Kevin J. Gutzwiller
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Applying Landscape Ecology in Biological Conservation

With a Foreword by Richard T.T. Forman

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12

Human Conversion of Terrestrial Habitats

Peter August, Louis Iverson, and Jarunee Nugranad

12.1 Introduction

In this chapter, we describe how human activities change the abundance and quality of terrestrial habitats and discuss the ecological implications of these changes for biota. We begin by identifying fundamental principles associated with human conversion of terrestrial habitats and how fauna and flora respond to habitat conversion. We present a number of examples of how landscape ecologists and conservation biologists use these basic principles of land-cover change to develop management strategies to minimize ecological impacts from habitat loss. Next, we discuss principles for applying landscape ecology. We identify major voids in ecological theory and existing data that need to be filled for land managers to be better prepared to apply the principles of landscape ecology to biological conservation. Finally, we suggest research approaches that may be used to fill knowledge gaps. Although social and economic considerations are fundamental to land-cover change dynamics (Riebsame et al. 1994), detailed discussion of these factors is beyond the scope of this book; therefore, we focus our remarks on the ecological aspects of human conversion of terrestrial habitats.

12.2 Concepts, Principles, and Emerging Ideas

Human disturbance is the most significant contemporary agent of change in terrestrial ecosystems (Forman 1995). The rates with which natural habitats are lost, disturbed landscapes are created, species go extinct, and ecosystem processes are altered are higher now than they have been since the last cataclysmic event that impacted the planet 50 million years ago (Fastovsky and Weishampel 1996). Transformation of habitat can occur as a result of either natural or human activities (Table 12.1). The outcomes of some natural phenomena (e.g., fire, hurricane, flooding; Turner et al. 1997) are greatly modified by human influences. For example, dams will modify the rate and extent of flooding; forest removal and fragmentation will modify the effects of windstorms and overall climatic conditions.

TABLE 12.1. Possible types of land transformation by human influences (adapted from Forman 1995).

Cause of transformation	Type of human influence
Forest cutting	Direct
Urbanization	Direct
Corridor construction (road, rail, irrigation, utility)	Direct
Agriculture	Direct
Wetland drainage	Direct
Reforestation/restoration	Mostly direct, some indirect
Desertification	Mostly indirect, some direct
Chronic air pollution	Direct
Burning	Mostly direct, some indirect
Flooding	Mostly direct, some indirect
Bombing	Direct
Removal, mining	Direct
Herbicide	Direct
Release of non-native species	Direct and indirect

Human impacts occur at all scales, from site-specific to global, and they can occur rapidly or slowly (Figure 12.1).

When, where, and how rapidly natural landscapes are changed by human activities depends on a number of factors (Figure 12.2). Landscapes with significant biophysical constraints to development such as steep slopes, extreme climate, low soil fertility, or seasonal inundation are less prone to extensive human settlement than are landscapes without such impediments (Iverson 1988; Fuentes 1990; LaGro 1994). Reliable, safe access is a prerequisite to human development of landscapes. Some conduits for transportation are naturally occurring (e.g., rivers and sea) and have long provided human access to remote landscapes; other transportation conduits are products of human engineering (e.g., roads and rail) and permit access to undeveloped landscapes (Forman and Alexander 1998). The creation of a reliable access system is frequently the precursor to sudden and dramatic landscape conversions in both historical and modern times (LaGro and DeGloria 1992; Greene 1997; Pedlowski et al. 1997).

Human conversion of natural landscapes is precipitated by social, economic, and political factors, but it is bounded by environmental constraints (Ojima et al. 1994). Human population growth is a fundamental driving force in land conversion; as population numbers increase, the need to produce or extract more food, fuel, and fiber, and to develop infrastructure to support homes and commerce increases (Meyer and Turner 1992; Figure 12.3). Economic development is frequently the cause of broad-scale and rapid conversion of landscapes. This is clearly seen in the rapid loss of tropical forests because of logging, or the creation of large residential communities in suburban expansion (Browder et al. 1995; Scheer and Mintcho 1998).

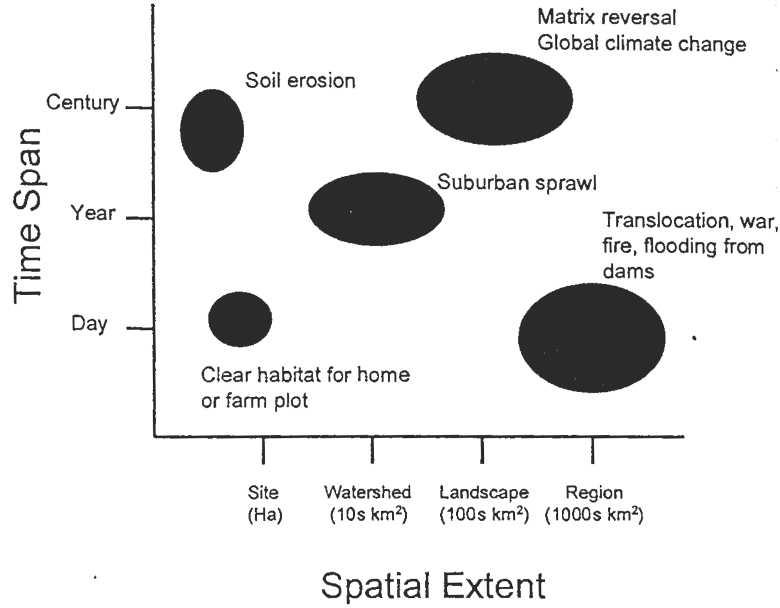

FIGURE 12.1. Human disturbance of terrestrial ecosystems occurs across a spectrum of time and spatial scales. Adapted from Forman (1995).

Anthropogenic disturbance of natural landscapes results from harvesting of environmental resources (e.g., forest, mineral, animal), farming, creation of residential opportunities, and commerce. The rate and extent of conversion can be rapid and extensive (Turner et al. 1998). For example, much of the native forest and prairie ecosystems of the northeastern and midwestern United States were rapidly transformed to pasture and cropland in the 18th and 19th centuries (Iverson 1988; Foster 1995). Massachusetts had an average deforestation rate of 1.37% per year during the period 1845–1875, whereas the Illinois deforestation rate was about 1% per year from 1850 to 1924 (Figure 12.4). During the period 1850–1900 in the United States, the human population tripled to 76 million, while the area of cropland increased over four times, from 31 million to 129 million ha (MacCleery 1992).

