Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence

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ESSAY REVIEW

Species loss in fragments of tropical rain forest: a review of the evidence

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Summary

1. A review of the literature shows that in nearly all cases tropical rain forest fragmentation has led to a local loss of species. Isolated fragments suffer reductions in species richness with time after excision from continuous forest, and small fragments often have fewer species recorded for the same effort of observation than large fragments or areas of continuous forest.

2. Birds have been the most frequently studied taxonomic group with respect to the effects of tropical forest fragmentation.

3. The mechanisms of fragmentation-related extinction include the deleterious effects of human disturbance during and after deforestation, the reduction of population sizes, the reduction of immigration rates, forest edge effects, changes in community structure (second- and higher-order effects) and the immigration of exotic species.

4. The relative importance of these mechanisms remains obscure.

5. Animals that are large, sparsely or patchily distributed, or very specialized and intolerant of the vegetation surrounding fragments, are particularly prone to local extinction.

6. The large number of indigenous species that are very sparsely distributed and intolerant of conditions outside the forest make evergreen tropical rain forest particularly susceptible to species loss through fragmentation.

7. Much more research is needed to study what is probably the major threat to global biodiversity.

Key-words: biodiversity, conservation biology, extinction, habitat fragmentation, species richness.

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Introduction

There can be little doubt that the lowland forests of the wet tropics are the most species-rich of all terrestrial ecosystems. Unfortunately, these masterpieces of biological diversity and complexity are under the continuing threat of destruction from human activity. Tropical forest clearance and conversion are root causes of the current global biodiversity crisis, yet surprisingly our scientific understanding of the link between tropical deforestation and species extinctions is very poor (Simon 1986; Heywood & Stuart 1992; Smith *et al.* 1993; Heywood *et al.* 1994).

This paper reviews studies of the effects of fragmentation on the biological diversity of tropical rain forest. Whilst recognizing that biological diversity is exhibited at levels above and below that of the species,

so little is known about the genetic and community diversity of tropical rain forest in relation to habitat fragmentation that species richness is inevitably the major focus of the review. I have deliberately avoided purely theoretical papers. My aims are first to survey the facts and secondly to make some suggestions as to what they imply in terms of possible generalizations.

Biodiversity loss in tropical rain forest fragments

Deforestation in the tropics often involves the conversion of landscapes with continuous forest to ones with remnant forest patches set in a matrix of non-forest vegetation. This manipulation of tropical environments has consequences for biodiversity at both the landscape and the forest-fragment level. Factors such as fragment size, degree of isolation and

time since excision from the continuous forest may directly influence the biodiversity of a fragment and hence, in a complex manner, the biodiversity of the collection of fragments that occupies the landscape.

Studies of biological diversity in fragments of tropical rain forest are listed in Table 1. Initial impressions from collating these include that of a strong bias toward research on birds and the large number of studies to come out of one particular project, namely the Biological Dynamics of Forest Fragments (for-

merly Minimum Critical Size of Ecosystems) Project, based near Manaus in Amazonian Brazil. Non-avian taxa have received little attention; plants, surprisingly, and invertebrates, particularly at sites other than Manaus, have rarely been studied in the context of tropical forest fragmentation. This heavy reliance on one taxonomic group (birds) and one locality (Manaus) for conclusions about the influence of fragmentation on the biodiversity of tropical forest is unsatisfactory, since it requires acceptance of the lar-

Table 1. Summary table of studies on species richness in fragmented tropical rain forest

