CHAPTER 5

Habitat fragmentation and landscape change

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Broad-scale destruction and fragmentation of native vegetation is a highly visible result of human land-use throughout the world (Chapter 4). From the Atlantic Forests of South America to the tropical forests of Southeast Asia, and in many other regions on Earth, much of the original vegetation now remains only as fragments amidst expanses of land committed to feeding and housing human beings. Destruction and fragmentation of habitats are major factors in the global decline of populations and species (Chapter 10), the modification of native plant and animal communities and the alteration of ecosystem processes (Chapter 3). Dealing with these changes is among the greatest challenges facing the "mission-orientated crisis discipline" of conservation biology (Soulé 1986; see Chapter 1).

Habitat fragmentation, by definition, is the "breaking apart" of continuous habitat, such as tropical forest or semi-arid shrubland, into distinct pieces. When this occurs, three interrelated processes take place: a reduction in the total amount of the original vegetation (i.e. habitat loss); subdivision of the remaining vegetation into fragments, remnants or patches (i.e. habitat fragmentation); and introduction of new forms of land-use to replace vegetation that is lost. These three processes are closely intertwined such that it is often difficult to separate the relative effect of each on the species or community of concern. Indeed, many studies have not distinguished between these components, leading to concerns that "habitat fragmentation" is an ambiguous, or even meaningless, concept (Lindenmayer and Fischer 2006). Consequently, we use "landscape change" to refer to these combined processes and "habitat fragmentation" for issues directly associated with the subdivision of vegetation and its ecological consequences.

This chapter begins by summarizing the conceptual approaches used to understand conservation in fragmented landscapes. We then examine the biophysical aspects of landscape change, and how such change affects species and communities, posing two main questions: (i) what are the implications for the *patterns* of occurrence of species and communities?; and (ii) how does landscape change affect *processes* that influence the distribution and viability of species and communities? The chapter concludes by identifying the kinds of actions that will enhance the conservation of biota in fragmented landscapes.

5.1 Understanding the effects of landscape change

5.1.1 Conceptual approaches

The theory of island biogeography (MacArthur and Wilson 1967) had a seminal influence in stimulating ecological and conservation interest in fragmented landscapes. This simple, elegant model highlighted the relationship between the number of species on an island and the island's area and isolation. It predicted that species richness on an island represents a dynamic balance between the rate of colonization of new species to the island and the rate of extinction of species already present. It was quickly perceived that habitat isolates, such as forest fragments, could also be considered as "islands" in a "sea" of developed land and that this theory provided a quantitative approach for studying their biota. This stimulated many studies in which species richness in fragments was related to the area and isolation of the fragment, the primary factors in island biogeographic theory.

The development of landscape ecology contributed new ways of thinking about habitat fragments and landscape change. The concept of patches and connecting corridors set within a matrix (i.e. the background ecosystem or land-use type) became an influential paradigm (Forman and Godron 1986). It recognized the importance of the spatial context of fragments. The environment surrounding fragments is greatly modified during landscape changes associated with fragmentation. Thus, in contrast to islands, fragments and their biota are strongly influenced by physical and biological processes in the wider landscape, and the isolation of fragments depends not only on their distance from a similar habitat but also on their position in the landscape, the types of surrounding land-uses and how they influence the movements of organisms (Saunders *et al.* 1991; Ricketts 2001).

The influence of physical processes and disturbance regimes on fragments means that following habitat destruction and fragmentation, habitat modification also occurs. Mcintyre and Hobbs (1999) incorporated this complexity into a conceptual model by outlining four stages along a trajectory of landscape change. These were: (i) intact landscapes, in which most original vegetation remains with little or no modification; (ii) variegated landscapes, dominated by the original vegetation, but with marked gradients of habitat modification; (iii) fragmented landscapes, in which fragments are a minor component in a landscape dominated by other land uses; and (iv) relict landscapes with little (<10%) cover of original vegetation, set within highly modified surroundings. This framework emphasizes the dynamics of landscape change. Different stages along the trajectory pose different kinds of challenges for conservation management.

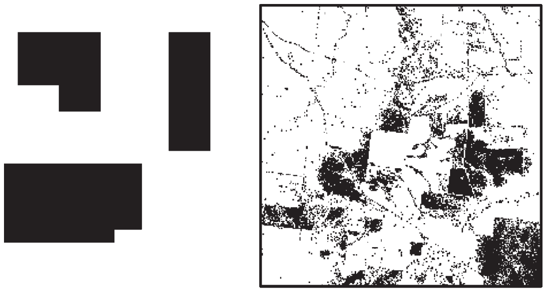
Many species are not confined solely to fragments, but also occur in other land uses in modified landscapes. In Nicaragua, for example, riparian forests, secondary forests, forest fallows, live fences, and pastures with dispersed trees each support diverse assemblages of birds, bats, dung beetles and butterflies (Harvey *et al.* 2006). To these species, the landscape represents a mosaic of land uses of differing quality, rather than a contrast between "habitat" and "non-habitat". Recognizing landscapes as mosaics emphasizes the need to appreciate all types of elements in the landscape. This perspective is particularly relevant in regions where cultural habitats, derived from centuries of human land-use, have important conservation values.

Different species have different ecological attributes, such as their scale of movement, life-history stages, longevity, and what constitutes habitat. These each influence how a species "perceives" a landscape, as well as its ability to survive in a modified landscape. Consequently, the same landscape may be perceived by different taxa as having a different structure and different suitability, and quite differently from the way that humans describe the landscape. A "species-centered" view of a landscape can be obtained by mapping contours of habitat suitability for any given species (Fischer *et al.* 2004).

5.1.2 Fragment vs landscape perspective

Habitat fragmentation is a landscape-level process. Fragmented landscapes differ in the size and shape of fragments and in their spatial configuration. Most "habitat fragmentation" studies have been undertaken at the fragment level, with individual fragments as the unit of study. However, to draw inferences about the consequences of landscape change and habitat fragmentation, it is necessary to compare "whole" landscapes that differ in their patterns of fragmentation (McGarigal and Cushman 2002). Comparisons of landscapes are also important because: (i) landscapes have properties that differ from those of fragments (Figure 5.1); (ii) many species move between and use multiple patches in the landscape; and (iii) conservation managers must manage entire landscapes (not just individual fragments) and therefore require an understanding of the desirable properties of whole landscapes. Consequently, it is valuable to consider

a) b)



Individual fragments
size
shape
core area
vegetation type
isolation

Whole landscapes
compositional gradients
diversity of land-uses
number of fragments
aggregation
structural connectivity

Figure 5.1 Comparison of the types of attributes of a) individual fragments and b) whole landscapes.

the consequences of landscape change at both the fragment and landscape levels.