Suburban sprawl (also known as urban sprawl, edge cities, or metropolitan fringe) is the creeping of residential neighborhoods and light commerce into rural or natural landscapes surrounding urban centers (Browder et al. 1995; Scheer and Mintcho 1998). Sprawl can occur slowly (over decades) and consist of a gradual incursion of homes and residential developments into natural habitats, or it can occur extremely fast (over years) with the rapid building of large residential compounds that consist of hundreds of homes. In America, sprawl and commercial development are significant causes for the loss of rural and agricultural landscapes (Ilbery and Evans 1989; LaGro 1994) and are consistently cited as top-ranking threats to biodiversity (Flather et al. 1998; Wilcove et al. 1998).

In many cases, landscapes that have been modified by human activities are in a continual process of change. Some human-dominated landscapes remain in a dis-

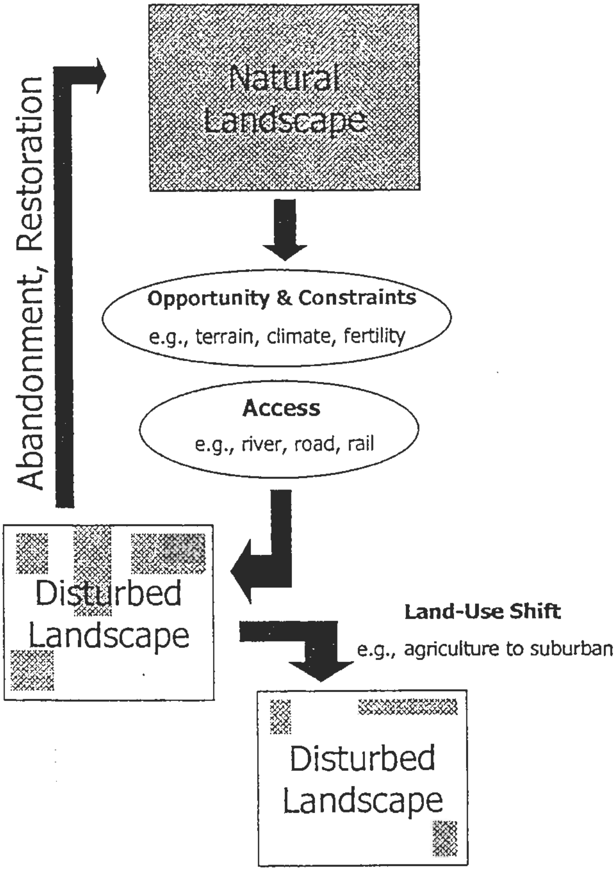

FIGURE 12.2. General sequence of events in the conversion of natural landscapes to disturbed landscapes and their continued disturbance or return to a natural or seminatural condition. Crossed-hatched areas in boxes symbolize the extent and pattern of undisturbed terrestrial habitats.

turbed state as evidenced by the large metropolitan centers of the world, other landscapes shift to another form of human disturbance, and some landscapes revert back to a natural condition through succession (Figure 12.2; Turner and Ruscher 1988; Odum and Turner 1990). Once abandoned, agricultural landscapes tend to revert back to a forested or prairie condition depending on the surrounding matrix and the long-term impacts of agricultural practices on soils, nutrients, and hydrological patterns (O'Keefe and Foster 1998).

From the above, we can deduce two basic principles that come into play when human activities convert natural habitats to a disturbed condition: *Principle 1—A safe, reliable, low-cost (time, energy) system (road, river, rail) to access landscapes is a prerequisite to human conversion of terrestrial habitats. Principle 2—Barring*

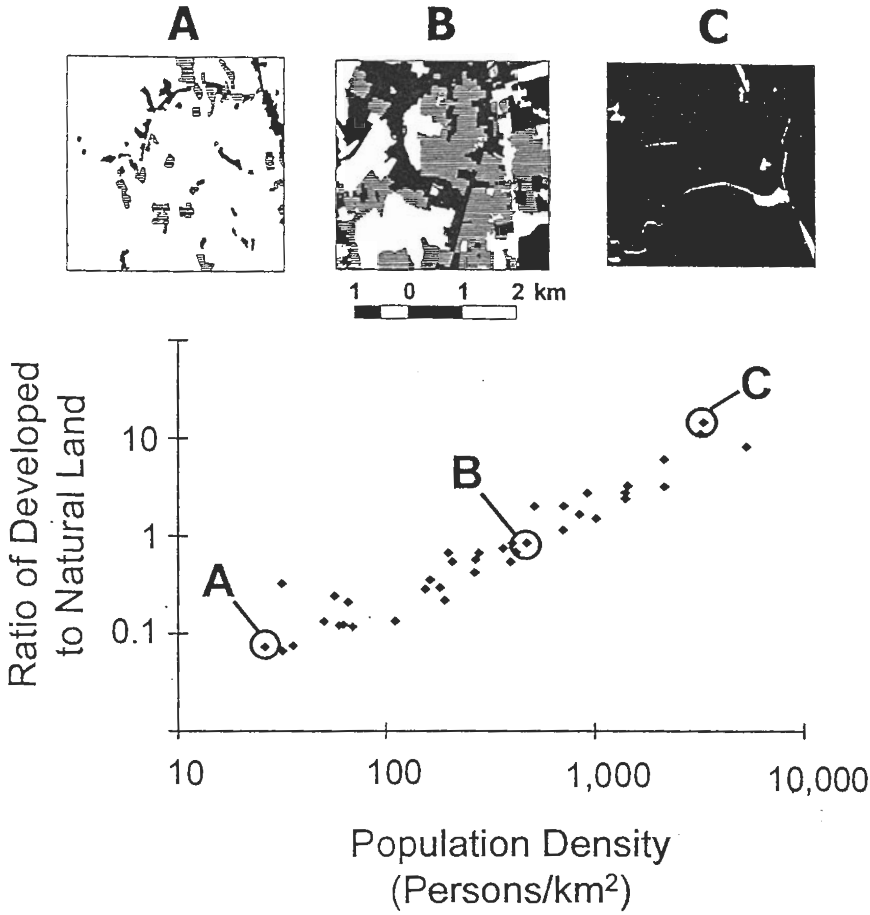

FIGURE 12.3. Relationship among human population density, natural and disturbed habitats, and the landscape matrix among Rhode Island (RI), USA towns spanning a continuum of human population density (1990 census data). The ratio of disturbed habitat (residential, commercial, and industrial [shaded black]) to natural habitat (forests, water, wetlands, and brushlands [shaded white]) is derived from 1988 land-cover data. Agricultural lands are hatched. Insets show a representative landscape for (A) a low-density rural community (West Greenwich, RI), (B) a medium-density community (Portsmouth, RI), and (C) a high-density community (Providence, RI). Note the matrix shift from natural (white shade) to developed (black shade) habitats.

profound changes to the soil and hydrological properties of a landscape that may occur during human modification, terrestrial habitats are resilient and can revert back to a natural condition if left undisturbed.

