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Review

Biological Consequences of Ecosystem Fragmentation: A Review

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Abstract: *Research on fragmented ecosystems has focused mostly on the biogeographic consequences of the creation of habitat "islands" of different sizes, and has provided little of practical value to managers. However, ecosystem fragmentation causes large changes in the physical environment as well as biogeographic changes. Fragmentation generally results in a landscape that consists of remnant areas of native vegetation surrounded by a matrix of agricultural or other developed land. As a result, fluxes of radiation, momentum (i.e., wind), water, and nutrients across the landscape are altered significantly. These in turn can have important influences on the biota within remnant areas, especially at or near the edge between the remnant and the surrounding matrix. The isolation of remnant areas by clearing also has important consequences for the biota. These consequences vary with the time since isolation, distance from other remnants, and degree of connectivity with other remnants. The influences of physical and biogeographic changes are modified by the size, shape, and position in the landscape of individual remnants, with larger remnants being less adversely affected by the fragmentation process. The dynamics*

Resumen: *La investigación sobre los ecosistemas fragmentados se ha enfocado principalmente en las consecuencias biogeográficas de la creación de "islas" de hábitat de diferentes tamaños y ha sido de muy poco valor práctico para los manejadores del recurso. Como quiera que sea, la fragmentación de los ecosistemas causa grandes cambios en el medio ambiente físico así como en el ámbito biogeográfico. La fragmentación resulta generalmente en terrenos que consisten de áreas remanentes de vegetación nativa rodeada de una matriz de tierras agrícolas u otras formas de uso de la tierra. Como un resultado de esto, el flujo de la radiación, del momentum (ej. el viento), del agua y de los nutrientes a través de la tierra son alterados significativamente. Esto en su turno, puede influenciar e la biota dentro de las áreas remanentes, especialmente en o cerca de los límites entre los remanentes y la matriz que los rodea. El aislamiento de las áreas remanentes por la tala también tiene importantes consecuencias para la biota y estas consecuencias varian con, el tiempo desde el momento del aislamiento, la distancia hasta los otros remanentes y el grado de conección entre ellos. La influencia de los cambios físicos y biogeográficos es modificada por el tamaño, la forma y la posición en el terreno de remanentes individuales siendo los remanentes grandes los menos afectados adversamante por el proceso de fragmentación. La dinámica de las áreas remanentes son dirigidas*

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of remnant areas are predominantly driven by factors arising in the surrounding landscape. Management of, and research on, fragmented ecosystems should be directed at understanding and controlling these external influences as much as at the biota of the remnants themselves. There is a strong need to develop an integrated approach to landscape management that places conservation reserves in the context of the overall landscape.

predominantemente por factores que surgen en el terreno circundante. El manejo y la investigación de los ecosistemas fragmentados debería de dirigirse tanto al entendimiento y control de estas influencias externas como a las biotas remanentes en sí. Hay una fuerte necesidad para el desarrollo de un enfoque integrado en el manejo de tierras que coloca a las reservas para la conservación en el contexto del terreno en general.

Introduction

Since the development of agriculture, the natural vegetation cover of every continent except Antarctica has been extensively modified. A cycle of agricultural development followed by overexploitation of the land has been repeated throughout recorded history. Forman (1987) quotes Plato's (ca. 2350 BP) description of how an area of ancient Greece was stripped of its soil following clearing and grazing, leaving "the mere skeleton of the land." Overexploitation and the use of inappropriate agricultural practices have led to desert encroachment, as in the Sahel region in North Africa (Le Houérou & Gillet 1986; Ehrlich & Ehrlich 1987), and to extensive loss of soil, often with disastrous and dramatic consequences, as in the Dust Bowl of the United States (Hudson 1981).

The process of land clearing and the consequent environmental degradation is continuing rapidly in many regions such as Southeast Asia and South America, particularly in areas of tropical rain forest (Myers 1988). Australia provides an example of recent agricultural development, with vast areas being cleared over the last 100 years for cereal cropping and stock grazing (Saunders & Hobbs 1989; Hobbs & Hopkins 1990; Saunders et al. 1990). In some regions over 93% of the native vegetation has been removed and the agricultural land that has replaced it is subject to extensive wind and water erosion or soil salinization, with consequent pollution of water supplies for drinking and irrigation.

One legacy of the extensive removal of native vegetation is that the remaining vegetation is usually in fragmented patches across the landscape. These patches or remnants are situated in different positions in the landscape and on different soil types, possess different vegetation types, and vary in their size, shape, isolation, and type of ownership. Over much of the world, conservation of regional biotas depends entirely on the retention and management of these remnants. Conservation managers are therefore faced with the dual issues of whether the remnants have any practical conservation values, and if they do, of how they must be managed to retain these values (Saunders et al. 1987*a*).

