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Forest fragmentation and biodiversity: the case for intermediate-sized conservation areas

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Summary

Understanding the effects of forest fragmentation on biodiversity is essential for successful and efficient forest conservation. Four factors may cause loss of biodiversity in forest fragments: the effect of non-random sampling of the original forest, reduced forest size, isolation and edge effects. A review of 58 papers on effects of forest fragmentation reveals that general conclusions from fragmentation research are biased due to a focus on birds, on size-effects rather than isolation, and on species presence rather than population sizes. Perhaps the most important finding is that current knowledge on fragmentation effects is based mainly on studies in small fragments (<10 ha). These are dominated by edge effects, can not contain viable populations for many species and are rarely the focus of conservation programmes. Studies of small fragments can not be extrapolated to larger-sized, protected areas, and do not necessarily support the case for needing extremely large, protected areas. Conservation of medium-sized, strategically-located areas may be a more efficient option for biodiversity conservation, given financial, social and logistic limitations. More research is needed on forest fragments that are representative of the sizes of real-world protected areas (i.e. >10 000–100 000 ha) and should focus on the biological and human-induced processes which determine species persistence.

Keywords: biodiversity, forest conservation, forest fragmentation, edge effects

Introduction

Isolation of forest patches is caused by human activities such as logging, conversion to agriculture, and road construction (McCloskey 1993; Skole & Tucker 1993; FAO 1995; Vogelmann 1995). The resulting forest fragments are surrounded by agriculture, urban landscapes, plantation forests, secondary forests or wastelands. In general, forest fragmentation can be expected to cause local extinctions of original forest species, and fragmented forests will contain fewer of the original forest species than continuous forests. Efficient programmes to conserve forest biodiversity require an ability to predict the scale of losses of biodiversity which will occur as a result of the fragment's representativeness, size and degree of isolation. Currently, the scientific basis for predictions of species extinction rates resulting from deforestation and fragmentation is weak (Simberloff 1992). Models based on island-biogeography theory

(MacArthur & Wilson 1967) predict much higher extinction rates than empirical studies have reported (Heywood & Stuart 1992; Heywood *et al.* 1994; Turner & Corlett 1996).

Forest biodiversity conservation is an area of major international concern (ITTO 1993; Heywood & Watson 1995). Despite this, only limited financial resources are available for conservation programmes and these need to be used efficiently, especially in developing tropical countries. Many conservation plans advocate the establishment of extremely large protected forest areas, but observation suggests that socioeconomic constraints limit the success of such ambitious schemes. Many 'paper parks' exist only in plans and on maps. A set of strategically placed reserves of a size which is consistent with resources available for their protection may be a more realistic option (Boyle & Sayer 1995). Since these areas will inevitably be 'fragments', knowledge of the effects of forest fragmentation on rates of species loss is essential. However, research has dealt almost exclusively with fragments of 100 ha or less. The protected areas which are established to conserve forest biodiversity are several orders of magnitude larger than this. We have extracted information on the size of nature conservation areas in tropical forest countries from Collins *et al.* (1991) for Asia, Sayer *et al.* (1992) for Africa, and Harcourt & Sayer (1996) for South America. These publications give partial lists of areas established by the late 1980s. They indicate that the average size of National Parks in Brazil is 340 000 ha, in Indonesia is 345 000 ha and in Zaire is 1.2-million ha. There are 118 National Parks and equivalent strict Nature Reserves in the three countries, of which only 18 are less than 10 000 ha.

In this paper we attempt to use the existing literature on the biological impacts of fragmentation to draw conclusions about the viability of different size classes of conservation area. We review 58 original papers reporting on studies in forest fragments. The aggregate number of fragments in these studies was 1488, but several studies presented data from the same fragments so the actual number of fragments covered by this review is somewhat lower than this total (see Appendix 1 for general information and references). The studies focused on various changes and processes in forest fragments, which may affect rates of species loss.

Processes affecting species persistence in forest fragments

Forest fragmentation may negatively influence the forest's original biodiversity at the levels of genes, species, and species associations. The effect of forest fragmentation on biodiversity can either be a direct result of non-random 'sampling' of a certain forest area (representativeness), or indirect, resulting from chains of causes and effects. Different 'fragmentation factors' may affect species persistence in different ways (Fig. 1).