The transformation of terrestrial landscapes to landscapes dominated by human uses results in measurable changes to the composition and pattern of habitats, and the fauna and flora that occur in them (Table 12.2). Undisturbed landscapes typi-

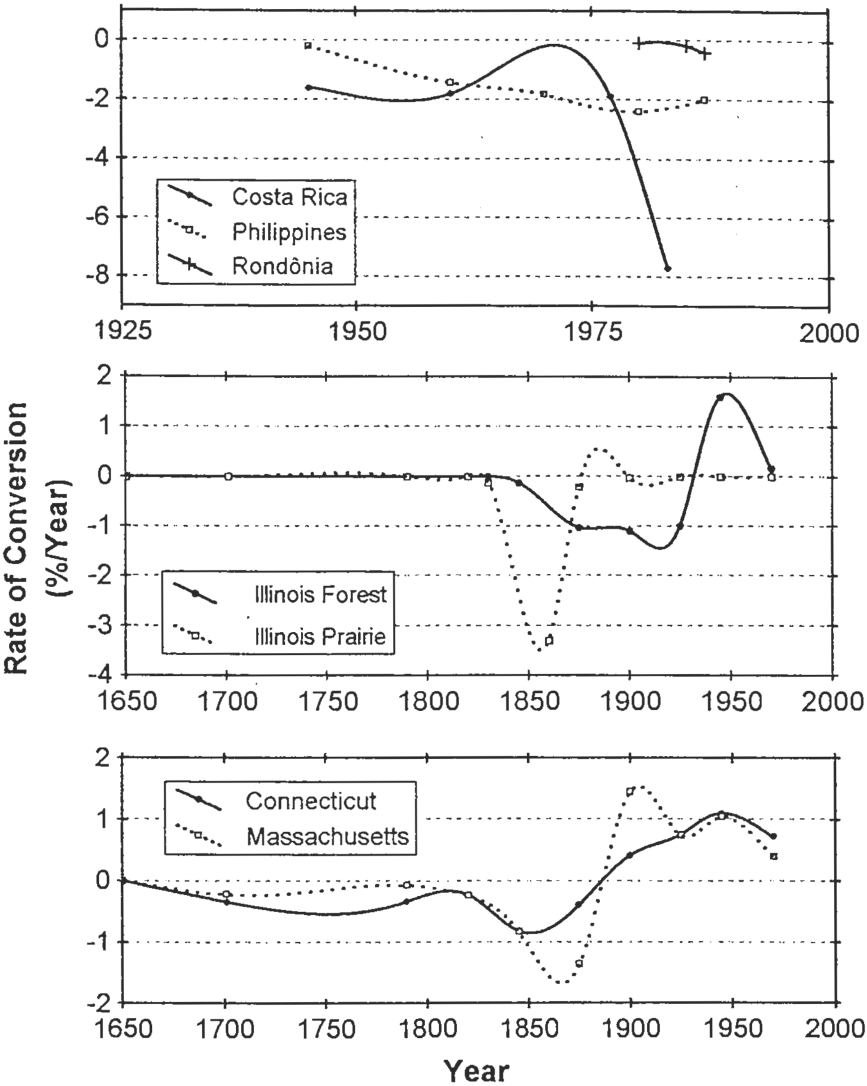

FIGURE 12.4. Rates of conversion (percent area/year) for various states and countries. Conversion rates are based on the amount of remaining forest (and prairie for Illinois) at the beginning of the time interval. Negative values indicate conversion from natural to disturbed habitats. Positive rates of conversion indicate a reversion from disturbed to natural condition (some smoothing of the trends has been done). Data are from Foster (1995, Connecticut and Massachusetts), Iverson (1991, Illinois forest and prairie), Sader and Joyce (1988, Costa Rica), Kummer and Turner (1994, Philippines), and Malingreau and Tucker (1988, Rondônia, Brazil).

TABLE 12.2. Typical changes in landscape and biological characteristics during the conversion of natural lands to human-dominated landscapes.

Landscape and biological characteristics	Landscape condition			Explanation	References†
	Natural	Transition	Disturbed		
Native/core habitat	Extensive	Medium	Uncommon	Native vegetation is lost or replaced with non-native species	1, 10, 11 12, 13, 15
Patch size	Large	Medium	Small	Large contiguous tracts of habitat are broken up	1, 2, 10, 13, 16
Patch shape	Complex	Simple	Simple	Human-modified edges tend to be rectilinear	7, 14, 17
Patch density	Low	Low to medium	Low to high	As fragmentation occurs, the landscape becomes more subdivided	10, 13, 16, 18
Edge density	Low	Moderate	High	Edge habitats become more common as conversion increases	2, 10, 13, 18
Connectedness	High	High to medium	Low	Patches become isolated	4, 10, 13
Landscape heterogeneity	Medium	High	Low to medium	Moderate disturbance can create a diverse landscape	2, 10, 16,
Roads	Few	Some to many	Many	Roads provide access for development or resource extraction	11, 12, 15, 18
Human population density	Low	Low to moderate	Low to high	Highly disturbed landscapes can have low human populations (e.g., farmlands, commercial forests) or high density (cities)	11, 17
Richness of native species	High	Moderate	Low	Native species are frequently replaced with non-native taxa as development proceeds	3, 4, 5
Richness of introduced/weedy species	Low	Moderate to high	Moderate to high	Generalist or non-native species frequently dominate heavily disturbed landscapes	2, 3, 18
Neotropical migratory birds	High	Moderate	Low	Migrants are often highly sensitive to disturbance	2, 3, 5
Predators	Normal	Depressed or elevated	Depressed or elevated	Domestic pets can increase predator density; natural predators usually decline	4, 6, 9, 12, 18
Wide-ranging species	Normal	Moderate	Depressed	As patches become smaller and isolated, less contiguous habitat is available for wide-ranging taxa	9
Core forest species	High	Moderate	Low	Species requiring large tracts of undisturbed habitat are impacted as landscapes become fragmented	1, 2, 5, 18
Total species diversity	Medium	High	Low to medium	Intermediate levels of disturbance often create complex landscapes that support high species diversity	1, 2, 4

