and Bierregaard 1995 for an example). However, matrix resistance also will depend on the dispersal mechanisms of a given species (whether it is random or influenced by habitat quality), and the scale at which a species moves (Ricketts 2001). If a species is very vagile and populations are not subdivided among patches, then the landscape will be patchy and continuous. Connectivity is therefore a species-specific phenomenon—an outcome of species-specific dispersal behavior and movement patterns (e.g., whether the main form of movement is flying or crawling) and how these interact with patterns of landscape cover. For these reasons, a simple map of vegetation cover may not correspond to a map of connectivity for a given species (Ingham and Samways 1996), and it may not reveal whether a landscape is connected or fragmented (Wiens et al. 1997; With 1999).

Consideration of matrix conditions is particularly important for connectivity in forest landscapes. This is because, unlike agricultural areas, logged and regenerated lands will often immediately or eventually provide suitable habitat for many species (Pattemore and Kikkawa 1975; Loyn 1985a; Smith 1985). Even the structural complexity provided by exotic plantations can provide connectivity for forest species (including some that otherwise could not move through an agricultural landscape) (Renjifo 2001). Hence, changes in matrix conditions that might even be relatively minor may substantially enhance connectivity for many taxa. There are many factors influencing not only the suitability of the matrix as habitat, but also the suitability of the matrix for movement in managed forests. These include the type and extent of silvicultural practices in the matrix (Bennett 1990a; Machtans et al. 1996; Vesely and McComb 1996; see Chapter 8), partial retention of original stands (Taylor 1991; Thillay 1997), and rotation length (Curtis 1997; see Chapter 7).

Understanding relationships between matrix conditions and the movement behavior of target organisms is fundamental to analyses of connectivity. Even

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frogs could breed and travel across the matrix (cleared pasture) that surrounded the rainforest fragments, indicating that the remnants were not true isolates for these taxa (Tocher et al. 1997; see Chapter 14). The matrix may be particularly important in forest ecosystems where either (1) remnants (e.g., old-growth patches) are surrounded by a matrix that regenerates following harvesting and can eventually provide suitable habitat for a significant proportion of the forest-dependent biota, or (2) enough structural attributes of the original stand are retained in the matrix to allow forest-dependent taxa to persist there.

Hence, the effects of fragmentation in forest environments where protected areas are embedded within a matrix of regenerating or structurally enriched forest may be quite different from those in many agricultural systems where the surrounding matrix is often thought to be unsuitable, or "hostile," for forest biota (McGarigal and McComb 1995; Estades and Temple 1999).

In summary, traditional perspectives on fragmentation effects like those based on ocean-island models and on island biogeography theory are often inappropriate where the matrix is not wholly inhospitable (Pither and Taylor 1998; Ricketts 2001). Understanding fragmentation effects requires an understanding of how biota use all landscape components, including the matrix (Laurance 1991a; Åberg et al. 1995; Flather and Sauer 1996).

Metapopulation Dynamics

A metapopulation is a "set of local populations which interact via individuals moving between local populations" (Hanski and Gilpin 1991). Hanski and Simberloff (1997) contend that the metapopulation paradigm is most useful when successful interpatch dispersal is infrequent and migration distances are limited. Hastings (1993) suggested from simulation modeling that populations could be considered to be "independent" where dispersal rates between them were less than 10 percent.

The concept of metapopulation dynamics has been used widely to describe the spatial arrangement of subpopulations of species in fragmented environments

(e.g., Arnold et al. 1993; Hanski and Thomas 1994; McCullough 1997), particularly those taxa susceptible to localized extinction and recolonization (Hanski 1998). Most models of metapopulation dynamics are simplified and do not consider the strongly influential effects of the matrix on patch processes and interpatch dispersal. As noted by Wiens (1997a), most metapopulation models assume that the "the matrix separating subpopulations is homogeneous and featureless." Perhaps this is a relict of island biogeography theory, which some workers consider to be a precursor of metapopulation theory (Wiens 1995). Therefore, predictions from many population models are unlikely to be accurate because of the simplifying assumptions they make about matrix suitability and patch-matrix interrelationships (see Pope et al. 2000). This has led some workers to suggest that simple forms of metapopulation modeling should not be used in population management in real landscapes (e.g., Doak and Mills 1994; Fahrig and Merriam 1994).

By ignoring the matrix in a landscape that is thought to be fragmented, important factors can be overlooked in metapopulation modeling. Consideration of the matrix may reveal that a species is not distributed as a metapopulation at all (Hanski and Simberloff 1997). Including appropriate information on the matrix and how it is used by an organism should improve the understanding of the factors influencing the species distribution in patchy landscapes such as production forests.