In this paper we use the word *remnant* to define any patch of native vegetation around which most or all of the original vegetation has been removed (Saunders et al. 1987*a*). Remnants often have been called habitat islands and the changes that result from the isolation of these islands have been the subject of considerable debate in the literature. This debate has centered mostly on the equilibrium theory of island biogeography (MacArthur & Wilson 1963, 1967) and its applicability to conservation. In particular, the importance of size, shape, and design of single reserves and reserve systems, extinction and colonization rates, and species-area relationships have been much discussed (Wilson & Willis 1975; Diamond 1975, 1976; May 1975; Terborgh 1976; Whitcomb et al. 1976; Simberloff & Abele 1976*a*, 1982; Pickett & Thompson 1978; Game 1980; Margules et al. 1982; Boecklen & Gotelli 1984). Particular attention has been paid to the question of whether one large reserve could preserve more species than several small reserves adding up to the equivalent area of the larger reserve (the so-called SLOSS, or "single large or several small" debate; Simberloff & Abele 1976*b*, 1984; Gilpin & Diamond 1980; Higgs & Usher 1980; Järvinen 1982; Willis 1984).

These questions have been reviewed elsewhere (Simberloff 1988) and are not examined in detail here. While of theoretical interest, most of these issues are of little practical value in managing fragmented systems (Zimmerman & Bierragaard 1986; Margules 1987; Hobbs 1988; Margules & Stein 1989). The species-area equation, for example, may give a manager a rough idea of how many species will be maintained on a remnant of a given area, but will yield absolutely no information on the practical issue of which habitats contribute most to species richness or on which species are most likely to be lost from the remnant. Simberloff (1986) stated, "It is also sad that unwarranted focus on the supposed lessons of island biogeography theory has detracted from the main task of refuge planners, determining what habitats are important and how to maintain them." Margules (1986), in a discussion about two conservation evaluation exercises, notes that, "no panel members in either exercise considered the species-area relationship or the equilibrium theory of island biogeography in their evaluations; at least not explicitly." In addition, the debates about reserve design and SLOSS are of limited relevance because, with very few exceptions, managers of conser-

vation reserves are faced with a fait accompli. Conservation considerations have rarely been taken into account during the development of areas for agriculture, mining, forestry, or other such uses. Conservation managers must work with the remnants left following these developments and virtually never have the opportunity to design a reserve network before an area is fragmented. There is an increasing need to utilize design criteria to improve conservation networks in already fragmented areas, but this requires a clear understanding of the problems created by fragmentation in the first place.

Hence we believe that research and discussion should focus on practical issues relating to the impact of fragmentation on natural ecosystems and managing remnants for conservation (Saunders et al. 1987*b*). We share the fear of Noss and Harris (1986) that conservation agencies have not realized the important biological consequences of ecosystem fragmentation and have therefore not developed policies to manage their remnants to maintain conservation values. The aim of this paper is to point out the physical effects of fragmentation, the biological consequences for natural ecosystems of these effects, and the options available for conservation research and management.

Characteristics of Fragmented Ecosystems

Fragmentation of the landscape produces a series of remnant vegetation patches surrounded by a matrix of different vegetation and/or land use. Two primary effects of this are an alteration of the *microclimate* within and surrounding the remnant and the *isolation* of each area from other remnant patches in the surrounding landscape. Thus, in a fragmented landscape there are changes in the physical environment as well as biogeographic changes. Most discussions of habitat fragmentation have concentrated on the biogeographic aspects, and the physical changes have received little attention. All remnants are exposed to these physical and biogeographic changes to a greater or lesser degree, but their effects are modified by the *size, shape,* and *position in the landscape* of individual remnants. We examine first the physical effects of fragmentation and then discuss the operation of the modifying factors.

Changes in Microclimate

Fragmentation of the landscape results in changes in the physical fluxes across the landscape. Alterations in fluxes of radiation, wind, and water can all have important effects on remnants of native vegetation.

1. RADIATION FLUXES

The energy balance of a fragmented landscape will differ markedly from one with a complete cover of native vegetation, especially where the native vegetation was dense before clearing. Removing native vegetation and replacing it with crop species with differing architecture and phenology alters the radiation balance by increasing the solar radiation reaching the ground surface during the day, changing the albedo, and increasing reradiation at night. These features vary depending on time of year; ploughing, crop growth, and harvesting produce an alternation of bare ground and varying degrees of vegetation cover (Geiger 1965; Milthorpe & Moorby 1974). In cleared areas, in general, daytime temperatures are higher and night temperatures lower than in naturally vegetated areas. This leads to greater temperature ranges both at the surface and in the upper layers of the soil, and an increased incidence of frost (Geiger 1965).

These changes in the cleared parts of the landscape impinge on the remnant native vegetation, especially at the edge between the two. Except near the equator, the orientation of the edge affects the degree to which solar radiation increases within a remnant at different times of year (Geiger 1965; Wales 1972; Ranney et al. 1981). Latitude also affects radiation input, and at high latitudes especially, where solar angles are low, a remnant edge can receive significantly more solar radiation than unfragmented areas receive (De Walle & McGuire 1973; Hutchinson & Matt 1976, 1977). Air temperatures at the edge of a forest remnant can be significantly higher than those found in either the interior of the remnant or the surrounding agricultural land (Geiger 1965; Kapos 1989).