Study	Locality	Taxonomic group	Landscape/fragment size(s)	Time since fragmentation
Bierregaard & Lovejoy 1989	Manaus, Brazil	Forest birds	3 × 1 ha, 3 × 10 ha and continuous	0–3 years
Malcolm 1988	Manaus, Brazil	Small mammals	1 × 100 ha, 3 × 10 ha isolated; 3 × 10 ha, 3 × 100 ha non-isolated	2 months–3 years
Zimmerman & Bierregaard 1986	Manaus, Brazil	Forest frogs	1 ha, 10 ha and continuous	?
Powell & Powell 1987, Becker et al. 1991	Manaus, Brazil	Euglossine bees	1 ha, 10 ha, 100 ha, continuous forest	<2 years, 8 years
Klein 1989	Manaus, Brazil	Dung & carrion beetles	1 ha, 10 ha and continuous	2–6 years
Fonseca de Souza & Brown 1994	Manaus, Brazil	Termites	1 ha, 10 ha and continuous	Isolated in 1980
Willis 1979	Sao Paulo, Brazil	Forest birds	21 ha, < 250 ha, 1400 ha	>100 years
da Fonseca & Robinson 1990	Atlantic forest, Brazil	Small mammals	2 × 60–80 ha, 3600 ha	20 years
Kattan et al. 1994	San Antonio, Colombia	Forest birds	Fragments totalling 700 ha	40–90 years
Leck 1979	Rio Palenque, Ecuador	Forest birds	87 ha	?
Willis 1974; Karr 1982a	Barro Colorado Island, Panama	Forest birds	1500 ha	60–70 years
Leigh et al. 1993	Gatun Lake, Panama	Trees	6 × <1 ha islands, continuous forest	70–80 years
Daily & Ehrlich 1995	Las Cruces, Costa Rica	Butterflies	7 at 3–30 ha, 1 of 227 ha	18–33 years
Estrada et al. 1993a,b, 1994	Los Tuxtlas, Mexico	Frugivorous mammals & birds, bats, non-flying mammals	35 fragments of 1–2000 ha	5–35 years
Askins et al. 1992	St Thomas & St John, US Virgin Islands	Winter-resident migratory birds	Two islands compared, 71 km² (38% forested) vs. 50 km²(88% forested)	>100 years
Brash 1987	Puerto Rico	Land birds	8628 km², 99·6% primary forest cleared, 32·7 % forest cover	>100 years mostly
Newmark 1989	Eastern Usambara Mountains, Tanzania	Forest birds	0·1–30 ha, 1520 ha	50–100 years
Corlett 1992, Turner et al. 1994	Singapore	Vertebrates, plants	620 km², 99·8% primary forest clearance, c. 5% forest cover	100–150 years
Thiollay & Meyburg 1988	Java	Forest falcons	530, 15 000, 25 000, 36 000 & 50 000 ha	Several centuries
Diamond et al. 1987	Bogor Botanic Garden, Indonesia	Breeding birds	86 ha	50 years
Pahl et al. 1988	Queensland, Australia	Arboreal marsupials	2·4–74 ha	2–>28 years
Laurance 1990, 1994	Queensland, Australia	Arboreal marsupials, small mammals	Continuous forest: 10 fragments of 1·4–590 ha	50–80 years

gely untested assumption that birds and Amazonian forest in Brazil truly represent all the major taxa and communities of tropical forest. In addition, with the focus of the Manaus project being on recently excised forest patches, few studies are left to provide information on fragments that have been isolated for decades or longer.

Several studies have shown declines over time in the diversity of resident forest birds within a fragment or group of fragments (Willis 1974, 1979; Leck 1979; Diamond, Bishop & van Balen 1987; Kattan, Alvarez-López & Giraldo 1994). Leck (1979) reported a loss of 25 species of bird from a highly isolated 87-ha forest fragment (at Rio Palenque in Ecuador) in just 5 years. Nearly a third of the species have been lost in 80 years from a fragmented area of montane forest at San Antonio in the Colombian Andes (Kattan *et al*. 1994). Barro Colorado Island, Panama, lost 45 breeding bird species in its first half century as a protected area (Willis 1974), though 32 of these were specialists of secondary forest and forest margin that were displaced because of successional development of the forest on the island. Out of 62 bird species breeding in the Bogor Botanical Garden (containing many mature forest trees, though hardly a proper forest), Indonesia, during 1932–52, 20 had disappeared by 1980–85, four were close to extinction and five more had declined noticeably (Diamond *et al*. 1987). Small fragments at Manaus showed brief increases in forest bird diversity and density after isolation as displaced birds took refuge in remnant forest patches, but these measures soon fell to levels below those recorded before isolation (Lovejoy *et al*. 1986; Bierregaard & Lovejoy 1989).