Types of Metapopulations

Hanski and Gyllenberg (1993) describe some different forms of metapopulation structure, where a metapopulation structure is defined as "a system of habitat patches which is occupied by a metapopulation and which has a certain distribution of patch sizes and interpatch distances" (Hanski and Gilpin 1991). Two extreme forms of metapopulation structure were recognized by them—the Mainland-Island structure and the Levins structure (Figure 2.6). The Mainland-Island metapopulation structure has two major features: (1) a large "mainland" area in which populations are secure and rarely (if ever) suffer extinction, and (2) an array of small patches in which extinctions can be relatively common events. The mainland provides a source of dispersalists to recolonize the patches and

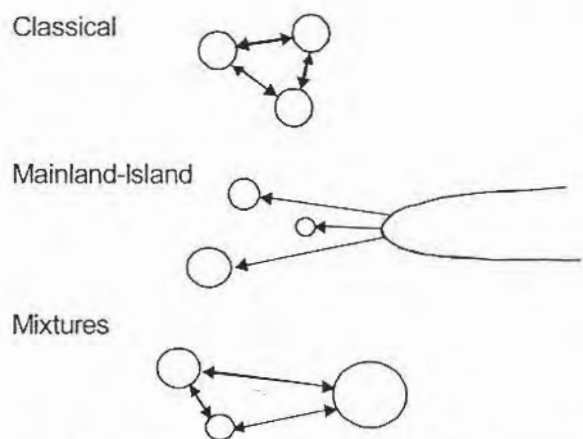


FIGURE 2.6. Types of metapopulations. Classical metapopulations are demonstrated by the Levins (1970) model (see text) in which all patches are the same size and equidistant. "Mainland" in the mainland-island model refers to a large area of habitat whose populations never suffer extinction. The mixtures model falls between the classical and mainland-island models in terms of patch size and distance.

reverse localized extinctions. A number of species of butterflies are thought to exhibit a Mainland-Island metapopulation structure (Harrison et al. 1988; Hanski and Thomas 1994).

The Levins metapopulation structure (from Levins 1970) is characterized by all the patches being the same size. There is no "mainland." Localized extinctions in the patches are reversed by recolonization from other patches (Hanski and Gyllenberg 1993). Harrison (1991) believed that most metapopulation structures will be characterized by patches that vary in size and spatial location—in other words, they will fall between the two extremes illustrated by the Mainland-Island and Levins models.

Metapopulations in the Real World

An increasing number of species have been identified that display various types of metapopulation dynamics (e.g., Hill et al. 1996; Carlson and Edenhamn 2000). Nevertheless, it is not clear whether metapopulations are common in real landscapes (Hastings and Harrison 1994; Harrison and Taylor 1997; but see Niemien and Hanski 1998). Dispersal is essential to the maintenance of metapopulation dynamics (Hanski 1999b), but for some species it may not occur across a hostile

matrix. Therefore, it is not appropriate to assume that all patchily distributed taxa function as metapopulations (Hanski and Simberloff 1997). For example, a study of geckos in Western Australia showed that animals were isolated populations confined to woodland patches with no movement across the matrix (Sarre et al. 1995).

Studies of the matrix also have revealed that some patchily distributed species are not distributed as metapopulations. If a species exhibits metapopulation structure, then patches close to occupied patches should be more likely to be occupied than more distant ones (see Smith 1994; Koenig 1998). There should, in turn, be spatial dependence in its distribution pattern. Statistical tests for seventy-six species of birds living in eucalypt patches of the Tumut Fragmentation Experiment in southeastern Australia (see Chapter 13) found no evidence of spatial dependence, suggesting that metapopulation dynamics were not occurring in any of these taxa (Lindenmayer et al. 2001a). In the same study, extensive surveys of the radiata pine matrix surrounding eucalypt fragments showed that many species used the matrix (see Chapter 13).

The occurrence of species in the matrix can create problems in the application of metapopulation models that ignore matrix effects. For example, Lindenmayer et al. (1999d) found poor predictive ability for Hanski's (1994b) incidence metapopulation model for two species of arboreal marsupials that persisted in the matrix. McCarthy et al. (2000) found that the ability of their target species (the white-throated treecreeper [*Cormobates leucophaeus*]) to forage both in habitat fragments and in the surrounding matrix (termed "landscape complementation"; Dunning et al. 1992) significantly reduced the fit between model-predicted and actual values for patch occupancy. Estades (2001) found that when matrix habitat had value as a food resource, traditional patch size effects tended to dissipate significantly.