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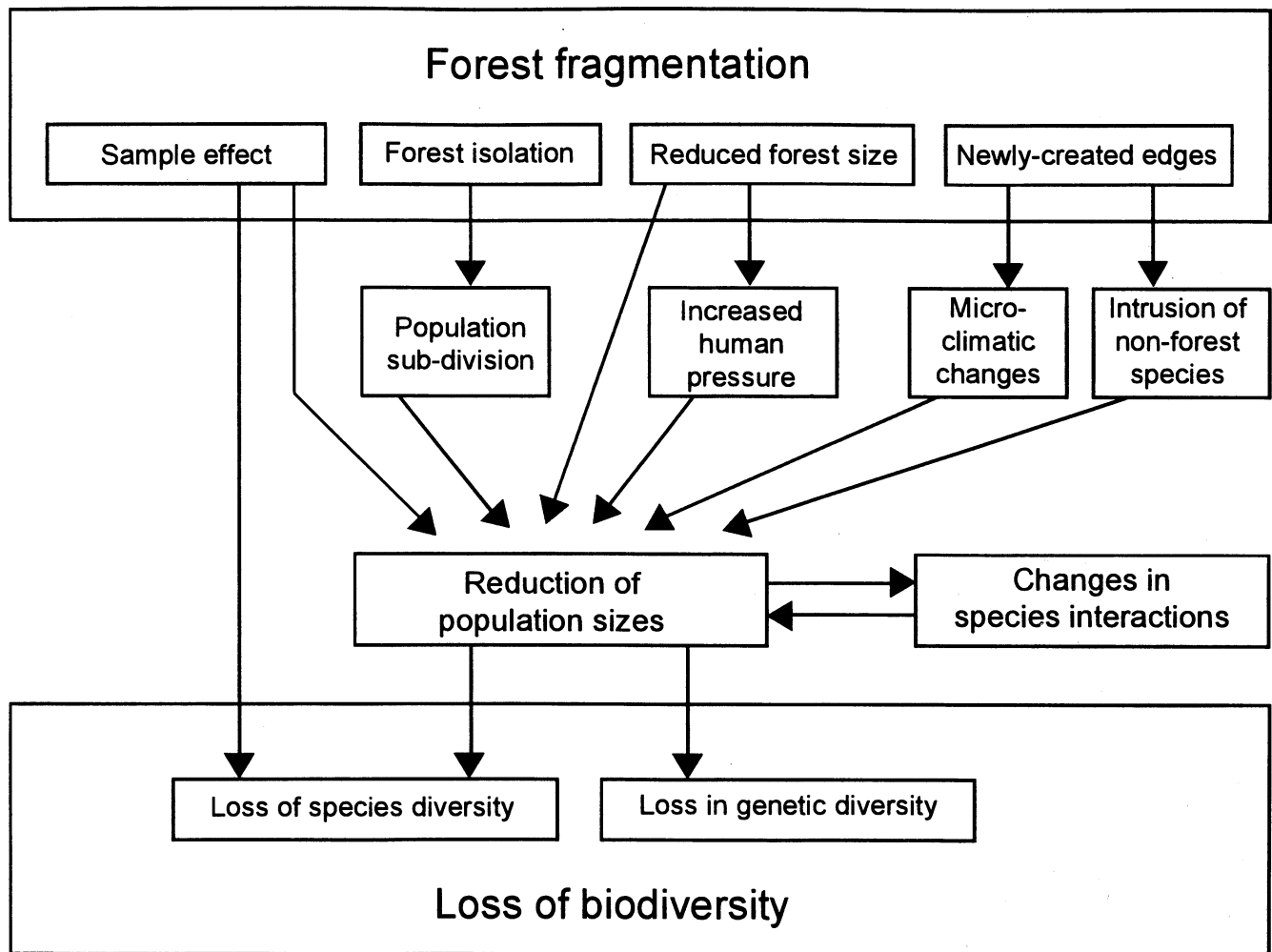


Figure 1 A schematic representation of the theoretical ways in which four forest fragmentation factors (sample effect, forest isolation, reduced forest size and newly-created forest edges) may cause reduction of population sizes which may result ultimately in loss of biodiversity. Arrows indicate causal relations.