Native species density	Medium to high	High	Low to medium	Native species are often outcompeted by invasives in disturbed habitats	4, 5, 10
Probability of extinction	Low	Moderate	High	Native taxa have a high probability of extinction as habitat patches become small and isolated	4
Edge-related mortality	Low	Moderate to high	High	Edge habitat increases mortality and decreases productivity for some species, such as ground-nesting birds	6, 8

† [1] Franklin and Forman (1987), [2] Miller et al. (1997), [3] Germaine et al. (1998), [4] Bolger et al. (1997a), [5] Hanowski et al. (1997), [6] Bayne and Hobson (1997), [7] O'Neill et al. (1988), [8] Esseen and Renhorn (1998), [9] Woodroffe and Ginsberg (1998), [10] Pearlstine et al. (1997), [11] Pedlowski et al. (1997), [12] LaGro (1994), [13] Dunn et al. (1990), [14] Turner and Ruscher (1988), [15] LaGro and DeGloria (1992), [16] Ambrose and Bratton (1990), [17] Iverson (1988), [18] Nilon et al. (1995).

cally have large amounts of native habitat, and landscape diversity is maintained by geomorphological properties of the area and naturally occurring disturbance such as fire, flood, landslide, and so on (Turner et al. 1997; Nichols et al. 1998). In contrast, human-disturbed patches are often simpler in shape than are naturally occurring patches; landscape edges defined by human uses tend to be rectilinear, whereas edges defined by natural processes are curvilinear. In heavily disturbed settings, fragments of original habitat become disconnected from one another and become isolated islands. Edge habitats can increase considerably in disturbed landscapes. In cases of extreme human disturbance, there can be a total shift in matrix habitat (Figure 12.3).

The results of human conversion of landscapes—loss of native habitat, small isolated remnant patches of native habitat, and increased edge—have profound effects on the fauna and flora of the region (Table 12.2). As native habitat decreases in extent, populations of resident plants and animals decrease in size and become more vulnerable to local extinction (Lande 1988, 1995; Andrén 1994). The sequence of impacts to local biota is largely scale-dependent. Large predators and wide-ranging taxa are first affected by habitat loss and fragmentation. Specialist taxa, such as species requiring large homogeneous expanses of native habitat, are frequently lost, whereas generalist taxa that can exist in natural or disturbed settings may dominate the biota. Species of plants and animals that are not native to the landscape are brought into the ecological setting as human disturbance continues. For example, domestic cats (*Felis cattus*) that accompany residential communities represent a new predator to transitional ecosystems and can have a profound impact on bird and small mammal populations. Horticultural and invasive plants frequently outcompete native flora and result in significant changes to habitats (Stohlgren et al. 1999). Loss and fragmentation of native habitat increases the amount of edge habitat. Some species, such as deer (*Odocoileus* sp.), Wild Turkeys (*Meleagris gallopavo*), and Brown-headed Cowbirds (*Molothrus ater*), benefit from edge, but others are negatively impacted (Paton 1994; Hartley and Hunter 1998). The changes in climate and ecology that occur in habitat edges can extend far into patches of native habitat. Edge contrast (sharp or gradual) and the types of adjacent land uses are important parameters in assessing the ecological impact of edge (Forman 1995).

A growing body of evidence shows that the ecological context (i.e., surrounding matrix habitat) of patches is as important (or sometimes more so) to resident biota as are the ecological conditions within the patch. Bird communities in plantation forests (Hanowski et al. 1997), oak (*Quercus* spp.) woodland (Sisk et al. 1997), and remnant deciduous forests patches in Chile (Estades and Temple 1999) all showed greater sensitivity to habitats surrounding occupied patches than they did to the composition and structure of vegetation within the patches.

In addition to the two previously mentioned principles that relate to landscape conversion, three principles summarize the ecological implications of such disturbances: *Principle 3—Human disturbance reduces the amount and alters the spatial properties (patch size, amount of edge, connectedness) of native habitat. Principle 4—Loss of native habitat results in the loss of resident species of plants* *and animals; non-native species frequently invade and can sometimes dominate disturbed landscapes. Principle 5—Habitat context is a very important characteristic of patches, and the biota within a patch are often affected by the habitat(s) surrounding it.*

12.3 Recent Applications

The principles of landscape ecology that bear on human conversion of terrestrial habitats can play a significant role in reducing the negative impact of human disturbance. However, our review of primary literature and government documents, as well as contacts with colleagues, indicated that the principles identified in the preceding section have rarely been applied on the ground to ameliorate these impacts. In contrast, the principles have been very important in directing the focus of recent ecological research. It is this type of use of the principles that we discuss in this section. These principles have been used in landscape planning; recent examples of such applications are discussed in Section IV of this book but not in this chapter. Here, we focus on research associated with three basic classes of anthropogenic land-cover change—forest and farmland conversion, suburban sprawl, and human resettlement. These three classes of conversion account for much of the historical and current human disturbance to natural ecosystems on the planet (Houghton 1994).

12.3.1 Forest and Farmland Conversion

Cutting forests for wood products or clearing native vegetation to allow for the planting of crops or creation of pasture are, by areal extent, the most significant human activities resulting in the loss of natural habitat world-wide (Myers 1980). The contemporary landscapes of many developed countries, for example much of western Europe and the United States, are defined by historical conversions for farming and forestry. Broad-scale conversions are now occurring over much of the tropical world in a fashion similar to what occurred in the United States 150 to 300 years ago (Figure 12.4) and in Europe before then. If suburban sprawl is viewed as a gradual nibbling away of natural or rural landscapes, conversion for forestry or farming must be considered a large and sudden bite. The time course for conversion and the details of the ecological impacts vary by region and land use. Swanson et al. (1990) found that extensive cutting of native forests in the Pacific Northwest of the United States resulted in the loss of older-age-class forests, created a mosaic of forest patches of different seral stages, increased sedimentation and alteration of coarse woody debris, and led to significant changes in local hydrology and stream ecosystem health. Similarly, conversion of natural landscapes for farming and pasture resulted in major losses of native habitat, as evidenced by the near total loss of tall-grass prairie in America (Iverson 1988), and it created a mosaic in which remnant patches of forest or native vegetation were isolated or loosely connected by narrow hedgerows (Merriam 1991).