The consequences of increasing solar radiation at the edges of remnants are not clear. The indications are, however, that a different suite of species may come to occupy this altered habitat. Lovejoy et al. (1986) report that fragmentation in tropical forests results in the rapid growth of vines and other secondary vegetation in a 10–25 m strip around the remnant edge. This may effectively seal off the remnant and maintain an environment within the remnant similar to that that existed prior to fragmentation (F. Crome, personal communication). This also occurs to some extent in temperate regions (Gysel 1951; Trimble & Tryon 1966; Ranney et al. 1981).

Shade-tolerant species may become restricted to the interior parts of the remnant, with different species requiring different distances from the edge. The composition of remnant edges may be affected by edge aspect (Wales 1972; Palik & Murphy 1990). Distinct sets of "interior" and "edge" species have been recognized in landscapes that have been fragmented for a long time, for instance in the eastern United States (Ranney et al. 1981).

Nutrient cycling processes may be affected by increased soil heating and its effect on soil microorganism

and invertebrate numbers and activity (Klein 1989; Parker 1989), on litter decomposition, and on soil moisture retention. Changes in the radiation balance also affect larger fauna both directly and indirectly through altering resource availability (via changes in plant growth and phenology). Lovejoy et al. (1986) attribute changes in butterfly community composition in tropical forest fragments partly to increased insolation within small remnants. Increased radiation load and dessication rates may lead to reduced foraging opportunities. Saunders (1982) considered that elevated temperatures in fragmented landscapes reduced the foraging time available to adult Carnaby's cockatoos (*Calyptorhynchus funereus latirostrus*) and contributed to their local extinction. Alternatively, some species dependent on temperature thresholds may be able to forage for longer periods. For instance, the strongly dominant ants of the *Iridomyrmex* genus are known to forage only when insolation and temperatures are high, and other ant species forage only when *Iridomyrmex* is absent (Greenslade & Halliday 1983; Andersen 1987). Increased insolation and ambient temperatures could then increase the foraging time available to *Iridomyrmex* but reduce it for subordinate species.

Altered temperature regimes can also have the effect of destabilizing competitive, predator-prey, and parasitic interactions. Geiger (1965) quotes the example of the timber pest *Ocneria monacha*, which lays eggs on tree trunks. Elevated springtime temperatures on trunks at the forest edge allow larvae to emerge before their parasites, which emerge from the cooler forest floor. This gives the pest a head start and results in population buildups.

2. WIND

With the removal of surrounding vegetation, the entire pattern of momentum transfer over the landscape is altered. As air flows from one vegetation type to another, the wind profile adjusts to the new roughness characteristics. When air flowing over one vegetation type comes to a boundary with a new vegetation type, the upper part of the wind profile initially retains the characteristics of the previous vegetation type, but the lower part takes on new characteristics reflecting the roughness of the new vegetation type. The wind profile does not fully equilibrate with the new vegetation for some distance. Rules of thumb for wind profile measurements give the minimum "fetch" (i.e., the minimum distance from the vegetation boundary that will ensure that the profile has taken on the characteristics of the vegetation under study) as 100–200 times the height of the vegetation under study (Monteith 1975; Grace 1983; Jones 1983). Turbulent transfer is important for the transport of atmospheric gases, and gas fluxes above vegetation are controlled by these processes. It follows, then, that these processes must be significantly modified in remnant vegetation areas, where the wind profile will not be in equilibrium with the remnant vegetation (Jarvis & McNaughton 1986). Given the fetch requirements, a woodland with 20-m-tall trees would need to be at least 2–4 km wide before wind profiles would resemble those in an unfragmented situation. The implications of this for plant gas exchange and growth have not been examined, but could be significant.

A more obvious effect of landscape fragmentation is that remnants are subjected to increased exposure to wind. This may result in damage to the vegetation, either through direct physical damage (Moen 1974; Grace 1977), or by increasing evapotranspiration with reduced humidity and increased dessication (Tranquillini 1979; Lovejoy et al. 1986). Direct physical damage can take the form of wind pruning (Caborn 1957) or windthrow of trees. Distinct edge structures have been found to develop at the edges of tree plantations (Fraser 1972), and this is likely to be the case for remnant areas also (see Ranney et al. 1981 for a discussion of edge structures). Trees near the edge of recently isolated remnants are particularly at risk of windthrow since they have matured within a closed canopy and have therefore developed in the absence of strong winds and lack the necessary support mechanisms to deal with such winds. Windthrow of dominant trees results in changes in the vegetation structure and increased availability of regeneration gaps, allowing recruitment, particularly of pioneer or light-demanding species. Increased litter fall through tree damage is likely to alter soil surface characteristics and hence the habitat of ground-dwelling fauna. Similarly, increased exposure to wind may remove loose bark and reduce the substrate available for bark-dwelling invertebrates, and hence also reduce their availability as a food resource. Increased wind turbulence due to clearing has been shown to affect the breeding success of birds by creating difficulties in landing due to wind shear and vigorous canopy movement (Brett 1989; Reville et al. 1990). In the case of tropical forests, fragmentation can result in hot, dry winds blowing into remnant areas from the surrounding cleared areas, with the probable result of increased tree mortality (Lovejoy et al. 1986) and prevention of regeneration of species whose successful establishment requires humid conditions or persistent soil moisture (Janzen 1986). This may also be important in the regeneration of species in other areas, such as those with mediterranean climates, where successful establishment requires adequate soil moisture (e.g., Gordon et al. 1989; Williams & Hobbs 1989). This effect will be lessened in cases where the edges of remnants are sealed off by rapid secondary growth.