The Matrix, Interpatch Dispersal, and Interpatch Movements

Interpatch dispersal can be strongly influenced by the surrounding matrix (Wiens 1997b). Andrén and Delin (1994) found that managed forests had no negative ef-

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fects on interpatch dispersal by the red squirrel (*Sciurus vulgaris*). Thus, conditions in the matrix can strongly influence the degree of isolation of patches, which may be more or less than typically revealed by simple euclidean distances in landscape models of population dynamics (Ricketts 2001). Most existing computer models for metapopulation dynamics assume that the matrix is totally unsuitable breeding and foraging habitat and does not influence the success of interpatch dispersal and that taxa have random dispersal patterns. Nonrandom dispersal patterns and the effects of matrix conditions on dispersal were found to be significant in the dynamics of butterfly populations (Conradt et al. 2000). Lindenmayer et al. (2000a) found greater congruence between the predictions of a metapopulation model and actual field data for patch occupancy when the effects of matrix conditions on dispersal were included in the model specifications. Most metapopulation models do not consider movement in the context of the mosaic nature of most real landscapes (Cale 1999). Linear distance may actually be a poor measure of connectivity and/or isolation (Wegner and Merriam 1979). Two fragments far apart with high connectivity will be less isolated than closely spaced ones with low interpatch connectivity (Haila 1999).

Forecasts from metapopulation models will also be very poor for animals that cannot use the matrix but can readily disperse through it. Metapopulation models generally do not accommodate changes in home range sizes that can occur with habitat fragmentation (e.g., Barbour and Litvaitis 1993), changed landscape mosaics (Milne et al. 1992), or frequent movements between many patches to gather spatially separated food resources (e.g., Boone and Hunter 1996). Concepts such as the *central place foraging theory* are relevant to how matrix conditions and their relationships with patch configuration influence patchily distributed organisms (Recher et al. 1987; Lindenmayer et al. 1993a). For example, modeling of an Australian kingfisher, the laughing kookaburra (*Dacelo novaeguineae*), produced inaccurate estimates of patch occupancy because birds appear to alter home range movements in response to landscape change, and to move between many different patches to gather

food—in other words, classic metapopulation models did not fit (Lindenmayer et al. 2001b).

Spatial and Temporal Changes in Matrix Suitability

Most metapopulation models assume that the matrix and the patches it contains are homogeneous (Wiens 1997a) and that the habitat suitability of both landscape elements will not change on a spatial or temporal basis. Yet, in wood production forests the reverse will often occur and habitats will become suitable for many taxa with increasing time after harvesting, especially if matrix-based management strategies are adopted. Spatially explicit models like the one developed by Possingham and Davies (1995) can be useful in this regard. Different habitat-quality values can be assigned to any number of patches in this model. These habitat-quality values can, in turn, have varying temporal trajectories depending on, for example, regrowth of cutover stands in the matrix (Lindenmayer and Possingham 1995a).

All models invariably simplify the systems they attempt to portray (Burgman et al. 1993). Metapopulation models are no different in this regard (Hanski 1999a), and models like Hanski's (1994b) incidence function model consistently favor simplicity above model complexity (Ludwig 1999). However, it is essential to consider temporal and spatial variation in matrix conditions when applying metapopulation modeling to dynamic managed landscapes. It is also vital to check model assumptions before models are applied to real landscapes and real conservation problems (Wiens 1994; Pope et al. 2000). In some patchily distributed populations there will be no conformity to a metapopulation structure (1) where the matrix is so hostile that it precludes movement and relict populations are confined only to totally isolated habitat patches, (2) where the matrix is sufficiently suitable to facilitate frequent movements between habitat patches, and (3) where conditions in the matrix are suitable enough to allow organisms to forage or live there.

The incorporation of these sorts of considerations into modeling frames may ultimately lead to new generations of spatially explicit population models that include some of the complexity that characterizes real

landscapes and the responses of biota to it (e.g., Gustafson and Gardner 1996; Hokit et al. 1999).

Connectivity and Corridors

Determining what constitutes connectivity for a given species or group of organisms is a critical issue in conservation biology. Much work has focused on corridors, yet connectivity in forests involves much more than just the establishment of wildlife corridors (Wiens 1997a), and the connectivity role of the matrix (see Chapter 1) has often been overlooked. This is particularly true in forest environments—the majority of corridor studies have been in agricultural landscapes (Saunders and Hobbs 1991; Gustafsson and Hansson 1997). Dynamic matrix conditions can have a fundamentally important influence on connectivity in forest ecosystems (Lindenmayer 1998).

Although the establishment of wildlife corridors is common in wood production forests (reviewed by Lindenmayer 1998), assessments of their effectiveness in contributing to connectivity cannot be made without consideration of the matrix (Noss 1987; Simberloff and Cox 1987; Beier and Noss 1998). Moreover, if there is continued habitat loss in the surrounding matrix, the establishment of corridors may make only a limited contribution to biodiversity conservation (Rosenberg et al. 1997; Harrison and Bruna 2000).