For a variety of social and economic reasons, farming and forestry are declining in many regions of the world, and landscapes that were under cultivation or pasture are reverting back to a more natural ecological condition. Research by David Foster and colleagues in New England has chronicled the land-use history of this region. Their research demonstrates the long-term changes that occur in ecosystem patterns and processes, and the resiliency of natural habitats when human impacts are curtailed (Foster 1992, 1995; Foster et al. 1992, 1998). The precolonial (16th and early 17th centuries) landscape of New England was dominated by forest and wetland. Aboriginal human occupants cultivated lowland habitats in close proximity to rivers and streams, and they used fire to maintain fields and clear understory vegetation to facilitate travel and enhance the quality of habitat for game animals (MacCleery 1992). Occupation of the New England landscape by European colonists occurred in the 18th and 19th centuries. In approximately 200 years, much of the native forest of the region was cut and the land cleared for crops or pasture (Figure 12.4). In the 19th century, the Industrial Revolution precipitated a major change in land use and human settlement; farms were abandoned, cities grew, and industry developed along the major waterways (a source of energy and a transportation conduit). The abandoned farms reverted to forest in the 20th century (Figure 12.4). The pattern and species composition of contemporary forests has, however, been significantly altered when compared with precolonial forests. For example, many of the oak-hickory (*Quercus* spp., *Carya* spp.) forests in the eastern United States were established during a time of high fire and forest clearing (Abrams 1994). Today, red maple (*Acer rubrum*) is emerging as an increasing dominant over much of this region (Abrams 1998).

The landscape patterns observed by Foster and colleagues in their research mimic patterns found in other parts of the world. For example, in the southeastern United States and western Europe, lands that were intensively farmed in the 19th and early 20th centuries have been replaced by forest (Turner and Ruscher 1988; Preiss et al. 1997). In other areas, the farmland has remained relatively constant or is being converted to residential areas, a shift from one form of intensive human impact to another (Browder et al. 1995; Greene 1997). These research studies of land-cover change over long time scales clearly demonstrate the ecological resiliency of terrestrial habitats.

12.3.2 Suburban Sprawl

The principles described in Section 12.2 have provided direction for a number of excellent research projects on the ecological impacts of suburban sprawl. Sprawl destroys native habitat and creates isolated patches of remnant native habitat (Figure 12.3). Germaine et al. (1998) found that non-native horticultural plants that accompany residential development can expand into natural or seminatural habitats on the fringe of sprawl. Luken and Thieret (1996) found that ecological communities can shift from being dominated by native taxa to communities infiltrated by aggressively superior introduced species or species tolerant of human disturbance. The composition of ecological communities shifts as wide-ranging taxa and large predators are replaced by large numbers of smaller predators, both native and introduced (e.g., domestic cats; Soulé et al. 1988). Studies in the United Kingdom have shown that house cats have a significant impact on nearby bird and small-mammal communities, especially at the fringe of villages and neighborhoods that abut natural or seminatural landscapes (Churcher and Lawton 1987; May 1988). Some species of large predators may continue to exist in the face of human intrusion. For example, interactions between mountain lions (*Felis concolor*) and humans are becoming more common as sprawl encroaches on largely undisturbed habitats in the western United States (Torres et al. 1996; Torres 2000).

The studies by Bolger, Soulé, and colleagues (Soulé et al. 1988; Bolger et al. 1997a,b) have done an excellent job of measuring the ecological impacts of habitat fragmentation due to suburban sprawl in coastal southern California. The native flora of the region is coastal sage scrub and chaparral (Davis et al. 1995), and this landscape has exceptional levels of habitat diversity, species diversity, and endemism. The authors found that the size of remnant patches of shrub habitat and how long they had been isolated from other patches of habitat were critical variables in explaining variation in the number and diversity of chaparral-specialist birds and rodents; the smaller the patch and the longer the isolation, the fewer the resident species. Distance to the closest edge of residential habitat was a significant predictor of the distributions of many bird species. Some taxa were tolerant of human disturbance and occurred most often in edge habitats, whereas others were intolerant of disturbance and only occurred in core habitat.

12.3.3 Human Resettlement

As a means to relieve overpopulation pressures in urban centers, a number of national governments have initiated ambitious human resettlement programs that strive to relocate large numbers of citizens to underdeveloped or underutilized landscapes. Two recent examples are the Indonesian Transmigration from the densely populated island of Java to the sparsely populated islands of Sumatra and Kalimantan (MacKinnon 1996), and the Brazilian settlement of Rondônia in the Amazon Basin. Ecologists have studied the land-cover changes in Rondônia for a decade, and this research has been very important in clarifying the patterns and impacts of human invasion of undisturbed habitats.

The Brazilian government has had a policy of settling the Amazon Basin region of the country for over a century (Dale et al. 1993; Dale et al. 1994a,b; Pedlowski et al. 1997). The area is large (3.3 million km^2) and is rich in natural resources. In 1970, a road was built to provide reliable overland transportation from Rondônia to neighboring Brazilian states. During the next two decades, the human population density increased by an order of magnitude (from 100,000 to over 1,000,000 people). Most of the colonists cleared small patches of forest and planted crops and pasture. New patches were cleared every two years, and previously farmed patches were sold to cattle ranchers. Cattle ranchers removed any remnant forest habitat on the previously farmed patches and grazed cattle on the cleared lands. The changes in the Rondônian landscape have been systematically monitored with AVHRR and TM satellite data (Malingreau and Tucker 1988; Skole and Tucker 1993). From 1970 to 1993, over 52,500 km^2 of forest were destroyed. Much of the forest loss occurred adjacent to roads, the total length of which increased at a phenomenal rate (1,400 km in 1979, 25,000 km in 1988; Dale et al. 1994a,b). Similar conversion rates have historically been seen elsewhere in the world (Figure 12.4), usually as a result of a rapid influx of people and new access to the land.

The rapid settlement of Rondônia and concomitant habitat changes created an exceptional opportunity to study the ramifications of many of the principles described in Section 12.2. Dale et al. (1994b) modeled the probability of extinction of nine groups of animals from the Brazilian Amazon under three scenarios of land-use conversion over a 40-year period. Animals were characterized by their gap-crossing ability and area requirements. If a species could readily cross gaps, its fate was proportional to the amount of remaining forest and was not sensitive to fragmentation per se. If, however, a species had large area requirements and would only cross small gaps, the rate of habitat loss for this species was disproportionately greater than was the rate of forest clearing. Tropical frogs fared the worst of all species, with their habitat shrinking to as little as 39% of the remaining forest land after seven years of land conversion.