5.2 Biophysical aspects of landscape change

5.2.1 Change in landscape pattern

Landscape change is a dynamic process. A series of "snapshots" at intervals through time (Figure 5.2) illustrates the pattern of change to the original vegetation. Characteristic changes along a time trajectory include: (i) a decline in the total area of fragments; (ii) a decrease in the size of many fragments (large tracts become scarce, small fragments predominate); (iii) increased isolation of fragments from similar habitat; and (iv) the shapes of fragments increasingly become dominated by straight edges compared with the curvilinear boundaries of natural features such as rivers. For small fragments and linear features such as fencerows, roadside vegetation, and riparian strips, the ratio of perimeter length to area is high, resulting in a large proportion of "edge" habitat. An increase in the overall proportion of edge habitat is a highly influential consequence of habitat fragmentation.

At the landscape level, a variety of indices have been developed to quantify spatial patterns, but many of these are intercorrelated, especially with the total amount of habitat remaining in the landscape (Fahrig 2003). Several aspects of the spatial configuration of fragments that usefully distinguish between different landscapes include: (i) the degree of subdivision (i.e. number of fragments), (ii) the aggregation of habitat, and (iii) the complexity of fragment shapes (Figure 5.3).

Some kinds of changes are not necessarily evident from a time-series sequence. Landscape change is not random: rather, disproportionate change occurs in certain areas. Clearing of vegetation is more common in flatter areas at lower elevations and on the more-productive soils. Such areas are likely to retain fewer, smaller fragments of original vegetation, whereas larger fragments are more likely to persist in areas less suitable for agricultural or urban development, such as on steep slopes, poorer soils, or regularly inundated floodplains. This has important implications for conservation because sites associated with different soil types and elevations typically support different sets of species. Thus, fragments usually represent a biased sample of the former biota of a region. There also is a strong historical influence on landscape change because many fragments, and the disturbance regimes they experience, are a legacy of past land settlement and land-use (Lunt and Spooner 2005). Land-use history can be an effective predictor of the present distribution of fragments and ecosystem condition within fragments. It is necessary to understand ecological processes and changes in the past in order to manage for the future.

5.2.2 Changes to ecosystem processes

Removal of large tracts of native vegetation changes physical processes, such as those relating to solar radiation and the fluxes of wind and water (Saunders *et al.* 1991). The greatest impact on fragments occurs at their boundaries; small remnants and those with complex shapes experience the strongest "edge effects". For example, the microclimate at a forest edge adjacent to cleared land differs from that of the forest interior in attributes such as incident light, humidity, ground and air temperature, and wind speed. In turn, these physical changes affect biological processes such as

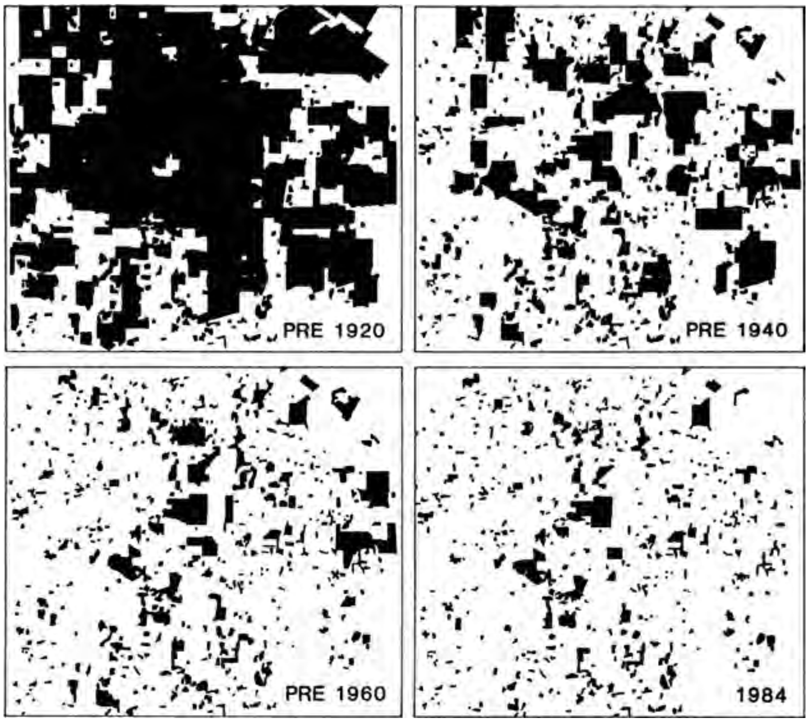


Figure 5.2 Changes in the extent and pattern of native vegetation in the Kellerberrin area, Western Australia, from 1920 to 1984, illustrating the process of habitat loss and fragmentation. Reprinted from Saunders *et al.* (1993).

litter decomposition and nutrient cycling, and the structure and composition of vegetation.

Changes to biophysical processes from land use in the surrounding environment, such as the use of fertilizers on farmland, alterations to drainage patterns and water flows, and the presence of exotic plants and animals, also have spill-over effects in fragments. Many native vegetation communities are resistant to invasion by exotic plant species unless they are disturbed. Grazing by domestic stock and altered nutrient levels can facilitate the invasion of exotic species of plants, which markedly alters the vegetation in fragments (Hobbs and Yates 2003) and habitats for animals.

The intensity of edge effects in fragments and the distance over which they act varies between processes and between ecosystems. In tropical forests in the Brazilian Amazon, for example, changes in soil moisture content, vapor pressure deficit, and the number of treefall gaps extend about 50 m into the forest, whereas the invasion of disturbance-adapted butterflies and beetles and elevated tree mortality extend 200 m or more from the forest edge (Laurance 2008). In most situations, changes at edges are generally detrimental to conservation values because they modify formerly intact habitats. However, in some circumstances edges are deliberately managed to achieve specific outcomes. Manipulation of edges is used to enhance the abundance of game species such as deer, pheasants and grouse (see Box 1.1). In England, open linear "rides" in woods may be actively managed to increase incident light and early successional habitat for butterflies and other wildlife (Ferris-Kaan 1995).

Changes to biophysical processes frequently have profound effects for entire landscapes. In highly fragmented landscapes in which most fragments are small or have linear shapes, there may be little interior habitat that is buffered from edge effects. Changes that occur to individual fragments accumulate across the landscape. Changes to biophysical processes such as hydrological regimes can also affect entire landscapes. In the Western Australian wheatbelt (Figure 5.2), massive loss of native vegetation has resulted in a rise in the level of groundwater, bringing stored salt (NaCl) to the surface where it accumulates and reduces agricultural productivity and transforms native vegetation (Hobbs 1993).