Sample effects

Forest fragments are 'samples' of a larger area of forest and may exclude patchily distributed species that were present in the original area (Wilcox 1980). The extent to which the forest fragment represents the original forest depends on the proportion of the landscape converted into non-forest, the spatial arrangement of the remaining fragments, the size of the fragments and the spatial distribution of original forest species. Selectivity of deforestation will affect the representativeness of forest fragments. For example, lowland forests in flat areas are generally cleared before forests on steep slopes in the uplands are cleared, as is the case on Java (Thiollay & Meyburg 1988). As a result, groups of species, or complete communities, may be eliminated.

Fragment size

The reduction in forest area due to fragmentation will result in a decrease in population sizes of forest species. For species with a patchy distribution, the abundance in a fragment will depend on the location and size of the fragment. For species that naturally occur at high densities, population size may not be reduced to critically low numbers in forest fragments of reasonable size (e.g., Klein 1989; De

Souza & Brown 1994). Species occurring at low densities will suffer from considerable reduction in population size, and may become vulnerable to local extinction as a result of stochastic events or reduced genetic fitness. Reduced forest size will also make fragments more accessible for logging, hunting and gathering (Janzen 1986), which can also contribute to species loss (Turner 1996).

Transformation of a large forest area into several fragments results in population subdivision. The nature of the habitat separating the fragments, and the capacity of individuals, seeds or pollen to cross gaps, will determine the effective size of resulting population(s) (Hanski 1989). Altered microclimatic conditions (high temperature, low moisture, strong wind), and increased susceptibility to predation, may inhibit movement, or even completely impede crossings of inter-fragment areas (Powell & Powell 1987; Bierregaard & Lovejoy 1989).

Isolation

Clearly, the effect of fragment isolation differs among species, depending on their mobility, dispersal mechanism or pollination agent (Wilcox 1980). Laurance (1991a) has reported on the effects of an animal's degree of habitat specialization and behavioural avoidance

of open habitats on extinction proneness. Some species, or their propagules, can cross large areas of non-forest vegetation (e.g., raptors; Thiollay & Meyburg 1988), whereas for other species an inter-fragment distance of 80–100 m or less can act as a strong barrier (Mader 1984; Powell & Powell 1987; Temple & Cary 1988; Klein 1989).

Open vegetation outside forest fragments (grassland, agricultural fields, plantation forest) results in higher air temperatures, wind speeds and light availability, and a drier air and soil moisture regime, in the edge zones of forest fragments (for review see Murcia 1995). The depth to which microclimatic influences extend depends on the steepness of microclimatic gradients, and on the structure of the edge vegetation; a more dense vegetation buffers the intrusion of microclimatic changes (Lovejoy *et al.* 1986; Williams-Linera 1990; Saunders *et al.* 1991). In temperate, as well as tropical regions, these microclimatic changes were found to penetrate over 50 m into the forest (Ranney *et al.* 1981; Kapos 1989; MacDougall & Kellman 1992; Young & Mitchell 1994). Pioneer and agricultural species may benefit from the altered microclimate in the edge zone, and may out-compete original forest species (Janzen 1983; Lovejoy *et al.* 1984; Laurance 1991*b*; Brothers & Spingarn 1992). Laurance (1991*b*) found non-forest species invading up to 500 m into fragments surrounded by pasture. Non-forest species may also introduce pests and diseases into fragments, and, in this way, affect viability of original forest species (Janzen 1986).

The processes described above may result in a reduction in the population sizes of forest species. Clearly, the time scale of such changes differs between species, depending on their life cycle; long-lived species such as tropical trees will show a decline in adult population only a long time after forest fragmentation (Lovejoy *et al.* 1983; Turner & Corlett 1996).

A drastic population reduction may result in a population size below a minimum viable level. The size of the minimum viable population will depend on the species' life cycle, demography and breeding system (Schaffer 1981; Soulé 1987; Nunney & Campbell 1993), but is ultimately determined by vulnerability to stochastic fluctuations in population size and reduced genetic fitness (Schaffer 1981; Gilpin & Soulé 1986; Lande 1993). Permanent local extinction is avoided when individuals or propagules are exchanged with other fragment populations, i.e., when a metapopulation is established (Hanski 1989, 1994). Young *et al.* (1996) reviewed literature on the population genetic consequences of habitat fragmentation for plants. They concluded that, for the species examined so far, genetic variation usually is reduced by fragmentation. They attribute this to genetic 'bottlenecks' at the time of fragmentation and subsequent inbreeding in small populations, but they note that there is no direct evidence of the latter. Significantly, they point to evidence of fragmentation thresholds above which genetic variation is not lost, and to situations where fragmentation may lead to increased gene flow amongst remnant populations. Their overall conclusion is that the genetic effects of fragmentation appear to be more varied than simple population genetics models would predict, and that remnant populations can play a significant role in maintaining the genetic diversity of a species.