Other studies have contrasted forest fragments of different sizes, often including data gathered from extensive forest tracts for comparison. It is a fairly trivial result to show that a small fragment contains fewer species of a certain taxon than a large one, but many of these studies have shown that diversity measured with the same sampling effort is lower in small fragments. Fragment size varies very greatly in these studies, being largely dependent on the taxonomic group in question. Tree community composition has been studied in fragments less than 1 ha in extent (Leigh *et al*. 1993), whereas forest raptor diversity has been investigated in blocks of forest of up to 50 000 ha (Thiollay & Meyburg 1988), indicating the very elastic nature of the concept of forest fragment.

The studies at Manaus have shown that small fragments contain fewer species of understorey birds (Lovejoy *et al*. 1986), small mammals (Malcolm 1988; Bierregaard *et al*. 1992), primates (Bierregaard *et al*. 1992), frogs (Zimmerman & Bierregaard 1986), dung and carrion beetles (Klein 1989), euglossine bees (Powell & Powell 1987; Becker, Moure & Peralta 1991) and termites (Fonseca de Souza & Brown 1994) than larger fragments or areas in continuous forest.

Similar results have been found in other tropical localities: generally for fragments that have been isolated for greater periods of time (Willis 1979; Thiollay & Meyburg 1988; Pahl, Winter & Heinsohn 1988; da Fonseca & Robinson 1990; Laurance 1990; Newmark 1991; Estrada, Coates-Estrada & Meritt 1993a, 1994; Estrada *et al*. 1993b; Leigh *et al*. 1993; Laurance 1994; Daily & Ehrlich 1995). For instance, 2–9 understorey bird species were captured during mist-netting in seven 50–100-year-old fragments less than 3 ha in area in the Eastern Usambara Mountains, Tanzania; while 26 species were caught over a similar period in a 520-ha fragment nearby (Newmark 1991).

There are also some data for species loss associated with deforestation on a larger spatial scale. Brash (1987) reported that the loss of 99·6% of Puerto Rico's primary forest had been associated with a 12% loss of land bird species. Singapore has undergone a similar degree of deforestation (99·8%) and suffered a higher level of species loss (Corlett 1992; Turner *et al*. 1994), estimates of which include 26% of the vascular plant flora, 28% of the resident avifauna and 44% of the species of freshwater fish. In the US Virgin Islands St John, despite being smaller than St Thomas, had more species of wintering migrant birds (mostly warblers) and in greater abundances (Askins, Ewert & Norton 1992). This is probably because St John still had 88% forest cover as opposed to 38% on St Thomas.

Analysis of the literature makes it difficult to refute the hypothesis that forest fragmentation leads to the local loss of biodiversity, though few studies can be said to have been entirely rigorous in their methodology, particularly regarding the extent to which observations were replicated. Further and better studies are to be encouraged. But it is also necessary to step beyond treating tropical rain forest communities as mere species totals. It is imperative, from the perspectives of both ecologists and conservation biologists, to understand the underlying mechanisms of species loss in forest fragments and to identify groups that are particularly susceptible to extinction.

Mechanisms of species loss in forest fragments

It has been shown that fragmentation often leads to the local extinction of species but we need to know the mechanism of extinction if we are to try to stop this, or to study the process as a means of gaining insight into community structure. Several possibilities are available, at least some of which are covered below.

DEFORESTATION-RELATED DISTURBANCE

Some species will be exterminated because by chance their habitats within the landscape will all be destroyed. Species distribution patterns are usually patchy in the tropical rain-forest landscape and this increases the likelihood of certain species being exter-

minated by fragmentation (Diamond 1980; Fonseca de Souza & Brown 1994).

There is a tendency to oversimplify the fragmentation process by viewing the fragmented landscape as a deforested matrix containing patches of undisturbed forest. Reality is much more complex. Deforestation will undoubtedly affect the remnant fragments: trees will be felled, watercourses will be altered, animals will be hunted, fire or smoke will penetrate the fragments. These events are all likely to be deleterious to biodiversity: indeed disturbed fragments at Los Tuxtlas, Mexico, had a significantly lower diversity of non-flying mammals than undisturbed ones (Estrada *et al.* 1994); but the events defy analysis within any simple ecological model of diversity loss.