12.4 Principles for Applying Landscape Ecology

The sciences of landscape ecology and conservation biology provide many important insights into the management and monitoring of human conversion of terrestrial habitats. These ecological insights are the basis for the application principles we discuss in this section. In Figure 12.5, we illustrate the various points in the conversion sequence where land managers can intercede to eliminate or minimize adverse ecological impacts to biodiversity. The scientific principles described in this chapter guide planning and regulatory activities to prevent (or reduce) land uses that adversely impact ecosystems, help determine the most important measurements necessary to monitor the rate and extent of human disturbance, assess the response of populations and communities of native biota to change, and assist in the development and implementation of restoration activities to return impacted ecosystems to their natural form and function.

A critically important venue for minimizing the ecological impact of human activities is the institution where local land-use controls are established (LaGro 1994; Rookwood 1995). Depending on the form of governance and the ownership patterns of the land, venues may be town or county planning boards, or federal agencies such as the U.S. Forest Service or the U.S. Bureau of Land Management. The topic of ecologically sustainable environmental planning is taken up in detail in Section IV of this book, so our discussion is brief and focuses on

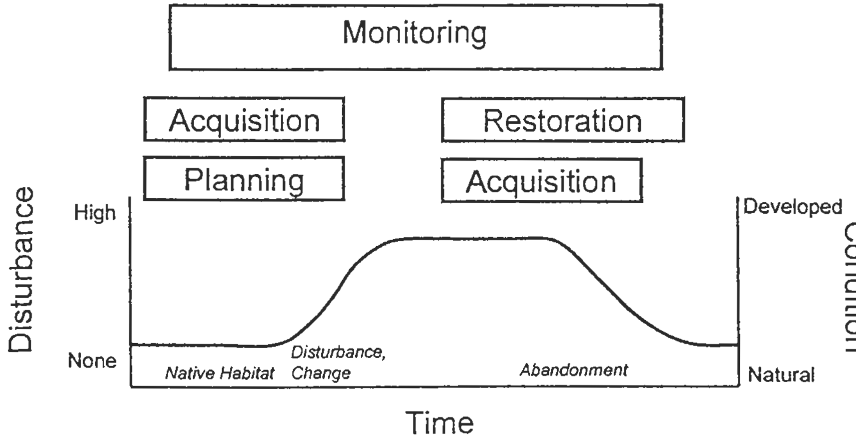

FIGURE 12.5. Time course for human conversion of terrestrial habitats and intervention opportunities (in boxes) for land managers.

how ecological principles described in Section 12.2 can be incorporated into the planning process.

Land-use managers and planners at regional and local levels are critically important players in the conservation process, and the principles of landscape ecology provide guidance to many of the decisions they must make. Carefully constructed zoning regulations can prevent destructive land uses in ecologically sensitive areas. For example, we have shown that a reliable method of access frequently precedes rapid settlement of undisturbed habitats and that creating or enhancing safe and reliable access to rural or wilderness landscapes is a precursor to future land-use change (see Section 12.2); therefore, transportation planners should assess the ecological impacts their projects will likely induce. This fundamental principle has been applied in wilderness regions of the United States where human access is restricted to nonmotorized methods of transportation (e.g., hiking, canoeing; The Wilderness Act of 1964 [16 U.S. C 11 21]).

Native species composition, population sizes, and community structure are severely impacted when native habitat is reduced to small, isolated patches in close association with highly disturbed land uses (Section 12.2). Therefore, two simple design principles for planners and land managers are as follows: maintain connections (corridors) among tracts of native habitat (Bueno et al. 1995), and ensure that remnant patches of natural habitat are as large as possible. Corridors that are naturally defined on the landscape, such as stream networks, should be maintained in an undisturbed condition to permit natural flux of species, energy, and materials (Harris 1984; Ahern 1995; Rosenberg et al. 1997). The amount and form of edge impacts the quality of habitat within a patch. In most cases, land management goals should be to minimize edge-to-core ratios. Edge contrast can be an important landscape characteristic and, when possible and appropriate, gradual edges rather than abrupt transitions from natural to impacted land uses should be designed. Gradual contrast can be achieved by surrounding natural regions of the landscape with buffer zones having only slight or moderate disturbance (Koslowski and Vass-Bowen 1997). Patch size is nearly always the most important variable defining the level of impact to species and communities; small patches are heavily impacted, and large patches are less-impacted. Therefore, environmental planners should minimize the extent of high-disturbance land uses adjacent to or near existing natural habitats.

Ecological monitoring is necessary to measure the rate and extent of human conversion of terrestrial habitats. Through monitoring, we quantify habitat loss, changes in landscape structure (patchiness, isolation of habitats), and the loss and gain of species and communities. Furthermore, continual ecological monitoring is the only way to determine if planning, regulatory, or conservation programs and policies to control human disturbance actually work (Goldsmith 1991). With adequate monitoring, we can shift our thinking and management strategies in a timely manner as new knowledge is acquired, a process called adaptive management (Stanford 1996).

Perhaps the most effective tool that planners and land managers have to stop human conversion of terrestrial habitats is to obtain ownership or development rights to the land. This strategy can occur at all scales, from continental initiatives (Soulé and Terborgh 1999) to municipal-scale programs (Peck 1998). Landscape ecology and the basic principles describing the changes that occur in species and populations that have experienced extensive habitat loss (see Section 12.2) have much to offer the process of creating and managing bioreserves. Some simple design or management objectives are as follows: refuges should be as large as possible and be connected with nearby refuges by protected corridors of habitat, round refuges offer the greatest core area of protected land relative to edge habitats, land adjacent to refuges should be managed as a buffer zone with only limited opportunity for major anthropogenic impacts, and disturbance regimes within refuges may have to be managed to maintain landscape diversity. Indeed, these simple principles are becoming entrenched within environmental planning and bioreserve design protocols (Noss et al. 1997; Peck 1998; Baydack et al. 1999).

The long-term resiliency of terrestrial habitats is an important principle to bear in mind while developing conservation plans or designing refuge systems. Habitats that are presently degraded, but have the potential to revert to a successional stage that has value for native fauna and flora (MacCleery 1992), may be important targets for conservation (Nichols et al. 1998). The cost to acquire degraded lands may be less than that of pristine habitats, and their geographic position in the landscape can fill important gaps in conservation networks.

12.5 Knowledge Gaps

Several areas of theoretical and empirical research must be advanced if we are to reconcile the need to accommodate human needs for space and natural resources with the need to protect biodiversity. Here we identify knowledge gaps that we feel are the most crucial to fill because of their constraining influence on our ability to convert principles of landscape ecology into hands-on planning, management, and restoration programs.