If conditions in the matrix are hostile, then large corridors linking large retained patches may be required to retain connectivity for some species. Conversely, given suitable matrix conditions, reliance on corridors to provide connectivity may be minimized (Rosenberg et al. 1997) and corridor widths reduced (Forman 1995; Lindenmayer 1998). Only a limited amount of movement may then be required to “rescue” populations in reserves or habitat remnants and limit losses of genetic variability or limit population decline (Stacey and Taper 1992; Mills and Allendorf 1996). For example, an average of only one migrant per generation (every three to four years) was predicted to stem losses of expected heterozygosity from patchy populations of arboreal marsupials (Lindenmayer and Lacy 1995a).

The matrix will be a filter rather than a complete barrier to movement for many organisms (Gascon and Lovejoy 1998). Forman (1995) termed the control of the matrix over connectivity as “resistance” and hypothesized that barriers to movement across the matrix will be reduced if patch conditions resemble those in the matrix (see Stouffer and Bierregaard 1995 for an example). However, matrix resistance also will depend on the dispersal mechanisms of a given species (whether it is random or influenced by habitat quality), and the scale at which a species moves (Ricketts 2001). If a species is very vagile and populations are not subdivided among patches, then the landscape will be patchy and continuous. Connectivity is therefore a species-specific phenomenon—an outcome of species-specific dispersal behavior and movement patterns (e.g., whether the main form of movement is flying or crawling) and how these interact with patterns of landscape cover. For these reasons, a simple map of vegetation cover may not correspond to a map of connectivity for a given species (Ingham and Samways 1996), and it may not reveal whether a landscape is connected or fragmented (Wiens et al. 1997; With 1999).

Consideration of matrix conditions is particularly important for connectivity in forest landscapes. This is because, unlike agricultural areas, logged and regenerated lands will often immediately or eventually provide suitable habitat for many species (Pattimore and Kikkawa 1975; Loyn 1985a; Smith 1985). Even the structural complexity provided by exotic plantations can provide connectivity for forest species (including some that otherwise could not move through an agricultural landscape) (Renjifo 2001). Hence, changes in *matrix conditions that might even be relatively minor* may substantially enhance connectivity for many taxa. There are many factors influencing not only the suitability of the matrix as habitat, but also the suitability of the matrix for movement in managed forests. These include the type and extent of silvicultural practices in the matrix (Bennett 1990a; Machtans et al. 1996; Vesely and McComb 1996; see Chapter 8), partial retention of original stands (Taylor 1991; Thillay 1997), and rotation length (Curtis 1997; see Chapter 7).

Understanding relationships between matrix conditions and the movement behavior of target organisms is fundamental to analyses of connectivity. Even

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if a habitat patch is close to another occupied patch and well within typical dispersal distances, it may be isolated because of hostile conditions in the matrix (Taylor et al. 1993). In many other cases, dispersal pathways used by organisms will not always conform to designated corridors (Gustafson and Gardner 1996; Lindenmayer 1998; Cale 1999).

Conservation management strategies applied throughout the matrix may provide better connectivity than wildlife corridors for species that disperse randomly (e.g., cabbage butterfly [Fahrig and Paloheimo 1988] and eastern screech-owl [*Otus asio*; Belthoff and Ritchison 1989]). In Australia, matrix suitability can allow migratory and nomadic species such as native pigeons and honeyeaters access to resources that fluctuate in temporal and spatial availability (Date et al. 1996; Price 1999). Connectivity via stepping stones or dispersed islands of potentially suitable habitat may be the best way for these and other mobile species (like butterflies and bats), which can move readily across the matrix between roosting areas and foraging locations (Lumsden et al. 1994; Schultz 1998; Law et al. 1999). Individual structures, such as trees and logs, can also function as stepping stones.

Most existing knowledge about connectivity and the matrix comes from theory (e.g., Murphy and Noon 1992) and simulation modeling (e.g., Burkey 1989; Boone and Hunter 1996; Lindenmayer and Possingham 1996). Since robust empirical data linking matrix conditions and connectivity are presently limited (Nicholls and Margules 1991; Bennett 1998), carefully designed studies of the interrelationships between matrix conditions and connectivity are badly needed (see Chapter 17).