RESTRICTION OF POPULATION SIZE

At present, a consideration of the demographic and genetic effects of the restriction of population size through the fragmentation of tropical forest must remain largely theoretical since very few relevant data have been published. In theory, a small fragment will support a smaller population of a given species than a larger one. As a fragment gets very small, populations will fall below viable levels and extinction will ensue. Tiny relict patches may contain 'ecologically extinct' populations of species doomed because of their small size. Small populations may be more liable to fluctuations which will inevitably include local extinctions; and they will also tend to suffer from genetic drift and inbreeding that reduce genetic variation, increase homozygosity and, in the long term, reduce fitness (Caughley 1994; Mills & Smouse 1994). However, Leung, Dickman & Moore (1993) did not find any reduction in heterozygosity in populations of the rodent *Melomys cervinipes* in small fragments (2·5, 7·5 and 97·5 ha) of rain forest in northern Queensland, isolated for more than 60 years by clearance for pastures, compared with a population from a large forest tract. However, an island population did show reduced heterozygosity, showing that migration between the fragments in the agricultural landscape was occurring and that it helped to maintain genetic diversity.

PREVENTION OR REDUCTION OF IMMIGRATION

If the deforested matrix is inhospitable to forest species there will be little or no immigration of individuals to colonize fragments after isolation. Studies have shown that many forest species will not cross even relatively small deforested zones (Dale *et al.* 1994): for example, forest beetles were markedly affected by a 100-m-wide break in tree cover (Klein 1989), as were forest birds (Bierregaard *et al.* 1992). Isolation distance has been shown to influence the species richness of tropical forest fragments (Estrada *et al.* 1993a;

Laurance 1994). The failure of many animals to move between fragments can also restrict the immigration of plant species when these animals include seed dispersers; gene flow will also be restricted if they are pollinators. Certain animal species may be relatively nomadic, or migrate seasonally through the forest (Loiselle & Blake 1992). If they avoid crossing open areas, they are unlikely to utilize fragmented habitats so the conservation value of isolated forest patches will diminish.

The nature of the matrix may play a major role in determining the movement between forest fragments. The possibilities range from open water (causing hilltops to become islands because of the flooding of valleys after dam construction) to secondary forest or tree-crop plantations. Few forest animals may be willing or able to cross the former, but many may utilize the latter. There are reports that some small patches of rain forest in Malaysia contain a surprisingly high diversity of wildlife, including large mammals, apparently because they receive little human disturbance and are surrounded by extensive tree plantations (Bennet & Caldecott 1981; Duff, Hall & Marsh 1984). This raises the possibility that swathes of secondary forest or planted trees might form valuable corridors to increase the connectedness of primary fragments and maintain higher rates of immigration to them. With regard to tropical wildlife, evidence in favour of this hypothesis comes from studies on mammals (Laurance 1990; Leung *et al.* 1993; Estrada *et al.* 1994) and butterflies (Daily & Ehrlich 1995) and by implication from the paucity of mammalian rain-forest specialists in the unconnected fragments of monsoon forest in Northern Australia (Bowman & Woinarski 1994).

Immigration is probably an important phenomenon for the maintenance of high local levels of diversity in tropical forests. Studies of tree diversity have shown that a substantial portion of the species in a tropical rain forest plot are rare, i.e. sparsely represented (Hubbell & Foster 1983; Gentry 1988), as indeed they must be where so many species are packed in. The few long-term studies of tropical tree populations show that there is turnover in the composition of the rare species complement in a given area of forest (Hubbell & Foster 1983; Primack & Hall 1992). Rare tree species often exhibit higher turnover rates per individual in their populations than common ones, at least in Sarawak (Primack & Hall 1992). Thus a considerable fraction of the diversity in a plot is supplied by tiny transient populations of rare trees (Hubbell & Foster 1986). In isolated fragments the rare species will die out relatively rapidly and not be replaced by other species because of a failure of immigration.

EDGE EFFECTS

The edges of forest fragments are the boundaries between forest and non-forest and are thus transition

zones between the two. The relative importance of edges increases as fragment size decreases, and edge effects may become highly influential. Such phenomena have been reviewed recently by Murcia (1995). For instance, forest microclimate is strongly influenced by distance to the periphery of a fragment. These effects appear to be properties of the edge and not restricted to fragments. Roads passing through forest produce similar effects, as may large gaps in the forest canopy.