Increased wind speeds at remnant edges have the secondary effect of increasing the transfer of material such as dust and seeds in from the surrounding matrix. Gei-

ger (1965) gives an example where particulate matter deposition at the edge of a forest remnant increased by 40% over that in the open. Transfer of nutrients by saltation of surface soil particles is also possible, and strong gradients in soil nutrient levels have been found at the edges of remnant areas (Muir 1979; Cale & Hobbs 1991). Wind can deposit seeds of nonnative species over considerable distances into remnant areas (Hobbs & Atkins 1988). Transfer of insects and disease organisms into remnant areas may also be increased.

3. WATER FLUX

Fragmentation of the landscape results in modification of the local water regime by altering the various components of the hydrological cycle. Removal of native vegetation changes the rates of rainfall interception and evapotranspiration, and hence changes soil moisture levels (Kapos 1989). The pathways by which water penetrates the soil may also be markedly altered (Bormann & Likens 1979; Nulsen et al. 1986; Peck & Williamson 1987; Sharma et al. 1987; Bell 1988). Replacement of deep-rooted perennial species with herbaceous crop or pasture species leads to greatly reduced evapotranspiration and increased surface- and groundwater flows. The hydrological system in general becomes much less buffered with more extreme run-off events (Hornbeck 1973; Simons 1989). Increased surface water flows lead to increased erosion and transport of particulate matter (e.g., Bormann et al. 1974). Topsoil removed from high in the catchment ends up as sediment in the river system. Transport of nutrients into streams also increases (Likens et al. 1970). Rises in water tables can bring stored salts to the surface and cause secondary salinity, with considerable impacts on both remnant vegetation and the surrounding agricultural matrix (Peck 1978; Williamson et al. 1987). Movement of stored salts, nutrients, and pesticides washed from cleared land can have significant impacts on river systems (Kendrick 1976; Karr & Schlosser 1978).

The impact of these changes on an individual remnant depends greatly on its position in the landscape (Swanson et al. 1988). Remnants at the top of a catchment can be expected to be relatively little affected by changes in water flux, whereas remnants on midslopes and valley bottoms will be more affected. Remnants in run-off areas can be expected to experience more erosion, while those in run-on areas will experience more soil deposition, especially on the up-slope edge.

Further impacts on remnant areas can be expected following management operations in the surrounding matrix that alter hydrological processes. Thus irrigation, water storage, or drainage may affect remnant areas. An extreme example of this is found in the fens of eastern England, where drainage has led to peat shrinkage and a drop of 4 m in land level in 130 years. Remnant areas of natural wetland now require pumping systems to retain adequate water levels (Hutchinson 1980; Rowell 1986).

Changes in water fluxes and associated particulate and nutrient fluxes can have important influences on the biota of remnants. Altered patterns of erosion lead to changes in drainage patterns and the production of new substrates for plant colonization. Of particular importance is the deposition of nutrient-rich material in run-on areas, which can act as a focus for invasion by species requiring disturbance and/or nutrient enrichment for successful establishment (Hobbs & Atkins 1988). Changes in surface and soil moisture levels could also lead to changes in decomposition rates, altered seedbed characteristics, and changes in habitat for ground-dwelling fauna.

Isolation

Landscape fragmentation has two important consequences for the biota. First, there is a reduction in the total area of habitat available, with possible increased densities of surviving fauna in the remnants, and second, the habitat that is left is broken up into remnants that are isolated to varying degrees (Lovejoy et al. 1984, 1986; Haila & Hanski 1984; Wilcove et al. 1986). The time since isolation, the distance between adjacent remnants, and the degree of connectivity between them are all important determinants of the biotic response to fragmentation.

1. TIME SINCE ISOLATION

Upon isolation, a remnant is likely to have more species than it will be capable of maintaining, and species will be lost as the changes brought about by fragmentation take effect (Miller & Harris 1977; Miller 1978; Wilcox 1980; Harris 1984). This process of "species relaxation" is considered an inevitable consequence of area reduction and isolation, on the basis of island biogeographical predictions. However, the various mechanisms by which local extinctions occur will result from the physical changes discussed above and resulting changes in biotic interactions. The rate of species relaxation will differ among different taxa. The most rapid extinctions are likely in species that depend entirely on native vegetation, those that require large territories, and those that exist at low densities. Dispersal behavior and demography will determine the response of individual species to fragmentation (Karieva 1987).