12.5.1 Theoretical Voids

Integration of Ecological Theory and Land-Use Planning

There is a lack of communication between scientists and land-use planners. Each group has a strong tradition of research and application within their respective disciplines, but there is little integration of science and practical land-use management. This lack of interdisciplinary interaction is perhaps the most significant gap in our ability to apply the principles of landscape ecology to on-the-ground natural resource management. We need to develop a means to integrate ecological theory with the land-use planning process. Likewise, we must integrate planning theory as a significant driving force into the ecological assessment of landscapes and regions. Planners and economists have developed tools to assess the social and financial impacts of development scenarios (Wegener 1994; Landis 1995), but ecologists have just begun to provide planners the same ability to assess ecological impacts (Linehan et al. 1995). Until a better connection is made between ecology and planning, land managers will have limited knowledge of the real impact of their decisions on fauna and flora within their jurisdiction.

Detecting Anthropogenic Change

If we are to manage human impacts at landscape scales, it is essential that we know rates and patterns of habitat conversion. Measuring and monitoring human impact of terrestrial ecosystems is a large and complex task; the variables measured, the technologies used, and the indices computed differ markedly depending on the size of the target landscape. Geographic information systems (GIS) and remote sensing technologies are fundamental tools for measuring the extent and pattern of land-use change (Iverson et al. 1989; Johnson 1990; August et al. 1996; Jensen 1996). Critical data for monitoring projects may be aerial photography or orthophotography for small areas, or satellite-based imagery for large regions (Dunn et al. 1990). Technological advancement in Earth imaging science is proceeding faster than is the research community's ability to identify the best suite of sensors, classification and change detection protocols, and summary indices to define accurately human impact on the Earth.

Predictive Mapping of Biota and Biodiversity

If we are to understand the impacts of land-use conversion and other human disturbances on biota, we must have the ability to measure or predict the distribution and abundance of fauna and flora. With the onset of better GIS capability, better landscape data on the environment, and geographically referenced records of biota, this area of research is rapidly changing (e.g., Franklin 1998; Wiser et al. 1998). Franklin (1995) has reviewed the field of biodiversity mapping and the many methods now available for such work. The Gap Analysis Program (Scott et al. 1993) uses a GIS approach to determine suitable habitat for a suite of animals. Our own work has enabled the prediction of species richness (Iverson and Prasad 1998a; Nichols et al. 1998), and particular tree species importance at local (Iverson et al. 1997) and regional (Iverson and Prasad 1998b) scales of analysis. Predictive mapping of various animal species is also undergoing rapid growth (e.g., Dettmers and Bart 1999; Mladenoff et al. 1999). However, it is common to find that the predictive models explain a relatively small portion of the variance. Additional research on what constitutes the critical input data to improve these models is required.

Land-Conversion Models

There is a need to develop better models to determine the most appropriate locations on the landscape for habitat conversions to occur and where they are most likely to occur (Wegener 1994). Modeling the spread of urban areas and other land-use changes more than 30 years into the future is rich in uncertainty, and more research is needed in this area (Landis 1995). Consideration of landscape ecological principles in land-use planning, via model development and outputs, is needed to ensure that planners identify spatial configurations of landscape development that permit sustainable ecological goods and services.

Conversion-Impact Models

We do not have the ability to model the impact of habitat conversion of the distribution and abundance of biota. Initial attempts to model impacted populations and communities are site-specific and not yet transferable to other areas (Friesen et al. 1995; Blair 1996; White et al. 1997; Rottenborn 1999). Research is needed to model the integrated effects of projected land-use conversion on the fauna and flora of the impacted area (Naiman et al. 1993; Lawton 1999).

12.5.2 Empirical Voids

Role of Habitat Corridors

Despite decades of research, we still do not know when and where corridors should be used to connect patches of habitat. Furthermore, we do not have a set of design guidelines to determine the optimal corridor width or habitat composition. It will be difficult or impossible for land managers and ecological planners to be effective if ecologists remain uncertain about the long- and short-term benefits of connected habitats (Simberloff et al. 1992; Rosenberg et al. 1997).

Fragmentation Versus Habitat Abundance

We do not yet know the relative importance of habitat loss versus fragmentation with respect to impacts on biota. In many cases, the two factors are correlated; as habitat is lost, remaining patches become increasingly fragmented. However, there is increasing evidence (e.g., McGarigal and McComb 1995; Trzcinski et al. 1999) that habitat abundance, rather than patchiness, is the dominant landscape feature controlling biotic integrity. If true, this tendency will have far-reaching implications in the way we integrate human activities into natural habitats at the landscape scale.

Role of Landscape Matrix

We do not understand the interactions that occur between habitat patches and their surrounding matrix. Much of our thinking about the relationships between patches and matrix has it roots in the theory of island biogeography advanced by MacArthur and Wilson (1967). The importance of island (patch) size, shape, and distance from source habitats is fundamental to landscape ecology. However, island biogeography is based on the notion that the matrix within which islands lie (e.g., oceanic islands in the sea, mountaintops in the desert) is totally unsuitable for resident biota. In terrestrial landscapes, this may not be the case because the matrix can have varying degrees of suitability for species occupying patches. Recent research suggests that the ecological context of patches of native habitat is critically important to the biota of the patch (Hanowski et al. 1997; Sisk et al. 1997; Estades and Temple 1999).

12.6 Research Approaches

12.6.1 Approaches for Theoretical Research

Integration of Ecological Theory and Land-Use Planning

Research is needed to develop a process to incorporate ecological thinking into land-use planning, and vice-versa. Central to this is knowing how human conversion of terrestrial habitats impacts species and communities. Long-term research in transitional landscapes, such as that conducted in urban long-term ecological research projects (Grove and Burch 1997), can provide knowledge needed for the integration of ecological theory and land-use planning. Publication of integrative treatises that promote unification of ecological science and land management are essential. Important also are the efforts of professional societies (e.g., International Association for Landscape Ecology) that provide forums for communication and interaction among planners and scientists.

Detecting Anthropogenic Change

Only recently have satellite-based data that have high spatial resolution (<5-m pixel size) and multispectral information content (e.g., Ikonos imagery) become publicly available. These data, in theory, provide an excellent basis to monitor detailed changes in land use over small areas (Li 1998). Satellite-based data sources (e.g., Spot, Landsat, AVHRR) that produce imagery at coarser scales (10–1,000-m pixel size) are valuable sources of data for measuring change over extensive regions (Skole and Tucker 1993; Laporte et al. 1998). GIS and remote sensing technology enable us to measure changes in the extent of natural habitats or levels of disturbance, patch characteristics, edge metrics, connectedness, landscape diversity, and other landscape metrics (O'Neill et al. 1997). What constitutes the best suite of landscape metrics to measure is, however, still an open question (O'Neill et al. 1988; Gustafson 1998).