Subjects and findings of fragmentation studies to date

The theoretical literature on fragmentation is quite large (e.g., Simberloff & Abele 1982; Wilcox & Murphy 1985; Boecklen & Simberloff 1986; Zimmerman & Bierregaard 1986; Murcia 1995),

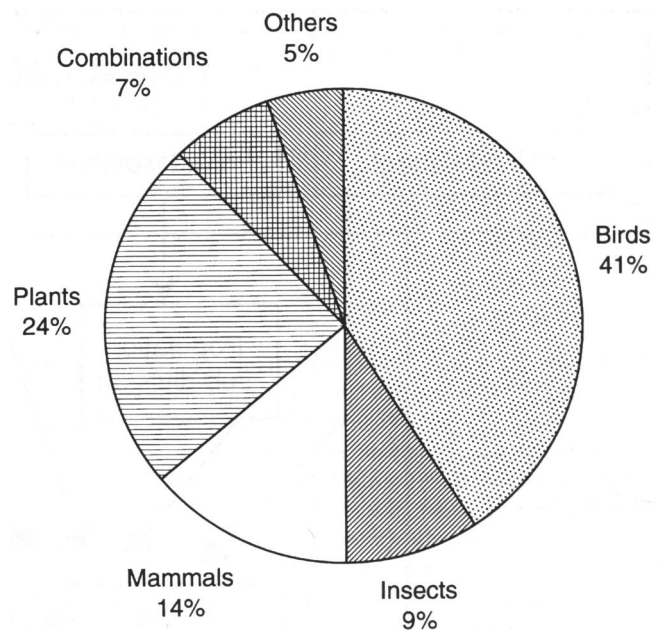


Figure 2 Distribution of the species groups studied in the 58 original forest fragmentation papers reviewed (see Table 1).

but there are relatively few empirical studies of what actually has happened in isolated pieces of forests. We have reviewed 58 of the studies which measured the impact of fragmentation on species persistence (Table 1).

Species studied

Birds are the most intensively studied species group (Fig. 2; see review by Andrén 1994). This can be attributed to the abundance of ornithologists and the advanced state of knowledge of bird taxonomy and geographical distribution (e.g., Whitcomb *et al.* 1981; Opdam *et al.* 1984). Plants are the second-most studied taxonomic group. Plant population sizes and species diversity have often been

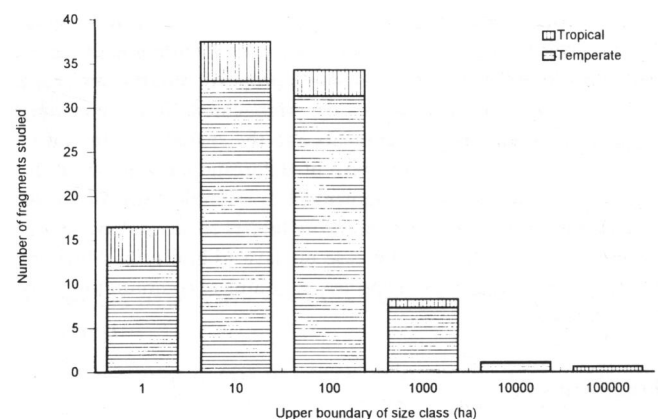


Figure 3 Size distribution of the 1488 forest fragments studied in the 58 papers reviewed (see Table 1) for temperate and tropical forest areas. Note that several papers refer to studies carried out in the same fragment and the actual aggregate number of fragments covered by the studies cited is less than 1488.

Table 1 List of 58 reviewed fragmentation studies classified per taxonomic group with information on size distribution of studied fragments, studied factors (S = size; I = isolation; SI = size & isolation; E = edge; O = other) and their findings (P = population size; D = species diversity; PD = population size & species diversity; G = genetic diversity; I = species interaction; U = uncertain or no effect). Numbers in columns indicate the number of fragments studied in that size class.