5.3 Effects of landscape change on species

Species show many kinds of responses to habitat fragmentation: some are advantaged and increase in abundance, while others decline and become locally extinct (see Chapter 10). Understanding these diverse patterns, and the processes underlying them, is an essential foundation for conservation. Those managing fragmented

Box 5.1 Time lags and extinction debt in fragmented landscapes
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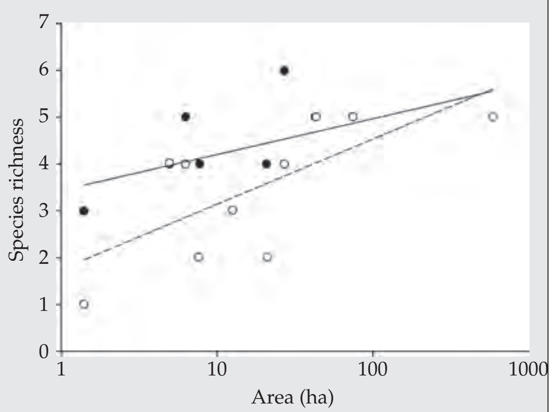
Habitat destruction and fragmentation result in immediately visible and striking changes to the pattern of habitat in the landscape. However, the effects of these changes on the biota take many years to be expressed: there is a time-lag in experiencing the full consequences of such habitat changes. Long-lived organisms such as trees may persist for many decades before disappearing without replacement; small local populations of animals gradually decline before being lost; and ecological processes in fragments are sensitive to long-term changes in the surroundings. Conservation managers cannot assume that species currently present in fragmented landscapes will persist there. Many fragments and landscapes face impending extinctions, even though there may be no further change in fragment size or the amount of habitat in the landscape. We are still to pay the 'extinction debt' for the consequences of past actions.

Identifying the duration of time-lags and forecasting the size of the extinction debt for fragmented landscapes is difficult. The clearest insights come from long-term studies that document changes in communities. For example, large nocturnal marsupials were surveyed in rainforest fragments in Queensland, Australia, in 1986–87 and again 20 years later in 2006–07 (Laurance *et al.* 2008). At the time of the first surveys, when fragments had been isolated for 20–50 years, the fauna differed markedly from that in extensive rainforest. Over the subsequent 20 years, even further changes occurred. Notably, the species richness in fragments had declined further (see Box 5.1 Figure), with most declines in the smaller fragments. By 2006–07, one species, the lemuroid ringtail possum (*Hemibelideus lemuroides*), was almost totally absent from fragments and regrowth forests along streams and its abundance in these habitats was only 0.02% of that in intact forest (Laurance *et al.* 2008).



Box 5.1 Figure A change in the species-area relationship for mammals in rainforest fragments in Queensland, Australia, between 1986 (filled circles) and 2006 (open circles) illustrates a time-lag in the loss of species following fragmentation. Data from Laurance *et al.* (2008).

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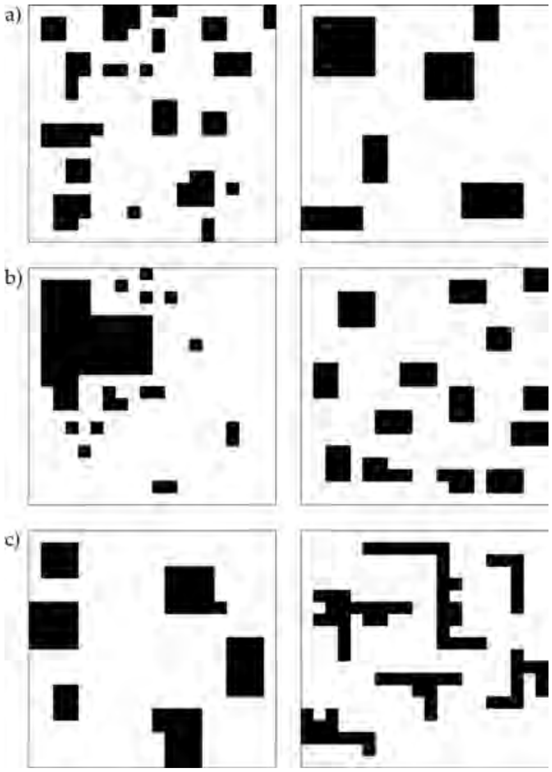


Figure 5.3 Variation in the spatial configuration of habitat in landscapes with similar cover of native vegetation: a) subdivision (many versus few patches); b) aggregated vs dispersed habitat; and c) compact vs complex shapes. All landscapes have 20% cover (shaded).

landscapes need to know which species are most vulnerable to these processes.

5.3.1 Patterns of species occurrence in fragmented landscapes

Many studies have described the occurrence of species in fragments of different sizes, shapes, composition, land-use and context in the landscape. For species that primarily depend on fragmented habitat, particularly animals, fragment size is a key influence on the likelihood of occurrence (Figure 5.4). As fragment size decreases, the frequency of occurrence declines and the species may be absent from many small fragments. Such absences may be because the fragment is smaller than the minimum area required for a single individual or breeding unit, or for a self-sustaining population.

Some species persist in fragmented landscapes by incorporating multiple fragments in their territory or daily foraging movements. In England, the tawny owl (*Strix aluco*) occupies territories of about 26 ha (hectares) in large deciduous woods, but individuals also persist in highly fragmented areas by including several small woods in their territory (Redpath 1995). There is a cost, however: individuals using multiple woods have lower breeding success and there is a higher turnover of territories between years. Species that require different kinds of habitats to meet regular needs (e.g. for foraging and breeding) can be greatly disadvantaged if these habitats become isolated. Individuals may then experience difficulty in moving between different parts of the landscape to obtain their required resources. Amphibians that move between a breeding pond and other habitat, such as overwintering sites in forest, are an example.

Other attributes (in addition to fragment size) that influence the occurrence of species include the type and quality of habitat, fragment shape, land use adjacent to the fragment, and the extent to which the wider landscape isolates populations. In the Iberian region of Spain, for example, the relative abundance of the Eurasian badger (*Meles meles*) in large forest fragments is

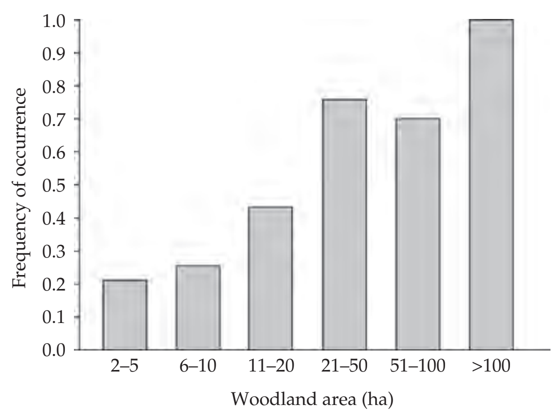


Figure 5.4 Frequency of occurrence of the common dormouse (*Muscardinus avellanarius*) in ancient semi-natural woods in Herefordshire, England, in relation to increasing size-class of woods. Data from Bright *et al.* (1994).

significantly influenced by habitat quality and forest cover in the wider landscape (Virgos 2001). In areas with less than 20% forest cover, badger abundance in forests was most influenced by isolation (i.e. distance to a potential source area >10 000 ha), whereas in areas with 20–50% cover, badgers were most influenced by the quality of habitat in the forest fragments.