Extinction Proneness

Species vary widely in their response to habitat loss and fragmentation; some decline, while others remain unchanged or even increase (Saunders and Ingram 1995; Dooley and Bowers 1998). In an effort to better predict species responses to landscape change, correlations between extinction proneness and particular traits of species (such as diet, body size, life history strategy, longevity and fecundity, habitat require-

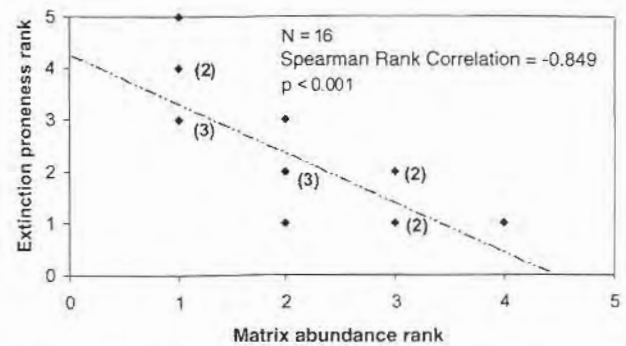


FIGURE 2.7. Correlations between extinction proneness and use of the matrix by sixteen species of nonflying mammals in North Queensland (redrawn from Laurance 1991a). The solid dots show plotted values between matrix abundance and extinction proneness. The values in brackets are the number of species with the same plotted value. The diagonal line is the fitted relationship between the two parameters. Extinction proneness (y-axis) is ranked from high (5) to low (1). Matrix abundance is scaled from 1 to 5, with 1 indicating that a species was never detected in the matrix and a value of 5 indicating that a species was commonly observed in the matrix.

ments, and type of locomotion) have been the focus of many studies (e.g., Terborgh 1974; Karr 1982; Pimm et al. 1988; Robinson and Quinn 1988; Burbidge and McKenzie 1989; Lawler 1993; Gaston and Blackburn 1995). Extinction-prone species appear to include large wide-ranging taxa (often predators), rare species, or species that are sparsely distributed. One crucial factor in assessing the likelihood of species persistence is occurrence in matrix habitats.

Sixteen nonflying species of Queensland mammals were studied to determine correlations between extinction proneness and ecological traits such as body size, longevity, fecundity, trophic level, diet, and population abundance both in rainforest patches and in the surrounding modified landscape matrix (Laurance 1991a). The best predictor of persistence was the abundance of the species in stands of regrowth forest and pastures in the landscape matrix surrounding the rainforest fragments (Figure 2.7). Species that were rare or absent in the matrix were also those most likely to have been lost or to have declined substantially in the rainforest fragments (e.g., brown antechinus [*Antechinus stuartii*], Atherton antechinus [*Antechinus godmani*], and tiger quoll [*Dasyurus maculatus*]) (Laurance 1991a, 1997a). Several factors may explain

these findings. Animals lost from the matrix may be lost from an entire region (and hence also habitat fragments). Conversely, individuals dispersing from matrix habitats may "rescue" declining populations in the fragments (Laurance 1997a).

Persistence in the matrix and resilience to extinction proneness has also been demonstrated in other studies. The Wog-Wog Fragmentation Experiment in southeastern Australia (Margules 1992) showed that the species of beetles that inhabited the radiata pine matrix surrounding fragments of eucalypt forest were most likely to persist in the fragments (Davies et al. 2000). Similar outcomes have been found for insects in Scandinavian forests (Ås 1999), as well as in studies of temperate and tropical bird populations (Blake 1983; Howe 1984; Diamond et al. 1987; Renjifo 2001).

Reserve Selection

Around the world, reserve systems have generally been developed on an ad hoc basis (Terborgh 1992; see Chapter 5). In an attempt to improve systems of protected areas (e.g., to enhance their representativeness), reserve selection methods have been developed, such as gap analysis (e.g., Scott et al. 1993; Stoms et al. 1998) and mathematical algorithms (Kirkpatrick 1983; Williams et al. 1996; Pressey 1997). There are numerous hypothetical examples of these approaches for the selection of reserves (Bedward et al. 1992; Nicholls and Margules 1993; Noss and Cooperrider 1994; see Chapter 5). However, the potential contribution of the matrix to species persistence is often ignored by these methods (Burgman and Lindenmayer 1998). The focus is on species captured within reserves, usually without regard to their status in surrounding matrix lands. However, many of the organisms that persist in the matrix will also be the ones most likely to occur in the reserve system. The inclusion of the matrix will add considerably to the efficiency of reserve design because reserve selection routines can be focused principally on taxa that can be conserved *only* in the protected areas. Diamond (1976) recommended that the selection of reserves should be made on the basis of the species that require them for survival. Therefore, while the stated goal of a network

of reserves has traditionally been to adequately represent the biodiversity of a region, more efficient and refocused reserve design approaches could be those that target species not captured adequately in sensitively managed matrix lands.

Lewis et al. (1991) described some reserve design algorithms that better account for matrix conditions and showed how the buffering potential of adjacent matrix lands could significantly influence protected area outcomes in the Australian state of Tasmania (see also Nix 1997). As noted by Wiens (1989):

To establish reserves according to ecological insights requires both a consideration of broad-scale landscape configurations and knowledge of the ecological requirements of species that are important in particular situations.