Populations that are too small to be viable may persist for long periods simply because of the longevity of individuals. For example, in remnants in the Western Australian wheatbelt, female trapdoor spiders *Anidiops villosus* can live for at least 23 years (Main 1987), and small Australian passerines of about 25 g may live over 20 years (Australian Bird Banding Scheme records). It may take several hundred years to lose some species

such as long-lived trees, especially since adult plants are often less sensitive to changed environmental conditions than seedling and juvenile stages. Alterations in disturbance regime in remnant areas may prevent successful regeneration (Hobbs 1987; Bond et al. 1988). Presence of a species in a remnant is thus no guarantee of its continued existence there; successful reproduction and recruitment are required. Managers therefore may need to examine the age structure of species on remnants to identify vulnerable species to be targeted for special management.

Time since isolation will therefore determine how far down the "relaxation track" any given remnant has traveled. Recently isolated remnants can be expected to continue losing species; this process may continue for relatively long periods in the absence of interventive management (Soulé et al. 1988; Saunders 1989). Long-isolated remnants can be expected to have lost a proportion of the species originally present, and gained an additional component of invading species that are capable of establishing in the fragmented system. It is thus wrong to consider only species numbers and not species composition when discussing species diversity in remnant areas: species numbers can potentially increase in fragmented systems where invasive and edge species can establish, but the numbers of species originally found in the area may continue to decline (Verner 1986; Murphy 1989; Webb 1989; Harris & Scheck 1991).

It is commonly assumed that at some stage the remnant will reequilibrate with the surrounding landscape. It is, however, questionable whether a new stable equilibrium will be reached since the equilibration process is liable to be disrupted by changing fluxes from the surrounding matrix, disturbances, and influx of new invasive species. The final equilibrium can be likened to an idealized endpoint that is never likely to be reached, in much the same fashion as the climatic climax is now conceptualized in succession theory. Management of remnant areas will thus be an adaptive process directed at minimizing potential future species losses.

2. DISTANCE FROM OTHER REMNANTS

The ability of species to colonize a remnant depends to some extent on the distance of the remnant from other areas of native vegetation, be they other remnants or nearby uncleared areas. Colonizing ability is related to dispersal mode, with wind-dispersed and vagile species more likely to arrive at isolated remnants. However, whether such species become successful colonists depends on physical and biotic factors such as nutrient availability and competitive interactions (Vepsäläinen & Pisarski 1982). Animal species may have the physical ability to disperse long distances, but lack the behavioral repertoire to traverse the matrix surrounding the remnant; the matrix becomes an effective barrier to movement. Organism size is also important, and 100 m over agricultural fields may be a complete barrier to dispersal for small organisms such as invertebrates (Mader 1984) and some species of bird (Saunders & de Rebeira 1991). The persistence of such species on a remnant would then depend entirely on the retention of enough suitable habitat to maintain sufficient numbers to withstand the risks of extinction (Soulé 1987*a*; Ewens et al. 1987). Some evidence exists that fragmentation of large populations into subpopulations may decrease the risk of overall species extinction even though local extinctions may occur (Higgs 1981; Quinn & Hastings 1987). It seems likely that different species will respond differently to the creation of subpopulations and that knowledge of the details of an organism's behavior will be necessary to predict its response (Karieva 1987; Merriam 1991).

3. CONNECTIVITY

Associated with the effects of distance is the degree to which individual remnants are connected in some way to adjacent areas. The issue of connectivity and the usefulness of corridors connecting remnants has received increasing attention in the literature (MacClintock et al. 1977; Wegner & Merriam 1979; Baudry 1984; Forman & Baudry 1984; Merriam 1984; Harris 1984, 1985; Fahrig & Merriam 1985; Noss & Harris 1986; Bridgewater 1987; Simberloff & Cox 1987; Noss 1987; Soulé et al. 1988), and was the subject of a recent symposium (Hobbs et al. 1990; Saunders & Hobbs 1991*a*). Corridors are generally believed to provide benefits such as enhanced biotic movement, extra foraging areas, refuges during disturbances, and enhancement of the aesthetic appeal of the landscape. In some areas they significantly add to the area of native vegetation left following fragmentation.

Simberloff & Cox (1987) pointed out that most of the work on the value of corridors has not been sufficiently controlled to demonstrate an unequivocal role in increasing immigration and/or decreasing extinctions. An increasing number of studies, however, now indicate that corridors are of value for movement, at least for a subset of the biota (papers in Saunders & Hobbs, 1991*a*). Simberloff and Cox (1987) also discussed potential disadvantages of corridors, which include facilitation of the spread of disease, pests, and fire and other disturbances, increased predation, and high costs of maintaining linear remnants with high edge:area ratios. The relative merits of corridors and their required characteristics (i.e., width, composition, etc.) will vary from place to place and will depend on the target species. Detailed predictions of corridor value in reducing isolation of remnant areas are not possible without information on the movement of individual species across the landscape. Such information is, however, difficult

and time-consuming to collect (Saunders & de Rebeira 1991). Nevertheless, while such data are being gathered, we need to take the approach that corridors do have value for biotic movement and attempt to retain a good corridor network wherever possible (Harris & Scheck 1991; Saunders & Hobbs 1991*b*).