A key issue for conservation is the relative importance of habitat loss versus habitat fragmentation (Fahrig 2003). That is, what is the relative importance of *how much* habitat remains in the landscape versus *how fragmented* it is? Studies of forest birds in landscapes in Canada and Australia suggest that habitat loss and habitat fragmentation are *both* significant influences, although habitat loss generally is a stronger influence for a greater proportion of species (Trczinski *et al.* 1999; Radford and Bennett 2007). Importantly, species respond to landscape pattern in different ways. In southern Australia, the main influence for the eastern yellow robin (*Eopsaltria australis*) was the total amount of wooded cover in the landscape; for the grey shrike-thrush (*Colluricincla harmonica*) it was wooded cover together with its configuration (favoring aggregated habitat); while for the musk lorikeet (*Glossopsitta concinna*) the influential factor was not wooded cover, but the configuration of habitat and diversity of vegetation types (Radford and Bennett 2007).

5.3.2 Processes that affect species in fragmented landscapes

The size of any population is determined by the balance between four parameters: births, deaths, immigration, and emigration. Population size is increased by births and immigration of individuals, while deaths and emigration of individuals reduce population size. In fragmented landscapes, these population parameters are influenced by several categories of processes.

Deterministic processes

Many factors that affect populations in fragmented landscapes are relatively predictable in their effect. These factors are not necessarily a direct consequence of habitat fragmentation, but arise from land uses typically associated with subdivision. Populations may decline due to deaths of individuals from the use of pesticides, insecticides or other chemicals; hunting by humans; harvesting and removal of plants; and construction of roads with ensuing road kills of animals. For example, in Amazonian forests, subsistence hunting by people compounds the effects of forest fragmentation for large vertebrates such as the lowland tapir (*Tapir terrestris*) and white-lipped peccary (*Tayassu pecari*), and contributes to their local extinction (Peres 2001).

Commonly, populations are also affected by factors such as logging, grazing by domestic stock, or altered disturbance regimes that modify the quality of habitats and affect population growth. For example, in Kibale National Park, an isolated forest in Uganda, logging has resulted in long-term reduction in the density of groups of the blue monkey (*Cercopithecus mitza*) in heavily logged areas: in contrast, populations of black and white colobus (*Colobus guereza*) are higher in regrowth forests than in unlogged forest (Chapman *et al.* 2000). Deterministic processes are particularly important influences on the status of plant species in fragments (Hobbs and Yates 2003).

Isolation

Isolation of populations is a fundamental consequence of habitat fragmentation: it affects local populations by restricting immigration and emigration. Isolation is influenced not only by the distance between habitats but also by the effects of human land-use on the ability of organisms to move (or for seeds and spores to be dispersed) through the landscape. Highways, railway lines, and water channels impose barriers to movement, while extensive croplands or urban development create hostile environments for many organisms to move through. Species differ in sensitivity to isolation depending on their type of movement, scale of movement, whether they are nocturnal or diurnal, and their response to landscape change. Populations of one species may be highly isolated, while in the same landscape individuals of another species can move freely.

Isolation affects several types of movements, including: (i) regular movements of individuals between parts of the landscape to obtain different requirements (food, shelter, breeding sites); (ii) seasonal or migratory movements of species at regional, continental or inter-continental scales; and (iii) dispersal movements (immigration, emigration) between fragments, which may supplement population numbers, increase the exchange of genes, or assist recolonization if a local population has disappeared. In Western Australia, dispersal movements of the blue-breasted fairy-wren (*Malurus pulcherrimus*) are affected by the isolation of fragments (Brooker and Brooker 2002). There is greater mortality of individuals during dispersal in poorly connected areas than in well-connected areas, with this difference in survival during dispersal being a key factor determining the persistence of the species in local areas.

For many organisms, detrimental effects of isolation are reduced, at least in part, by habitat components that enhance connectivity in the landscape (Saunders and Hobbs 1991; Bennett 1999). These include continuous "corridors" or "stepping stones" of habitat that assist movements (Haddad *et al.* 2003), or human land-uses (such as coffee-plantations, scattered trees in pasture) that may be relatively benign environments for many species (Daily *et al.* 2003). In tropical regions, one of the strongest influences on the persistence of species in forest fragments is their ability to live in, or move through, modified "countryside" habitats (Gascon *et al.* 1999; Sekercioglu *et al.* 2002).

Stochastic processes

When populations become small and isolated, they become vulnerable to a number of stochastic (or chance) processes that may pose little threat to larger populations. Stochastic processes include the following.

- Stochastic variation in demographic parameters such as birth rate, death rate and the sex ratio of offspring.
- Loss of genetic variation, which may occur due to inbreeding, genetic drift, or a founder effect from a small initial population size. A decline in genetic diversity may make a population more vulnerable to recessive lethal alleles or to changing environmental conditions.
- Fluctuations in the environment, such as variation in rainfall and food sources, which affect birth and death rates in populations.
- Small isolated populations are particularly vulnerable to catastrophic events such as flood, fire, drought or hurricanes. A wildfire, for example, may eliminate a small local population whereas in extensive habitats some individuals survive and provide a source for recolonization.

5.3.3 Metapopulations and the conservation of subdivided populations

Small populations are vulnerable to local extinction, but a species has a greater likelihood of persistence where there are a number of local populations interconnected by occasional movements of individuals among them. Such a set of subdivided populations is often termed a "metapopulation" (Hanski 1999). Two main kinds of metapopulation have been described (Figure 5.5). A mainland-island model is where a large mainland population (such as a conservation reserve) provides a source of emigrants that disperse to nearby small populations. The mainland population has a low likelihood of extinction, whereas the small populations become extinct relatively frequently. Emigration from the mainland supplements the small populations, introduces new genetic material and allows recolonization should local extinction occur. A second kind of metapopulation is where the set of interacting populations are relatively similar in size and all have a likelihood of experiencing extinction (Figure 5.5b). Although colonization and extinction may occur regularly, the overall population persists through time.