Edge Effects

Distinct edges or boundaries are created between clearcut and unlogged areas (Matlack 1993; Esseen 1994; Parry 1997). Profound modifications of biological and physical conditions can occur at these boundaries; these modifications are typically referred to as *edge effects* (Wilcove 1985; Temple and Cary 1988; Yahner 1988; Reville et al. 1990; Chen 1991; Chen et al. 1992; Kremsater and Bunnell 1999).

The magnitude of many types of edge effects is often related to the level of contrast between the matrix and other landscape units; where the contrast is high, there will be more intense interactions and spatially extensive edge influences (Laurance and Yensen 1991; Mesquita et al. 1999). The extent of the area of the matrix supporting such high-contrast conditions can also influence the magnitude of edge effects. For example, microclimate edge effects may be greater where a large clearcut abuts a retained patch than where the cutover is small (Lindenmayer et al. 1997a). An assessment of conditions in the matrix is therefore fundamental to an understanding of the impacts of various kinds of biotic and abiotic edge effects. It is also vital to the development of buffering protocols in the matrix that aim to better protect sensitive habitats in forest landscapes. For example, the width of buffer strips to protect riparian areas from pesticides and to

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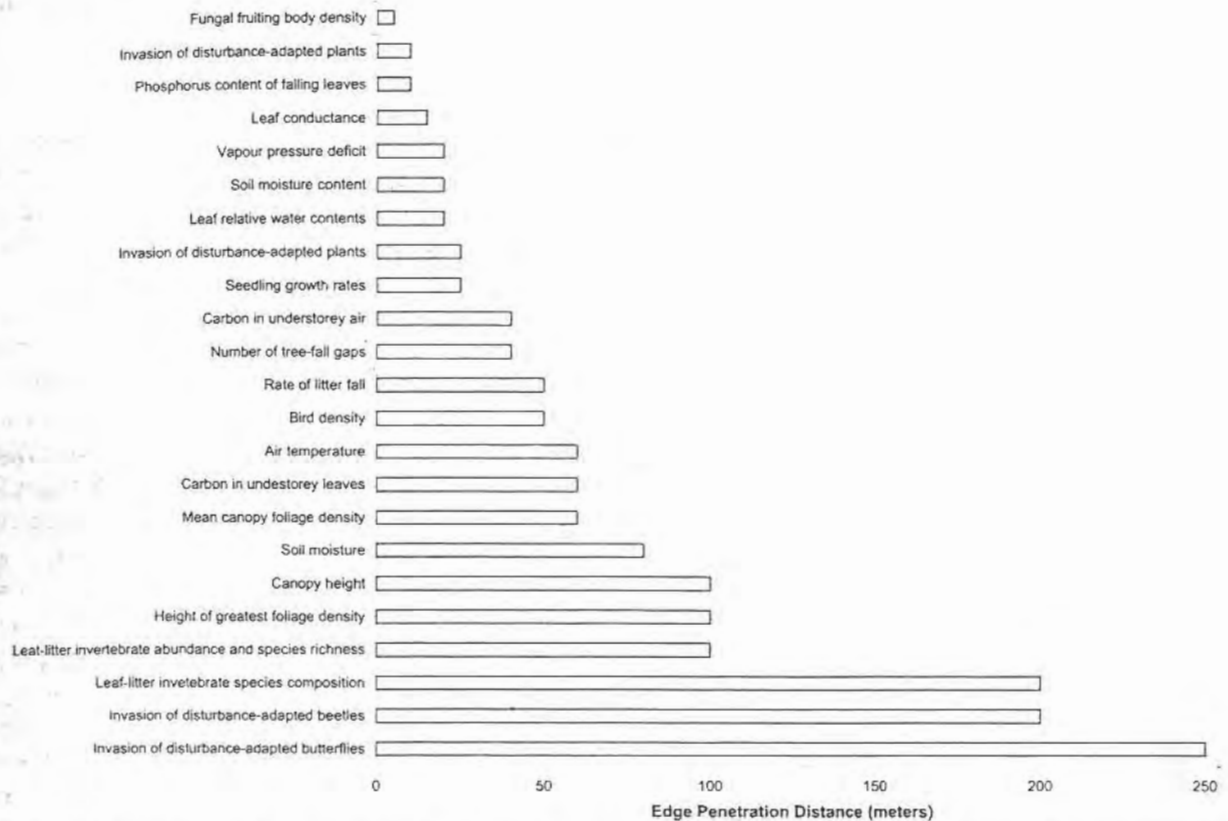


FIGURE 2.8. Variation in edge penetration for a range of measures in the Biological Dynamics of Forest Fragments Project in Brazil. See Chapter 14 for further details (modified and redrawn from Laurance et al. 1997).

reduce in-stream invertebrate mortality (more than 50 meters in Australian eucalypt plantations; Barton and Davies 1993) may be quite different from that required to mitigate changed wind patterns that may otherwise penetrate several hundred meters from cut-over boundaries (Harris 1984; Saunders et al. 1991).