Besides using wall-to-wall imagery to monitor human impacts, there remains immense value to plot-level assessments to understand ecological trends occurring spatially and temporally at ground level. Three national examples exemplify these data. The Forest Inventory and Analysis data of the U.S. Forest Service has data for over 100,000 forested plots across the eastern United States (Scott 1998). The National Resources Inventory of the U.S. Natural Resources Conservation Service is a longitudinal survey of soil, water, and related environmental resources designed to assess conditions and trends every five years on nonfederal United States lands (Nusser and Goebel 1997). The North American Breeding Bird Survey of the U.S. Fish and Wildlife Service provides field survey data on bird distributions for much of North America (Flather and Sauer 1996).

Predictive Mapping of Biota and Biodiversity

Improvement of models to predict the extent and abundance of species and communities can be achieved by several actions. The models will only ever be as good as the data from which they are built. First and foremost, local and regional biota must be inventoried and monitored (National Research Council 1993). Extensive and intensive surveys are needed, and the information should be entered into readily available databases. The National Biological Information Infrastructure (Anonymous 1998) provides one source for biological data to be distributed in clearinghouse fashion. Global positioning devices should be standard for any survey operations so that exact locations can be recorded in coordinates that can be easily entered into GIS databases (August et al. 1994). Ecologically meaningful environmental data should be acquired at a fine resolution with wall-to-wall coverage. Satellite imagery provides much of this information, but additional data are critical. Digital elevation models, at a scale of at least 1:24,000, are needed for modeling the variation in the abundance of flora and fauna across specific landscapes. Soils information is critical in identifying particular texture, depth, pH, drainage, or nutrient regimes especially related to specific organisms.

Land-Conversion Models

Land-use-change models have, for the most part, been based on or calibrated by historical trends. As such, there is a great dependency on adequate spatial data that describes the land use of an area at several previous intervals. To be most useful, these data should be in digital format over wide spatial extents. Unfortunately, these types of data sets are scarce; they need to be built from historical photographs and maps, and this is a slow and laborious process. The incorporation of less-used variables into land-use-change models should be explored. Variables related to human attitudes, quality of life, potential future transportation systems, and job locations in the age of telecommunications may become relatively more important than traditional land-capability, road network, and human population density variables in land-use-change models.

Conversion-Impact Models

There is no shortage of empirical research showing the ecological effects of habitat conversion at landscape scales (Friesen et al. 1995; Blair 1996; Rottenborn 1999). However, ecologists are only now trying to consolidate this knowledge into predictive models that strive to assess future impacts to biodiversity based on various land-use-change scenarios (Sisk et al. 1994; Freemark 1995; Lawton 1999). An excellent example of this kind of endeavor is the work of White et al. (1997), who developed a model to measure the gain or loss of species under six land-use scenarios ranging from complete build-out (maximum development of all developable lands) to immediate protection of all undeveloped lands in Monroe County, Pennsylvania. Their model attempts to predict the fate of individual species of mammals, birds, reptiles, and amphibians based on species-specific habitat requirements and the fate of those habitats under the different development scenarios. Their analysis is a benchmark beginning for the development of predictive planning tools to assess human impacts to local and regional patterns of biodiversity and should be extended to different landscapes and different land-use change scenarios. Metapopulation theory also offers considerable potential insight into the ecological impacts of land-use conversion. For example, the models developed by Wahlberg et al. (1996) have been used successfully to identify critically important patches of habitat for Fritillary Butterfly (*Melitaea diamina*) populations in moist meadow patches on the Finnish landscape.

12.6.2 Approaches for Empirical Research

Role of Habitat Corridors

Controlled experiments, such as those of Haddad (1999), need to be conducted across various landscapes and with various organisms to determine the overall importance of corridors. "Created" landscapes consisting of isolated and connected patches of habitat have been a productive method to measure the importance of corridors (Rosenberg et al. 1997). Organisms should be classified as to their requirements for corridor type and width, and a database that summarizes the work should be built. Only then can the modeling community begin to predict potential outcomes of conversions, which leave corridors as the primary protection against loss of biodiversity, at a species or guild level. Dale et al. (1994b) used an approach like this to evaluate the effects of tropical deforestation on biodiversity. Experimental determination of what species (or classes of species) benefit from corridors and what design principles should be followed when creating corridors are essential baseline data.

Fragmentation Versus Habitat Abundance

Much of the research on the ecological effects of habitat loss and fragmentation has been based on observational studies. Few well-controlled experimental studies exist to clarify cause-and-effect relationships between habitat change and concomitant changes in biota. The urban–rural landscape gradient is an interesting setting for these studies because it offers a continuum of patch-mosaic configurations along a relatively short distance (e.g., Bolger et al. 1997b; Germaine et al. 1998). The results of this research need to be categorized by organism and by guild, in a database, so that the modeling community can better use the work. The long-term studies of Lovejoy and colleagues (Bierregaard et al. 1992) in the Amazonian forest islands project constitute an excellent model for such experiments.

The scale of habitat patches relative to movement and space needs of the resident species is an important parameter to consider in analysis of habitat abundance versus patchiness (Fahrig 1997). If native species will tolerate levels of fragmentation that were previously considered excessive, planners and land managers will have greater flexibility in establishing development plans and policies that do not negatively impact the ecological integrity of the landscape. Carefully controlled studies comparing biodiversity among different geometric (patchy versus contiguous) configurations of landscapes should provide insight into the factors most important in maintaining viable populations and ecological communities.

Role of Landscape Matrix

Realization of the importance of the matrix in determining species' fates after disturbances is increasing, even for those species that spend very little time in the matrix. Landscapes with patches occurring in a variety of matrix habitats, for example wetland patches surrounded by disturbed habitats (residential areas) and natural matrix (upland forest), will be useful settings for this research. The fundamental question to answer is how much of the total variation in population and community characteristics is explained by the landscape ecological context of patches versus the habitat content of patches. This can be achieved observationally or experimentally. In an observational approach, community composition can be measured in a large number of landscape patches in a diversity of matrix settings. These data can be analyzed using multivariate statistical procedures to estimate the total variation explained by patch content and matrix type (McGarigal and McComb 1995). In an experimental approach, the fate of communities and populations can be monitored in landscape patches that have been created with varying levels of internal habitat complexity in a diversity of matrix settings.

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