The silver-spotted skipper (*Hesperia comma*), a rare butterfly in the UK, appears to function as a metapopulation (Hill *et al.* 1996). In 1982, butterflies occupied 48 of 69 patches of suitable grassland on the North Downs, Surrey. Over the next 9 years, 12 patches were colonized and seven populations went extinct. Those more susceptible

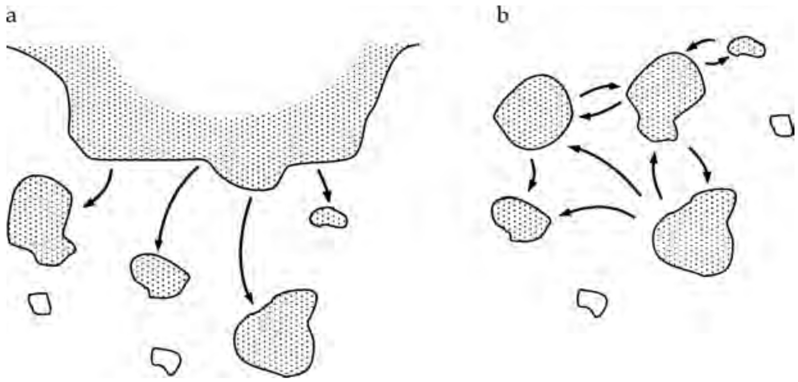


Figure 5.5 Diagrammatic representation of two main types of metapopulation models: a) a mainland-island metapopulation and b) metapopulation with similar-sized populations. Habitats occupied by a species are shaded, unoccupied habitat fragments are clear, and the arrows indicate typical movements. Reprinted from Bennett (1999).

to extinction were small isolated populations, whereas the patches more likely to be colonized were relatively large and close to other large occupied patches.

The conservation management of patchily-distributed species is likely to be more effective by taking a metapopulation approach than by focusing on individual populations. However, "real world" populations differ from theoretical models. Factors such as the quality of habitat patches and the nature of the land mosaic through which movements occur are seldom considered in theoretical models, which emphasize spatial attributes (patch area, isolation). For example, in a metapopulation of the Bay checkerspot butterfly (*Euphydryas editha bayensis*) in California, USA, populations in topographically heterogeneous fragments were less likely to go extinct than those that were in topographically uniform ones. The heterogeneity provided some areas of suitable topoclimate each year over a wide range of local climates (Ehrlich and Hanski 2004).

There also is much variation in the structure of subdivided populations depending on the frequency of movements between them. At one end of a gradient is a dysfunctional metapopulation where little or no movement occurs; while at the other extreme, movements are so frequent that it is essentially a single patchy population.

5.4 Effects of landscape change on communities

5.4.1 Patterns of community structure in fragmented landscapes

For many taxa—birds, butterflies, rodents, reptiles, vascular plants, and more—species richness in habitat fragments is positively correlated with fragment size. This is widely known as the species-area relationship (Figure 5.6a). Thus, when habitats are fragmented into smaller pieces, species are lost; and the likely extent of this loss can be predicted from the species-area relationship. Further, species richness in a fragment typically is less than in an area of similar size within continuous habitat, evidence that the fragmentation process itself is a cause of local extinction. However, the species-area relationship does not reveal which particular species will be lost.

Three explanations given for the species-area relationship (Connor and McCoy 1979) are that small areas: (i) have a lower diversity of habitats; (ii) support smaller population sizes and therefore fewer species can maintain viable populations; and (iii) represent a smaller sample of the original habitat and so by chance are likely to have fewer species than a larger sample. While it is difficult to distinguish between these mechanisms, the message is clear: when habitats are fragmented into smaller pieces, species are lost.

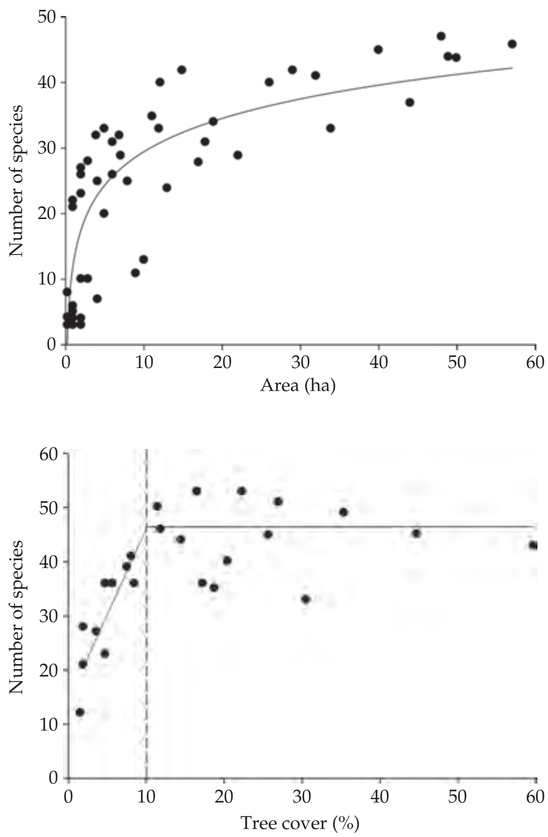


Figure 5.6 Species-area relationships for forest birds: a) in forest fragments of different sizes in eastern Victoria, Australia (data from Loyn 1997); b) in 24 landscapes (each 100 km^2) with differing extent of remnant wooded vegetation, in central Victoria, Australia (data from Radford *et al.* 2005). The piecewise regression highlights a threshold response of species richness to total extent of wooded cover.

Factors other than area, such as the spatial and temporal isolation of fragments, land management or habitat quality may also be significant predictors of the richness of communities in fragments. In Tanzania, for example, the number of forest-understory bird species in forest fragments (from 0.1 to 30 ha in size) was strongly related to fragment size, as predicted by the species-area relationship (Newmark 1991). After taking fragment size into account, further variation in species richness was explained by the isolation distance of each fragment from a large source area of forest.

Species show differential vulnerability to fragmentation. Frequently, species with more-specialized ecological requirements are those lost from communities in fragments. In several tropical regions, birds that follow trails of army ants and feed on insects flushed by the ants include specialized ant-following species and others that forage opportunistically in this way. In rainforest in Kenya, comparisons of flocks of ant-following birds between a main forest and forest fragments revealed marked differences (Peters *et al.* 2008). The species richness and number of individuals in ant-following flocks were lower in fragments, and the composition of flocks more variable in small fragments and degraded forest, than in the main forest. This was a consequence of a strong decline in abundance of five species of specialized ant-followers in fragments, whereas the many opportunistic followers (51 species) were little affected by fragmentation (Peters *et al.* 2008).

The way in which fragments are managed is a particularly important influence on the composition of plant communities. In eastern Australia, for example, grassy woodlands dominated by white box (*Eucalyptus albens*) formerly covered several million hectares, but now occur as small fragments surrounded by cropland or agricultural pastures. The species richness of native understory plants increases with fragment size, as expected, but tree clearing and grazing by domestic stock are also strong influences (Prober and Thiele 1995). The history of stock grazing has the strongest influence on the floristic composition in woodland fragments: grazed sites have a greater invasion by weeds and a more depauperate native flora.