The intensity of edge effects, or the area of a patch subject to significant edge influence or modification, depends on many variables. The magnitude of an edge effect is dependent on the parameter of interest (which has its own unique pattern of response; see Figure 2.8)—whether it is an environmental variable (e.g., air temperature), an ecological process (e.g., rate of organic matter decomposition), or a community interaction (e.g., predation of one species by another). The magnitude of edge effects will also be influenced by the extent of the area of the matrix supporting

high-contrast conditions. For example, Lindenmayer et al. (1997a) found that windthrow significantly increased in retained strips of forest when the adjacent clearcut was large rather than small cutblocks.

Edge effects are not uni-directional processes. In addition to edge effects penetrating from the matrix into adjacent patches, forest patches can exert edge influences on adjacent harvested areas. The effects of retained trees on light and other microclimatic factors are well known in the forestry literature. Similarly, Lindenmayer et al. (2001a) found the occurrence of birds in the matrix was strongly related to their occurrence in adjacent retained patches (see Chapter 13). It is important to be cognizant of the reciprocal nature of edge influences, but in the remainder of this section we concentrate on the impacts of edge processes ema-

nating from the matrix and penetrating into adjacent retained patches.

Edges of forest along boundaries with cutovers may be subject to significant microclimatic changes, such as increased temperatures and decreased humidity that extend for varying distances from an edge. Edge influences may be limited or extend for tens or hundreds of meters into a forest depending upon the environmental variable, physical nature of the edge, and weather conditions at the time of measurement (Moore 1977; Miller et al. 1991; Chen et al. 1992; Parry 1997). In some cases, edge effects can lead to the degradation of habitat in protected areas such as wildlife corridors (Lindenmayer et al. 1997a) and can disrupt connectivity between larger reserved areas (Lovejoy et al. 1986).

Wildlife biologists have known for many decades that certain game species have strong preferences for edge environments where foraging and hiding/thermal cover are close together (Leopold 1933; Patton 1974; Matlack and Litvaitis 1999). Large populations of white-tailed deer (*Odocoileus virginianus*) in the northern United States may exert considerable grazing pressure on food plants that occur at forest edges (Johnson et al. 1995), including endangered taxa (Miller et al. 1992). This can limit stand regeneration (Tilghman 1989) and alter patterns of species diversity in plants (Miller et al. 1992) and birds (McShea and Rappole 2000).

Studies in the Northern Hemisphere have documented negative vertebrate responses to forest edges, including interior forest species (i.e., those requiring *habitats away from edge environments*) (Gates and Gysel 1978; Andrén and Angelstam 1988; Telleria and Santos 1992; Terborgh 1992; Rudnicki and Hunter 1993; Paton 1994; Rich et al. 1994; Robinson et al. 1995). Many bird species in tropical forests are interior species (Terborgh 1989; Frumhoff 1995) and tend to avoid edges. This is, in part, because the efficiency of foraging patterns is impaired if home ranges or territories are transgressed by nonhabitat or edge conditions (McCullin 1998). Another important factor influencing species responses in edge environments is a lack of food—Burke and Nol (1998) provide an example in which the abundance of arthropods was significantly lower along the edges of small woodlots than in

the interior of larger patches, resulting in a negative effect on bird populations.

Elevated levels of nest predation along edges may not be a general phenomenon characteristic of all habitats and landscapes (Berg et al. 1992; Hanski et al. 1996, reviewed by Lahti 2001). Many studies in which significant nest predation effects have been observed are in agricultural landscapes where there are large contrasts between vegetation remnants and the surrounding environment (e.g., Andrén 1992; Bayne and Hobson 1997, 1998; Hannon and Cotterill 1998). Conversely, nest predation at edges may be limited or absent in landscapes with low levels of contrast (Schmiegelow et al. 1997), such as continuous Australian eucalypt forest dissected by minor bush tracks or juxtaposed native forest and exotic softwood plantations (Lindenmayer et al. 1999e). Sargent et al. (1998) showed that nest predation effects in hardwood fragments in South Carolina (United States) were lower if they were adjacent to pine stands rather than agricultural fields.

Certain types of edge effects can vary in their impacts between different forested ecosystems. Forest edges on the boundary of clearcuts in Sweden are characterized by reduced bird species diversity (Hansson 1983), but no such pattern occurs in clearcut forest edges in the northeastern United States (Rudnicki and Hunter 1993). Similarly, patterns of brood parasitism characteristic of edge environments in many northern hemisphere landscapes appear to be rare in parts of the Southern Hemisphere, such as in Australia (but see Luck et al. 1999). Even within North America, increased nest predation and brood parasitism seen in studies on the eastern side of continent are not common in the west (Kremsater and Bunnell 1999; Marzluff and Restani 1999). Notably, a recent review of the literature (Lahti 2001) has shown that the majority of studies did not find increased nest predation at edges.