<i>Studies per taxonomic group</i>	<i>Upper limit of size classes of studied fragments (ha)</i>						<i>Factors</i>	<i>Findings</i>	
	10^0	10^1	10^2	10^3	10^4	10^5			10^6
<i>Birds</i>									
Askins <i>et al.</i> 1987		8	18	16	4			S	PD
Bierregaard & Lovejoy 1989	5	4						SI	PD
Blake & Karr 1984		4	6	2				SI	PD
Diamond <i>et al.</i> 1987			1					S	PD
Estrada <i>et al.</i> 1993	3	6	9	12				S	D
Forman <i>et al.</i> 1976	3	5	2					S	I
Gibbs & Faaborg 1990		1	4	1				S	P
Haila <i>et al.</i> 1993	2	11						S	U
Lynch & Whigham 1984*		35	216	18	1			SI	P
Mills 1995	3	10						S	P
Newmark 1991	5	3	2	1				SI	D
Nores 1995					2	4	3	SI	D
Opdam <i>et al.</i> 1984	17	19						SI	D
Porneluzi <i>et al.</i> 1993		1	7	3				S	P
Robinson <i>et al.</i> 1995*			6	20	6	1		SI	I
Schieck <i>et al.</i> 1995		4	12	4	1			S	U
Stouffer & Bierregaard 1995	5	4						S	U
Telleria & Santos 1992	14	5	6	4				S	I
Telleria & Santos 1995	11	5	7	4				S	P
Thiollay & Meyburg 1988				1		4		S	PD
Van Dorp & Opdam 1987	10	185	40					SI	D
Villard <i>et al.</i> 1995*		7	40	3				S	PD
Whitcomb <i>et al.</i> 1981		15	7	8				SI	D
Willson <i>et al.</i> 1994	3	5		3				S	PD
<i>Plants</i>									
Brothers & Spingarn 1992*	1	6						E	P
Dzwonko & Gawronski 1994		4						I	PD
Dzwonko & Loster 1989	59	4	3					SI	PD
Esseen 1994	5							O	P
Levenson 1981	7	31	5					S	U
Norton <i>et al.</i> 1995		5	4	3	2			S	P
Rankin-de Merona cited in Bierregaard (1992)		1	1					E	P
Scanlon 1981		16	6	1				S	D
Simberloff & Gotelli 1984	31	10	9	1				S	P
Sizer cited in Bierregaard (1992)		1						E	U
Van Dongen <i>et al.</i> 1994	3	4	4	1				I	G
Weaver & Kellman 1981		10						SI	U
Young & Mitchell 1994	2	3						O	P
Young <i>et al.</i> 1993		8						S	U
<i>Mammals</i>									
Bennett 1990	5	19	15					I	P
Laurance 1990		4	5	1				SI	D
Laurance 1994		4	5	1				S	PD
Malcolm 1994	4	1	1					SI	PD
Matthiae & Stearns 1981	4	16	2					S	D
Pahl <i>et al.</i> 1988		4	7					S	D
Rylands & Keuroghlian 1988		4	1					S	D
Van Apeldoorn <i>et al.</i> 1994	7	30	12					SI	P
<i>Insects</i>									
Baz & Garcia-Boyero 1995		3	4	5	1			SI	D
Becker <i>et al.</i> 1991	2	2	1					S	U
De Souza & Brown 1994	1	1						S	D
Klein 1989	3	3						S	PD
Powell & Powell 1987	1	1	1					S	P
<i>Combinations</i>									
Aizen & Feinsinger 1994	5	4	1					S	I
Howe 1984*	25	14						S	PD
Rosenberg & Raphael 1986		6	29	11				S	D
Santos & Telleria, 1994	3	4	2	2				S	I
<i>Others</i>									
Kapos 1989	2		2					E	U
Laurance 1991b		4	5	1				E	U
Ranney <i>et al.</i> 1981		8	1					E	U

* Number of fragments in size classes is approximate for this reference.

studied in relation to edge effects (e.g., Ranney *et al.* 1981; Esseen 1994; Young & Mitchell 1994). Insects have received relatively less attention, in spite of their important contribution to total species diversity (e.g., Powell & Powell 1987; Klein 1989; Didham *et al.* 1996). The over-representation of bird studies may result in biased general conclusions, since effects of fragmentation on birds will differ from those on groups of less mobile species (Wilcox 1980). Extrapolation between organisms with different capacities of movement and dispersal will not normally be possible.