The composition of animal communities in fragments commonly shows systematic changes in relation to fragment size. Species-poor communities in small fragments usually support a subset of the species present in larger, richer fragments (Table 5.1). That is, there is a relatively predictable change in composition with species "dropping out" in an ordered sequence in successively smaller fragments (Patterson and Atmar 1986). Typically, rare and less common species occur in larger fragments, whereas those present in smaller fragments are mainly widespread and common. This kind of "nested subset" pattern

Table 5.1 A diagrammatic example of a nested subset pattern of distribution of species (A–J) within habitat fragments (1–9).

Species	Fragments								
	1	2	3	4	5	6	7	8	9
A	+	+	+	+		+	+	+	+
B	+	+	+		+	+	+	+	
C	+		+	+	+	+	+		+
D	+	+	+	+	+			+	
E	+	+	+	+	+	+			
F		+		+					
G	+		+	+					
H	+	+							
I	+	+	+						
J	+								

has been widely observed: for example, in butterfly communities in fragments of lowland rainforest in Borneo (Benedick *et al.* 2006).

At the landscape level, species richness has frequently been correlated with heterogeneity in the landscape. This relationship is particularly relevant in regions, such as Europe, where human land-use has contributed to cultural habitats that complement fragmented natural or semi-natural habitats. In the Madrid region of Spain, the overall richness of assemblages of birds, amphibians, reptiles and butterflies in 100 km^2 landscapes is strongly correlated with the number of different land-uses in the landscape (Atauri and De Lucio 2001). However, where the focus is on the community associated with a particular habitat type (e.g. rainforest butterflies) rather than the entire assemblage of that taxon, the strongest influence on richness is the total amount of habitat in the landscape. For example, the richness of woodland-dependent birds in fragmented landscapes in southern Australia was most strongly influenced by the total extent of wooded cover in each 100 km^2 landscape, with a marked threshold around 10% cover below which species richness declined rapidly (Figure 5.6b) (Radford *et al.* 2005).

5.4.2 Processes that affect community structure

Interactions between species, such as predation, competition, parasitism, and an array of mutualisms, have a profound influence on the structure of communities. The loss of a species or a change in its abundance, particularly for species that interact with many others, can have a marked effect on ecological processes throughout fragmented landscapes.

Changes to predator-prey relationships, for example, have been revealed by studies of the level of predation on birds' nests in fragmented landscapes (Wilcove 1985). An increase in the amount of forest edge, a direct consequence of fragmentation, increases the opportunity for generalist predators associated with edges or modified land-uses to prey on birds that nest in forest fragments. In Sweden, elevated levels of nest predation (on artificial eggs in experimental nests) were recorded in agricultural land and at forest edges compared with the interior of forests (Andrén and Angelstam 1988). Approximately 45% of nests at the forest edge were preyed upon compared with less than 10% at distances >200 m into the forest. At the landscape scale, nest predation occurred at a greater rate in agricultural and fragmented forest landscapes than in largely forested landscapes (Andrén 1992). The relative abundance of different corvid species, the main nest predators, varied in relation to landscape composition. The hooded crow (*Corvus corone cornix*) occurred in greatest abundance in heavily cleared landscapes and was primarily responsible for the greater predation pressure recorded at forest edges.

Many mutualisms involve interactions between plants and animals, such as occurs in the pollination of flowering plants by invertebrates, birds or mammals. A change in the occurrence or abundance of animal vectors, as a consequence of fragmentation, can disrupt this process. For many plant species, habitat fragmentation has a negative effect on reproductive success, measured in terms of seed or fruit production, although the relative impact varies among species (Aguilar *et al.* 2006). Plants that are self-incompatible (i.e. that depend on pollen transfer from another plant) are more susceptible to reduced reproductive success than are self-compatible species. This difference is consistent with an expectation that pollination by animals will be less effective in small and isolated fragments. However, pollinators are a diverse group and they respond to fragmentation in a variety of ways (Hobbs and Yates 2003).

Changes in ecological processes in fragments and throughout fragmented landscapes are complex and poorly understood. Disrupted interactions between species may have flow-on effects to many other species at other trophic levels. However, the kinds of changes to species interactions and ecological processes vary between ecosystems and regions because they depend on the particular sets of species that occur. In parts of North America, nest parasitism by the brown-headed cowbird (*Molothrus ater*) has a marked effect on bird communities in fragments (Brittingham and Temple 1983); while in eastern Australia, bird communities in small fragments may be greatly affected by aggressive competition from the noisy miner (*Manorina melanocephala*) (Grey *et al.* 1997). Both of these examples are idiosyncratic to their region. They illustrate the difficulty of generalizing the effects of habitat fragmentation, and highlight the importance of understanding the consequences of landscape change in relation to the environment, context and biota of a particular region.

5.5 Temporal change in fragmented landscapes

Habitat loss and fragmentation do not occur in a single event, but typically extend over many decades. Incremental changes occur year by year as remaining habitats are destroyed, reduced in size, or further fragmented (Figure 5.2). Landscapes are also modified through time as the human population increases, associated settlements expand, and new forms of land use are introduced.

In addition to such changes in spatial pattern, habitat fragmentation sets in motion ongoing changes within fragments and in the interactions between fragments and their surroundings. When a fragment is first isolated, species richness does not immediately fall to a level commensurate with its long-term carrying capacity; rather, a gradual loss of species occurs over time—termed "species relaxation". That is, there is a time-lag in experiencing the full effects of fragmentation (see Box 5.1). The rate of change is most rapid in smaller fragments, a likely consequence of the smaller population sizes of species and the greater vulnerability of such fragments to external disturbances. For example, based on a sequence of surveys of understory birds in tropical forest fragments at Manaus, Brazil, an estimate of the time taken for fragments to lose half their species was approximately 5 years for 1 ha fragments, 8 years for 10 ha fragments, and 12 years for a 100 ha fragment (Ferraz *et al.* 2003).

Ecological processes within fragments also experience ongoing changes in the years after isolation because of altered species interactions and incremental responses to biophysical changes. One example comes from small fragments of tropical dry forest that were isolated by rising water in a large hydroelectric impoundment in Venezuela (Terborgh *et al.* 2001). On small (< 1 ha) and medium (8–12 ha) fragments, isolation resulted in a loss of large predators typical of extensive forest. Seed predators (small rodents) and herbivores (howler monkeys *Alouatta seniculus*, iguanas *Iguana iguana*, and leaf-cutter ants) became hyperabundant in these fragments, with cascading effects on the vegetation. Compared with extensive forest, fragments experienced reduced recruitment of forest trees, changes in vegetation composition, and dramatically modified faunal communities, collectively termed an "ecological meltdown" (Terborgh *et al.* 2001).