The tall and relatively continuous evergreen canopy of the rain forest shades the forest interior producing a comparatively dark, cool and humid microclimate (Fetcher, Oberbauer & Strain 1985). Thus, a fragment edge will produce a gradient in microclimatic conditions, though not necessarily a simple one (Malcolm 1994; Murcia 1995). Increases in photosynthetically active radiation (Williams-Linera 1990; MacDougall & Kellman 1992) and air temperature, and decreases in relative humidity, have been recorded when forest edges are compared with interiors (Kapos 1989; Brown 1993). Such effects on the microclimate have been shown to extend up to 40 m inwards from the forest boundary in fragments at Manaus (Kapos 1989). Others have reported less dramatic effects (7–12 m, MacDougall & Kellman 1992; 15–25 m, Williams-Linera 1990), ameliorated over time as the new edge of a forest develops. Repetition of measurements after 4 years at the Manaus site showed a less marked and more complex edge influence on microclimate (Camargo & Kapos 1995). At a larger spatial scale, remote sensing has revealed that the edges of forest blocks have average canopy temperatures up to 2 C° warmer than central areas (Nichol 1994).

Edge phenomena in the physical environment may have direct effects on the forest community, though these are much less well documented. The altered microclimate may be unsuitable for certain species, effectively reducing the fragment size further for some forest animals, increasing mortality rates of forest plants near the edge and reducing recruitment to their populations. Changes in forest structure near edges have been found. These include a greater tree density (Williams-Linera 1990, 1993), an increased understorey and reduced overstorey density of foliage (Malcolm 1994), a greater mortality and rate of resulting disturbance (Lovejoy *et al.* 1986; Laurance 1991a; Leigh *et al.* 1993), and a higher density of disturbance-associated species (Laurance 1991a), though the latter was not found by Williams-Linera (1990). Newly created edges expose trees unused to strong winds to the turbulent atmosphere outside the forest, thus increasing mortality from windthrow (Lovejoy *et al.* 1986). This process may erode the fragment, reducing further its effective size.

An edge-related phenomenon that has received much attention in the temperate zone is increased predation at birds' nests. Fewer studies have been conducted in the tropics. Burkey (1993) has shown

that the chance of bait chicken eggs being found by egg-eating animals is significantly higher at rain forest edges than interiors in Belize and Mexico. However, Gibbs (1991) found that, while boundaries between primary and secondary forest in Costa Rica showed this edge effect, the periphery of primary forest meeting open pasture did not differ significantly from the forest interior in rates of egg attack. Nest predation is probably higher in fragments compared with continuous forest (Loiselle & Hoppes 1983; Sieving 1992). This may be due to the presence of nest predators that are either edge specialists or avoiders of the forest interior. Brash (1987) reported that the nest-predatory bird *Megarops fuscatus* and a warble fly chick-parasite were found at greater abundances in smaller forest fragments on Puerto Rico. Loss from nests may be a major influence on recruitment to bird populations and might be paralleled by predation on adult birds and other forest vertebrates.

In conclusion, fragment edges may be inhospitable to some, and possibly a majority of, forest species leading to an effective reduction in fragment size, and making fragment shape (via periphery to area relationships) an important determinant of fragment quality. However, edges may not be universally adverse to forest organisms. The choice of breeding pool by five species of forest frog in Brazil appeared unaffected by forest edges (Gascon 1993) and several species of small mammal increased in abundance near the margins of forest fragments in Queensland (Laurance 1994), possibly because these rodents found superior foraging in the dense, tangled growth at the forest fringe. The hemiepiphyte *Oreopanax capitatus* (Araliaceae) was restricted to edge zones in the lower montane forest of Mexico (Williams-Linera 1992).

HIGHER-ORDER EFFECTS

If certain animal or plant groups are more susceptible to local extinction through fragmentation than others, a change in community structure within the fragment is highly likely, which may ultimately lead to further changes and more extinctions, producing second- and higher-order effects. A good example involves the loss of army ants from neotropical forest fragments (Lovejoy *et al.* 1986). The ant colonies require large areas (> 30 ha) of forest to supply sufficient food. The disappearance of the ants from smaller fragments is associated with the rapid loss of a small and specialized group of insectivorous birds that follow army ant colonies feeding on insects disturbed by the swarming ants (Willis 1974, 1979; Lovejoy *et al.* 1986).