Differences in invertebrate community composition have been observed between edge and interior environments (e.g., Keals and Majer 1991; Hill et al. 1992; Scougall et al. 1993). Populations of invertebrates such as amphipods responded negatively to increased levels of exposure, moisture, and temperature regimes at the edges of forest fragments in southeastern New South Wales (Margules et al. 1994b). Other examples of edge responses in insects have been docu-

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Edge environments can exert a strong influence on plant species (Laurance 1991b). Plant reproduction, growth, and mortality may respond to edges, depending upon the species and specifics of the edge. Chen et al. (1992) observed positive responses in tree reproduction and growth of surviving mature trees in old-growth forests bordering on recent clearcuts. Negative effects included accelerated mortality of mature trees due to windthrow.

Edge effects vary according to the type of harvesting prescriptions employed in the cutover area (e.g., clearcutting or shelterwood) and will generally decline (but rarely disappear completely) with the development of regenerating forest (Savill 1983). This is because the magnitude of edge effects is strongly related to the contrast in structure between harvested areas and retained patches.

Understanding various types of biotic and abiotic edge effects and their relationships to matrix conditions is fundamental to the development of appropriate buffering protocols that can make the matrix management more protective of sensitive areas in forest landscapes (see Chapters 3 and 6).

The Matrix and the Importance of Habitat

The study of habitat is essential for the evolving fields of landscape ecology and conservation biology. Because habitat is an organism-specific concept (Whittaker et al. 1973), an understanding of habitat is needed to determine what constitutes a suitable patch or a fragmented landscape for a particular species. Habitat information is also fundamental to matrix management and, in turn, to any comprehensive plan for conserving forest biodiversity. The availability of habitat is one of the primary factors influencing the distribution and abundance of organisms (Caughley 1978; Krebs 1978), and an understanding of distribution patterns through the use of habitat analysis can be crucial for determining (1) if the areas suitable for a particular species are also those targeted for forestry operations, (2) if areas that are not logged provide ef-

fective refugia or reserves, and (3) if logging practices alter the characteristics of a forest in ways that (temporarily or permanently) influence the distribution of a species, and, if so, how might logging practices be modified to mitigate such impacts?

Habitat analysis (*sensu* Morrison et al. 1992) also can be useful for determining relationships between the species' distribution and abundance and structural and floristic conditions in forests (Urban and Smith 1989; Block and Brennan 1993; Pearce et al. 1994). This information is useful for matrix management because it is central to identifying (1) the structural and floristic attributes that need to be retained to conserve particular species (Adams and Morrison 1993; Lindenmayer 1994a; see Chapter 8), (2) how many of these stand and/or landscape characteristics are needed (McComb and Lindenmayer 1999), and (3) how such attributes should be spatially arranged (Nelson and Morris 1994).

Increasingly, the importance of habitat is being recognized in landscape ecology and conservation biology. The loss of habitat is a key driver in species loss (Fahrig 1999) and, conversely, the maintenance of habitat across many spatial scales is a fundamental plank of any comprehensive approach for the conservation of forest biodiversity. We believe it is the overarching goal of matrix management. General principles to achieve this goal are the topic of the next chapter.

Conclusion

In this chapter, we have explored only a small subset of the significant themes in landscape ecology and conservation biology. The aim was not criticize either discipline but, rather, to highlight the importance of the matrix as a fundamental landscape component and to demonstrate the complexity that characterizes all real-world landscapes. Serious deficiencies arise in many aspects of conservation biology theory when the matrix is overlooked or relegated to the status of nonhabitat. Such oversights are understandable given the complexity of landscapes—and conservation biologists and landscape ecologists have often been forced to select relatively simple theories and approaches as part of preliminary attempts to understand landscapes. Much has

already been learned from testing existing theories and approaches. Greater efforts should now be made in conservation biology and landscape ecology to include the roles and contributions of the matrix.

We believe that much of ecology (including conservation biology and landscape ecology) is significantly more difficult than other areas of science such as physics and chemistry. Applied ecology (and, hence, ecologically sustainable forest management) is unlike physics and chemistry in that there are few general

principles that can be applied generically. Given such complexity, unique approaches to conserving biodiversity will be necessary that reflect different landscapes, species assemblages, and many other factors (including social ones). Accounting for the inherent complexity that characterizes forest ecosystems does not mean that developing robust plans for conserving biodiversity is impossible. In Chapter 3, we propose a framework and a set of associated generic, multiscaled principles to tackle the problem.