Almost all fragmentation studies describe the response of a single species or several species from one taxonomic group, e.g., beetles, euglossine bees, under-storey birds and small mammals. Information on changes in interactions of plants and pollinators, or prey and predator species, is scarce (Aizen & Feinsinger 1994; Santos & Telleria 1994). Further research on inter-species' dependencies and ecological processes in fragmented forests will be of importance in predicting species extinctions resulting from forest fragmentation (Terborgh, 1992; Estrada *et al.* 1993; Harrington *et al.* 1997).

Size of fragments studied

A relatively small proportion of fragmentation research has been conducted in the tropics and of all forest fragments that were studied in the papers reviewed, more than 50% were smaller than 10 hectares (Fig. 3). Species that occur at low densities and cannot disperse between fragments will usually fail to maintain a minimum viable population in fragments of this size. Also, species requiring a home range larger than a few hectares, and which are unable to expand their home range to incorporate several fragments, will risk extinction in these small areas.

The large edge-to-core ratio in small forest fragments dramatically reduces the area of suitable habitat for many obligate forest species. Several studies indicated that in one-ha forest fragments edge conditions predominate, and no core area remains in which the original forest microclimate is maintained (Esseen 1994; Young & Mitchell 1994). Assuming a 50-m penetration depth of microclimatic changes, almost half of the area of a 10-ha circular forest fragment is affected. For edge effects penetrating 200–500 m, as found by Laurance (1991*b*) for forest fragments with a non-circular shape, the fraction of forest area affected by edge conditions is even greater. Furthermore, small fragments rarely are representative of the original forest, since they cannot include much habitat variability. It seems reasonable to conclude that fragments smaller than *c.* 100 ha should not be a main focus of biodiversity conservation, although they may still be valuable as components of a matrix habitat (Turner & Corlett 1996).

The sizes of the forest fragments that have been the object of these studies are several orders of magnitude smaller than the major protected areas in tropical countries. Species persistence in small fragments is determined largely by edge effects and extreme reduction in population size. These may not be the most important processes determining species persistence in the protected areas which are the mainstay of real-world forest conservation programmes. There is much empirical evidence to suggest that extrapolation between the two scales is not justified.

Fragmentation factors studied

Of the fragmentation factors that may affect biodiversity (see Fig. 1), fragment size has been the focus of the majority of the studies

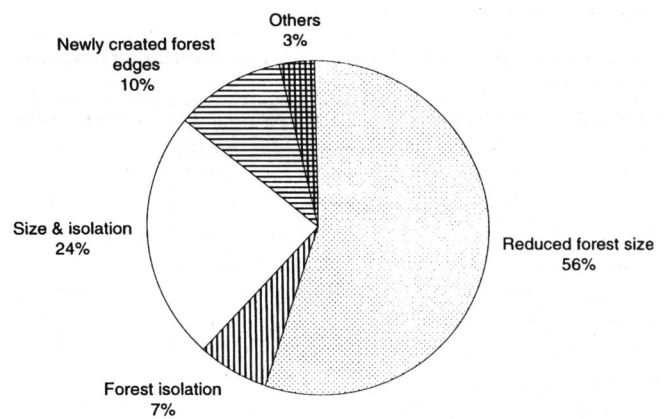


Figure 4 Distribution of the fragmentation factors studied in the 58 original forest fragmentation papers reviewed (see Table 1).

(Fig. 4). Effects of isolation are studied less frequently, presumably since isolation is more difficult to quantify, as it depends on both the distance to surrounding fragments and the characteristics of the inter-fragment vegetation. Since different measures of isolation have been used in fragmentation studies (e.g., Opdam *et al.* 1984; Laurance 1990), comparison of isolation effects is difficult.

Effects on species survival and diversity

The fragmentation studies reviewed emphasize decreased population sizes and reduction of species diversity as the two most significant effects of forest fragmentation (Fig. 5). For many studies in which an effect on species diversity was detected, the findings were based solely on presence or absence data (Fig. 5), and not on population sizes (e.g., Baz & Garcia-Boyer 1995; Nores 1995). Lack of information on population sizes of species present may lead to underestimates of longer-term fragmentation effects. Haila *et al.* (1993) noted that a reduction in population size, or of species diversity, of mobile bird species in temperate forest fragments, may be caused by natural variability in patch occupancy (e.g., shifting territory locations), rather than by reduced forest size or increased isolation.