5.6 Conservation in fragmented landscapes

Conservation of biota in fragmented landscapes is critical to the future success of biodiversity conservation and to the well-being of humans. National parks and dedicated conservation reserves are of great value, but on their own are too few, too small, and not sufficiently representative to conserve all species. The future status of a large portion of Earth's biota depends on how effectively plants and animals can be maintained in fragmented landscapes dominated by agricultural and urban land-uses. Further, the persistence of many species of plants and animals in these landscapes is central to maintaining ecosystem services that sustain food production, clean water, and a sustainable living environment for humans. Outlined below are six kinds of actions necessary for a strategic approach to conservation in fragmented landscapes.

5.6.1 Protect and expand the amount of habitat

Many indicators of conservation status, such as population sizes, species richness, and the occurrence of rare species, are positively correlated with the size of individual fragments or the total amount of habitat in the landscape. Consequently, activities that protect and expand natural and semi-natural habitats are critical priorities in maintaining plant and animal assemblages (see also Chapter 11). These include measures that:

- Prevent further destruction and fragmentation of habitats.
- Increase the size of existing fragments and the total amount of habitat in the landscape.
- Increase the area specifically managed for conservation.
- Give priority to protecting large fragments.

All fragments contribute to the overall amount and pattern of habitat in a landscape; consequently, incremental loss, even of small fragments, has a wider impact.

5.6.2 Enhance the quality of habitats

Measures that enhance the quality of existing habitats and maintain or restore ecological processes are beneficial. Such management actions must be directed toward specific goals relevant to the ecosystems and biota of concern. These include actions that:

- Control degrading processes, such as the invasion of exotic plants and animals.
- Manage the extent and impact of harvesting natural resources (e.g. timber, firewood, bushmeat).
- Maintain natural disturbance regimes and the conditions suitable for regeneration and establishment of plants.
- Provide specific habitat features required by particular species (e.g. tree hollows, rock crevices, "specimen" rainforest trees used by rainforest birds in agricultural countryside).

5.6.3 Manage across entire landscapes

Managing individual fragments is rarely effective because even well managed habitats can be degraded by land uses in the surrounding environment. Further, many species use resources from different parts of the landscape; and the pattern and composition of land uses affect the capacity of species to move throughout the landscape. Two broad kinds of actions relating to the wider landscape are required:

- Manage specific issues that have degrading impacts across the boundaries of fragments, such as pest plants or animals, soil erosion, sources of pollution or nutrient addition, and human recreational pressure.
- Address issues that affect the physical environment and composition of the land mosaic across broad scales, such as altered hydrological regimes and the density of roads and other barriers.

5.6.4 Increase landscape connectivity

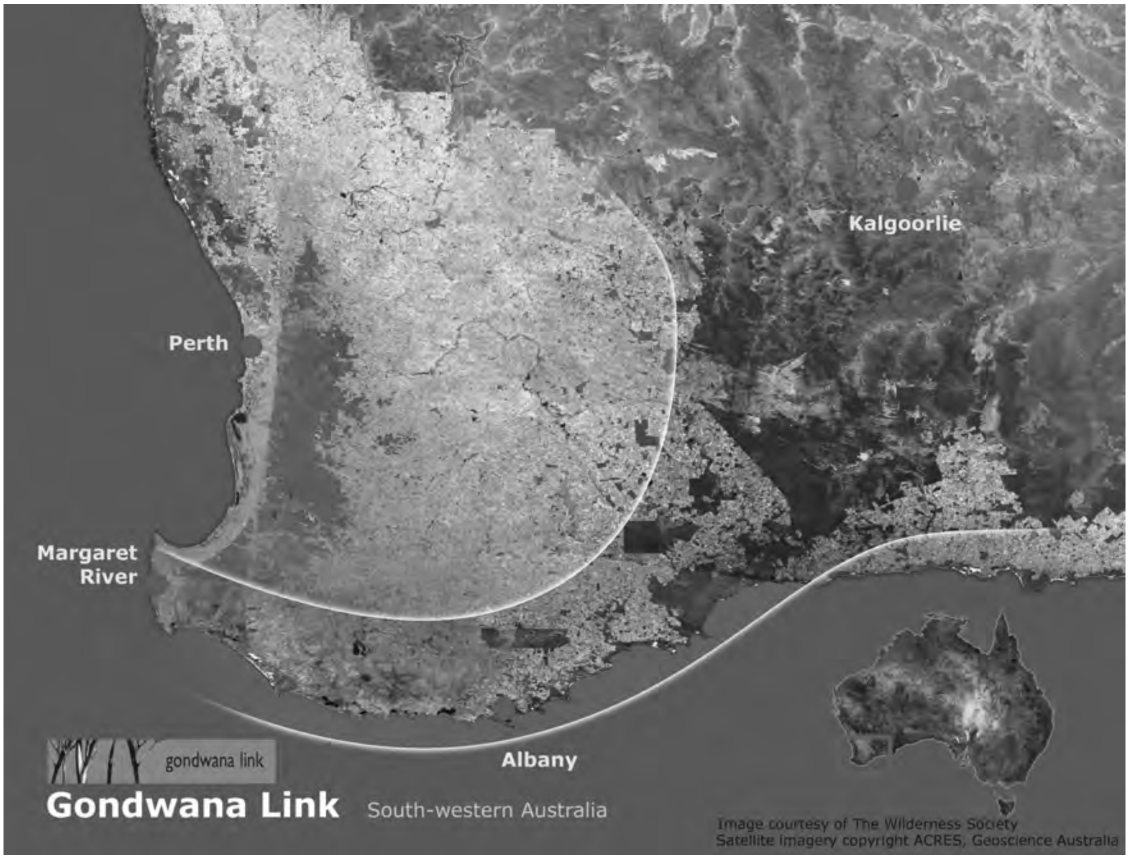
Measures that enhance connectivity and create linked networks of habitat will benefit the conservation of biota in fragmented landscapes. Connectivity can be increased by providing specific linkages, such as continuous corridors or stepping stones, or by managing the entire mosaic to allow movements of organisms. Actions that enhance connectivity include:

- Protecting connecting features already present, such as streamside vegetation, hedges and live fences.
- Filling gaps in links or restoring missing connections.
- Maintaining stepping-stone habitats for mobile species (such as migratory species).
- Retaining broad habitat links between conservation reserves.
- Developing regional and continental networks of habitat (see Boxes 5.2 and 5.3).

Box 5.2 Gondwana Link: a major landscape reconnection project
Denis A. Saunders and Andrew F. Bennett

In many locations throughout the world, conservation organizations and community groups are working together to protect and restore habitats as ecological links between otherwise-isolated areas. These actions are a practical response to the threats posed by habitat destruction and fragmentation and are undertaken at a range of scales, from local to continental. Gondwana Link, in south-western Australia, is one such example of an ambitious plan to restore ecological connectivity and enhance nature conservation across a large geographic region.