4. CHANGES IN THE SURROUNDING LANDSCAPE

Removal of the vegetation from the area surrounding a remnant leads to the remnant becoming the only area of suitable habitat remaining for biota displaced by clearing. This may lead to the concentration of mobile elements of the biota in the remnants (Lovejoy et al. 1986). This concentration or crowding effect may be rapid and result in supersaturation of the remnant by some species. Crowding can alter intra- and interspecific interactions. Competition and predation, for example, can be increased, resulting in changes in fecundity and the potential ultimate collapse of the population. Resource availability is also affected by overexploitation; for instance, increased herbivory by large herbivores such as the elephant in African reserves can lead to quite dramatic changes in habitat (Spinage & Guiness 1971; Laws et al. 1975; Walker 1981).

Supersaturation results from the influx of species native to the area, but there are also potential influxes of new suites of species that have increased in abundance or established in the surrounding landscape following fragmentation. Such species include those that have been introduced in the process of agricultural development (pasture and crop plant species and livestock), other deliberate and accidental introductions, and native or migrant species that can take advantage of the new habitat conditions caused by fragmentation.

Natural communities vary in their susceptibility to invasion, although there is still debate over which characteristics render one community more invasible than another (Fox & Fox 1986; MacDonald et al. 1986; Crawley 1987; Usher 1988; Rejmánek 1989). For vegetation, establishment of nonnative species seems to be enhanced by some form of disturbance, especially if this increases the availability of a limiting resource (Hobbs 1989; Panetta & Hopkins 1991). Thus the opening of light gaps in dense forests where light was limiting could enhance invasion, whereas in nutrient-limited systems, nutrient input significantly increases the performance of nonnatives, especially in conjunction with soil disturbance (Hobbs & Atkins 1988). Invasion may be restricted to the edge of remnants if disturbance factors decline with distance from edge (Cale & Hobbs 1991; Panetta & Hopkins 1991), but species with wind- or animal-dispersed seeds can establish in suitable areas within a remnant, away from the edge. Invading species can establish, for example, from seeds carried in by, or deposited in feces of, animals that feed in the area surrounding the remnant but use the remnant for shelter. An example from Western Australia is the Wedge-tailed Eagle (*Aquila audax*), which breeds or roosts in remnants but forages on carrion in the surrounding farmland, bringing parts of sheep carcasses back to the roost to consume them. Wool from carcasses carries seed that is dropped under the roost tree. Nutrient input from eagle droppings and the disturbance caused by other scavanging animals provides a focus for the establishment of nonnative species (Saunders, personal observation). Thus, even in the absence of deliberate disturbance within remnant areas, invasions may occur.

Invasive species can have significant impacts on the plant communities within remnants; for instance, invading plant species can significantly alter the fuel structure and hence fire regime, and can inhibit the regeneration of native species (Wycherly 1984; Macdonald et al. 1989; Panetta & Hopkins 1991). Nonnative herbivores, including stock, can also dramatically change vegetation structure and prevent regeneration. Species that increase because of landscape modification can also have significant impacts on the rest of the biota. For instance, in North America increased pressure from nest predators and parasites such as the Brown-headed Cowbird (*Molothrus ater*) has affected passerine bird populations in fragmented systems (Brittingham & Temple 1983; Wilcove 1985; Andren & Angelstam 1988). Similarly, the Galah (*Cacatua roseicapilla*) has moved into all agricultural areas in Australia as a result of the development of cereal cropping and the provision of watering points for stock (Saunders et al. 1985). It now roosts in remnant woodland areas, often competing with other indigenous hole nesters (Saunders & Ingram 1987; Saunders 1990), and can damage tree foliage and bark, in extreme examples causing tree mortality.

Modifying Influences

1. REMNANT SIZE

The smaller a remnant is, the greater the influence external factors are likely to have. In small remnants, ecosystem dynamics are probably driven predominantly by external rather than internal forces. Of importance here are "edge effects" (Williamson 1975; Janzen 1983; Harris 1988; Yahner 1988). Larger remnants have a bigger core area that is unaffected by the environmental and biotic changes associated with edges. Here, we regard edge effects as mainly detrimental; this is opposite to the traditional view that edges and ecotones are beneficial to wildlife (Harris 1988). The difference is that remnant edges are created by removal of the surrounding vegetation and place the remainder in juxtaposition with a completely altered surrounding matrix.

Noss and Harris (1986) have pointed out that we do not know the minimum critical size an ecosystem needs

to be to preserve its characteristic species diversity and species composition (Lovejoy & Oren 1981). In fact the "minimum dynamic area" of Pickett and Thompson (1978) or "the smallest area with a natural disturbance regime which maintains internal recolonization sources" would probably exist only in the largest conservation parks.