Despite this example, relatively little research has been conducted on higher-order effects, but a number of anecdotal cases point to fragmentation-related changes in community structure as being of great importance and interest (Terborgh 1992). Habitat fragmentation is likely to affect most severely those

animals with requirements for very large areas of undisturbed forest. Large carnivores are particularly susceptible to local extermination through the fragmentation of tropical forest, and are generally under strong additional pressure from other human activities. The absence of megapredators is liable to release control on vertebrate herbivore and medium- to small-sized carnivore (mesopredator) populations, though larger species of the former are unlikely to be allowed to increase greatly because they are frequently also the prey of human hunters. A scarcity of predators may lead to a reduction of diversity in the prey fauna as one or a few species come to dominate and out-compete the rest. This suggestion may explain the low diversity of small mammals in 60–80-ha forest fragments in the Atlantic coast forests of Brazil (da Fonseca & Robinson 1990) and a more structured (apparently less randomly assembled) small mammal community in small fragments in Queensland (Laurance 1994). Mesopredator release, namely the expansion of mesopredator populations after reduction or removal of megapredator control, has been implicated in increased nest predation in tropical forest fragments (Loiselle & Hoppes 1983; Sieving 1992; Laurance, Garesche & Payne 1993).

Very small fragments may lose most of their vertebrate fauna and this can affect the floristic composition of the forest. Leigh *et al.* (1993) hypothesized that the tiny islands in Lake Gatun, Panama, had become dominated by a handful of large-seeded, wind-throw-resistant trees that thrive in the absence of mammalian seed-predators. For these same islands, Adler (1994) found strong asynchrony in reproductive activity between fragmented populations of the frugivorous rodent *Proechimys semispinosus*. This he ascribed to floristic differences between the islands that had led to differing temporal patterns of resource availability. Asynchrony might reduce migration and gene flow between populations. In larger forest fragments small mammals may increase in abundance and act as efficient seed and seedling predators, greatly influencing tree regeneration (Laurance 1994).

Tropical rain forest is often identified as an ecosystem with a heavy dependence on mutualistic species interactions for its stability. Many plant species in the rain forest are reliant on animals as agents of dispersal for either pollen or seeds or both. If habitat fragmentation causes the extinction of certain important pollinating or seed-dispersing animals, this could severely limit regeneration of these plant species and hence initiate an extinction vortex (Howe 1984; Bond 1994). However, evidence to support this process in tropical rain forest is limited (Bond 1994; Bowman & Woinarski 1994). Most plant species appear not to be so specialized in either their pollinators or dispersers as to be affected rapidly by fragmentation-related extinction, though reproductively unsuccessful populations of trees may persist for centuries because of the longevity of their members.

IMMIGRATION OF EXOTICS

The deforested matrix of a fragmented landscape is often dominated by alien species, because few of the native species are tolerant of the extremely exposed conditions in the cleared areas. There may be a tendency for these exotics to start to invade the fragments. Continuous forest areas are less vulnerable to invasion because environmental conditions may not favour establishment of the aliens; much of the forest will be outside the range of dispersal of those species; and the undisturbed community may be resistant to the establishment of exotic species. The considerably greater susceptibility of oceanic island communities, compared with those of continents, to disruption by exotic species (Loope & Mueller-Dombois 1989) indicates that communities indeed have an inherent resistance to invasion. Whitmore (1991), in a review of invasive woody plants in the humid tropics, cited the case of *Pittosporum undulatum* in montane forest in Jamaica as the sole example of undisturbed forest being successfully invaded. However, small fragments are within dispersal range (Willson & Crome 1989) and the strong tide of alien invaders may overwhelm the native community (Janzen 1983; Simberloff 1992). The greater frequency of disturbance in and around fragments may also favour their invasion (Laurance 1991a).

Extinction proneness

Some species are more susceptible to rapid extinction through the fragmentation of tropical rain forest than others. In tropical Australia, the proneness of mammals to extinction appears to be inversely related to tolerance towards conditions in the prevailing matrix vegetation of the fragmented landscape (Laurance 1990, 1991b). At Los Tuxtlas, Mexico, vertebrate frugivores with low population densities, low mobility and specialized habitats were the most susceptible to habitat fragmentation (Estrada *et al.* 1993b), with terrestrial mammals exhibiting a greater likelihood of local extinction than volant species or birds. Fragmentation has led to the loss of the largest mammals at Los Tuxtlas (Estrada *et al.* 1994). In a study of the mammal faunas of islands of the Sunda Shelf that would have been linked by land to the Asian continent during the Pleistocene, Heaney (1984) showed that the smallest islands were characterized by a sharp reduction in the number of large carnivore species. These so called land-bridge islands may not be directly analogous to forest fragments, but the results illustrate the generally accepted premise that only very large areas of forest can maintain populations of top predators.