The southwest region of Australia is one of the world's 34 biodiversity "hotspots". It is particularly rich in endemic plant species. The region has undergone massive changes over the past 150 years as a result of development for broadscale agricultural cropping and raising of livestock. Over 70% of the area of native vegetation has been removed. The remaining native vegetation consists of thousands of fragments, most of which are less than 100 ha. Many areas within the region have less than 5–10% of their original vegetation remaining.



Box 5.2 Figure Diagrammatic representation of the Gondwana Link in south-west Western Australia. Shaded areas indicate remnant native vegetation.

continues

Box 5.2 (Continued)

This massive removal of native vegetation has led to a series of changes to ecological processes, producing a wide range of problems that must be addressed. Without some form of remedial action, over 6 million hectares of land (30% of the region's cleared land) will become salinized over the next 50 years, over 50% of vegetation on nature reserves will be destroyed, around 450 endemic species of plant will become extinct, over half of all bird species from the region will be adversely affected, and no potable surface water will be available in the region because of water pollution by salt.

Addressing the detrimental ecological consequences involves the revegetation, with deep-rooted trees and shrubs, of up to 40% of cleared land in the region. Gondwana Link is an ambitious conservation project involving individuals, local, regional and national groups addressing these detrimental ecological consequences. The objective of Gondwana Link is to restore ecological connectivity across south-western Australia. The aim is to provide ecological connections from the tall wet forests of the southwest corner of the state to the dry woodland in the arid interior. This will involve protecting and replanting native vegetation along a "living link" that stretches over 1000 km from the wettest corner of Western Australia into the arid zone (see Box 5.2 Figure and Plate 6). It also involves protecting and managing the fragments of native vegetation that they are reconnecting.

The groups believe that by increasing connectivity and restoring key habitats they will enable more mobile species that are dependent on native vegetation to move safely between isolated populations. This should reduce the localized extinctions of species from isolated fragments of native vegetation that is happening at present. Gondwana Link should also allow species to move as climatic conditions change over time. The revegetation should also have an impact on the hydrological regime by decreasing the amount of water entering the ground water, and reduce the quantity of sediment and pollution from agriculture entering the river and estuarine systems.

In addition to addressing environmental issues the project is speeding up the development of new cultural and economic ways for the region's human population to exist sustainably.

Relevant website

- Gondwana Link: http://gondwanalink.org/index.html.

Box 5.3 Rewilding
Paul R. Ehrlich

Some conservation scientists believe that the ultimate cure for habitat loss and fragmentation that is now spreading like ecological smallpox over Earth is a radical form of restoration, called rewilding in North America. The objective of rewilding is to restore resilience and biodiversity by re-connecting severed habitats over large scales and by facilitating the recovery of strongly interactive species, including predators. Rewilding is the goal of the "Wildlands Network," an effort led by Michael Soulé and Dave Foreman (Foreman 2004). The plan is to re-connect relatively undisturbed, but isolated areas of North America, into extensive networks in which large mammals such as bears, mountain lions,

continues

Box 5.3 (Continued)

wolves, elk, and even horses and elephants (which disappeared from North America only 11 000 years ago) can roam free and resume their important ecological roles in ecosystems where conflict with humans would be minimal. Rewilding would restore landscape linkages—employing devices from vegetated overpasses over highways to broad habitat corridors—allowing the free movement of fauna and flora and accommodation to climate change. The cooperation of government agencies and willing landowners would eventually create four continental scale wildways (formerly called MegaLinkages):

Pacific Wildway: From southern Alaska through the Coast Range of British Columbia, the Cascades, and the Sierra Nevada to the high mountains of northern Baja California.

Spine of the Continent Wildway: From the Brooks Range of Alaska through the Rocky Mountains to the uplands of Western Mexico.

Atlantic Wildway: From the Canadian Maritime south, mostly through the Appalachians to Okefenokee and the Everglades.

Arctic-Boreal Wildway: Northern North America from Alaska through the Canadian arctic/subarctic to Labrador with an extension into the Upper Great Lakes.

Many critical ecological processes are mediated by larger animals and plants, and the recovery, dispersal, and migration of these keystone and foundation species (species that are critical in maintaining the structure of communities disproportionately more than their relative abundance) is essential if nature is to adapt to stresses such a climate change and habitat loss caused by energy development, sprawl, and the proliferation of roads. Rewilding will help restore ecosystems in the Wildways to structural and functional states more like those that prevailed before industrial society accelerated the transformation of the continent. Similar rewilding projects on other continents are now in the implementation stage—as in the "Gondwana Link" in Australia (see Box 5.2). The possible downsides to rewilding include the spread of some diseases, invasive species, and fires and the social and economic consequences of increased livestock depredation caused by large, keystone predators (as have accompanied wolf reintroduction programs) (Maehr *et al.* 2001). Careful thought also is needed about the size of these Wildways; to be sure they are large enough for these species to again persist in their "old homes". Nonetheless, it seems clear that such potential costs of rewilding would be overwhelmed by the ecological and economic-cultural benefits that well designed and monitored reintroductions could provide.

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5.6.5 Plan for the long term

Landscape change is ongoing. Over the long-term, incremental destruction and fragmentation of habitats have profound consequences for conservation. Long-term planning is required to sustain present conservation values and prevent foreclosure of future options. Actions include:

- Using current knowledge to forecast the likely consequences if ongoing landscape change occurs.
- Developing scenarios as a means to consider alternative future options.
- Developing a long-term vision, shared by the wider community, of land use and conservation goals for a particular region.

5.6.6 Learn from conservation actions

Effective conservation in fragmented landscapes demands that we learn from current management in order to improve future actions. Several issues include:

- Integrating management and research to more effectively evaluate and refine conservation measures.
- Monitoring the status of selected species and ecological processes to evaluate the longer-term outcomes and effectiveness of conservation actions.

Summary

- Destruction and fragmentation of habitats are major factors in the global decline of species, the modification of native plant and animal communities and the alteration of ecosystem processes.
- Habitat destruction, habitat fragmentation (or subdivision) and new forms of land use are closely intertwined in an overall process of landscape change.
- Landscape change is not random: disproportionate change typically occurs in flatter areas, at lower elevations and on more-productive soils.
- Altered physical processes (e.g. wind and water flows) and the impacts of human land-use have a profound influence on fragments and their biota, particularly at fragment edges.
- Different species have different ecological attributes (such as scale of movement, life-history stages, what constitutes habitat) which influence how a species perceives a landscape and its ability to survive in modified landscapes.
- Differences in the vulnerability of species to landscape change alter the structure of communities and modify interactions between species (e.g. pollination, parasitism).
- Changes within fragments, and between fragments and their surroundings, involve time-lags before the full consequences of landscape change are experienced.
- Conservation in fragmented landscapes can be enhanced by: protecting and increasing the amount of habitat, improving habitat quality, increasing connectivity, managing disturbance processes in the wider landscape, planning for the long term, and learning from conservation actions undertaken.

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