Larger remnants usually contain greater habitat diversity than smaller ones. A collection of smaller reserves may, however, cover a greater array of habitats than a single large one simply because a single large reserve will not contain all of the habitats likely to occur in a region. These arguments have been discussed in detail elsewhere and will not be pursued here. It is important, however, to recognize that the process of fragmentation is generally not random (Usher 1987). Land clearance usually occurs on a selective basis, with the best soil types being cleared first. For example, in southwest Western Australia, settlers selectively cleared woodlands because they occurred on the heavier soils best suited for agriculture. As a result, woodland communities are now poorly represented in conservation reserves and most woodland remaining on farms is in a highly degraded state (Saunders & Hobbs 1989). Few reserves in the area are large enough to contain representative samples of all preexisting vegetation types. Kitchener et al. (1980*a*, *b*, 1982) found, however, that even relatively small reserves (i.e., 30 ha) could be rich in some groups of fauna, but whether these populations are viable in the long term is debatable (see Saunders 1989).

Remnant size determines the potential size of populations of component species. Clearly, the number of individuals of any particular species that a given remnant will support depends on organism size and requirements. The larger the remnant, the more likely it is that populations will be large and more likely to resist chance extinctions (Gilpin & Soulé 1986; Soulé 1987*a*). Retaining populations in the long term may require large population sizes (of the order of hundreds or very much greater; Shaffer 1987), although the actual numbers required will depend on the life history and population growth rate of the species involved. Pimm et al. (1988) confirm that over a few decades extinction risk does decrease with population size, but they found no extinctions among British island birds numbering over 18 pairs. The issue of minimum population size has been discussed extensively in the literature (see Soulé 1987*b*), but there is still no real resolution as to what constitutes a minimum viable population. There has been extensive modeling of the concept, but little experimental work.

Larger populations tend to have higher levels of heterozygosity than small isolated populations. Current thinking is that heterozygosity is beneficial. Species that have gone through genetic "bottlenecks" are likely to suffer a reduction in heterozygosity with consequent loss of ability to adapt to changing conditions. Species isolated on remnants may go through such genetic bottlenecks because of small population sizes, and deliberate transfer of individuals between populations may be required (Boecklen & Bell 1987). However, the general assumption that heterozygosity is essential for long term population viability is still open to debate.

Large reserves may have some disadvantages; in particular, the possibility of disease spreading through entire populations on a large reserve has been discussed. However, there is a wide range of species' life histories and distribution patterns in the biota, and the effects of reserve size are largely species-specific. Species that have large area requirements or that require combinations of different habitats are likely to survive only in relatively large areas, whereas organisms with small, localized populations and simple habitat requirements can survive on smaller remnants. However, all will be affected by the disruption of physical ecosystem processes that result from fragmentation and were discussed earlier.

2. SHAPE

The shape of a remnant is important only for relatively small areas; there is some size beyond which shape does not really matter. However, for small remnants, shape determines the perimeter:core (or edge:interior) ratio. Long, thin remnants have proportionally much more edge than square or round remnants (Diamond 1975; Wilson & Willis 1975), and are more open to detrimental edge effects. However, some vegetation types, such as riparian strips, are naturally thin, and corridors are by definition generally long thin remnants (although the wider they are the more useful they may be to aid movement of biota; Saunders & Hobbs 1991*b*). Long, thin remnants may also, depending on their orientation, lie along environmental gradients and thus contain more vegetation types and habitats than a square reserve of similar area. Linear features are thus part of the natural and fragmented landscape, and there is no point in trying to develop optimal design principles that do not take them into account; the most important question is how to manage the remnants, whatever shape they are, so as to minimize external effects.

3. POSITION IN LANDSCAPE

The position of a remnant in the landscape has important influences on all the features so far discussed. It affects prefragmentation patterns of geomorphology, soil, and vegetation, and hence determines the structure and vegetation composition of any given remnant area. It also significantly affects postfragmentation processes.

For instance, there is an important distinction between remnants that are predominantly run-on versus those that are predominantly run-off. This influences not only the hydrological regime of the remnant, but also the movement of soil, nutrients, and seeds into and out of the remnant area.

Lessons for Management

Management of fragmented ecosystems has two basic components: (1) management of the natural system, or the internal dynamics of remnant areas, and (2) Management of the external influences on the natural system. For large remnant areas, the emphasis should be on managing the internal dynamics, including, for instance, the disturbance regime and population dynamics of key organisms. For small remnants, on the other hand, management should be directed primarily at controlling the external influences. Janzen (1983, 1986), however, has pointed out that external influences can be important whatever the remnant size.

Since most impacts on remnant areas originate from the surrounding landscape, there is clearly a need to depart from the traditional notions of reserve management, and look instead toward integrated landscape management. It will become increasingly difficult to maintain remnants of native vegetation if the management practices in the surrounding matrix have continuous adverse impacts on them. Traditional reserve management stops at the reserve boundary; fluxes of water, particulates, and organisms do not. Placing the conservation reserves firmly within the context of the surrounding landscape and attempting to develop complementary management strategies seems to be the only way to ensure the long term viability of remnant areas (Hobbs & Saunders 1991). This has important implications for land managers since it involves a radically new way of viewing management and requires that neighboring land uses, and hence neighboring landowners, interact in a positive way. This is difficult, but not impossible, and there are encouraging examples of attempts at this type of integrated management (e.g., Fitzgerald Biosphere Project 1989; Bradby 1991).