For neotropical avifaunas classified by major ecological guild, extinctions in fragmented forests are summarized in Table 2. It is difficult to distinguish any clear trend from the data. This may be because

Table 2. Avifaunal extinctions as a percentage of their guild for five neotropical rain forest sites. Data from Brash (1987) and Kattan et al. (1994)

Site	Guild		
	Raptors	Insectivores	Frugivores
Brazil	54	74	57
Panama	22	22	16
Ecuador	56	18	33
Colombia	33	31	36
Puerto Rico	14	7	22

the studies cover forests over a wide range of spatial scale. A number of authors have emphasized a heavy loss among raptors and large frugivores (Leck 1979; Willis 1979; Brash 1987; Kattan et al. 1994). Brash (1987) points out that this may be a phenomenon exacerbated by direct human pressure on these species. Large frugivores generally require extensive forest in order to have sufficient fruit to sustain their populations. Fragmentation often leads to local domination by smaller generalist frugivores that are more tolerant of the matrix vegetation and able to switch diets opportunistically, thus flourishing in the altered landscape (Willis 1979). In their literature review, Johns & Skorupa (1987) also identified large frugivores as the ecological group of primates that was most sensitive to forest disturbance. However, in a study of neotropical land-bridge islands Gotelli & Graves (1990) could find no evidence for greater extinction proneness among larger-bodied bird species. Successful colonizers of such islands tend to be species that are widespread on continents (Faaborg 1979), possibly indicating that narrowly endemic species may be particularly susceptible to fragmentation-related extinction. This appears to be the case for butterflies in Costa Rica (Thomas 1991). Katten et al. (1994) reported that bird species at the edges of their geographical range or ecological tolerance were particularly sensitive to habitat fragmentation. However, Karr (1982b) found for forest birds that strong variability in population size was a more important predictor of extinction probability than was rarity.

Turner et al. (1994) identified epiphytic orchids as having been particularly susceptible to forest fragmentation in Singapore. The reasons for their extinction proneness are a matter for speculation. Changes in forest microclimate with fragmentation may be to blame, but epiphytic pteridophytes have been much less susceptible to local extinction (Turner et al. 1994). Meave & Kellman (1994) noted that natural fragments* of riparian forest in Belize appear depauperate

*Natural fragments are those patches of forest surrounded by non-forest vegetation where recent human activity was not the primary agency responsible for their formation and is not responsible for their maintenance as fragments. A universally tenable and succint definition of natural fragment may not be possible, but they clearly differ from the fragments that are the focus of this review, which were created in historically recent times by people clearing forest.

in dioecious and mammal-dispersed species compared with continuous forest, possibly because the poor persistence in small populations of the former and the limited dispersal of the latter disadvantage these two functional groups of plants.

Conclusions

Enough studies have been conducted for us to conclude safely that the fragmentation of tropical rain forest is a major threat to local biodiversity, though the increased pressure on wildlife from greater human activity in fragmented landscapes may make a major contribution to the negative impact. Various mechanisms are responsible for the local extinction of species in fragmented forest but, as yet, it is not possible to quantify the relative importance of different factors such as restriction of population size, forest edge effects or invasion of exotic species. Rare and patchily distributed species, and those with requirements for a large range or specialist habitats seem particularly susceptible to fragmentation. Tolerance of the matrix conditions is a characteristic frequently associated with species that can survive in fragmented forest.