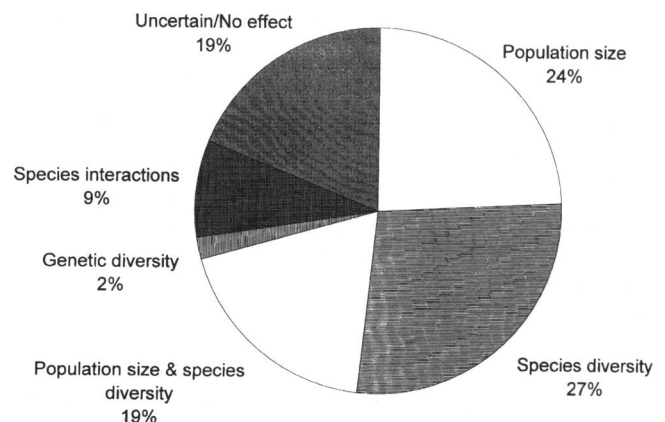


Figure 5 The effects of fragmentation identified in the 58 original forest fragmentation papers reviewed (see Table 1).

Conclusions

From the overview of studies presented here, it is clear that knowledge of effects of forest fragmentation on biodiversity is inadequate for effective planning of conservation programmes. It is apparent that it is extremely difficult to isolate different fragmentation effects in empirical studies, and many authors have actually looked at combined edge, area and isolation effects, without genuinely controlling each factor. The overall picture is based on studies in small fragments, focusing on particular taxonomic groups, testing for effects of fragment size more than isolation, and for effects on short-term survival of species rather than changes in factors such as gene frequency, levels of heterozygosity and interactions among species which will determine their long-term viability.

The general findings of the fragmentation studies presented here probably can not be extrapolated to larger areas. The implicit assumption that forest biodiversity can be conserved only in very large fragments (e.g., Meffe & Carroll 1994) is neither supported nor refuted by the empirical studies reviewed.

Perceptions of conservation managers and decision makers may have been influenced excessively by unjustified extrapolations of the results of research on small fragments. Protected area plans overestimate fragmentation effects and underestimate the social, political and logistic difficulties inherent in the protection of extensive reserves located in remote frontier areas (Sayer 1995). Strategically-targeted systems of Reserves, whose management needs correspond more closely to the resources available to support conservation, probably represent a better option for conservation. Empirical evidence suggests that Reserves as small as 1000 ha can play an important role in biodiversity conservation (Heywood & Stuart 1992; Turner & Corlett 1996). The relationship of 50% species loss for 90% habitat reduction postulated by MacArthur & Wilson (1967) is an inadequate basis for conservation planning. There is almost certainly an inflection in the species/area curve above which the rate of species loss declines. The habitat size at which this inflection occurs will differ between organisms, but Turner & Corlett (1996) make a strong case for increased persistence of plant species in fragments as small as 100 ha. However, birds and mammals may be more vulnerable in fragments of this size, and certainly will require significantly larger habitat areas (Corlett & Turner 1997).

In order to further refine the ability to predict species loss in isolated protected areas, it will be necessary to study the impact of fragmentation on the ecological interactions between species and on changes in gene frequency and heterozygosity in fragmented populations. The susceptibility of species in isolated protected areas to random demographic factors and environmental fluctuations may prove ultimately to be the most important factor in determining extinction risk. In countries with weak nature conservation institutions, there is abundant anecdotal evidence that the impacts of hunting and other anthropogenic influences are much greater in fragments. However, to some extent this may be a function of the fact that smaller fragments are not perceived to be important for conservation. It is interesting to note that of the nine National Parks in Indonesia having an area of more than 100 000 ha, six have major internationally-funded conservation projects. Of the seven National Parks with areas between 10 000 and 100 000 ha, only one benefits from significant international support. The conclusion of this paper is that the greatest area of uncertainty lies in understanding the species conservation potential, and risks for areas, in the size range of 10 000–100 000 ha, but that very little of the current research is relevant to this issue. It may be possible to demonstrate that pro-

tected areas in this medium-size range could support viable populations of most species for periods of at least several hundreds of years. Focusing more conservation resources on areas in this size range could allow major cost savings and improvements in efficiency in conservation programmes. Pragmatic decisions will then have to be taken as to when the theoretical, very long-term risks to biodiversity in forest fragments are outweighed by the financial, social and logistic advantages of smaller, more manageable reserves.

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