The landscape approach to management is also essential since several remnant areas taken together may represent a system over which components of the biota travel to meet habitat and food requirements. The loss of a single component of such a network could severely affect the capability of the remaining remnants to carry out the same functions, if for instance a particular species or habitat was lost. Such a network consists not only of the designated reserves, but also other remnant areas and linkages between them.

The goal of conservation management usually is to maintain species diversity, and the method of achieving this is to attempt to maintain representative examples of each ecosystem or community type present before fragmentation. To do this, we need to know the distributions of species and communities and then select areas that represent them. In general, there are two possible scenarios. In the first, we have a system that is about to be fragmented and we have to design the ideal set of reserves for the area. In the second, we have an already-fragmented system that we need to make the most of. Most theories in conservation biology, including virtually all the discussions of island biogeography in relation to reserves, have dealt with the first scenario, whereas it is the second scenario that we most frequently have to confront. Here we present a series of guidelines for management in this situation.

1. The initial step must be to determine the minimum subset of the existing remnants that are required to represent the diversity of a given region (Margules et al. 1988; Margules & Stein 1989). This requires that we have some knowledge of the distribution of species or ecosystem types. Clearly, it would be desirable to have all existing remnants available for this purpose, but in many cases this is not achievable, and there must be priorities for reserve retention or acquisition.

2. The system must then be managed to maintain the diversity of species or ecosystems. The question of whether management should be for individual species or whole ecosystems is largely irrelevant, because individual species require functioning ecosystems to survive. Management guidelines will be area-specific, but the need to manage external influences is universal.

3. Priorities for management must be established. Clearly there are many problems to be tackled, and usually there are limited resources available for the job. There must therefore be a clear priority ranking to ensure that resources are deployed optimally. Problems that are likely to disrupt ecosystem processes and hence threaten the viability of a remnant area should be given high priority for treatment.

4. Continuous management is needed to maintain remnant areas in their current state, due to the constant pressure of altered internal dynamics and external influences. Here again, the allocation of scarce management resources must be considered. Effort should go into maintaining some remnant areas in as near a "natural" state as possible, but it will not be feasible to do this for all remnants. There is a strong case to be made for letting some areas degrade so that they become less natural but are easier to manage and still retain some conservation value (Bridgewater 1990). This is not as radical as it may sound, since the process is ongoing in many remnant areas anyway. Once we accept that many remnants now contain "synthetic" communities that are not likely ever to return to their pristine state, management priorities become easier to set.

Research Requirements

Research to date on fragmented ecosystems has provided few answers on the issues of practical importance to management. It is just as important to set priorities for research as for management, and in the same way, research costs must be taken into account since resources for research are also limited. For instance, is it better to concentrate on single-species studies that can produce results with direct practical application but are very costly and time-consuming, or should we concentrate on the community/ecosystem approach that is cheaper but may yield more equivocal results? Clearly, balanced use of both approaches is needed. We have identified a number of priority areas that require research effort (see also Soulé & Kohm 1989).

1. A major priority is to understand the effects of external factors. Comparisons of pre- and postfragmentation systems will be particularly useful (Lovejoy et al. 1986; Margules 1987). Effects of changes in radiation and water fluxes are particularly important, as is the biotic invasion process.

2. Changes in internal processes since fragmentation also require further investigation. In particular, the interaction between internal and external processes is likely to be of critical importance.

3. Isolation factors need to be better understood. In particular, rates of genetic change in isolated populations require study, as does the question of whether reduction in genetic variability is important. We also require more and better data on the role of corridors in allowing biotic (and hence genetic) movement in fragmented landscapes.

4. While theoretical studies have their place, there is an urgent need for field experimentation in both management and restoration. While such experiments are costly to set up, it is possible to make use of many situations that offer ready-made experiments. Our understanding of succession has benefited greatly from the study of abandoned old fields, and in the same way, we can use current or past management activities as large-scale experiments; there is plenty of experimental material around (McNab 1983; Hopkins & Saunders 1987; Pimm 1986; Jordan et al. 1987; Hobbs & Hopkins 1990). Research has much to gain from a close liaison with management, especially if management operations actually can be carried out as designed experiments and the results suitably monitored.

Conclusions

Emphasis in the literature has been on the design of nature reserves, but we are usually too late to do anything except try to maintain the remnants left following fragmentation. Emphasis also has been on biogeographic explanations for the patterns of species loss after fragmentation, whereas a whole suite of physical and biotic parameters are significantly altered in the fragmented system and have significant impacts on remnant biota. In particular, the switch from predominantly internally driven to predominantly externally driven dynamics is a key factor in the fragmented system. Management and research should focus on this factor. There is a pressing need for an integrated approach that treats the landscape as a whole instead of as a collection of separate biotic and legal entities.

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