It is probably a mistake to assume that all tropical rain forest communities will react in an exactly similar way to fragmentation. In their resistance and resilience to fragmentation, forests may differ significantly between continents or over much smaller spatial scales. Puerto Rico and Singapore provide interesting comparisons in this respect. Both islands have suffered a similar massive loss of primary forest, mostly from nineteenth century deforestation, but Singapore's biodiversity has been more seriously reduced. Of the two islands, Puerto Rico has a considerably greater cover from extensive secondary forests which have been colonized by many native woody species (Lugo 1988). Singapore also has large areas of secondary forest, often containing primary forest fragments, yet its secondary forests remain relatively species-poor after more than a century of succession (Turner et al. 1994), indicating that the Puerto Rican forest community may be more resilient than the Singaporean one. Explanations for this might include the greater absolute size of fragments on the larger island of Puerto Rico and a stronger selection pressure in favour of fragmentation tolerance, brought to bear on the Puerto Rican biota through greater geographical isolation, a more seasonal climate and the greater likelihood of catastrophic winds in the Caribbean hurricane belt.

Only extensive tracts of forest can contain a full complement of the indigenous biota of a region and therefore guarantees of security from disruption for such tracts must be the first priority of conservationists. It is imperative to prevent fragmentation if at all possible. I would argue that evergreen tropical forests are particularly sensitive to fragmentation because a large portion of their species are both very

sparsely distributed through the community and also intolerant of open sites. Thus, both the absolute number of species and the proportion of the complete biota under threat from fragmentation are greater than for any other biome. Nowhere else is there such a sharp distinction between highly diverse primary forest and the species-poor early successional matrix.

This however, does not mean that already fragmented tropical forests should be ignored or neglected (Turner *et al.* 1994). Many forest types in the humid tropics now occur only as fragmented remnants: e.g. the Atlantic rain forest of Brazil, and the tropical dry forests of Central America and Indo-China. Even small fragments continue to possess relatively high levels of diversity many years after excision (Turner *et al.* 1994). Certain species may be able to survive indefinitely in fragmented landscapes. For example, Robbins *et al.* (1987, 1992) found that many migrant birds made good use of fragmented forests in the Neotropics; Stouffer & Bierregaard (1995) discovered that understorey hummingbirds, in stark contrast to insectivorous species, persist in diversity and abundance in small fragments at Manaus; and Ferrari & Diego (1995) reported that two threatened species of primate, *Callithrix flaviceps* and *Alouatta fusca*, were surviving in many small fragments of the Atlantic coast forests of Brazil. Even single remnant trees may conserve, at least in the short term, some epiphytic orchid species (Williams-Linera, Sosa & Platas 1995).

Meave & Kellman (1994) argued that, because natural fragments of tropical rain forest possess high levels of plant diversity, forest fragmentation need not necessarily lead to mass extinction. This view may be over optimistic: these natural forest patches may have species numbers similar to those of equivalent areas in continuous forest in that region, but they do not approach the very high diversity of the core rain forest blocks. Undoubtedly the natural fragment assemblages were derived over a long period of time and have not suffered from damaging human interference. Man-made fragments of rain forest are literally created 'overnight' and will contain a community, elements of which have over many generations received little selection pressure for fragmentation tolerance.

Where do we go from here?

We know so little about this enormous and urgent problem that more research undoubtedly has to be done. I would emphasize further work on forest fragments that have been isolated for a considerable period of time. It is information on the long term viability of fragments, and on the nature of the new equilibrium point that they will reach that will be of greatest value in planning conservation strategies. Research priorities must include studies to identify those groups which, in the long term, are most affected by habitat fragmentation, and research into the dynamics and

genetic diversity of small populations. Probably the most interesting area of research will be into the second- and higher-order effects of fragmentation. These will present a great challenge to ecologists but are of high potential for pure as well as applied science. One approach to understanding the diversity and community structure of tropical forest might be through the natural deconstruction experiments of habitat fragmentation. Major difficulties will include finding the right controls for such observations, unravelling the multiplicity of factors involved, and the inevitable stochasticity or even chaos of natural systems. The effectiveness of corridors and buffer zones in ameliorating the negative impacts of fragmentation also needs critical attention. The ultimate challenge will be to resynthesize species-rich rain forest from its tattered remnants. Emphasis on field studies is important. This area of research suffers greatly both from the emotional hyperbole of the ill-informed and from the academic hypertrophy of theoreticians and modellers.

Finally, it is salutary to reflect upon how much of the ecological research which has provided the foundations for our theories concerning tropical rain forest communities was actually conducted in fragments such as Barro Colorado Island, Panama.

Acknowledgements

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